The diet of Eurasian perch larvae in lakes with different zooplankton assemblages

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Eurasian perch has a great ecological importance in freshwaters as it is often a dominating predatory fish in ecosystems. The knowledge of perch feeding patterns, strategies, and adaptivity to food environment in their early life stages is essential to understand its population development and dynamics. It has been demonstrated that there exists a positive relationships between preferred prey availability and larval feeding success. We examined the diet of larval perch in their natural habitats of different zooplankton assemblages in three small lakes with varying ecological status. In each lake, both pelagial and littoral were studied. We found significant relation between zooplankton biomass in the lake and zooplankton biomass consumed by fish larvae. The most important food objects were crustaceans (*Bosmina longirostris*, *Chydorus sphaericus*). Ciliates were consumed only in one lake. Our results show that perch larvae are flexible in their choice of food and can adapt to different food environments.

Introduction

During the larval stage, fish undergo significant changes in their morphology and physiology. These changes include alterations in body shape, the development of fins, and the ossification of their axial skeleton. Additionally, numerous organs, such as the gut, kidneys, eyes, and swim bladder, undergo structural and functional changes to meet the fish's nutritional demands and help them adapt to their environment (McMenamin and Parichy 2013). Based on

larval metamorphoses, developmental step L1 indicates the start of exogenous food ingestion to L6, when rays have developed in all fins and the first signs of septa formation in the olfactory pits (Peňáz 2001). This is the final larval stage before the juvenile period begins (characterized by scales development on the body surface and gradual attainment of adult body shape). According to the "critical period" hypothesis (Hjort 1914, 1926), first-feeding larvae failing to find suitable planktonic prey in sufficient quantity result in high larval mortality and a reduction

in year-class strength. After the first period of exogenous feeding, the following larval stages (L2-L6) may have a period of lower mortality rate (McCasker *et al.* 2014). But even then, not only the food supply but also the composition of food is critical for larval survival and faster larval development into larger, less vulnerable juveniles (Zingel *et al.* 2012). Some studies have also demonstrated that when accounting for prey selectivity of larvae, the positive relationships between selected prey availability and larval feeding success, growth and survival is evident (Mayer and Wahl 1997; Robert *et al.* 2009; Murphy *et al.* 2013). Still, larval fish diet is often poorly resolved without sufficient taxonomical resolution of zooplankton of the actual prey field of larvae as well as the diet composition and prey preference (Robert *et al.* 2014). This, however, can bias the understanding of factors and processes affecting larval survival and growth performance in their natural environment. Therefore, field-based research providing knowledge of major fish species feeding patterns and adaptivity to food environment in their early life is of great importance to understand its population development and dynamics, and also in revealing the key linkages in food web supporting the recruitments.

The Eurasian perch (*Perca fluviatilis*) is a piscivorous freshwater fish common in large parts of Europe and Asia inhabiting almost all types of running and standing waters (Froese and Pauly 2021). It is ecologically important and one of the most valuable commercial and recreational freshwater fish species in Europe (Vainikka *et al.* 2012, Heermann *et al.* 2013).

Perch is widespread in different types of water bodies, which shows the ability of this species to adapt to different feeding conditions. However, the abundance and growth rate of perch can be very different in different environments (Rask 1983).

In lakes, perch spawns in the shallow littoral areas around the shoreline. Perch produce very small larvae (hatching roughly at 5.4 mm and 0.7–0.8 mg), which are at first very fragile and vulnerable to several problems, e.g. failure of development, cannibalism, predation, starvation (Overton and Paulsen 2005). Soon after hatching in littoral, part of the larval perch population

are known to move to the open water area (Urho 1996). An important question is how the available zooplankton communities in these habitats meet the dietary requirements of the larvae. Zooplankton communities can be very diverse varying greatly in time and space. As perch larvae in different environments are forced to select only from available zooplankton resources it is somewhat complicated to examine their feeding preferences. An additional problem that may interfere with the understanding of the diet of perch larvae is the fact that only three major metazooplankton groups are usually included in the zooplankton analyses: rotifers, cladocerans and copepods. This applies both in the environment and in the food of the larvae. However, several studies have shown that unicellular ciliated protist can account for more than two-thirds of the total biomass of zooplankton communities in some waterbodies (Zingel and Nõges 2008, Zingel and Nõges 2010). It has also been shown that the proportion of ciliate biomass in the perch larval diet can exceed 60% (Zingel *et al.* 2012). Thus, if we ignore ciliates, both in the zooplankton community and in the larval food, we can get a skewed picture of the diet of perch larvae.

The main objective of this study was to examine comprehensively the diet of larval perch in their natural habitats of different zooplankton assemblages. We aimed to focus on larvae of larger developmental stage (L6; Peňáz 2001) that is shifted from the first exogenous feeding to an intensive oral feeding capable for ingestion of prey sizes of a wider range. For this stage of larvae, the metamorphosis is completed. Their resistance towards the most environmental factors are increasing and the natural mortality rate decreases (Peňáz 2001). At this stage (L6) perch larvae are clearly capable to express selectivity when choosing amongst different food objects and the chance is much smaller that their food selectivity is influenced by some kind of failure of development. At the same time, their food consumption has increased, compared with the early larval stages (L1–L2), which allows a better quantitative assessment of zooplankton intake. If only few planters are ingested, the results from stomach content analyses may be more random. We assessed how the diet of these larval populations respond to the different availability of
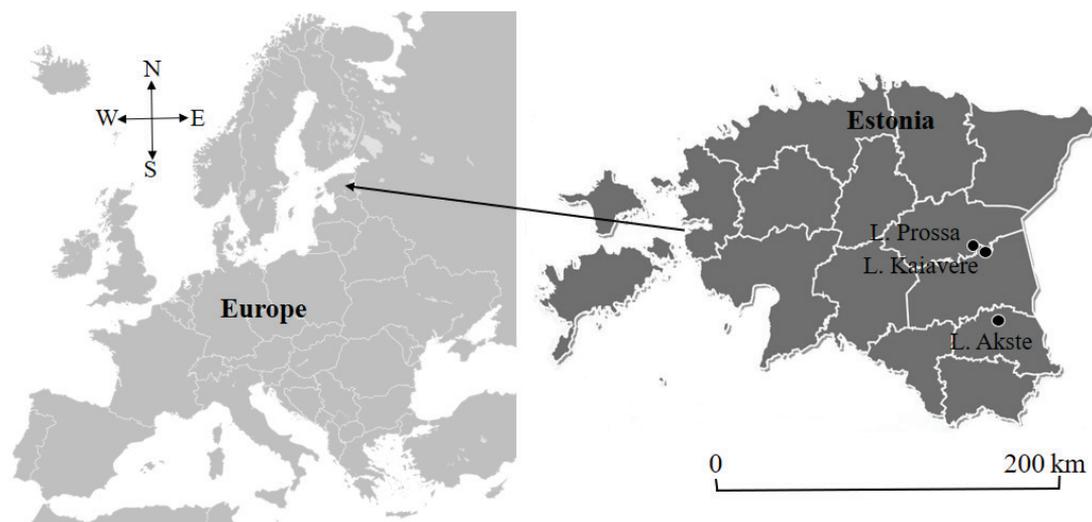
Fig. 1. Location of three study lakes (Akste, Kaiavere, Prossa) in Estonia (locations are marked by black dots).

food (ciliates and metazooplankton). For our study we selected three small and shallow lakes with varying ecological status. Shallow lakes were selected because they are the most abundant lentic freshwater bodies at a global scale and very common also in the Europe. They are very important scientifically, economically, and socially (Meerhoff and Jeppesen 2009, Mayer and Pilson 2019). In each lake we sampled additionally both open water pelagic (an open water column without aquatic vegetation, depth > 2 m, distance from the shore line > 50 m) and macrophyte rich littoral zones (an inshore area covered with macrophytes, depth < 2 m, distance from the shore line < 50 m). These two habitats were selected to broaden our assortment of different zooplankton assemblages available for perch larvae as it is known that zooplankton communities can differ considerably between the pelagic and littoral zone (e.g. Walseng *et al.* 2006). Our work addressed the following research questions:

1. What is the larval perch diet composition and how food consumption patterns differ across different zooplankton assemblages?
2. What kind of zooplankton community structure favours the consumption of ciliates and in which conditions they become dietary important?
3. What are the most important food objects in terms of selectivity and dietary importance for larval perch in stage L6?

Based on the larval food composition we further assessed how the perch larvae are linked to the food webs in lakes and biotopes assessed. Specifically, we followed the potential connection with the microbial food web (via consumption of ciliates) for this stage of perch larvae.

Material and methods

Study sites

Surveys were conducted on sixth of June in 2019 in three small and shallow lakes in Estonia (North Europe) (Fig. 1) varying in nutrient status, macrophyte coverage, and with different colour and hardness of water (Zingel *et al.* 2006) — Lake Kaiavere is an eutrophic plankton-dominated lake, Lake Prossa is an eutrophic macrophyte-dominated lake and Lake Akste is a semi-dystrophic lake. Characteristic morphological features and physico-chemical conditions of the study lakes during the survey can be found in Table 1; macrophyte community indices in Karus *et al.* (2022).

Sampling and analyses

All lakes were sampled in the afternoon. As soon after hatching in littoral, part of the perch

population move to the open water area (Urho 1996), the larval perch diet was assessed in both habitats of the lakes — littoral (an inshore area covered with macrophytes) and pelagic areas (an open water column without aquatic vegetation and depth > 2 m). Samples for zooplankton (ciliates, metazooplankton (multicellular zooplankton belonging to rotifers, cladocerans and copepods)) and larval fish were collected from these two habitats of each lake.

Ciliates, metazooplankton and water-chemistry samples were collected and analysed from depth-integrated lake water (with 0.5 m interval, mixed in a tank) using a Ruttner water sampler. For each sampling site, the physio-chemical parameters of temperature, oxygen, pH and conductivity were determined with a portable YSI Professional Plus instrument (YSI Inc., USA). For ciliates, an intact depth-integrated lake water sample was used and the final sample volume was 200 ml. For metazooplankton samples, 10 L of depth-integrated water for each habitat and lake was poured through a 48-µm-mesh net and the concentrated sample (200 ml) was passed to the sample bottle. Ciliate and metazooplankton samples were preserved with acidified Lugol's solution (0.5% final concentration). For ciliates' sample counting, an inverted microscope (Nikon Eclipse Ti-U; Nikon Instruments Europe B.V., Amstelveen, the Netherlands) at 400–1000× magnification

was used. Utermöhl (1958) technique was applied for abundance, biomass and community composition analyses. The entire contents of each Utermöhl chamber were surveyed. For ciliate biomass calculations the first 20 specimens encountered for each taxon were measured. Biovolumes of each taxa were estimated by assuming simple geometric shapes. Ciliate carbon content was determined from the measured volumes of cells by using a conversion factor of 190 fg C µm^{-3} (Putt and Stoecker 1989). For community composition analysis, ciliates were usually identified to genus by consulting several works (Kahl 1930, 1931, 1932, 1935, Foissner and Berger 1996, Foissner *et al.* 1991–95, Foissner *et al.* 1999). Metazooplankton samples were counted in triplicate subsets in Bogorov chamber under dissecting microscope (Nikon AZ100; Nikon Instruments Europe B.V., Amstelveen, the Netherlands) at 80× magnification. Crustacean and rotifer carbon biomasses were estimated using either the taxon-specific length-carbon relationships (Telesh *et al.* 1998, Manca and Comoli 2000), or length-dry weight relationships (Dumont *et al.* 1975, Bottrell *et al.* 1976) applying the carbon conversion factor of 0.48 mg C per mg dry weight (Andersen and Hessen 1991). Metazooplankton taxa accounting for 20% or more of the number or biomass were considered, respectively, as abundance and biomass dominants.

Table 1. Characteristic morphological and physico-chemical features of the study lakes (Akste, Kaiavere, Prossa) in spring, 2019.

Characteristic \ Lake	Akste		Kaiavere		Prossa	
Habitat/indices	littoral	pelagial	littoral	pelagial	littoral	pelagial
Location	58°10′10″N; 27°3′3″E		58°36′14″N; 26°40′31″E		58°39′2″N; 26°34′34″E	
Surface area (ha)	5.5		248		24.2	
Mean depth (m)	—		2.8		2.2	
Maximum depth (m)	4.3		5.0		4.2	
Water colour	reddish-brown		brownish-green		greenish-yellow	
Habitat/indices	littoral	pelagial	littoral	pelagial	littoral	pelagial
Temperature (°C)	23.0	20.10	20.05	17.68	20.05	17.78
Sechhi depth (m)	0.5	0.7	0.5	1.4	1.0	2.3
Total phosphorus (mg/L)	0.028	0.018	0.003	0.003	0.003	0.003
Total nitrogen (mg/L)	0.87	0.81	1.68	1.52	1.23	1.19
Oxygen content (mg/L)	8.65	8.3	11.97	8.80	14.68	13.75
Oxygen saturation (%)	101.1	92.3	131.65	93.3	163.25	146.53
pH	6.07	5.67	8.43	8.28	8.36	8.13
Conductivity (µS/cm)	19.05	18.83	419.3	422.95	365.05	344.58

Larval fish communities were sampled using a conical bongo net (mouth diameter 50 cm, mesh size 0.5 mm) in pelagic and a scoop-net (mouth diameter 40 cm, mesh size 0.5 mm, equipped with a 2 m handle) in littoral areas of the lakes by drawning the nets through the habitat's water column. Larval fish samples collected with different methods were preserved in ethanol for further analyses and to estimate larval fish diet. Fish larvae were killed according to the Estonian legislation (Nõukogu määrus 2009), Estonian animal welfare laws, guidelines and policies, appropriate permits for animal collections and animal welfare issues were sought and approved by the local committees (permit number: 10-1/19/52). Fish were euthanized with overdose of ethanol (20 mL/L) before immersing fish into preservative concentration of ethanol (70%) (AVMA 2020). At this dose (20 mL/L), alcohol induces anesthesia (Deitrich *et al.* 1989), and prolonged immersion produces death via respiratory depression causing anoxia. This is not equivalent to immersing fish directly into preservative concentrations of ethanol (70%), which is not acceptable as a euthanasia method (AVMA 2020). Caught larval fish species were identified in the laboratory according to Koblitskaya (1981), measured (total length) and weighed. Larval developmental steps were identified in the laboratory according to Koblitskaya (1981) and Peňáz (2001) using corresponding external morphological features.

The larval cut contents were analyzed according to Fukami *et al.* (1999), and Sutela and Huusko (2000). Larval fish feeding particularly on ciliates was calculated on the basis of first gut quarter methodology as suggested by Zingel *et al.* (2012). Samples were gently filtered through 0.8-mm pore-size black isopore filters (Poretics). Ciliates with DAPI-stained clearly visible nuclei in the gut were counted on a Leica DMBR fluorescence microscope at 1000× magnification using blue (470/40 nm, OG515) and ultraviolet light (360/40 nm, GG420). Metazooplankton remains in larval gut contents were analysed according to Hyslop (1980). At least 20 larvae from each lake and habitat were analysed for gut content analyses. All found food objects were measured using calibrated oculars. Biovolumes were estimated by assuming simple geomet-

ric shapes. Ciliate and metazooplankton carbon weights were estimated as stated earlier for ciliate and metazooplankton samples analyses from the water column.

Indices of dietary importance

To evaluate larval fish prey importance, feeding homogeneity and strategies at the population level we calculated several indices of dietary importance: Ivlev's selectivity index (E_i) and percent index of food items relative importance ($IRI_i\%$).

Feeding selectivity of the fish was assessed using Ivlev's (s)electivity index, E_i (Ivlev 1961), to describe the degree of selection or avoidance of certain prey organisms by larvae (index values between –0.3 and +0.3 represent nonselective feeding (Lazzaro 1987)):

$$E_i = (r_i - n_i) / (r_i + n_i), \quad (1)$$

where r_i is the relative abundance (% by number) of prey category i in the diet of fish and n_i is the relative abundance (% by number) of prey category, i, in the environment; r_i and n_i were calculated as follows:

$$r_i = 100 \times \Sigma f_i / \Sigma f, \quad (2)$$

where f is the total number of all food items in the gut contents and f_i is the number of food item, i, in the gut contents. r_i represents the average value over the perch population studied in a specific lake and biotope.

$$n_i = 100 \times \Sigma e_i / \Sigma e, \quad (3)$$

where e is the total number of all food items in the surrounding environment and e_i is the number of food item, i, in the surrounding environment. n_i represents the average value in a specific lake and biotope.

To assess the importance of different prey items in larval diet the food items relative importance index (IRI_i) was calculated. IRI_i was calculated on the basis of three different indices — numbers (r_i), mass (w_i) and frequency of occurrence (fo_i) in diet and it shows, which food items
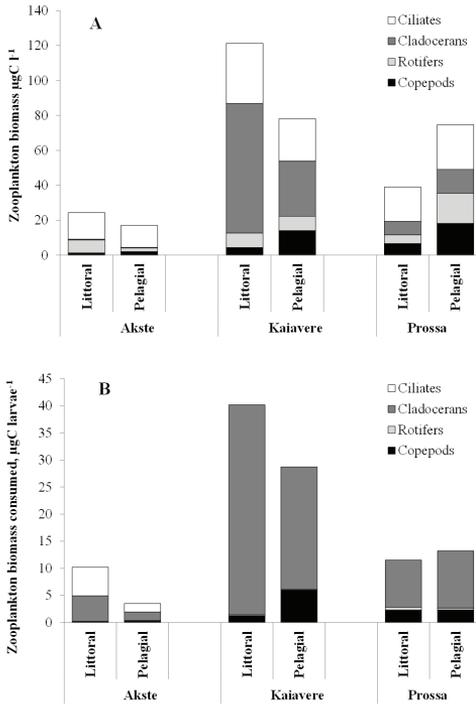
Fig. 2. (**A**) Zooplankton carbon biomass and (**B**) average zooplankton carbon biomass consumed by perch larvae in littoral and pelagial sites of Lakes Akste, Kaiavere and Prossa, in spring, 2019.

are relatively the most important concerning all these three afore-mentioned indices.

$$\mathrm{IRI}_i = (r_i + w_i) \times (\mathrm{fo}_i), \qquad (4)$$

where r_i (percent by number) is the same as in Eq. 2; w_i (percent by weight) and fo_i (frequency of occurrence), were calculated for each prey item i as follows:

$$w_i = 100 \times \Sigma m_i \,/\, \Sigma m, \qquad (5)$$

where m is the total weight of all food items in the gut contents and m_i is the weight of food category, i, in the gut contents. w_i represents the average value over the perch population studied in a specific lake and biotope.

$$\mathrm{fo}_i = 100 \times \Sigma b_i \,/\, \Sigma b, \qquad (6)$$

where b is the number of all fish examined and b_i is the number of fish in which prey item, i, occurred.

We also compared the species lists for ciliates and metazooplankton found in different lakes and in littoral and pelagic areas using the Bray-Curtis dissimilarity index:

$$\mathrm{BC}_{ij} = 1 - 2C_{ij} \,/\, (S_i + S_j) \qquad (7)$$

where C_{ij} is the sum of the lesser values for only those species in common between both sites and S_i and S_j are the total number of specimens counted at both sites.

Statistical analysis

Statistical analyses were performed using STATISTICA 13.2 (StatSoft Inc., 2016) for ANOVA and regression analysis, and R programming language ver. 4.1.1 (R Core Team 2020) for PERMANOVA. We compared the species composition of both ciliates and metazooplankton between different lakes and also within each lake (between pelagial and littoral) using the Bray-Curtis dissimilarity indices and tested the differences through pseudo-F from a PERMANOVA with 9999 permutations (Clarke and Gorley 2006). We used regression analysis to test the relationship between the share of ciliates in larval perch diet and the share of ciliates in total lake zooplankton, and between zooplankton biomass in the lake and zooplankton biomass consumed by fish larvae. ANOVA was used to compare the amount of zooplankton biomasses consumed by perch larvae in different lakes and biotopes.

Results

Zooplankton

The zooplankton communities had clear differences in species composition (both ciliates and metazooplankton) between the lakes studied and between different habitats (pelagial and littoral) (Bray–Curtis dissimilarity, PERMANOVA, $F = 13.52$; $p < 0.05$).

The highest ciliate and metazooplankton biomasses occurred in Kaiavere (Fig. 2a). The lowest biomasses of ciliates and metazoo-
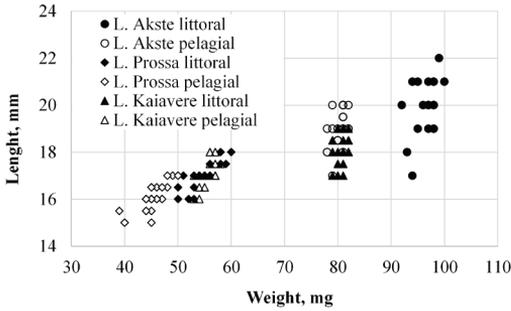
Fig. 3. The length and weight of larval perch in littoral and pelagial sites of Lakes Akste, Kaiavere and Prossa, in spring, 2019.
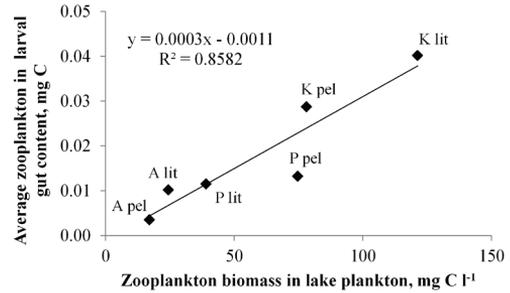

Fig. 4. The relationship between zooplankton biomass in a lake and average zooplankton biomass in larval perch gut content in Lakes Akste, Kaiavere and Prossa (both in pelagial and littoral), in spring, 2019. A lit = L. Akste littoral, A pel = L. Akste pelagial, K lit = L. Kaiavere littoral, K pel = L. Kaiavere pelagial, P lit = L. Prossa littoral, P pel = L. Prossa pelagial.

plankton occurred in Akste. In this lake, however, the relative share of ciliates in total zooplankton biomass was the highest comprising 62% and 74%, while this was 28% and 31% in Kaiavere and 51% and 34% in Prossa (in littoral and pelagial, respectively) (Table 2).

Perch larvae

Altogether, 122 perch larvae (61 larvae from both habitats) were analysed. From Akste, 42 larvae and from all the other lakes 40 larvae were dissected. Smallest larvae were found in pelagial habitat of Prossa (average ± SD: 16 ± 0.53 mm and 45 ± 2.33 mg) and largest in littoral habitat of Akste (average ± SD 20 ± 1.16 mm and 97 ± 2.06 mg) (Fig. 3). Considering ontogenetic steps, all studied larvae were in the same development stage, indicating therefore also on a similar age and making comparison on food consumption reasonable. Larval developmental steps were identified in the laboratory according to Koblitskaya (1981) and Peňáz (2001) using corresponding external morphological features (development of rays in fins, development of olfactory pits). All studied larvae were in the developmental step L6 (steps defined according to Peňáz 2001).

Larval diet

The amount of zooplankton biomass consumed by perch larvae was highest in Kaia-

vere and lowest in Akste (ANOVA; $F = 18.57$; $p < 0.01$; Fig. 2b). We found statistically significant relation (Regression analysis; $R^2 = 0.86$; $p = 0.008$; $n = 6$) between total zooplankton biomass per litre in the lake and average zooplankton biomass consumed by fish larvae (Fig. 4). In Lake Kaiavere and Lake Prossa the most consumed food items in terms of zooplankton biomass were cladocerans and in Lake Akste ciliates (Fig. 2b). Ciliates were not consumed in Kaiavere and Prossa. In Akste, we also compared the number of ciliates in the larval diet with the corresponding larval length, but found no significant relationship between the two (Regression analysis; littoral $R^2 = 0.003$; $p = 0.44$; $n = 21$; pelagial $R^2 = 0.0004$; $p = 0.90$; $n = 21$). In all lakes larvae consumed also small unidentified insect larvae but their relative importance was marginal (< 1% from consumed carbon biomass). Ciliates were the only zooplankton group that was negatively selected despite considerable consumption (Fig. 5), considering Ivlev's feeding selectivity index. Cladocerans were positively selected in all lakes. Nauplii and copepodites were mainly positively selected. Selectivity for rotifers showed greatest variability amongst studied lakes (Fig. 5). According to IRI index (Fig. 6) the most important food objects for larval perch were *Bosmina longirostris* (in Prossa and in littoral of Kaiavere), *Chydorus sphaericus* (in pelagial of Kaiavere) and ciliates (in Akste).

Table 2. Abundances of ciliates and metazooplankton, their mean weight (μg C), and larval perch ingestion on food objects (mean ± standard deviation) in lakes Akste, Kaiavere and Prossa, in spring, 2019.

	Akste		Kaiavere		Prossa	
	littoral	pelagial	littoral	pelagial	littoral	pelagial
Biomass						
Ciliate % in total zooplankton	62.4	73.9	28.4	31	50.5	34.3
Cladoceran % in total zooplankton	1.6	1.4	61.1	40.4	19.3	18.2
Copepod % in total zooplankton	5.4	12.3	3.6	18.1	17.2	24.4
Rotifer % in total zooplankton	30.6	12.4	6.9	10.5	13.0	23.1
Abundance						
Ciliates, cell L^{-1}	5762	4312	16726	5928	4301	8689
Metazooplankton, ind. L^{-1}	570	186	1376	1059	1360	2785
Cladocerans, ind. L^{-1}	1	3	205	62	18	63
Copepods, ind. L^{-1}	25	56	113	51	154	475
Rotifers, ind. L^{-1}	544	128	1059	946	1189	2247
Abundance of dominant taxa						
Bosmina longirostris, ind. L^{-1}	1	0	200	26	9	62
Keratella cochlearis, ind. L^{-1}	63	26	61	119	576	1160
Polyarthra spp., ind. L^{-1}	348	39	406	50	505	808
Nauplii, ind. L^{-1}	21	50	101	9	130	420
Cyclopoida copepodites, ind. L^{-1}	4	6	8	29	13	27
Abundance of other taxa in larval food						
Holopedium gibberum, ind. L^{-1}	n.f.	3	n.f.	n.f.	n.f.	n.f.
Chydorus sphaericus, ind. L^{-1}	n.f.	4	5	3	n.f.	n.f.
Trichocerca spp., ind. L^{-1}	1	6	1	n.f.	13	112
Mean weight						
Metazooplankton, μg C	0.0161	0.0240	0.0631	0.0509	0.0142	0.0176
Ciliates, μg C	0.0026	0.0029	0.0021	0.0041	0.0046	0.0029
Ingestion by larval fish						
Number of Ciliates, larvae^{-1}	55±28	58±35	0	0	0	0
Number of Cladocerans, larvae^{-1}	20±8	3±1	121±48	83±36	55±36	51±27
Number of Copepods, larvae^{-1}	2±1	4±2	25±10	32±15	59±27	51±22
Number of Rotifers, larvae^{-1}	19±10	14±6	27±9	31±11	37±13	30±8

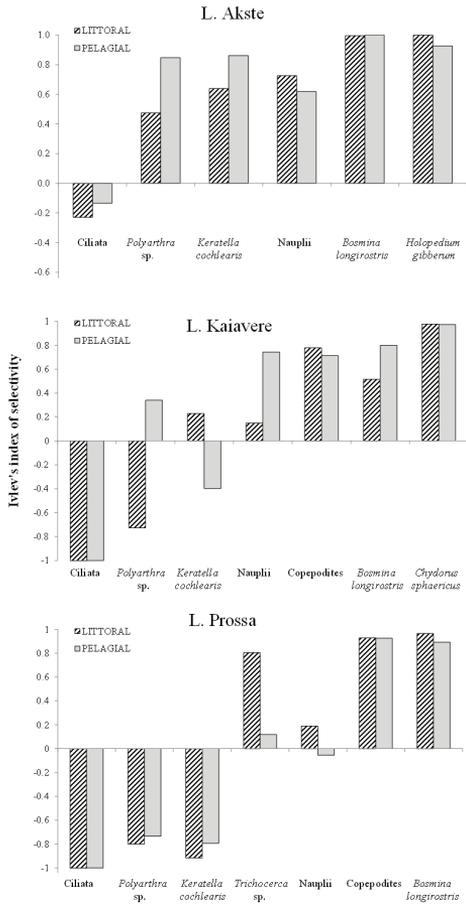n.f. — not found in the samples taken from water column.

Fig. 5. Values of Ivlev's index of selectivity (*E*) estimated for perch larvae inhabiting littoral and open-water sites of Lakes Akste, Kaiavere and Prossa, in spring, 2019.

Fig. 6. Values of index of food objects relative importance (IRI, %) estimated for perch larvae inhabiting littoral and open-water sites of Lakes Akste, Kaiavere and Prossa, in spring, 2019.

Discussion

In this research, the focus was on larvae of larger developmental stage (L6; Peňáz 2001) that is shifted from the first-feeding to a more advanced feeding capable for ingestion of both proto- and metazoan zooplankton. We found statistically relations between zooplankton biomass in the lake and zooplankton biomass consumed by fish larvae. Our main question was how these larval populations respond to the different availability of food (ciliates and metazooplankton); and further, how the perch larvae are linked to the food web in these conditions. We observed variable diet patterns of perch larvae across the habitats studied showing the flexibility of larval perch
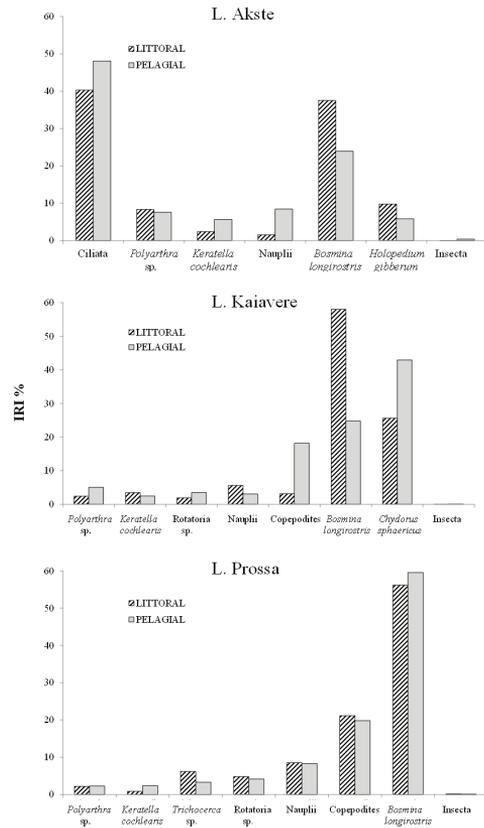
feeding behaviour. Larval populations differed in selectivity patterns, ingested food biomass per larvae and prey importance (IRI). The availability of food (zooplankton abundance, type) greatly affected the larval perch feeding patterns but pointed also to a different carbon pathway to larvae in these environments. We are fully aware that the zooplankton communities are highly variable and can change rapidly in terms of community assembly and biomass over time. Still, we opted in the current study to use a snapshot approach as also fish larvae develop rapidly. If we had sampled over a longer time period, then we have analysed larvae from different developmental stages, which are known to have different diets (Mayer and Wahl, 1997), and not the purpose of the current study. Our main aim was to see how different the food selectivity of

perch larvae from the same developmental stage is in the situation of different zooplankton availability. This again could not be done over long time period as larvae development is a continuous process.

In lakes Prossa and Kaiavere, the larval perch populations ingested only metazoan food. Ciliates were not consumed although the abundance and biomass of this source was high and generally large forms of ciliates prevailed in the assemblages (Table 2). In Lake Akste, ciliates were consumed and they were equally important diet source compared with metazooplankton in terms of ingested carbon biomass. Cilitaes were, however, selected against as a prey by larvae in Akste. All studied larval perch populations selected for crustacean prey. Small cladocerans, especially *Bosmina longirostris*, and juvenile forms of copepods (copepodites and nauplii) were the most selected food items. Opposite to other lakes, due to limited crustacean prey, some small rotifers (*Polyarthra* sp. and *Keratella cochlearis*) were also selected for in Akste. According to IRI index, across the populations studied, the small cladoceran *B. longirostris* seem to be the zooplankton species of great importance to support the larval perch diet. *B. longirostris* is a common spring dominant in cladoceran communities (e.g. Huusko *et al.* 1996) co-occurring with the larval hatching and their exogenous feeding. Other research has also pointed to the significant relationship between *Bosmina* and larval fish development. Limburg *et al.* (1999) tested whether growth and survival of fish larvae were enhanced in relation to a seasonal pulse ("bloom") of high zooplankton abundance in the Hudson River. They found that time period associated with the *Bosmina freyi* bloom, and not the copepod bloom, appears to have been related to successful striped bass (*Morone saxatilis*) recruitment. *Bosmina longirostris* evidently represents the suitably sized (in current study 240–350 µm) and shaped zooplankter, with relatively low swimming speed for larval ingestion at this stage. Despite there was a considerable amount of *Daphnia cucullata* in pelagial plankton in Kaiavere (28 ind L⁻¹), none of the larvae had ingested these relatively large cladocerans (average length 700 µm) with a long caudal spine. It seemed that both zooplankters body

shape and size were driving the choices of larval fish (Bremigan *et al.* 2003; Bremigan and Stein 1994; Mayer and Wahl 1997). Among rotifers, the species with long spines, such as *Kellicottia longispina* (Kellicott), *Filinia longiseta* (Ehrenberg) and also *Keratella quadrata* (O. F. Müller) were also not included into larval diet.

Our research has previously shown that ciliates can in certain situations be an important food items in the early stage of larval fish development (Zingel *et al.* 2012, 2019). When larvae grow, ciliates are gradually replaced with a larger and more evasive prey (Jackson and Lenz 2016) that are also more beneficial for larval fast growth (Lehtiniemi *et al.* 2007). Contrarily to that, we found in the current study that the smaller larvae in Lakes Kaiavere and Prossa consumed larger metazooplankton prey, but larger larvae in Lake Akste ingested also ciliates. The most reasonable explanation for this feeding behaviour is that in Akste the larvae living in the environment of low resources had to adapt to the limited availability of food and were forced to pick for ciliates to fill the gut and satisfy their energy demand. The size of the larvae at any given point in time cannot always reflect a direct relationship with the zooplankton available in this lake at that instant. Rather it reflects the past feeding conditions from the previous time periods. The availability of various zooplankters can change strongly over time as zooplankton population dynamics are affected by many different factors (Vanni 1987). As we opted in the current study to use a snapshot approach we lack the data concerning zooplankton availability during the former steps of larval development. It cannot be ruled out that at the beginning of the exogenous feeding the conditions were favourable for faster larval growth in Akste, but later there was a sharp decline in the zooplankton population for some reason. Our previous studies have demonstrated that ciliates are consumed only if their share in the total zooplankton biomass is relatively high (Zingel *et al.* 2019) and that exists a good accordance in the share of ciliates in total zooplankton and the share of ciliates in larval gut contents. As in the Akste the share of ciliates was highest in the zooplankton (> 60%), it makes sense that in that lake ciliates were also consumed by perch larvae. Despite the lower

food base, the larvae on the Akste littoral managed to assimilate the same amount of carbon biomass as on the littoral of Prossa.

In the littoral habitat of Kaiavere the zooplankton biomass was highest. In addition to that, the biomass of the most selected prey, small cladoceran *B. longirostris* was highest in Kaiavere, resulting also in the highest cladoceran consumption rate per larvae (Table 2). Generally, we found a statistical relation between zooplankton biomass in the study sites and zooplankton biomass consumed by fish larvae (Fig. 3a). This indicates that perch larvae can take advantage of the high zooplankton abundances that occur occasionally in some lakes — if prey numbers are high their capture rate is high as well.

Small and shallow, humic Akste, a lake type frequently occurring in northern boreal areas (e.g Juutinen *et al.* 2009), remains an interesting case in terms of larval perch feeding pattern, demonstrating different connections within the food web. In lakes of potential food shortage, like in Akste, the larvae may be longer linked with the microbial loop via feeding on ciliates. In such a situation the carbon transfer from microbial communities is more important to their ontogenetic development compared with the lakes of satisfactory level of metazoan food. In lakes Kaiavere and Prossa where the biomass of suitable crustacean prey was higher, perch larvae consumed only metazooplankters and were not anymore directly linked to the microbial source. It is important for us to understand how fish are linked to the food chain in different types of lakes so that we can recognize the most important connections and most crucial organisms for that kind of links.

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