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Shifts in Prey Selection and Growth of Juvenile Pikeperch (*Sander lucioperca*) over Half a Century in a Changing Lake Võrtsjärv

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ABSTRACT

Analysis of historical and recent data is essential to understand how eutrophication and/or climate change might trigger shifts in the feeding mode of fish and trophic dynamics of shallow lakes. To assess long-term changes in the diet and growth of juvenile pikeperch (*Sander lucioperca*), the prey selection and growth of pikeperch fry from Lake Võrtsjärv was investigated in 2007-2010 and compared with data from 1920 to 1970. Over the observed period, larger cladocerans have become less frequent in the diet as eutrophication has altered the zooplankton community. Furthermore, climate change has triggered a mismatch between the predator and its prey: the smelt population has collapsed but other fish fries are too large for YOY (young-of-the-year) pikeperch. However, the mean length of fish has decreased mainly due to the postponed diet shift.

Keywords: Climate Change; Eutrophication; YOY Pikeperch; Long-Term Changes; Diet Shift; Stomach Content Analysis

1. Introduction

Predator-prey interactions play a major role in aquatic ecosystems and thus can affect the whole biological community [1]. In this respect, the diet and ontogenetic dietary shift of juvenile pikeperch, *Sander lucioperca* (L.), have been studied quite extensively in many north temperate waters [2-9] as the size and structure of pikeperch populations are strongly dependent on their success at the juvenile stage [5,10]. However, due to eutrophication and climate change complex modifications in the feeding modes of fish are expected to take place [11]. Thus, there is a heightened need to research into long-term and developmental changes in diet, as pikeperch have a quite rigid ontogenetic feeding pattern [10] that is very sensitive to environmental changes, particularly to those influencing food web components. Nevertheless, there are only a few long-term data series on pikeperch fry diet and prey community that could be used as basis to study how eutrophication and/or climate change directly or indirectly might influence the diet, diet shift and growth of juvenile pikeperch.

The diet and growth of juvenile pikeperch have been studied several times since 1920 in a large shallow Lake Võrtsjärv [12-17]. Moreover, the probability of major shifts in the feeding modes of fish is especially high in shallow lakes [11] such as Lake Võrtsjärv. Therefore, Lake Võrtsjärv can be taken as a model for other shallow north temperate lakes under high anthropogenic and natural pressures to analyse the possible factors influencing the diet, diet shift and growth of juvenile pikeperch and hence the success of pikeperch populations.

Lake Võrstjärv has suffered a series of dramatic changes since 1950s, including human induced eutrophication, overfishing, warming and drastic water level fluctuations due to climate changes. As a consequence, its biota has altered and, therefore, also alterations in the diet and growth of pikeperch in the lake can be assumed. According to Tuvikene *et al*. [18], Lake Võrtsjärv has been under high anthropogenic pressure, primarily eutrophication, since the 1960s. In the 1980s, the discharge of nutrients into the lake by rivers increased steadily. However, from the 1990s onwards the loadings of nitrogen and phosphorus into the lake have decreased substantially. In consequence, changes in total phosphorus and total nitrogen concentration in water and water transparency have changed since the 1950s (**Table 1**). Additionally, the water temperature in Lake Võrtsjärv has increased significantly over the past half a century [19,20]. One result of these changes is the great difference in the food resources for the zooplanktivorous pikeperch in the lake.

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From the 1950s many large zooplankton species favored by oligo-mesotrophic conditions such as *Bythotrepes longimanus* Leydig*, Leptodora kindti* (Focke), *Diaphanosoma brachyurum* (Lieven), *Bosmina berolinensis* Imhof*, Cyclops kolensis* Lilljeborg and *Eudiaptomus gracilis* (Sars) completely or nearly disappeared from this water body [21,22]. Currently only small zooplankton species favored by eutrophic conditions like *Bosmina longirostris* (Müller), *Chydorus sphaericus* Müller, *Mesocyclops leuckarti* (Claus) and rotifers co-dominate [22-24]. Moreover, during recent decades the fish fauna of Lake Võrtsjärv has undergone several changes [25,26].

In the 19th century smelt (*Osmerus eperlanus eperlanus* m*. spirinchus* (Pallas)), which is considered to be the primary first prey fish for pikeperch [10,27], was rather common in Lake Võrtsjärv [28]. Before the mid-20th century, as a result of heavy fishing pressure [29], smelt disappeared from the lake. It was reintroduced from the nearby Lake Peipsi in 1950-1954 [16], however, according to Kangur *et al*. [25,30], climate change has continued to trigger a decrease in smelt populations. On the other hand, the abundance of ruffe (*Gymnocephalus cernuus* (L.)) and roach (*Rutilus rutilus* (L.)) is high in Lake Võrtsjärv [26] and their abundance increases consistently along a gradient of increasing productivity [31].

The purpose of this study was to explore if there has been a shift in prey selection and growth of juvenile pikeperch in a changing Lake Võrtsjlärv. In addition, an attempt was made to identify possible factors influencing the success of the pikeperch population in large shallow lakes. Therefore, studies since 1920 [12-17] on the diet, ontogenetic diet shift and growth of juvenile pikeperch were analysed to understand the long-term nature of pikeperch fry diet. This investigation concentrated on four different time periods: the 1920s, 1950s, 1960s-1970s and 2007-2010, as there have been significant shifts in living conditions and food supplies of juvenile pikeperch during those time periods. Furthermore, as there are no data on prey-predator length relationship since the 1950s, an additional investigation was carried out to obtain vital information for analysing diet shifts.

2. Materilas and Methods

2.1. Study Site

Lake Võrtsjärv, situated in the central part of Estonia (**Figure 1**), has a surface area of 270 km^2 and is the second largest lake in the Baltic region. It is a very shallow, turbid water body with a mean depth of only 2.8 m and a maximum depth of 6 m. Its water level is not regulated and fluctuates on average by 1.4 m each year [32]. The mean total phosphorus (TP) concentration in the lake water is 50 µg P·l^{-3} and the mean concentration of total nitrogen (TN) has been approximately 1.4 mg N·l^{-3} for the last decade [20]. Based on nutrient concentrations, the central part of the lake can be considered to be eutrophic, whereas the narrow and sheltered southern part is hypertrophic [33].

Figure 1. Location of Lake Võrtsjärv.

Table 1. Changes in total phosphorus (TP), total nitrogen (TN) concentration in water and water transparency (Secchi depth) [18,20] and shifts in zooplankton [21,22] as well as in fish community [13,16,26] in Lake Võrtsjärv since 1950s.

	1950s	1980s	2007-2010
TP, µg·l^{-3}	Undetectable	53	50
TN, mg·l^{-3}	0.1	1.6	1.4
Secchi depth, m	1.29	1.1	<1
Dominant zooplankton species by biomass	*D. cucullata*, *B. berolinensis*, *E. gracilis*, *L. kindti*, *B. c. coreconi*	*B. c. coreconi*, *C. sphaericus*	*C. sphaericus*, *B. longirostris*, *B. c. coreconi*, *M. leuckarti*
Dominant fish species	Perch, ruffe, roach, bream	Ruffe, perch, bream, smelt, vendace	Roach, ruffe, bream, pikeperch
OECD classification [33]	mesotrophic	eutrophic	eutrophic

2.2. Data Set

The historical data set on the diet and growth of juvenile pikeperch in Lake Võrtsjärv comprise three different time periods: the 1920s [12], 1950s [13] and 1960s-1970s [14-16]. The publications by Erm [13,14] and Haberman *et al*. [16] give an overview of the diet of YOY pikeperch in Lake Võrtsjärv in summer and autumn. The autumn length data of pikeperch fry in Lake Võrtsjärv were published by Schneider [12], Erm [13,14], Kangur [15] and Haberman *et al*. [16]. Altogether, the historical data set includes information on the diet of 551 and growth of 410 juvenile pikeperch. The samples for the growth and diet analysis were gathered with similar methods—monthly during the ice-free period from the pelagic zone of the lake using a bottom trawl. For growth analysis the standard length (SL) and the total mass (W) were measured. For the diet analysis only qualitative methods were used as the index of frequency of occurrence (*FO*) of different prey items was calculated:

$$FO\% = 100 \cdot \sum \frac{p_i}{p} \quad (1)$$

In this Equation (1) n_i represents the number of fish with *i* prey species consumed and *n* is the total number of fish examined [34].

The data set of the recent period (2007-2010) comprises results of the diet analysis in 2007-2008 [17] and of an investigation conducted in 2009-2010. To enable comparison of earlier data with the recent period, similar methods were used in sampling as described in publications since the 1950s. Pikeperch samples were collected in the summers and autumns of the years from 2007 to 2010 (**Table 2**) using a bottom trawl (height 2 m, width 12 m, 10 - 12 mm knot-to-knot mesh size at the cod-end). The trawl was towed by a ship for 15 min per haul at a speed of 5.5 - 6.2 km·h^{-1}. Trawl catches were carried out at noon, every sampling day one haul was carried through. Sampling was conducted in the pelagic zone of the lake, always in the same location. After capture, the pikeperch samples were frozen. In the laboratory, the SL and the W of each pikeperch individual were measured. The age was estimated from the length frequency distribution of the YOY and YAO (year-and-older) age groups (**Figure 2**). Each fish was dissected, the stomach contents were analysed under microscope and the food items were identified and counted.

Table 2. The number, age, standard length (SL) and weight (W) (± standard deviation) of examined juvenile pikeperch from Lake Võrtsjärv.

Sampling date	Number of individuals (*n*)	Age	SL (cm)	W (g)
8 Aug 2007	18	YOY	5.34 ± 0.61	1.74 ± 1.69
15 Aug 2007	37	YOY	5.47 ± 0.94	1.97 ± 2.56
3 Sept 2007	19	YOY	5.68 ± 0.31	1.9 ± 2.89
6 Nov 2007	11	YOY	6.18 ± 1.07	2.59 ± 2.23
30 June 2008	38	YAO	8.36 ± 0.41	6.49 ± 1.19
5 Aug 2008	4	YOY	4.2 ± 0.41	0.68 ± 0.31
29 Sept 2008	5	YOY	5.63 ± 1.39	2.19 ± 0.49
20 Oct 2008	6	YOY	6.39 ± 1.43	3.45 ± 1.43
13 Aug 2009	113	YOY	5.17 ± 0.38	1.46 ± 0.35
11 Sept 2009	30	YOY	5.29 ± 0.77	1.54 ± 0.32
20 Oct 2009	28	YOY	5.76 ± 1.49	1.87 ± 0.74
10 Nov 2009	35	YOY	5.20 ± 0.24	1.45 ± 0.15
4 May 2010	5	YAO	5.5 ± 0.31	1.27 ± 0.96
7 June 2010	5	YAO	9.32 ± 2.54	12.7 ± 9.21
13 July 2010	17	YOY	3.83 ± 0.31	0.71 ± 0.17
7 Sept 2010	5	YOY	5.83 ± 1.04	2.29 ± 1.41
27 Sept 2010	5	YOY	5.33 ± 0.29	1.54 ± 0.32

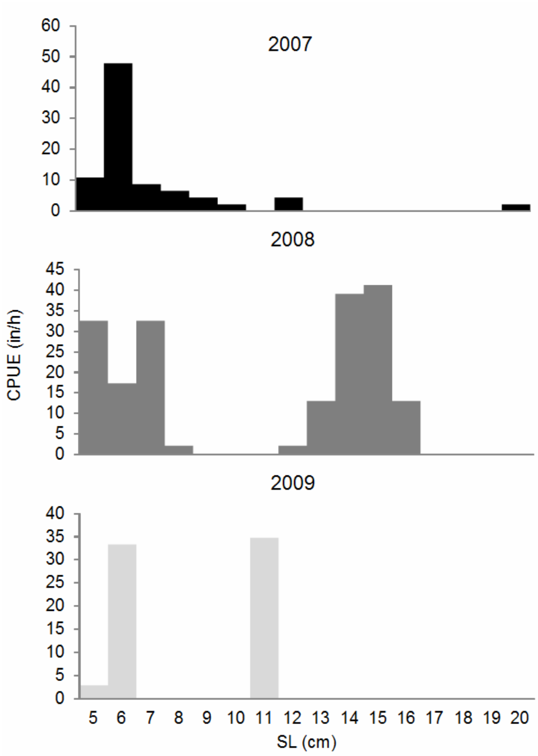

Figure 2. The Catch per unit effort (CPUE individuals per trawl hour) of juvenile pikeperch in Lake Võrtsjärv in 2007-2009 in autumn months.

For the diet analyses the index of frequency of occurrence (FO) was used. This index in itself is not a robust indicator of dietary changes, as the most common prey does not mean being the dominant. However, *FO* was the only basis on which diet comparison of historical and recent data could be conducted as it was the only parameter that was used to describe the diet of juvenile pikeperch in the 1950s [13]. To assess the potential prey community, 1673 juvenile fish, including bream (*Abramis brama* (L.)), ruffe, roach and perch (*Perca fluviatilis* (L.)) collected with the same trawl as pikeperch fries, were measured and weighed in 2009 and 2010 in the current investigation. Additionally, the prey-predator length relationship was calculated.

2.3. Data Analysis

Firstly, a logistic analysis was used to compare the diet of zooplanktivorous pikeperch in two investigated periods: the 1950s and the present (2007-2010). With the logistic analysis odd ratio (the ratio of the probability of occurrence) was found. Odds ratio shows the estimated difference in probability of a certain prey item occurring in the pikeperch diet in two investigated periods. Secondly, the ANOVA model was used to test the effect of different investigation periods—periods with abundant smelt population (1920s, 1960s-1970s) and periods with no smelt (1950s and from 1980s up to now)—on the standard length of the pikeperch fry. In the statistical tests, the level of significance (α) was set to 0.05. For statistical analysis, the programme R, version 2.11.0 was used [35].

3. Results

3.1. The Diet of Zooplanktivorous Pikeperch

In the 1950s the number of different species of zooplankton counted in YOY pikeperch stomach was 14 [13]. By the recent period (2007-2010), the number of prey species had decreased to seven. By then *B. longimanus, Alona* spp., *Alonopsis* spp., *Sida crystalline* (Müller), *Acroperus elongatus* (Sars), *Diaptomus* spp., *Achteres* spp. and *E. gracilis* had disappeared from the diet. In 2007-2010, the most common food object was *M. leuckarti*. This species occurred on average in 87% of the stomachs at the end of summer and in autumn (**Figure 3**).

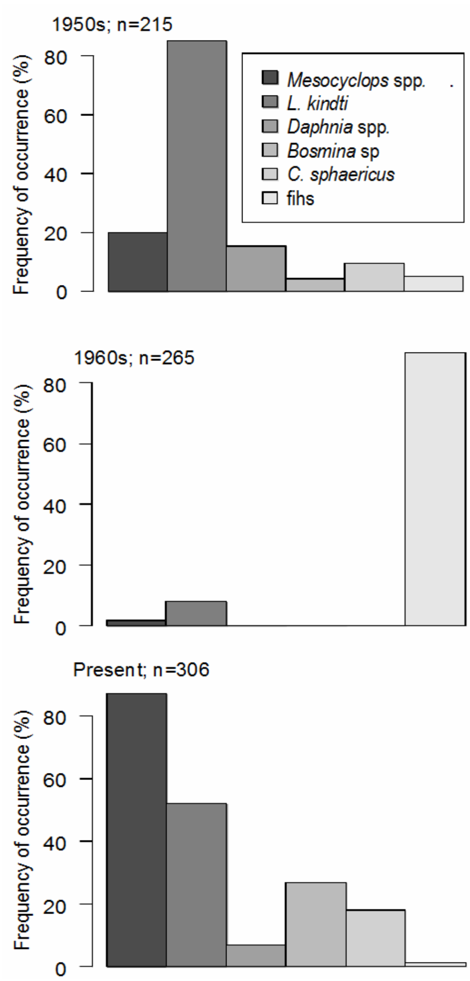

Figure 3. The average frequency of occurrence (%) of different prey items in the diet of juvenile pikeperch from August till October in different periods: the beginning of the 1950s [13], the 1960s [14,16] and 2007-2010 (authors data).

Compared to the 1950s, the probability that *M. leuckarti* occurs in the diet of juvenile pikeperch had increased significantly (Logistic analysis $n = 521$, $P < 0.001$): the odds ratio was 34.8, meaning that the estimated probability that *M. leuckarti* occurs in the diet in the recent period is 34.8 times higher than previously. At the beginning of the 1950s, the most common food object was *L. kindti* (*FO* 85%), however, recently the frequency of occurrence of this organism was found to be on average only 52%. The difference in the levels of *FO* of *L. kindti* was statistically significant (Logistic analysis, $n = 521$, $P < 0.001$) and the odds ratio was 7.6. In the 1950s *Bosmina* spp. and *Chydorus* spp. occurred in 4% and 9% of the YOY pikeperch stomachs, respectively. In 2007-2010 *Bosmina* spp. occurred in 25% and *C. sphaericus* in 15% of the stomachs. However, the only statistically signifycant (Logistic analysis, $n = 521$, $P < 0.001$) increase was for *Bosmina* spp., where the odds ratio was 3.6. *Daphnia cucullata* Sars was one of the subdominants in the 1950s in the diet of YOY pikeperch, when its *FO* was 15%. In the recent period the *FO* of *D. cucullata* was approximately 7%, whereas the decrease was significant (Logistic analysis, $n = 521$, $P < 0.001$).

3.2. Growth and the Ontogenetic Diet Shift

In the 1950s the standard length of pikeperch fry varied from 5.2 to 6.2 cm (**Table 3**) and 4.5% of juvenile pikeperch shifted to piscivory in their first autumn (**Figure 4**) as their potential prey fish was 86% - 91% of YOY pikeperch length (**Table 4**). However, the prey-predator length relationship decreased towards autumn and pikeperch was able to shift to piscivory in spring, being 7.6 - 8.5 cm in length [13].

In 2007 and 2008 the average autumn length (± standard deviation) of pikeperch fry was 6.2 ± 0.8 cm and 6.1 ± 0.9 cm, respectively [17]. In 2009 and 2010 it was 5.5 ± 1.1 cm and 5.6 ± 0.8 cm, respectively (**Table 3**). The autumn length of possible prey fishes was in the autumn of 2009 as follows: ruffe 4.2 ± 1.4 cm, roach 4.7 ± 0.3 cm, perch 5.5 ± 0.3 cm, bream 5.3 ± 0.9 cm (**Figure 4**) and in the autumn of 2010 ruffe was 5.3 ± 0.7 cm, roach 6.2 ± 0.4 cm, bream 6.3 ± 0.7 cm in length. Prey fishes were on average greater than 75% of the length of the pikeperch standard length (**Table 4**). The prey to predator length ratio increased towards autumn and did not change significantly in the spring of 2010. The diet shift to piscivory was not found among YOY in 2007, 2008 [17] and 2010. In the summer of 2009, 7% of YOY pikeperch had shifted to piscivory, however, in the autumn of the same year pikeperch samples did not comprise piscivorous individuals. In spring 2010, pikeperch fry as small as 5.4 cm were caught. Thus, the shift to piscivory can take place in the following summer: the 2007 year cohort shifted to piscivory at the end of June 2008, at a length of 8.4 ± 0.4 cm [17] and the 2009 year cohort at the beginning of June 2010, at a length of 9.3 ± 2.5 cm. In the recent period, the first fishes eaten by pikeperch were ruffe and pikeperch.

In the 1920s and in the 1960s-1970s YOY pikeperch gained length up to 12 cm in autumn as they started to eat fish (primarily smelt) already in their first midsummer, being only 3.5 cm in length [13]. Comparing periods with abundant smelt populations (1920s, 1960s-1970s) with periods with no smelt (1950s and from 1980s up to now) discrepancy in the autumn length of pikeperch fry can be observed. Furthermore, the differences in those investigation periods were statistically significant—1.5-fold increase in pikeperch length during periods of abundant smelt (ANOVA, n = 589, $P < 0.001$).

Table 3. The average standard length (SL) and total mass (W) of juvenile pikeperch for October and November in Lake Võrtsjärv [12-17], whereas *n* marks the number of fishes in each group.

	1920	1950	1951	1953	1954	1966	1968	1969	1970	2007	2008	2009	2010
SL (cm)	12.0	5.2	4.9	5.2	6.2	10.5	12.1	10.7	9.8	6.2	6.1	5.5	5.6
W (g)		1.46	1.25	1.3	3.4	15.9	24.2	15.6	14.0	2.15	2.7	2.1	1.91
n		40	48	50	7	186	28	7	44	30	11	64	10

Table 4. The average (± standard deviation) potential prey and pikeperch length relationship (%) in 1954 [13], 2009 and 2010 (author's data).

Food object	1954 Aug	1954 Oct	2009 Aug	2009 Oct	2009 Nov	2010 May	2010 June	2010 Sept
Ruffe	85.9	84.6	78.2 ± 6.4	75.5 ± 5.8	86 ± 7.9	83.9 ± 5.2	55.1 ± 3.7	95.3 ± 12.2
Perch	91.3	88.6	96.8 ± 4.9	96.8 ± 10.3	100.7 ± 4.4		79.8 ± 5.4	
Roach	91.3		82.9 ± 6.7	79.6 ± 5.9	90.6 ± 13.3	94.4 ± 0.7	57.9 ± 4.1	110.1 ± 6.25
Bream			82 ± 8.3	107.6 ± 18.6	90.9 ± 2.4	104.6 ± 6.5	60.5 ± 4.7	112.4 ± 14.1

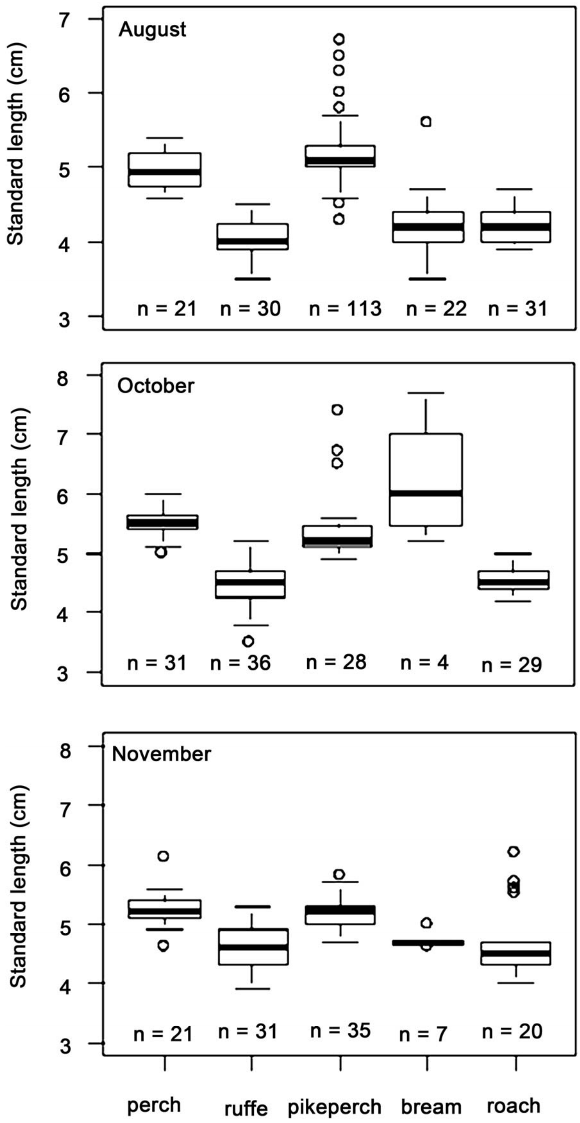

Figure 4. The autumn length of juvenile fish in Lake Võrtsjärv in August, October and November 2009. The box shows interquartile range, line inside the box indicates the median, whiskers show the 95% range of observed data and points are outliers, *n* marks the number of fish in each group.

4. Discussion

The diet, growth and recruitment to piscivory of juvenile pikeperch in Lake Võrtsjärv in four different time periods with dissimilar living conditions and food resources varied significantly. Comparison of the diets of juvenile pikeperch in Lake Võrtsjärv and in other shallow eutrophic European lakes [2,6,8-10] indicates that the diet of zooplanktivorous pikeperch in Lake Võrtsjärv was somewhat more similar to that in other lakes in 1950s than in the recent period. The type of food consumed by juvenile pikeperch is argued to depend mostly on the availability of zooplankton species [2]. According to Haberman *et al.* [23], in the course of eutrofication the food supplies of juvenile fish decrease. In Lake Võrtsjärv feeding conditions for pikeperch fry have been worsened by eutrophication as it has triggered the decrease of large zooplankters like *E. gracilis*, *B. berolinensis*, *Daphnia* spp. and *L. kindti* [23,24]. Thus, discrepancies between the trophic status and food resources of Lake Võrtsjärv in different time periods can evoke variations in the diet of juvenile pikeperch. Therefore, similar shifts in the diet of juvenile pikeperch may occur in other north temperate lakes in the case of ongoing eutrophication. Nevertheless, despite the variation in the diet and slight difference in growth, there were no differences in recruitment to piscivory. This, however, might indicate adaptation to the changed conditions caused by eutrophication or there is simply a threshold size in pikeperch growth that can be reached on zooplankton diet.

In years when the slender-bodied cold-water species smelt was abundant in Lake Võrtsjärv, YOY pikeperch did start to consume fish as early as in their first mid summer and the average length of YOY pikeperch was 1.5 times longer than in the years of postponed diet shift. In 2009-2010 the potential prey fish were found to make up on average more than 75% of the pikeperch's own length at the end of the first growing season. Furthermore, the prey to predator length ratio increased towards autumn and in the following spring; differently from the 1950s when the feeding opportunities were somewhat better and the prey to predator length ratio decreased towards spring. Consequently, pikeperch was not able to switch to piscivory before the second summer.

Sutela and Hyvärinen [36] point out that in the northern edge of pikeperch's distribution range juvenile pikeperch does not shift to piscivory even when smelt is present (**Figure 5**), as the summers are cool and pikeperch does not hatch before early June and prey fish are given a head start. Vice versa, in the southern part of its distribution area, pikeperch is able to predate on even YOY ruffe, perch, roach, bleak (*Alburnus alburnus* (L.)), pumpkinseed sunfish (*Lepomis gibbosus* (L.)) and monkey goby (*Neogobius fluviatilis* (Pallas)) in its first growing season [4,8,37] as there seems to be no mismatch between predator and its prey.

The mean air temperature in Estonia [39] and the water temperature in Lake Võrtsjärv have increased signifi-

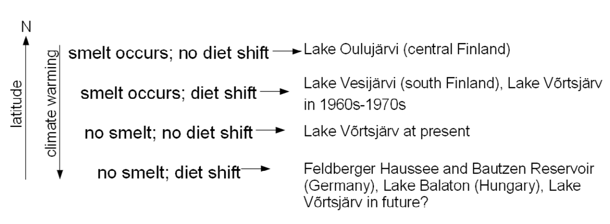

Figure 5. Possibilities for the diet shift in the first growing season for juvenile pikeperch in different latitudes and in changing climate [8,13,14,16,36-38].

cantly [19,20]. Thus, it is most likely that climate warming influences the recruitment success of juvenile pikeperch as warmer climate has already seriously affected the prey community structure. However, prey to predator size ratio depends not solely on the water temperature, but also on the rate at which water temperature increases during spring and early summer as pikeperch are shown to spawn later than most of their possible prey fish (smelt, ruffe, roach) [40]. Namely, if the water temperature rises gradually, pikeperch will have less size advantage to be able to capture the fry of prey fishes spawning at lower water temperatures. But if the water temperature rises rapidly, there will be a shorter gap between the hatching times of pikeperch compared to prey fishes. Thus, if the temperature rises rapidly, juvenile pikeperch may be capable of starting predation on ruffe, perch, roach etc. already in their first summer like in the southern part of pikeperch's distribution areas. On the contrary, when the temperature increases gradually in spring, pikeperch populations may seriously suffer due to shortage of suitable prey.

The growth of YOY pikeperch varied between periods with different prey communities: 1) period with abundant smelt population, 2) period with no smelt but high numbers of larger cladocerans and 3) period with no smelt and low numbers of larger cladocerans. The presence of suitable prey fish, e.g. smelt, rather than the presence of larger cladocerans, is the main factor influencing growth at the juvenile stage in Lake Võrtsjärv. Although it has been claimed that pikeperch growth depends largely on the availability of different prey items [10,41], particularly on the abundance of large-bodied cladocerans [2,5, 42], the length of individual fish in Lake Võrtsjärv has shown a reduction solely due to the postponed diet shift. Therefore, investigating long-term processes in one certain lake enriches results that can be gained from different study sites.

Pikeperch fries smaller than 6 cm SL do not survive their first winter [26,43]. Owing to climate changes winters have become warmer and wetter in Estonia [19,38, 44] and thus, as the current research demonstrated, juvenile pikeperch can survive the winter despite the growth acceleration triggered by ontogenetic diet shift and become piscivorous in their next summer. Similarly, with a warmer climate there will be an increase in fish winter survival [11,45]. Currently, populations of the first suitable prey fish, smelt, have collapsed due to the warmer climate, but juvenile pikeperch are able to survive only thanks to the changed environment, becoming the top-predator in their second growing season in Lake Võrtsjärv. Hereby, pikeperch fries are now zooplanktivorus considerably longer than previously and become piscivorous a year later.

In conclusion, there have been significant changes in the diet and growth of juvenile pikeperch in Lake Võrtsjärv since the 1950s. Furthermore, these changes are most probably related to eutrophication and climate change as these trigger changes in food supplies and living conditions. However, further research is needed to assess the exact effects of shifts in the environment on the population of pikeperch, the most important commercially fished species in the lake.

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