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Pikeperch cannibalism: effects of abundance, size and condition

Jyrki Lappalainen*, Mikko Olin & Mika Vinni

*Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland (*e-mail: Jyrki.T.Lappalainen@Helsinki.fi)*

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The possible effects of pikeperch abundance, size and condition on cannibalism were studied in 1999–2001 in two basins of lake Hiidenvesi, Finland. Cannibalism was found only during the warm summer of 1999 when the abundance of young-of-the-year (YOY) fish was the highest. In July 1999, YOY pikeperch were the smallest prey (2.5–3.5 cm TL) recorded from pikeperch stomachs. In September 1999, only the smallest YOY juveniles (6.5–8.6 cm) were predated of the available size-distribution of YOY juveniles in the lake (6.5–13.8 cm) showing that the risk of cannibalism was highest among the smallest juveniles. There was no effect of prey or predator condition on cannibalism.

Introduction

Cannibalism is common in teleost fish and has been connected to increased encounter rate between the prey and the predator, and to low food availability and quality (Polis 1981, Smith & Reay 1991 and references therein). The encounter rate, and thereby also the degree of cannibalism, should be increased either by the increased abundance of the predator or their prey (Smith & Reay 1991, Frankiewicz *et al*. 1999). Low food availability or quality can increase the duration and area of foraging activity of an individual (Polis 1981), which then may be more vulnerable to cannibalism or which may lead to increased cannibalistic behaviour (Smith & Reay 1991, Lovrich & Sainte-Marie 1997). When food availability or quality is low, the number of individuals with empty stomachs should increase (Ojaveer *et al*. 1999), which has been shown also to increase the likelihood of cannibalism (Lovrich & Sainte-Marie 1997).

Here we examine factors that may have affected the cannibalism of pikeperch (*Sander lucioperca*) observed within a project aiming to unravel the food web structure in lake Hiidenvesi (Vinni *et al*. 2000, 2004, 2005). Elsewhere, the proportion of cannibalistic pikeperch has been found to vary from 0% to 56% between populations (Campbell 1992, Hansson *et al*. 1997, Argillier *et al*. 2003, Keskinen & Marjomäki 2004), which has been connected to variations in the number of young-of-the-year (YOY) juveniles (Frankiewicz *et al*. 1999). Generally, YOY pikeperch are predated predators being age 1 or older specimens (Campbell 1992, Frankiewicz *et al*. 1999). However, it is currently unclear whether cannibalised YOY

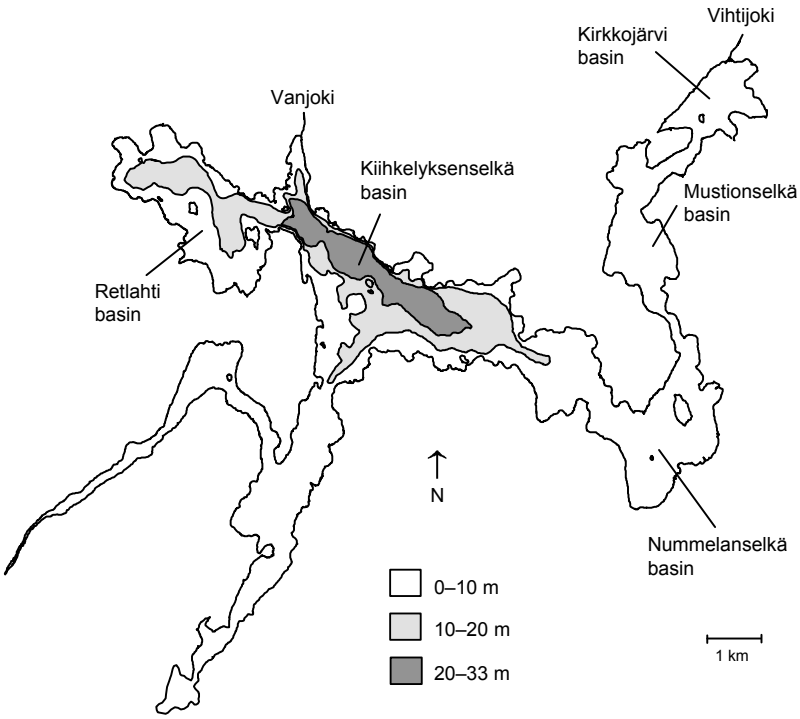

Fig. 1. Study area, lake Hiidenvesi, and different lake basins.

pikeperch are similarly sized than other prey species or the other YOY pikeperch available. Juanes (2003) showed that cannibalistic gadoids selected larger-sized conspecifics than non-cannibalistic species, whilst Macpherson and Gordoa (1994) found that Cape hake (*Merluccius capensis*) preferred smaller conspecifics. Hence, the role of prey size in pikeperch cannibalism needs to be studied.

The main aim of this study was to examine factors which could affect or promote the degree of cannibalism in pikeperch. Factors analysed were (i) the abundance and condition of both YOY and adult pikeperch in two lake basins, (ii) prey/predator ratio between cannibalized and other prey, and (iii) the size distribution of the cannibalised individuals relative to the size distribution of YOY juveniles in the lake. The two main hypotheses were that cannibalism should increase when (i) the abundance of YOY juveniles, adults or both are higher, and (ii) condition of either of the prey or the predator is lower. Although several studies have analysed some of the present factors included, none of these have analysed them simultaneously in any species.

Materials and methods

Study area

Hiidenvesi is a large (30.3 km^2) lake situated in southwestern Finland (60°24´N, 24°18´E) (Fig. 1). The lake consists of several basins with differing morphometry and water quality. Here, two of these basins, Kiihkelyksenselkä and Mustionselkä, were studied. Kiihkelyksenselkä basin has an area of 10.5 km^2, mean depth of 11.2 m and a maximum depth of 33 m. The basin has total P and total N concentrations of 40 μg l^{-1} and 1030 μg l^{-1}, respectively. Mustionselkä basin has an area of 2.7 km^2, and mean depth of only 1.7 m with a maximum of 4.5 m. The total P and N concentrations are 87 and 1140 μg l^{-1}, respectively (Horppila 2005).

The fish species and their abundances are quite different in the two basins. The total biomass and the percentage of cyprinids are higher in the more eutrophic part of the lake in Kirkkojärvi and Mustionselkä basins (Olin & Ruuhijärvi 2005). Bream (*Abramis brama*), white bream (*Abramis bjoerkna*) and blue bream (*Abramis ballerus*) are the most abundant species in these

basins, whereas roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*) are found in greater numbers in the less eutrophic Nummelanselkä and Kiihkelyksenselkä basins. Within percids, perch (*Perca fluviatis*) is less abundant in most eutrophic Kirkkojärvi and Mustionselkä basins, while the proportion of pikeperch is not dependent on the trophic state of the basin (Olin & Ruuhijärvi 2005). Smelt (*Osmerus eperlanus*) is the most abundant species in the least eutrophic and deepest Kiihkelyksenselkä basin (Malinen *et al*. 2005).

Pikeperch sampling and diet analysis

Diet analyses were conducted in pikeperch (age ≥ 1) collected using gillnets in Mustionselkä basin and with gillnets and trawl in Kiihkelyksenselkä basin in 1998, 1999 and 2000 (data set 1) (Table 1). Pikeperch were captured with bottom gillnets (height 1.8 m, length 30 m, mesh sizes 12–45 mm knot-to-knot). Nets were fished in 1.5–4 m depths in Mustionselkä basin and in 2–20 m depths in Kiihkelyksenselkä basin. In both basins, the fishing time with gillnets varied between 0.5 and 5 hours. The trawl (height 5 m, width 8 m and cod-end 3 mm mesh-size knot-to-knot) used was towed by two boats for approximately 20–30 min per haul, with a towing speed of ca. 1 m s^{-1}. After capture, pikeperch were chilled and stomach contents were analyzed in laboratory using a volumetric proportion method (Windell 1971). Pikeperch were aged from scales taken below the lateral line and above the anal fin for all pikeperch between 10 and 20 cm in autumn to separate YOY and older pikeperch (data set 1).

The possible effects of abundance and condition on cannibalism were analysed from pikeperch caught with NORDIC gillnets (height 1.5 m, length 30 m consisting of 12 panels, 2.5 m each, of different mesh sizes from 5 to 55 mm knot-to-knot) between July–September in years 1997–2001 (data set 2). The gillnet sampling was stratified and random (Appelberg *et al*. 1995, Olin *et al*. 2002). The two basins were divided vertically and horizontally into different zones, in which the net sites were chosen randomly. The nets were set overnight (fishing time 12 h).

Table 1. Number of studied pikeperch caught with trawl (T) and gillnets (G) in Mustionselkä basin (M) and in Kiihkelyksenselkä basin (K).

Month and year	Basin	Gear	Number of stomachs analysed	Number of cannibalistic pikeperch	Pikeperch with empty stomachs (*n*)
June 1998	M	G	29	0	8
June 1998	K	G	5	0	0
July 1998	M	G	12	0	4
July 1998	K	G, T	27	0	8
Aug 1998	M	G	5	0	2
Aug 1998	K	G, T	18	0	9
Sep 1998	K	T	50	0	17
Oct 1998	K	T	27	0	4
May 1999	K	T	9	0	4
May 1999	M	G	12	0	4
June 1999	K	T	7	0	0
June 1999	M	G	41	0	21
July 1999	K	T	34	0	12
July 1999	M	G	35	11	7
Aug 1999	K	T	8	0	2
Sep 1999	M	G	8	7	1
Oct 1999	K	T	27	0	6
May 2000	K	T	6	0	2
May 2000	M	G	12	0	0

The yearly sampling effort for each basin ranged from 6 to 46 net nights and was adjusted to the basin area and depth. Every basin and depth zone was sampled between 2–4 times per year.

Size distribution and condition of YOY pikeperch were analysed in fish collected with seining completed by the Uusimaa Regional Environment Centre in September 1999 in both Mustionselkä and Kiihkelyksenselkä basins (data set 3). The used seine had 150 m long wings and the height was 13 m. Mesh sizes were from 6 to 30 mm (bar length) in wings and 6 mm (bar length) in the cod end. The hauled area was 9.5 hectares in Kiihkelyksenselkä basin and 7.6 hectares in Mustionselkä basin. The total lengths and weights of YOY pikeperch were measured with 1 mm and 0.01 g precision in data set 1, and the adults with 1 cm and 1 g precision in data set 2.

Statistical analyses

The relationship between water temperature and $\log_{10}(x + 1)$ transformed YOY abundance was studied with correlation analysis separately for both basins. Mean surface water temperature was based on 3–4 measurements per basin recorded between 1 June and 14 July, and the YOY abundance on the number of YOY pikeperch caught with gillnets between July 15 and early September (data set 2). In a Baltic bay, the number of YOY juveniles correlated with the coming year-class strength of pikeperch already at the end of July (Kjellman *et al.* 2003), so the period of the highest mortality causing differences between years should have been stabilized at the time of the beginning of YOY sampling after 15 July in lake Hiidenvesi.

Analysis of covariance was used to compare the condition of pikeperch (age ≥ 1) between basins and years using $\log_{10}$-transformed weight as dependent variable and $\log_{10}$-transformed total length as a covariate (SAS Institute Inc. 1989). Homogeneity of slopes was tested before all analyses. Condition of pikeperch was compared between cannibalistic (CA) and non-cannibalistic (NCA) pikeperch in July 1999 (data set 1) and between years 1999 (CA) and 1998 (NCA) in Mustionselkä basin (data set 2). In addition, condition was compared between Mustionselkä basin (CA) and Kiihkelyksenselkä basins (NCA) in 1999 (data set 1). The differences in the numbers of empty stomachs of pikeperch (age ≥ 1) were compared with the χ^2-test between the years 1999 (CA) and 1998 (NCA) in Mustionselkä basin, and between Mustionselkä basin (CA) and Kiihkelyksenselkä basin (NCA) in 1999 (data set 1).

Analysis of covariance was not used to compare YOY conditions (data set 3), because the length–weight slopes were heterogeneous between basins. Therefore, only the length-weight relationships were estimated for the two basins with a model:

$$w = c + al^b \quad (1)$$

where w is weight (g), c is intercept, a and b are parameters, and l is total length (cm).

Logistic regression (SAS Institute Inc. 1989) was used to analyse whether the probability of cannibalism is dependent on prey length by comparing the number of YOY pikeperch caught with seining and the number of pikeperch recorded from pikeperch stomachs. The number of cannibalised YOY pikeperch was added to the number of YOY pikeperch caught from the lake, and were compared within length groups of 0.2 cm.

Results

Cannibalism and prey/predator ratio

Cannibalism of pikeperch was observed only in Mustionselkä basin in July and September 1999 (Fig. 2). In July 1999, 39.29% of pikeperch stomachs that contained food included pikeperch. In September, all pikeperch that had food in their stomachs were cannibalistic (Table 1). The piscivorous diet in Mustionselkä basin consisted, besides pikeperch, of cyprinids, such as roach, bream and bleak, and of percids, such as perch and ruffe (*Gymnocephalus cernuus*). The importance of smelt was much lower in Mustionselkä basin than in Kiihkelyksenselkä basin (Fig. 2).

In July 1999, cannibalised pikeperch (mean length = 2.81 cm, total range = 2.5–3.5 cm, n =

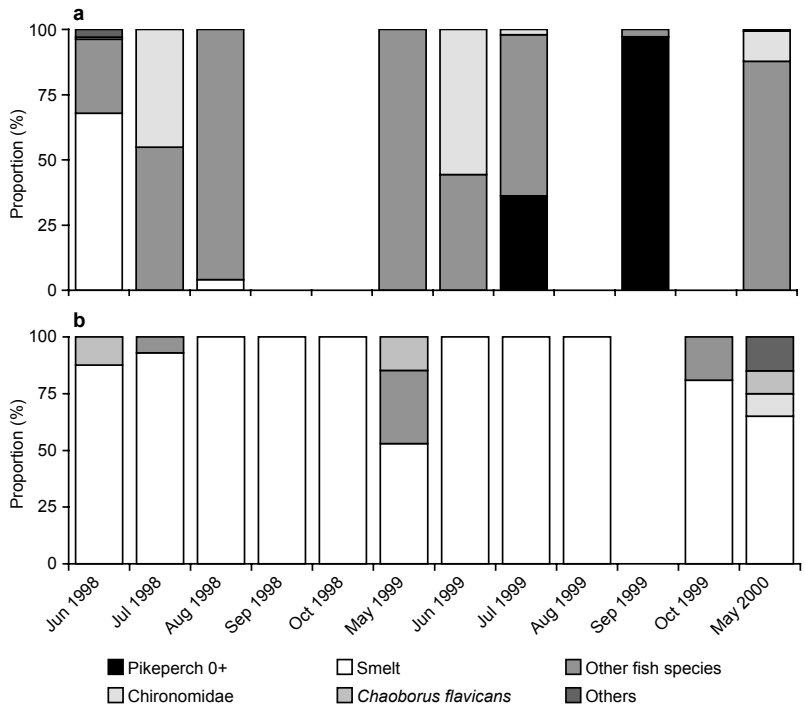

Fig. 2. Diet of pikeperch (age ≥ 1) in (**a**) Mustionselkä and (**b**) Kiihkelyksenselkä basins.

12) were among the smallest prey fishes (Fig. 3). In September, cannibalised pikeperch (mean length = 7.65 cm, total range = 6.5–8.6 cm, n = 15) were similar sized (Mann-Whitney U-test: p = 0.806) as smelt (mean length = 7.71, total range = 5.5–9.0 cm, n = 42) in Kiihkelyksenselkä basin (Fig. 3). However, based on the samples of YOY pikeperch collected using seine nets, cannibalised pikeperch were selected from the smallest end of the available size-distribution of YOY pikeperch in the basin (logit (CA) = 10.3983 – 1.7087 × length, $p < 0.0001$; Fig. 4).

The prey/predator ratio (PPR) decreased in relation to pikeperch size (Fig. 5). A comparison of the minimum and maximum size range of prey species by pikeperch in 24 lakes (Keskinen & Marjomäki 2004) with that found in lake Hiidenvesi showed that cannibalised pikeperch were smaller in July 1999 than those found by Keskinen and Marjomäki (2004) or other prey fishes in lake Hiidenvesi. In lakes studied by Keskinen and Marjomäki (2004), no cannibalism was observed. Also prey species were on average smaller in lake Hiidenvesi than those found by Keskinen and Marjomäki, probably due to the large proportion of smelt in the diet in lake Hiidenvesi.

Abundance and condition

The number of YOY juveniles correlated with the mean surface water temperature in both basins (Kiihkelyksenselkä basin: r = 0.917, p = 0.0282, n = 5; Mustionselkä basin: r = 0.924, p = 0.0247, n = 5). The YOY catches of pikeperch were the highest in 1999 in Mustionselkä basin among the studied years and basins (Fig. 6a). No large fluctuations in the number of older pikeperch (age ≥ 1) were observed (Fig. 6b), and cannibalism was found only during the year of the highest abundance of YOY pikeperch in Mustionselkä basin (Fig. 6c).

Analysis of covariance showed that the mean adult weight, using length as covariate, was not statistically significant between cannibalistic and non-cannibalistic pikeperch in Mustionselkä basin in July 1999 (Table 2). Similarly, no differences were found in mean adult weight between Mustionselkä and Kiihkelyksenselkä basins or between years 1998 and 1999 in Mustionselkä basin (Table 2). Even the differences in YOY conditions were small between basins according to length–weight relationships (Fig. 7). Thus, no clear effects of condition on cannibalism were

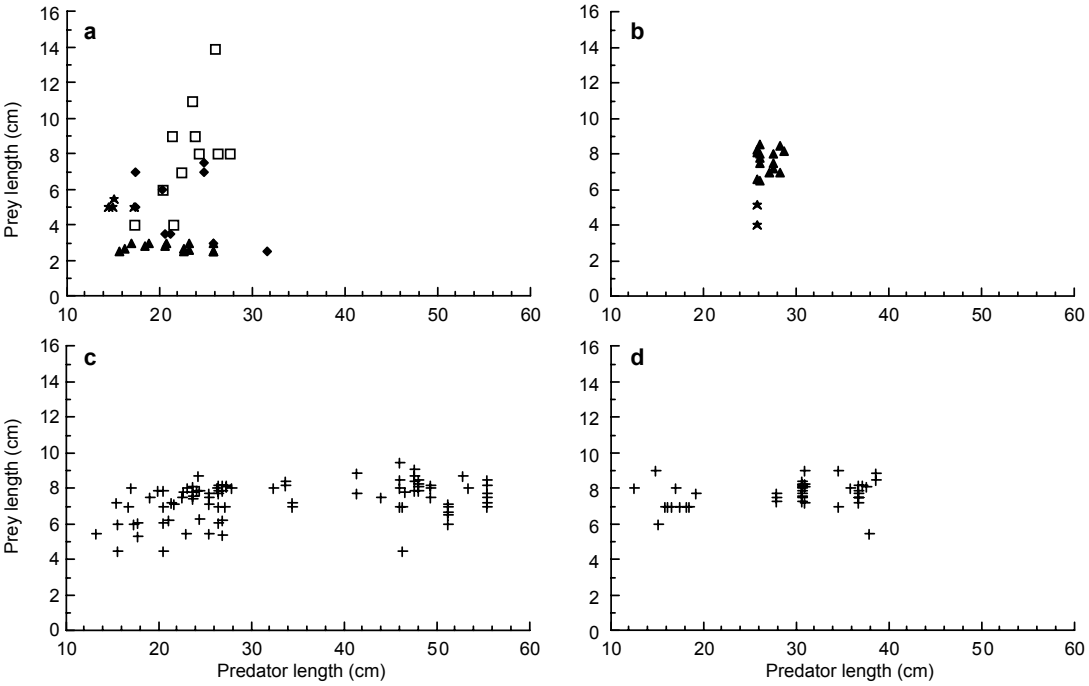

Fig. 3. Prey–predator lengths for pikeperch (age ≥ 1) in Mustionselkä basin (**a**) in May–July and (**b**) in September and in Kiihkelyksenselkä basin (**c**) in May–July and (**d**) in August–October in 1999. Cyprinids are marked with open squares, perch with black diamonds, ruffe with stars, pikeperch with black triangles, and smelt with crosses.

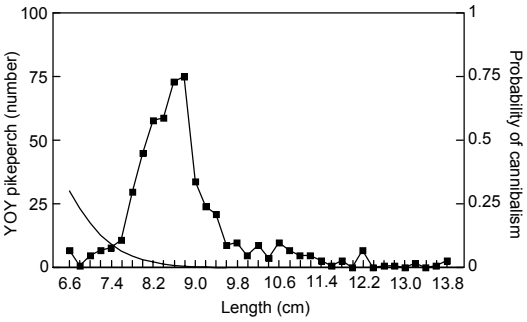

Fig. 4. Size distribution of YOY pikeperch in September 1999 in Mustionselkä basin (seine net, total n = 544) (solid line with squares, left axis) and probability of cannibalism estimated with logistic regression (solid line, right axis).

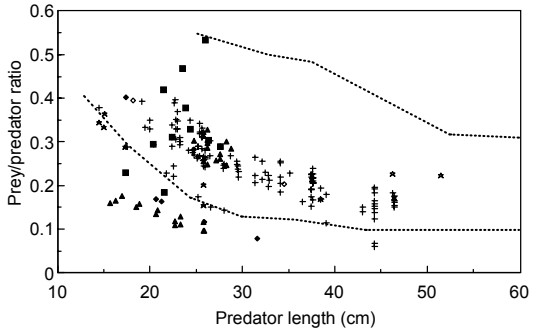

Fig. 5. Prey/predator ratio in relation to pikeperch length (age ≥ 1) in lake Hiidenvesi. Cyprinids are marked with black squares, perch with black diamonds, ruffe with stars, pikeperch with black triangles, and smelt with crosses. Dashed lines are for minimum and maximum prey/predator ratios of pikeperch in 24 other Finnish lakes (Keskinen & Marjomäki 2004).

found. The overall frequency of empty stomachs of pikeperch was similar in 1998 and 1999, 30.06% and 31.49%, respectively. Thereby, no statistical differences were found in the proportion of empty stomachs between years in Mustionselkä basin (χ^2-test: 1998 (NCA) and 1999 (CA), p = 0.6405) or between the two basins in 1999 (Kiihkelyksenselkä basin (NCA) and Mustionselkä basin (CA), p = 0.3748).

Discussion

The overall degree of cannibalism of pikeperch was low in lake Hiidenvesi. Of the 372 pikeperch analysed, 111 had empty stomachs, and only 18 adults were found to be cannibalistic with 27 YOY fish predated. Cannibalism was

observed only during the summer of highest abundance of YOY pikeperch. Frankiewicz *et al.* (1999) showed that the higher the abundance of YOY pikeperch, the higher the rate of adult cannibalism in Sulejów reservoir. Conversely, Kangur (2000) showed the importance of adult abundance on cannibalism in the Estonian side of lake Peipsi. When pikeperch catches were low in the lake, no cannibalism was observed (Pihu 1966), but when catches were high, cannibalism was also found (Kangur 2000). These two studies (Frankiewicz *et al.* 1999, Kangur 2000) confirm the importance of abundance of both the prey and the predator on cannibalism. In our study, cannibalism was related to the abundance of YOY pikeperch, which was correlated with water temperature similarly as shown for other northern (Lappalainen *et al.* 1995, Kjellman *et al.* 2003) and for some more southern populations of pikeperch (Buijse & Houthuijzen 1992). Typically, no stock–recruitment relationship was found for pikeperch (Willemsen 1977, Buijse *et al.* 1992), whereas near the northern limits of the distribution range of pikeperch the number of YOY juveniles both in mid summer (July) and in autumn (September, October) have been shown to be positively correlated with water temperatures during the same summer in June and in June to July, respectively (Lappalainen *et al.* 1995, Kjellman *et al.* 2003). Therefore, cannibalism may be more common during warm summers with high YOY abundance, such as noted in 1999. The mean air temperature in June and July 1999 was the 4th warmest (mean = 17.42 °C) measured at the weather station near lake Hiidenvesi between 1961 and 2000. Other, even warmer summers occurred in 1972 (mean = 17.86 °C), 1973 (mean = 17.94 °C) and 1988 (mean = 18.03 °C). All these warm summers produced strong year-classes of pikeperch elsewhere (Lehtonen & Lappalainen 1995, Kjellman *et al.* 2003), but the possible degree of cannibalism is not known. However, the existence of positive correlations between water temperature and year-class strengths (Lehtonen & Lappalainen

Table 2. Comparisons of mean weights (log_{10}-transformed) between (1) cannibalistic (CA) and non-cannibalistic (NCA) pikeperch in Mustionselkä basin in July 1999, (2) Mustionselkä basin (M) and Kiihkelyksenselkä basin (K) in 1999, and between (3) 1998 and 1999 in Mustionselkä basin.

Comparison		Least square mean	SE	*P*
1	CA	4.29	0.017	0.3487
	NCA	4.26	0.022	
2	Basin M	4.97	0.034	0.5240
2	Basin K	4.95	0.022	
3	Year 1998	3.96	0.029	0.9553
3	Year 1999	3.96	0.050	

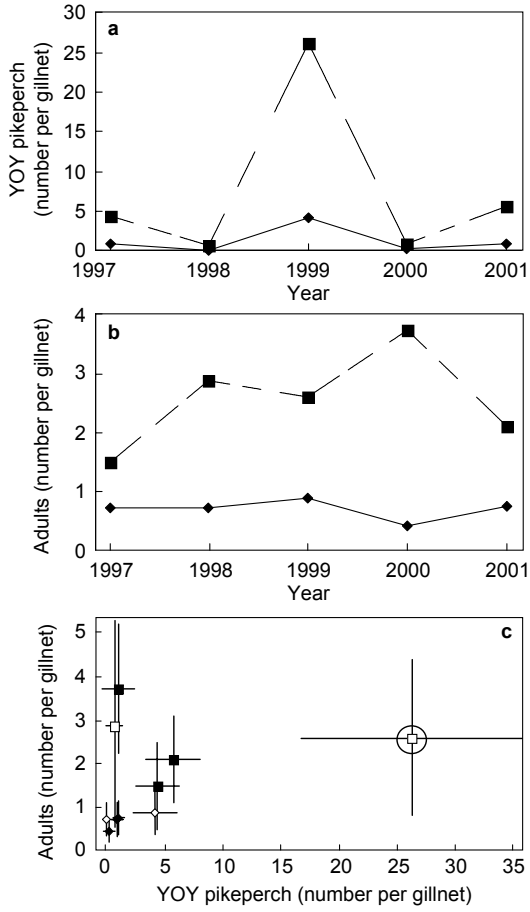

Fig. 6. (**a**) Number of YOY and (**b**) older pikeperch (age ≥ 1) per one gillnet in the Mustionselkä basin (marked with black squares and broken line) and in Kiihkelykselkä basin (marked with black diamonds and solid line) in 1997–2001. (**c**) Relationship between **a** and **b** in Mustionselkä basin (black squares) and in Kiihkelykselkä basin (black diamonds) in 1997–2001. Open markers are years with diet data and circled marker is year with noted cannibalism. Error bars are for 95% confidence limits.

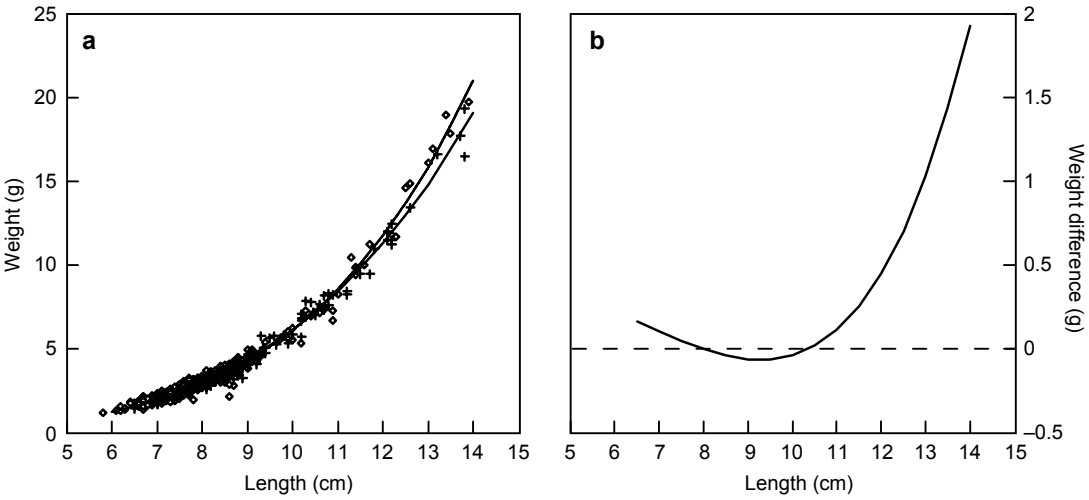

Fig. 7. (**a**) Length–weight relationships of age 0 pikeperch in Mustionselkä (Weight = 0.7581 + 0.0006 × length$^{3.9536}$; crosses) and in Kiihkelyksenselkä basins (Weight = 0.2239 + 0.0022 × length$^{3.441}$; diamonds) in September 1999. (**b**) Weight difference between Mustionselkä basin and Kiihkelyksenselkä basin based on **a**.

1995, Kjellman *et al*. 2003) suggests that cannibalism has not been effective enough to confound these correlations with temperature.

The size comparison of cannibalised YOY pikeperch with those caught from Mustionselkä basin showed that adult pikeperch positively selected smaller juveniles in September. This suggests active prey size selection (Turesson *et al*. 2002) among cannibalistic pikeperch. Also the size range of cannibalised YOY pikeperch was similar to that of the other prey used by non-cannibalistic pikeperch. If active selection is applicable, then the selection of pikeperch was based on suitable-sized prey rather than species, and it may only be due to the high abundance of juvenile pikeperch that these individuals were consumed. On the other hand, the situation could have been quite different in May and July when the highest variation in prey size was found. It is possible that the number of suitable-sized prey species was then low, and pikeperch had to prey on a wider size range of prey. Juanes (2003) suggested that the cannibalised prey of gadoids was larger than the other prey because the predator had higher capture success with familiar prey. The same phenomenon, but concentrating towards smaller prey sizes may have taken place in lake Hiidenvesi.

The prey/predator ratio (PPR) decreased in relation to pikeperch length in lake Hiidenvesi as shown for several marine piscivores (Scharf *et al*. 2000) and also for pikeperch (Keskinen & Marjomäki 2004). The decline in PPR is probably connected with the lower abundance of large-sized preys (Scharf *et al*. 2000, Juanes 2003). In Kiihkelyksenselkä basin, all size classes of pikeperch preyed on 6–8 cm smelt, which is probably due to the low number of smelt larger than 10 cm in the basin (Vinni *et al*. 2004). In Mustionselkä basin, the abundance of adult smelt is low and cyprinids are common, whereas in Kiihkelyksenselkä basin smelt is the most abundant pelagic species. Thus, the prey species eaten by pikeperch seem to match to species commonly occurring in the basins.

The abundance of other prey is often suggested to affect the cannibalism of pikeperch (Willemsen 1977, Campbell 1992, Argillier *et al*. 2003). If other prey is very abundant, the degree of cannibalism should be lower as compared with the situation when other prey is rare and the probability of cannibalism is increased. In lake Hiidenvesi, the overall degree of cannibalism is low, while in some more southern populations it is more common or even a necessity. In Sulejów reservoir, the number of YOY eaten was linearly correlated with their abundance (Frankiewicz *et al*. 1999), whereas in lake Egirdir, the introduction of pikeperch resulted in the loss of 17 origi-

nal fish species and high degree of cannibalism for pikeperch (Campbell 1992). The occurrence of cannibalism only in Mustionselkä basin is probably related to the shallowness of the basin, which should increase contacts between YOY pikeperch and older pikeperch, and could also be related to the low occurrence of other suitable-sized prey. Cyprinid fishes are very abundant in the basin, but with the presence of pikeperch smaller cyprinids, such as roach and bleak, stay near the littoral zone, which is not a typical habitat for piscivorous pikeperch (Brabrand & Faafeng 1993, Olin & Malinen 2003). The YOY pikeperch also show habitat shifts from the littoral zone to deeper waters in July (Urho *et al.* 1990), which matches closely with the date when the first signs of cannibalism was noted in lake Hiidenvesi.

The hypothesis that low condition increases cannibalism was not supported. However, Buijse and Houthuijzen (1992) showed that the condition of non-piscivorous YOY pikeperch decreased and that of piscivorous pikeperch increased towards the end of the growing season in lake IJssel. In lake Hiidenvesi, YOY pikeperch that were under the risk of cannibalism, were all non-piscivorous (< 9 cm) (Lappalainen *et al.* 2005). Therefore, the high abundance of non-piscivorous YOY juveniles could have increased food competition, duration and area of foraging activity, which then could have led to decreased condition and increased risk of cannibalism (i.e. Smith & Reay 1991). The analysis of the condition of preyed YOY pikeperch might have revealed whether the reduced condition could in fact enhance cannibalism.

To conclude, the results suggest that the cannibalism by pikeperch may be a relatively uncommon phenomena in lake Hiidenvesi. Cannibalism was only recorded in a year with the extremely high abundance of YOY juveniles, and only in a shallow basin. No clear effects of condition of adult or YOY fish on cannibalism were found. PPR ratio and size comparisons revealed that cannibalised YOY juveniles were either smaller (July) or similarly sized (September) than other prey fishes consumed, but the risk of YOY juveniles to be eaten by older pikeperch was higher within smaller sized juveniles than within larger sized ones in September.

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References

Appelberg, M., Berger, H.-M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J. & Rask, M. 1995: Development and intercalibration of methods in Nordic freshwater fish monitoring. — *Water, Air & Soil Pollut.* 85: 401–406.

Argillier, C., Barral, M. & Irz, P. 2003: Growth and diet of the pikeperch *Sander lucioperca* (L.) in two French reservoirs. — *Arch. Pol. Fish.* 11: 99–114.

Brabrand, Å. & Faafeng, B. 1993: Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: Predation risk versus pelagic behaviour. — *Oecologia* 95: 38–46.

Buijse, A. D. & Houthuijzen, R. P. 1992: Piscivory, growth, and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). — *Can. J. Fish. Aquat. Sci.* 49: 894–902.

Buijse, A. D., Van Densen, W. L. T. & Schaap, L. A. 1992: Year-class strength of Eurasian perch (*Perca fluviatilis* L.) and pikeperch (*Stizostedion lucioperca* (L.)) in relation to stock size, water temperature and wind in Lake IJssel, the Netherlands, 1966–1989. — In: Buijse, A. D. (ed.), *Dynamics and exploitation of unstable percid populations*: 31–69. Landbouwuniversiteit. Wageningen.

Campbell, R. N. B. 1992: Food of an introduced population of pikeperch, *Stizostedion lucioperca* L., in Lake Egirdir, Turkey. — *Aquacult. Fish. Manage.* 23: 71–85.

Frankiewicz, P., Dabrowski, K., Martyniak, A. & Zalewski, M. 1999: Cannibalism as a regulatory force of pikeperch, *Stizostedion lucioperca* (L.), population dynamics in the lowland Sulejów reservoir (Central Poland). — *Hydrobiologia* 408/409: 47–55.

Hansson, S., Arrhenius, F. & Nellbring, S. 1997: Diet and growth of pikeperch (*Stizostedion lucioperca* L.) in a Baltic Sea area. — *Fish. Res.* 31: 163–167.

Horppila, J. 2005: Project description and lake characteristics. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 59: 1–11.

Juanes, F. 2003: The allometry of cannibalism in piscivorous fishes. — *Can J. Fish. Aquat. Sci.* 60: 594–602.

Kangur, A. 2000: Feeding of pikeperch, *Stizostedion lucioperca* (L.), in Lake Peipsi. — *Proc. Estonian Acad. Sci. Biol. Ecol.* 49: 98–108.

Keskinen, T. & Marjomäki, T. J. 2004: Diet and prey size spectrum of pikeperch in lakes in central Finland. — *J. Fish Biol.* 65: 1147–1153.

Kjellman, J., Lappalainen, J., Urho, L. & Hudd, R. 2003: Early determination of perch and pikeperch recruitment in the northern Baltic Sea. — *Hydrobiologia* 495: 181–191.

Lappalainen, J., Erm, V. & Lehtonen, H. 1995: Pikeperch, *Stizostedion lucioperca* (L.), catch in relation to juvenile

density and water temperature in Pärnu Bay, Estonia. — *Fish. Manage. Ecol.* 2: 113–120.

Lappalainen, J., Vinni, M. & Kjellman, J. 2005: Diet, condition and mortality of pikeperch (*Sander lucioperca*) during their first winter. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 59: 207–217.

Lehtonen, H. & Lappalainen, J. 1995: The effects of climate on the year-class variations of certain freshwater fish species. — *Can. Spec. Publ. Fish. Aquat. Sci.* 121: 37–44.

Lovrich, G. A. & Sainte-Marie, B. 1997: Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricus) (Brachyura: Majidae), and its potential importance to recruitment. — *J. Exp. Mar. Biol. Ecol.* 211: 225–245.

Macpherson, E. & Gordoa, A. 1994: Effect of prey densities on cannibalism in Cape hake (*Merluccius capensis*) off Namibia. — *Mar. Biol.* 119: 145–149.

Malinen, T., Tuomaala, A. & Peltonen, H. 2005: Vertical and horizontal distributions of smelt (*Osmerus eperlanus*) and implications of distribution patterns for stock assessment. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 59: 141–159.

Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I. & Lumberg, A. 1999: Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. — *ICES J. Mar. Sci.* 56 (Suppl.): 33–40.

Olin, M. & Malinen, T. 2003: Comparison of gillnet and trawl in diurnal fish community sampling. — *Hydrobiologia* 506–509: 443–449.

Olin, M. & Ruuhijärvi, J. 2005: Fish communities in the different basins of L. Hiidenvesi in 1997–2001: effects of trophic status and basin morphology. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 59: 125–140.

Olin, M., Rask, M., Ruuhijärvi, J., Kurkilahti, M., Ala-Opas, P. & Ylönen, O. 2002: Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. — *J. Fish Biol.* 60: 593–612.

Pihu, E. H. [Пиху, Е. Х.] 1966: [The importance of pike, perch, pikeperch and burbot as biological control in Lake Peipsi-Pskov]. — *Hydrobiological Researches* 4: 235–248. [In Russian].

Polis, G. A. 1981: The evolution and dynamics of intraspecific predation. — *Annu. Rev. Ecol. Syst.* 12: 225–251.

SAS Institute Inc. 1989: *SAS/STAT user's guide*, ver. 6, 4th ed., vol. 2. — SAS Institute Inc., Cary, NC.

Scharf, F. S., Juanes, F. & Rountree, R. A. 2000: Predator size–prey size relationships of marine fish predators: interspecific variation and the effects of ontogeny and body size on trophic-niche breadth. — *Mar. Ecol. Prog. Ser.* 208: 229–248.

Smith, C. & Reay, P. 1991: Cannibalism in teleost fish. — *Rev. Fish Biol. Fish.* 1: 41–64.

Turesson, H., Persson, A. & Brönmark, C. 2002: Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. — *Ecol. Freshwat. Fish* 11: 223–233.

Urho, L., Hildén, M. & Hudd, R. 1990: Fish reproduction and the impact of acidification in the Kyrönjoki River estuary in the Baltic Sea. — *Environ. Biol. Fish.* 27: 273–283.

Willemsen, J. 1977: Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. — *J. Fish. Res. Bd. Can.* 34: 1710–1719.

Windell, J. T. 1971: Food analysis and rate of digestion. — In: Ricker, W. E. (ed.), *Methods for assessment of fish production in fresh waters*: 197–203. Blackwell, Oxford.

Vinni, M., Lappalainen, J. & Horppila, J. 2005: Temporal and size-related changes in the frequency of empty stomachs in smelt. — *J. Fish Biol.* 66: 578–582.

Vinni, M., Lappalainen, J., Malinen, T. & Peltonen, H. 2004: Seasonal bottlenecks in diet shifts and growth of smelt in a large eutrophic lake. — *J. Fish Biol.* 64: 567–579.

Vinni, M., Horppila, J., Olin, M., Ruuhijärvi, J. & Nyberg, K. 2000: The food, growth and abundance of five co-existing cyprinids in lake basins of different morphometry and water quality. — *Aquat. Ecol.* 34: 421–431.