

Tapio Keskinen

Feeding Ecology and Behaviour  
of Pikeperch, *Sander lucioperca* (L.)  
in Boreal Lakes



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## ABSTRACT

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Yhteenveto: Kuhan (*Sander lucioperca* (L.)) ravinnonkäyttö ja käyttäytyminen boreaalisissa järvissä

Diss.

Pikeperch is a predatory percid fish living in lakes and coastal areas in Europe. In this thesis, the role of pikeperch as a predator in freshwaters was studied by several methods. Diet and growth of pikeperch with respect to lake characteristics were studied. Smelt and perch were the most important prey species in Finnish lakes. The proportion of roach increased with pikeperch size and with total phosphorus content of a lake. Behaviour of pikeperch in a large boreal lake system was studied by tagging 21 pikeperch with ultrasonic transmitters. These telemetry studies showed that in the Päijänne lake system separate populations occurred, having different migrations and foraging tactics. Pikeperch always preferred the warmest available water. A bioenergetics model for pikeperch based on laboratory experiments was constructed. This bioenergetics model for pikeperch showed good fit in both the laboratory validation and field evaluation and was thus able to predict the food consumption of pikeperch based on the observed growth. The most important input variable in evaluation of uncertainty was activity coefficient, when uncertainty related to other input variables was taken account. The application of the bioenergetics model on a lake scale indicated that the pikeperch population could regulate the perch population after mass removal of fish and thus prevent recovery of the perch population. After intensive fishing, the perch population was dominated by young individuals and predation of pikeperch focused on these individuals. Increasing age of recruitment to the pikeperch fishery from 4 to 6 years doubled consumption by mass. The numbers of perch consumed depends on size-structures in both pikeperch and perch populations. These complex predator-prey interactions in a fish community mean that calculations by a simple model are only rough estimates, but they nevertheless suggest the high potential ability of pikeperch to regulate a perch population.

Keywords: Behaviour; bioenergetics model; diet; growth; pikeperch; predation; telemetry.

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# CONTENTS

## LIST OF ORIGINAL PUBLICATIONS

1	INTRODUCTION .....	9
1.1	Predation in fish communities.....	9
1.1.1	Direct and indirect effects of predation.....	9
1.1.2	Estimation of a predator's food consumption.....	10
1.2	Pikeperch as a top predator in lakes.....	10
1.2.1	The feeding biology of pikeperch.....	10
1.2.2	Behaviour of pikeperch.....	11
1.2.3	Pikeperch as a tool in biomanipulation.....	11
2	OBJECTIVES .....	13
3	MATERIAL AND METHODS .....	14
3.1	Diet of pikeperch in lakes (I).....	14
3.2	Growth of pikeperch in relation to lake characteristics and temperature (II, V) .....	15
3.3	Behaviour of pikeperch in the Päijänne lake system (III, IV).....	16
3.4	Bioenergetics model for pikeperch (V).....	18
3.5	Food consumption by the pikeperch population in L. Jyväsjärvi estimated by bioenergetics model.....	20
4	RESULTS AND DISCUSSION .....	24
4.1	The effect of environment on the diet and growth of pikeperch (I, II, V) .....	24
4.2	Pikeperch behaviour and migrations in a lake system (III, IV) .....	27
4.3	Bioenergetics model for pikeperch (V).....	30
4.4	Food consumption by the pikeperch population in L. Jyväsjärvi estimated by a bioenergetics model.....	32
5	CONCLUSIONS.....	39
	<i>Acknowledgements</i> .....	41
	YHTEENVETO.....	42
	REFERENCES.....	45



## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-V. Some additional data and results are also presented.

- I Keskinen, T. & Marjomäki, T. J. 2004. Diet and prey size spectrum of pikeperch in lakes in central Finland. *Journal of Fish Biology* 65: 1147-1153.
- II Keskinen, T. & Marjomäki, T. J. 2003. Growth of pikeperch in relation to lake characteristics: total phosphorus, water colour, lake area and depth. *Journal of Fish Biology* 63: 1274-1282.
- III Keskinen, T., Pääkkönen, J.-P. J., Lilja, J., Marjomäki, T. J. & Karjalainen, J. 2005. Homing behaviour of pikeperch (*Sander lucioperca*) following experimental transplantation. *Boreal Environment Research* 10: 119-124.
- IV Keskinen, T., Pääkkönen, J.-P. J., Lilja, J., Marjomäki, T. J. & Karjalainen, J. 2008. Home range, seasonal migrations and activity of pikeperch (*Sander lucioperca* (L.)) in a Finnish lake system. Submitted manuscript.
- V Keskinen, T., Jääskeläinen, J., Marjomäki, T. J., Matilainen, T. & Karjalainen, J. 2008. A bioenergetics model for pikeperch *Sander lucioperca* - construction, validation and evaluation of uncertainty of multiple input parameters. Submitted manuscript.

## RESPONSIBILITIES OF AUTHOR IN THE ARTICLES OF THIS THESIS

- I Original idea was joint. TK organised collection of samples and made stomach analysis and data analysis. TK wrote the first version of the manuscript, which was then finished together.
- II Original idea was joint. TK organised collection of samples and made growth analysis. Data analysis was done together. TK wrote the first version of the manuscript, which was then finished together.
- III Original idea was joint. J-PP was responsible for fish tagging. Field work was done by TK, JL, TJM and J-PP. TK made data analysis and wrote the first version of the manuscript, which was then finished together.
- IV Original idea was joint. J-PP and TK were responsible for fish tagging. Field work was done by TK, JL, TJM and J-PP. TK made data analysis and wrote the first version of the manuscript, which was then finished with TJM and JK.

V Original idea was by JK and TK. JJ and TM run the experiments. TK was responsible for organising collection of Hg samples and growth analysis. Model development was done by JK and TK. TJM was responsible for uncertainty evaluation. TK wrote the first version of the manuscript, which was then finished with TJM and JK.

# 1 INTRODUCTION

## 1.1 Predation in fish communities

### 1.1.1 Direct and indirect effects of predation

Predation is one of the main interactions between animal populations and this interaction between the fish populations in freshwaters can influence the function of the whole ecosystem. The direct effect of predation of the individual level is death or injury of the prey (Wootton 1990) but of the population level the effect of predation depends on the proportion of prey population consumed by the predator. The functional response of the predator to changes in the abundance of prey population can vary (Holling 1959). In general, consumption increases with the abundance of the prey. Optimal foraging theory assumes that a predator tries to maximise its net energy gain in unit time (Townsend & Winfield 1985). However, Sih & Christensen (2001) stated that the theory often falls down when predicting the diet of a predator attacking mobile prey. The reason was probably the inadequate information about key parameters for the models used. Moreover, Sih & Cristensen (2001) concluded that encounter rate and capture success are more important factors determining the observed diet of a predator than the active choice of a predator. This highlights the importance of other available prey when considering the effect of predation on one prey species or the prey selection of a predator. Piscivorous fish are often gape-limited predators (e.g. van Densen 1994). Thus, the predator-prey interactions are complicated systems affected by variations in size-structures and growth rates in both prey and predator populations (Tonn & Paszkowski 1986, Olson 1996, Persson et al. 1996, 1999). Moreover, Post et al. (2000) suggested that prey preference of the top predator has a major impact on system dynamics.

Beyond the direct effects, the risk of predation affects the behaviour of the prey species. For example, the risk of predation has been shown to influence the behaviour of perch (*Perca fluviatilis* L.). Increased predation risk diminished the foraging behaviour of perch (Magnhagen 2006) and had an effect on their

habitat use (Eklöv & Persson 1995, Persson et al. 1996). These changes led to decreased growth rate, which in turn decreased survival because mortality was size-dependent (e.g. Olson 1996). Thus, indirect effects of predation also affect the dynamics of fish communities.

### **1.1.2 Estimation of a predator's food consumption**

For management purposes, the interactions and their magnitude between predators and their prey are essential. To assess the effects of predatory fish at a population level, data for individual predators have to be expanded to the whole population level, which requires accurate estimates of stock size. At an individual level, the food consumption of a predator in terms of biomass will be transformed to individuals of each prey species. The consumption can be estimated by a bioenergetics model (Kitchell et al. 1977, Tarvainen et al. 2008) based on observed or estimated growth and temperatures or alternatively by gastric evacuation models based on intensive sampling in the field (e.g. Hansson et al. 1996, Principe et al. 2007). Both methods need data for diet composition.

In bioenergetics models, the food consumption estimate is based on the energy budget of the fish (Hanson et al. 1997). Input data consist of the observed specific growth, temperature and energy content of the diet. Specific temperature and mass dependent parameters are needed to run the model. The bioenergetics model has certain benefits compared to gastric evaluation models. There is less need for intensive sampling of stomach contents and bioenergetics models are easily applied to different circumstances, e.g. prey species and growth rates.

## **1.2 Pikeperch as a top predator in lakes**

### **1.2.1 The feeding biology of pikeperch**

Pikeperch (*Sander lucioperca* (L.)) is a large predatory percid fish living in lakes and coastal areas in Europe (Sonesten 1991). Pikeperch has been classified as a rapacious predator according to its behaviour and morphology (Elshoud-Oldenhave 1979). In boreal lakes pikeperch has been reported to consume mainly smelt (*Osmerus eperlanus* (L.)) and perch (Peltonen et al. 1996, Vehanen et al. 1998, II) in contrast to central Europe, where the main prey species are cyprinids (Dörner et al. 2007). Pikeperch is a gape limited predator (van Densen 1994, Dörner et al. 2007), which usually consumes prey fish with maximum length 50 % of its own length.

Pikeperch has been introduced in many waters and has caused changes in prey fish populations. In a British canal, introduced pikeperch decreased the number of cyprinids leading to a programme of removing pikeperch (Smith et al. 1996). In a lake in Turkey, introduction of pikeperch caused a collapse of

native fish stocks (Campbell 1992). In Finland, stocking of pikeperch is a very common management method of fish stocks. However, estimates of food consumption in relation to prey resources are scarce and are based on the bioenergetics model for related walleye (*Sander vitreus* (Mitchill)). Based on that model, Vehanen et al. (1998) estimated that in L. Oulunjärvi the pikeperch population did not regulate the vendace (*Coregonus albula* (L.)) population and in L. Köyliönjärvi the effect of pikeperch on coarse fish was minor (Salonen et al. 1996). More accurate estimates of the effect of European pikeperch predation on the fish communities, based on a specific and validated bioenergetics model, would often be required.

### 1.2.2 Behaviour of pikeperch

Previous telemetry studies of pikeperch behaviour have been carried out in river or channel systems (Koed et al. 2000, 2002, Poulet et al. 2005a,b), where migrations between seasons have been observed but between migration periods pikeperch were often stationary. Pikeperch in reservoirs were actively moving predators (Jepsen et al. 1999, Vehanen & Lahti 2003). Sites in these studies differ both as an environment and also geographically from the study area of this thesis. Before papers III and IV there were no published data on pikeperch migration behaviour in a boreal lake system, which includes several connected lakes. Studies based on the mark-recapture method in coastal areas of the Baltic Sea (Lehtonen 1979, Lehtonen & Toivonen 1987, Saulamo & Thoresson 2005) and in L. Hjälmaren in Sweden (Nyberg 1996) have shown migrations between seasons and also homing behaviour to the spawning site. However, the mark-recapture method is biased because usually data include only one observation after release of the marked fish, and there are no data about where it has been between these two occasions. Overall, recaptures are affected by the spatial and temporal distribution of fisheries.

The behaviour of pikeperch at a daily time scale is less studied. Jepsen et al. (1999) and Poulet et al. (2005a) concluded that pikeperch has its maximum activity at dusk. The temperature selection of pikeperch in the field has not been studied previously even though it is important information for application of bioenergetics models. Knowledge on the behaviour of pikeperch is important to evaluate the importance of pikeperch as a predator. This basic knowledge of migrations is also needed in fisheries management.

### 1.2.3 Pikeperch as a tool in biomanipulation

Anthropogenic eutrophication is a common problem in many Finnish lakes: land uses in the catchment area and waste waters from point sources increase the input of nutrients to lakes. Consequences of increased nutrient levels are accelerated primary production leading to algal blooms and oxygen depletion (e.g. Carpenter & Lathrop 1999). Eutrophication also affects the fish community decreasing the diversity and increasing the biomass (Jeppesen et al. 2000). Perch

is a dominant species in mesotrophic lakes and cyprinids dominate in eutrophic boreal lakes (Helminen et al. 2000, Olin et al. 2002).

Lake restoration is defined as a series of methods attempting to change the ecological condition of a eutrophicated lake. In a broad sense, it can include decrease of nutrient load, removal of coarse fish and stocking of predatory fish (e.g. Jeppesen et al. 2007). Biomanipulation usually means actions which try to change the food web of a lake. In many cases, coarse fish removal has been adopted as the main biomanipulation method, based on the theory of cascading effects (Carpenter et al. 1985). According to this theory, the decreased planktivory will lead to increased zooplankton biomass which effectively consumes phytoplankton. As compensatory or supportive methods for the fish removal, stockings of predatory fish have been suggested (Berg et al. 1997, Lathrop et al. 2002).

In eutrophicated lakes pike (*Esox lucius* L.), pikeperch and large perch are usually the most important predatory fishes (Hölker et al. 2007). All these predators have different foraging behaviour patterns and prey preferences (Hölker et al. 2007). The planktivorous and benthivorous fish community consisted of roach (*Rutilus rutilus* (L.)), small perch, ruffe (*Gymnocephalus cernuus* (L.)) bream (*Abramis brama* (L.)), white bream (*Abramis ballerus* (L.)) and bleak (*Alburnus alburnus* (L.)) (Helminen et al. 2000, Olin et al. 2002). The use of pikeperch as a tool in biomanipulation projects in order to consume and regulate the number of planktivory fish has been discussed (Salonen et al. 1996, Wysujack & Mehner 2002, Dörner & Benndorf 2003) and the main conclusions have been that pikeperch populations alone are not able to control the populations of coarse fish, so that effective fishing and other predators are also needed.

Fish remove for biomanipulation purpose by effective fishing is usually not economically profitable and needs an economics subsidy. In biomanipulation projects in L. Jyväsjärvi, central Finland, the cost per fish kg removed has been about 0.8 euros. In a German lake, Wysujack & Mehner (2002) estimated that predatory fish species (pike and pikeperch) consumed more than was removed by seine-fishing. Moreover, they estimated that a piscivore biomass of 21 % of the planktivore biomass was enough to consume the net growth of planktivores. However, those calculations are theoretical and very sensitive to changes in the dynamics of both prey and predator populations. An additional benefit of stocking predatory fish is the high economic value of predatory fish as a catch for both recreational and professional fishing. Strong pikeperch stocks can increase public interest in lakes and their restoration and protection. Unfortunately, maintaining abundant predatory fish stocks usually requires very restrictive fisheries management policy.

## 2 OBJECTIVES

The aim of this thesis was to analyze the importance of pikeperch as a predator in the fish community of boreal lakes. For management purposes, the obtained results are also applied as an example of a lake scale in order to estimate the effect of pikeperch population on its prey fish populations. Migration and movements of pikeperch were studied with ultrasonic telemetry in a large lake system. Several experimental and field studies were carried out:

- (a) to estimate the diet of pikeperch in relation to pikeperch size and trophic level of lake (I);
- (b) to estimate the effect of environmental factors on growth of pikeperch (II and V);
- (c) to describe the behaviour and habitat selection of pikeperch in lakes (III and IV);
- (d) to construct a bioenergetics model for pikeperch and to evaluate the effects of uncertainty in input parameters (V);
- (e) to estimate the effects of pikeperch predation on prey fish populations data lake scale using the constructed bioenergetics model (this thesis).

## 3 MATERIAL AND METHODS

### 3.1 Diet of pikeperch in lakes (I)

Diet of pikeperch was studied in Central Finland in 1996-1997. In total, 587 stomach contents samples were collected and analysed from 24 lakes varying in water quality and area. The total lengths ( $L_T$ ) of pikeperch varied from 128 to 805 mm. The number of stomach samples per lake was 6-84. Fish were caught by angling, gill net and trawling mainly during the open water season. The species of prey fish were identified and  $L_T$  estimated when possible. Estimated  $L_T$  of preys eaten was converted to initial weight (g) using equations given Koivurinta et al. (2000). The number of prey other than fish (mainly crustaceans) was low and thus their importance was negligible. All the sampled lakes had perch, roach, ruffe and bleak stocks, and the majority also had smelt, whitefish (*Coregonus lavaretus* (L.)) and vendace stocks.

In the data set, a correlation between the total length of pikeperch and phosphorus content of the lake was found. This correlation was removed by using only pikeperch  $L_T > 380$  mm or lakes with phosphorus content  $>10 \mu\text{l}^{-1}$  in analysis of pikeperch size or trophic status of the lake. When testing the effect of pikeperch size or lake phosphorus content on diet distribution prey species were divided in the three classes for  $\chi^2$ -test: smelt + coregonids, percids and cyprinids. The prey-to-predator size ratio (PPR) was calculated by the equation

$$100 * L_{T \text{ prey}} * L_{T \text{ pikeperch}}^{-1} \text{ (Turesson et al. 2002).}$$

The association between pikeperch  $L_T$  and prey  $L_T$  was tested by Spearman rank correlation.



### 3.2 Growth of pikeperch in relation to lake characteristics and temperature (II, V)

The pikeperch sampled for growth analysis from 41 central Finnish lakes were caught by gillnet, angling, trawling and trap nets. These lakes had area from 45 to 26 000 ha and maximum depth from 6 to 95 m. Water colour varied from 20 to 267 mg Pt l<sup>-1</sup> and total phosphorus content from 5 to 60 µg l<sup>-1</sup>. Most samples were from 1996-1997 and 97 % of the data belonged to year classes 1988-1994. The total length ( $L_T$ ) of sampled pikeperch varied from 143 to 805 mm. The ages of pikeperch were determined from scales taken from the area between the lateral line and pelvic fin. The total number of pikeperch aged at least 3 years was 1134. The number of samples per lake varied from 3 to 178. The relationship between  $L_T$  and scale radius ( $S$ ) was described by Fry's equation (Fry 1943, I). The values of  $a$ ,  $b$  and  $c$  were estimated by iterative least squares from scale data of pikeperch with length range 62-575 mm ( $N=487$ ). The length at age  $i$  ( $L_{Ti}$ ) of individual fish was back-calculated by Fry's equation (I).

The average of back calculated length at age 3 ( $L_{T3}$ ) was used as an index of growth in different lakes. This age was selected because pikeperch are immature at that age and the number of older and larger fish in exploited populations is usually low. Association of growth index ( $L_{T3}$ ) to lake characteristics (area, maximum depth, water colour and phosphorus content) was analysed by Kendall's nonparametric correlations and partial correlations.

Because temperature has a strong effect on growth of pikeperch (Ruuhijärvi et al. 1996), effect of temperature on growth was tested in year classes 1988-1994 in three different lakes located in Central Finland. The temperature sum of the epilimnion (days > 10°C) in the Kalkkinen channel (61°17' N; 25°43' E) was calculated and the association between average of year-class  $L_{T3}$  and the temperature sum of the two previous years was then analysed by Spearman correlations. The Kalkkinen channel is slightly more southern than these three study lakes (distance 30-110 km), but is representative to compare the differences between years.

The effect of temperature on pikeperch growth was also studied in laboratory experiments at 10, 14, 18 and 22 °C done originally for constructing a bioenergetics model for pikeperch (V). The experiments are described in detail in section 3.4. An instantaneous rate of growth ( $G$ ) was calculated for every temperature by equation

$$G = \ln (W_2/W_1),$$

where  $W_1$  is mass at the beginning and  $W_2$  at the end of the experiment. Difference in log ( $x+1$ ) transformed growth rate between temperatures was tested by ANOVA.

### 3.3 Behaviour of pikeperch in the Päijänne lake system (III, IV)

A total of 21 ( $L_T$  385 – 855 mm) pikeperch were tagged with ultrasonic transmitters during 2001-2003 in the Päijänne lake system (Fig. 1). Eight of these fish were from L. Päijänne (Vaajavirta) and 13 from L. Jyväsjärvi. The fish were anaesthetized with MS 222 or clove oil. The transmitter was inserted into the body cavity of a fish through a mid-ventral incision. The transmitters used were Sonotronics CT-82-2 and CTT-83 which operated at frequencies from 70 to 75 kHz. The guaranteed duration of the transmitter battery was 14 months. The length of transmitters was 64 mm, diameter 16 mm and weight in water 8 g. The CTT-83 transmitter had a temperature sensor, and temperature data were sent to the receiver as interval between pulses.

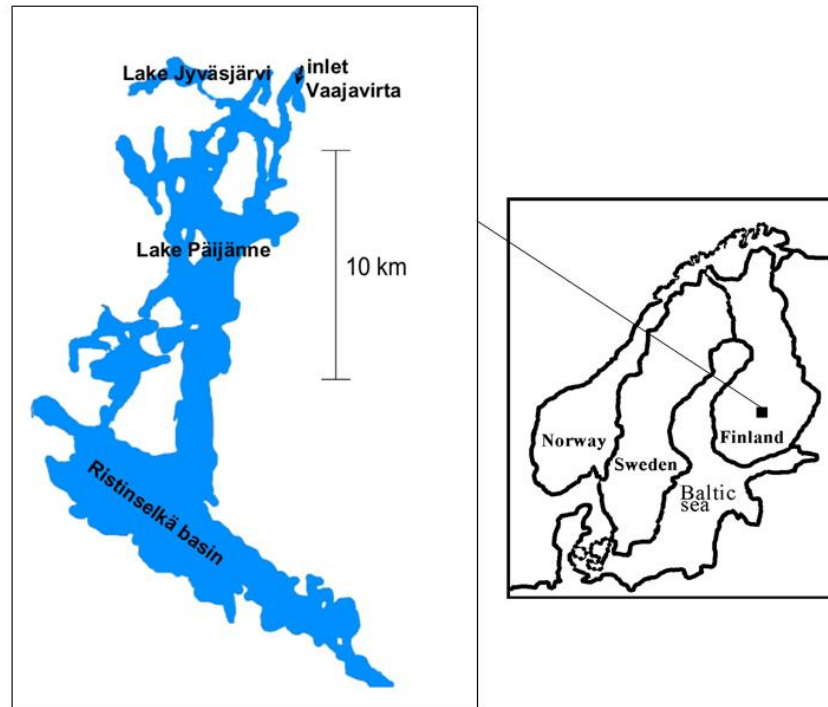


FIGURE 1 Study area in telemetry studies (III, IV).

Tracking was done manually from a boat or on ice. The position of the fish was determined using a hydrophone (Sonotronics DH-4) and a receiver (Sonotronics USR-5W) according to landmarks and marked on a map or by triangulation method. The bearing of the fish was measured using a compass and the position of the tracker by GPS. The average deviation of this method from the real position was 31.4 m. Data for locations collected were imported to Arc View software.

The tracking period of single fish varied from 9 days to 15 months. Tracking was done at least once per week during summer (June-September)

and once per month in other seasons. To get more detailed information about movements of pikeperch, fish were tracked intensively for 24 h in total 23 times. During these periods each fish was located at least 5 times.

To get information on the homing behaviour of pikeperch 6 fish were transplanted in L. Jyväsjärvi about 7 km west from the original capture location (L. Päijänne) and released there at least 1 day after tagging in summer 2001. A control group was 6 pikeperch originally captured and released in L. Jyväsjärvi. The effect of original capture place on remaining in L. Jyväsjärvi was tested with Fisher's exact test.

The whole data for 21 pikeperch were used when migration behaviour, activity and area of the home range in different time scales were analysed. In these analyses the period after transplantation of homing migration to original capturing location was excluded. After once returning to original location, it was assumed that observations of those fish were relevant to describe the behaviour of pikeperch. In these analyses, habitats were classified as thermally stratified (L. Jyväsjärvi) and unstratified (L. Päijänne, Vaajavirta). Thermally stratified areas were open lake areas and unstratified sites where the water current was obvious and prevented stratification.

Home range of pikeperch was studied in three different time scales: whole year, season and daily (IV). Time scale is an important component in definition of home range (Spencer & Cameron 1990, Heupel et al. 2004). The maximum linear distance between positions within a year was used as an index of the annual home range by an individual pikeperch. This index was calculated only for those fish ( $n=6$  and  $n=3$  overwintering in Lake Päijänne and Jyväsjärvi, respectively) which were tracked for at least one year. The areas of the seasonal home ranges were calculated by ArcView Animal Movement Analysis software using the Kernel home range method. This procedure calculates a core area where observations are located at 50 % probability. This probability has earlier been used as the core area of home range. According to Vokoun (2003) a minimum of 30 relocations should be available when calculating kernel density estimation of home range. These core areas can be one or more. If there was more than one area, the sum of these areas was used as an area of the home range. When determining the home range of an individual pikeperch in different seasons, the period from the beginning of May to the end of September was considered to be the summer season and from the beginning of January to the end of April the winter season. Only fish which were tracked over a whole season were included in the analysis. Daily home range within a 24-h period was calculated from data on the 24 h intensive tracking period as minimum convex polygon. The polygon was used as a method instead of the kernel home range because the number of observations in a 24-h period was under 30, usually 6-10. Data for the 24-h period during winter was available only for pikeperch overwintering in L. Jyväsjärvi.

Activity was described as a swimming speed (body length  $s^{-1}$ ) calculated from distance between two successive locations and time between these. A day was divided to dawn, day, dusk and night periods. Swimming speed was compared between summer and winter in L. Jyväsjärvi by independent t-test

after  $\log(x + 0.1)$  transformation of the data. The differences in activity between habitats and periods of the day were tested by repeated measures ANOVA using habitat as between subject factor and period of the day as within subject factor.

### 3.4 Bioenergetics model for pikeperch (V)

A specific bioenergetics model for European pikeperch was constructed based on the laboratory experiments. The model was validated with independent laboratory experiment data and also verified with a field test. Experiments included measurements of respiration (R), growth (G) and maximum food consumption ( $C_{\max}$ ) at different temperatures.

Oxygen consumption of pikeperch was measured at 12, 16, 18 and 24 °C in an intermittent-flow respirometer equipped with a polarographic oxygen sensor (YSI 5750). The respirometer system included three acrylic chambers with two different volumes of 147-148 and 3980-4025 ml for small and large pikeperch, respectively. Small fish (2.8-13.4 g) were from natural food fish culture ponds and large fish (70-285 g) were caught by angling or trawling in the Päijänne lake system. Fish were acclimated in experimental conditions from 2 weeks to 2 months. All fish were immature and starved for 2-3 days before experiments. Oxygen consumption in each chamber was recorded for 15 min every hour and the average rate during this period was extrapolated to obtain an hourly value. The oxygen electrode chamber and the fish chambers were flushed with fully aerated water 45 min every hour. Every measurement period lasted for 24 h. The oxygen consumption of the empty respirometer chambers (without fish) was measured before and after fish measurements and the bacterial consumption was subtracted from the total oxygen decline. The routine rate of oxygen consumption was the average of all hourly measurements excluding the three highest and three lowest values during experiment (Karjalainen et al. 1995). The flow rate of water in the chambers was low and in this respect the system was almost static. Specific dynamic action (SDA) was calculated as oxygen consumption increase during 18 hours after feeding in fed fish compared to starved fish at 12 and 18 °C. In these experiments fish were fed *ad libitum* with perch pieces before experiments.

Maximum food consumption of pikeperch was measured at 10, 14, 18 and 22 °C. Initial mass of pikeperch was 85-185 g and in every temperature was 4-5 fish. Pikeperch for the experiment were caught by angling or trawling from L. Päijänne watercourse and were acclimated under experimental conditions for at least 2 weeks before the experiments. Only individuals observed eating regularly in laboratory conditions were used in experiments. Fish were kept individually in aquaria for two consecutive 14 day periods. In these experiments fish were fed *ad libitum* once or twice per day with perch. In the beginning and at the end of both periods fish were anaesthetised and weighed.

The largest daily meal for every individual was used as an estimate of maximum food consumption.

Model construction was based on the basic energy balance equation (Hewett & Johnson 1992, Hanson et al. 1997)

$$C = (R+SDA) + (F+U) +G,$$

where C=food consumption, R=respiration, SDA=specific dynamic action, F=egestion, U=excretion and G=growth. Temperature and mass dependence functions of  $C_{max}$  and R were calculated from experimental data with nonlinear fitting. C was calculated as a proportion (p) of  $C_{max}$ . In the first phase (model I), the parameters derived from laboratory experiments of C and R were inserted to a previously used Wisconsin-type walleye model (Kitchell et al. 1977). Parameters of F and U were adopted from the walleye model. To improve the predictions of food consumption, the original model developed by Elliot (1976) was applied (model II). The Wisconsin- and Elliot-type models differ from each other in the calculation of parameter U. In Wisconsin-type models U is calculated as a proportion of assimilated food (C-F) whereas in the Elliot-type model it is calculated as a proportion of C. The parameter values used are presented in article V.

In verification, the data from maximum food consumption experiments were used. The observed and predicted individual food consumption value was compared. Verification was done both with Wisconsin-type and Elliot-type models. The success of verification was evaluated by three different methods (Mayer & Butler 1993); a linear regression between observed and predicted food consumption, the mean absolute percent error (MAE) and modelling efficiency ( $E_f$ ).

For validation of models, pikeperch were reared in the same kind of experimental conditions as when measuring the maximum food consumption. The individual food consumption predicted by bioenergetics models based on observed growth in the experiments was compared to the corresponding observed food consumption. The validation was done for model II, because it performed better in verification. The validation was also done for the pikeperch model by Salonen et al. (1996) and for the original walleye model (Kitchell et al. 1977). The success of validation was evaluated in the same way as in the verification step for all the validated models.

Field evaluation was carried out using mercury as a marker. Mercury concentration of pikeperch was analysed from samples collected from two Finnish lakes in 2002. Because smelt and perch are the main prey species of pikeperch (Peltonen et al. 1996, II), mercury content of whole perch and of smelt was analysed from the same lakes in 2006. Annual food consumption of pikeperch was calculated by model II using a 1 day time step for individual pikeperch after the first year by the same procedure as Trudel & Rasmussen (2001). The diet of pikeperch was assumed to comprise of 80 % smelt and 20 % perch in all age groups older than 1. The elimination rate and loss of mercury due to spawning was estimated by the model presented by Trudel &

Rasmussen (1997). The starting value of Hg concentration at age 1 was the same as in planktivorous smelt. The  $E_f$ , MAE and linear regression between observed and predicted Hg concentration were calculated as in the previous food consumption verification phase.

A numerical simulation technique Latin Hypercube Sampling (LHS) (a modified Monte Carlo approach using a form of stratified sampling, available in @RISK (Palisade Corporation 2004) software version 4.5), was applied to evaluate the effect on their predictions of uncertainty in input parameters to the bioenergetics and Hg mass balance models. An *a priori* probability distribution was generated for each of the 29 uncertain input parameters. The selected distribution for a parameter value is a fusion of published values, results of experiments presented and our expert knowledge, and aims to show the probabilities those different values are correct for pikeperch. Two thousand LHS realizations of input parameter values were generated and Hg concentration and food consumption estimates were calculated using model II for 12 individual pikeperch. The probability distributions of calculated Hg concentration and food consumption were assumed to represent the probability that different values were the correct average value for fish with a certain growth history, the width of distribution thus expressing uncertainty. The sensitivity of the output parameter values on different input parameters was evaluated using the sensitivity analysis procedure of @RISK (Palisade Corporation 2004) software. Spearman correlation coefficient was applied to evaluate the impact of probability distributions of different model parameters on the Hg concentrations and food consumption. Also the consumption calculated by the model for pikeperch (Salonen et al. 1996) and the original walleye model (Kitchell et al. 1977) were compared for the same individuals.

### **3.5 Food consumption by the pikeperch population in L. Jyväsjärvi estimated by bioenergetics model**

L. Jyväsjärvi is a eutrophic lake, which had earlier been in poor condition due to municipal waste waters, but has since recovered (Salonen et al. 2005). The most numerous fish species are perch and roach, pikeperch being the most important predatory species. The lake has undergone a biomanipulation project in 2004-2006 when 101 tons ( $300 \text{ kg ha}^{-1}$ ) of coarse fish was removed, of which about 27 tons ( $81 \text{ kg ha}^{-1}$ ) consisted of perch. The aim of the project was to decrease the biomass of cyprinids and small perch. A bioenergetics model for pikeperch (V) was applied in order to estimate the food consumption by the pikeperch population and its effects on the perch population in L. Jyväsjärvi (Fig. 2). The aim was to compare this consumption to the biomass removed by effective fishing and evaluate the possibility of pikeperch stocking as a biomanipulation method.

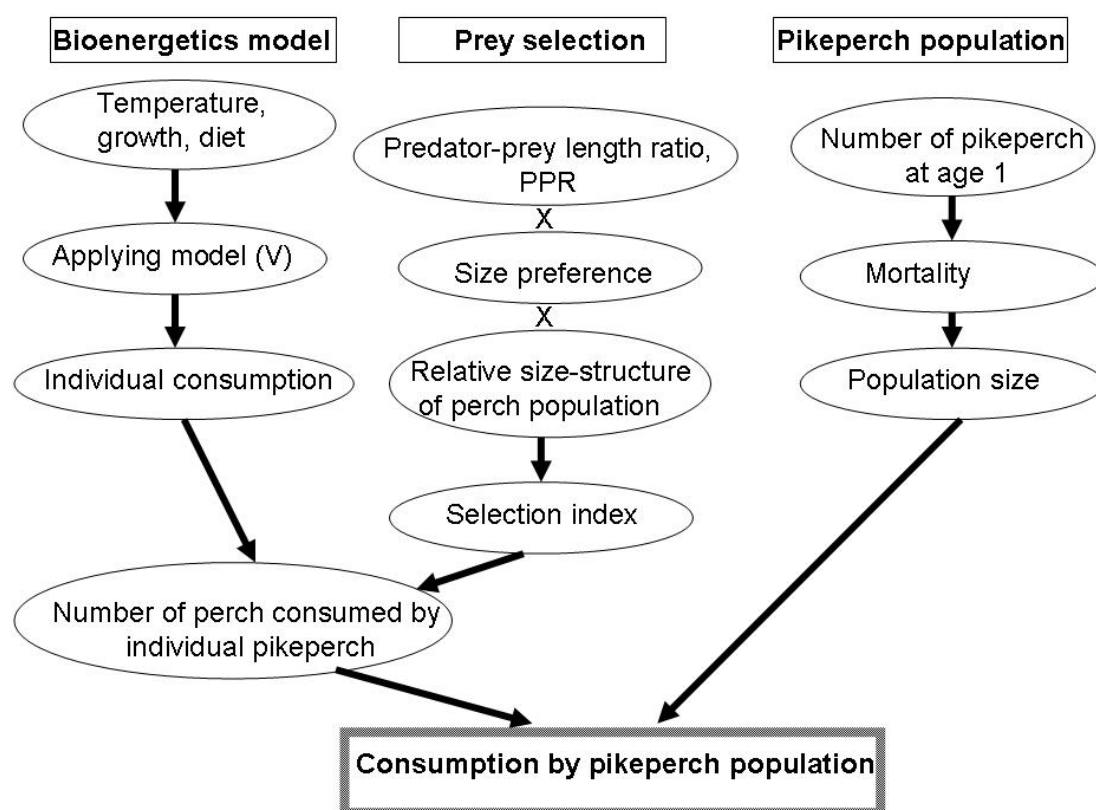


FIGURE 2 Schematic presentation of the model used in estimating the consumption by pikeperch of the perch population in L. Jyväsjärvi.

The age of pikeperch ( $n=32$ ) was determined from scales. When necessary, the age was also checked from coloured otoliths. The length in earlier years was back-calculated (II) and converted to mass by the length-mass equation. These growth estimates were used as input data in the bioenergetics model (V). There were no representative stomach samples from L. Jyväsjärvi. Annual consumption of each age-group was calculated assuming that pikeperch diet consisted of 80 % and 90 % of perch in 2004 and 2006, respectively. The rest of the diet was assumed to consist of smelt. This assumption was based on stable isotope analysis, which shows that in L. Jyväsjärvi perch was the main prey species for pikeperch (J. Syväranta, University of Jyväskylä, unpublished data). This was also supported by data from echo-sounding studies, which indicated that the smelt stock in L. Jyväsjärvi is sparse (T. Marjomäki, unpublished data).

The consumption of age-group 0+ perch by pikeperch age-group 1+ and older was assumed to start at the beginning of July when the total length of 0+ perch is about 2 cm. Thus a year was divided in two periods: a period before July, when no 0+ perch was consumed, and the rest of the year, when 0+ perch were present in the pikeperch diet. The preference for each perch age-group was based on the average length of perch in each age-group and data for preferred prey size of pikeperch (II, Turesson et al. 2002). This was done by calculating prey-to-predator size ratio (PPR) for all the perch age-groups. The minimum PPR value of perch consumed by pikeperch was set to 0.05, maximum

to 0.55 and highest preference to 0.25. The selection index for each age-group was then quantified by multiplying the preference of each PPR based on the average length of perch in this age-group and relative abundance of this age-group (Fig. 2). This selection index was calculated for all the pikeperch age-groups separately.

The food consumption of each age-group was first calculated for one individual by the bioenergetics model (V). The consumption of perch in grams was then transformed to number of perch of each age-group based on selection index. This individual consumption was then multiplied by the mean population size of each age-group of pikeperch during each period. The consumption by the whole pikeperch population was calculated by summing up the consumptions of each age-group.

The model was applied for two different situations in the L. Jyväsjärvi having differences in perch population size and structure. First, the food consumption by the pikeperch population was estimated before biomanipulation. Secondly, the effect of the pikeperch population on the perch population was estimated in 2006, which was the last year of the biomanipulation.

The size- and age distribution of the perch population in 2004 at the start of biomanipulation was assumed to represent the equilibrium situation before biomanipulation. The removal catches were weighed on every fishing day and random sample of about 30 kg was taken weekly during the fishing season in 2004-2006. The total mass and number of perch in the sample were measured and the average weight of perch and total number of perch in the catch were calculated. The total length of every perch in the sample was measured and 100 perch from every sample, representing different size-classes, were taken to the age determination. Ages of perch were determined by analysing opercula and scales. Based on this information, the length distribution of the whole perch catch was divided in to year-classes. The cohort size of year-class 2004 and older in the perch population was calculated by cohort analysis (Pope 1972), a modification of Virtual Population Analysis (Gulland 1983), based on the total catch of the fish removal project. The abundance estimates were calculated in daily steps. This method can be used in stock assessment, when natural mortality is low compared to fishing mortality, i.e. in intensively exploited fish stocks (e.g. Peltonen et al. 1999). The instantaneous natural mortality ( $M$ ) of perch older than 1 year in these calculations was assumed to be  $0.4 \text{ a}^{-1}$  (Persson et al. 2000). The terminal population was based on the catch of the three last days in 2006. Catchability was estimated as 0.03 per 10 traps  $\text{d}^{-1}$  for age-groups older than 1+. The number of 0+ perch (year-class 2004) at the beginning of July 2004 was calculated from their numbers at the beginning of May 2005, assuming that the instantaneous mortality ( $Z$ ) was  $1.71 \text{ a}^{-1}$  (Persson et al. 2000).

Because the accuracy of cohort analysis increases retrospectively, the estimates for year-class 2005 were of low accuracy. This year-class was not fully recruited in the removal catch in 2006. Thus, when estimating the population size of year-class 2005, the catchability of this year-class in cohort analysis was set to 0.005. The age distributions in years 2006 and 2005 estimated by cohort



analysis fit well with age distributions in gill net fishing in corresponding years, indicating good performance of the cohort analysis. Gill net sampling was carried out in 2001-2006. The gill nets had 9 mesh sizes (knot to knot) from 10 to 55 mm. The number of year-class 2006 in 2006 (0+) was estimated by comparing the catch per unit effort (CPUE) of this year-class (1+) in gill net fishing in August 2007 to the corresponding value of year-class 2005 (1+) in August 2006.

TABLE 1 Average back-calculated length ( $L_T$ , mm) and weight (g) of pikeperch in L. Jyväsjärvi at different ages, instantaneous natural mortality (M) and instantaneous fishing mortality (F) in pikeperch food consumption calculations.  $F_4$  and  $F_6$  are mean recruitment age of 4 and 6 years, respectively.

Age	Average length, mm	Average weight, g	M, a <sup>-1</sup>	F <sub>4</sub> , a <sup>-1</sup>	F <sub>6</sub> , a <sup>-1</sup>
1	80	4	1.50	0.0	0.0
2	157	31	0.80	0.0	0.0
3	255	137	0.15	0.0	0.0
4	350	369	0.15	0.8	0.0
5	445	784	0.15	0.8	0.0
6	551	1520	0.15	0.8	0.8
7	639	2417	0.15	0.8	0.8
8	702	3243	0.15	0.8	0.8
9	733	3705	0.15	0.8	0.8
10	761	4166	0.15	0.8	0.8
11	790	4684	0.15	0.8	0.8

The consumption by the pikeperch population was calculated for two different population sizes and structures. The pikeperch population in L. Jyväsjärvi consists of individuals which live in the lake at least during summer (III, IV) when most of the consumption takes place. In these scenarios the number of pikeperch at age of one year was 5055 or 10110 individuals (15 or 30 ind. ha<sup>-1</sup>). In all scenarios, the instantaneous natural mortality was set to 1.5, 0.8 and 0.15 in the first year, second years and subsequently, respectively (Lappalainen et al. 2005) (Table 1). The age of recruitment to the fishery was set to 4 (total length 37 cm) or 6 years (total length 55 cm). The instantaneous fishing mortality (F) after that was set to 0.8 up to the age of 11 years when practically all fish were caught. A recruitment age of 4 years corresponds to the legal size limit (37 cm) of pikeperch in Finland and an age of 6 years to the situation when fishing would be regulated to achieve higher recruitment age.

## **4 RESULTS AND DISCUSSION**

### **4.1 The effect of environment on the diet and growth of pikeperch (I, II, V)**

Smelt was the most numerous prey species for every size-class of pikeperch, the second being perch (I). In eutrophic lakes the proportion of perch and roach in pikeperch diet was higher than in oligotrophic lakes. These results for the diet of pikeperch generally accord with previous studies from Finnish lakes. In mesotrophic L. Oulujärvi smelt (Vehanen et al. 1998) and in eutrophic L. Vesijärvi (Peltonen et al. 1996) smelt and perch were the most important prey species for pikeperch. Prey-to-predator size ratio (PPR) decreased with total phosphorus content of a lake (I). Average total length of 3-year old pikeperch ranged from 179 to 333 mm in the studied lakes and correlated positively with total phosphorus concentration of the lake (II). In earlier studies total phosphorus has been reported to be positively correlated with pikeperch yield (Svårdson & Molin 1973) and success of introduction (Lehtonen et al. 1984). However, total phosphorus and water colour were positively correlated with each other but negatively with area and maximum depth. Partial correlation indicated that lake area has less impact on total length of 3-years old pikeperch than other variables. The results in papers I and II indicated that trophic status (measured as total phosphorus concentration) of the lake had a clear effect on pikeperch diet and growth rate.

The observed diet in stomach samples is a consequence of available prey and selection processes. The selection has been categorised to active and passive processes (Turesson et al. 2002, 2006). The passive processes include encounter rate, capture success and satiation, which are not solely dependent on the predator itself. Capture success is usually higher for relatively smaller prey (Christensen 1996, Einfalt & Wahl 1997), although for walleye and pikeperch no size-dependent capture success has been found when PPR is between 0.20-0.45 (Campbell 1998, Turesson et al. 2002). The active selection processes are the decision to approach or attack after detection of the prey by a predator.

According to optimal foraging theory (Townsend & Winfield 1985, Stephen & Krebs 1986, Sih & Christensen 2001) a predator tries to maximise net energy intake per unit time. Energy intake increases with prey size, but the handling time also increases, leading to some optimum PPR (Nilsson & Brönmark 2000, Turesson et al. 2002). This also depends on available preys. Altogether, based on earlier studies and paper I, a preferred PPR for pikeperch is 0.25-0.30 (Hansson et al. 1997, Campbell 1998, Turesson et al. 2002).

The potential prey assemblage of pikeperch differs in relation to trophic state of the lake. There is a shift from oligotrophic lakes dominated by salmonids (smelt and vendace) through mesotrophic lakes dominated by percids to eutrophic lakes dominated by cyprinids (Persson et al. 1991, Helminen et al. 2000, Olin et al. 2002). In eutrophic lakes, also the number of potential prey fish is also higher than in oligotrophic lakes. For example, in oligotrophic L. Puulavesi average pelagic fish density was  $< 6000 \text{ ind. ha}^{-1}$  (Marjomäki & Huolila 2001) and in eutrophic L. Vesijärvi  $> 20000 \text{ ind. ha}^{-1}$  before intensive trawl fishing (Peltonen et al. 1999). The higher densities of perch and roach in eutrophic lakes increase the encounter rate and make them more profitable prey. Thus, the changes in prey species proportions along the trophic gradient are simply consequences of available prey distributions. The average length of potential prey fish populations in the pelagic area of eutrophic lakes is usually small (Peltonen et al. 1996, Salonen et al. 1996). Turesson et al. (2006) have modelled prey size selection and concluded that, with increasing encounter rate, the proportion of high PPR values (0.4-0.5) in piscivore diets decreases. This is comparable to the situation when PPR decreases with increasing phosphorus concentration (I). The results are in accordance with optimal foraging theory. When high numbers of potential prey are available, it is possible to select prey with preferred PPR and achieve higher net energy intake in unit time. The satiation effect decreases PPR at high encounter rates (Turesson et al. 2006), while changes in prey species proportions can also affect PPR. Smelt is more slender than perch and roach and thus in the same PPR has less energy per individual. Thus, the average energy consumed by pikeperch from one prey fish could be even higher in eutrophic lakes, with lower PPR. Altogether, the higher growth rate in eutrophic lakes is probably due to better feeding conditions for pikeperch.

Prey length was not strongly associated with pikeperch length even though there was a trend for large pikeperch to consume larger prey. Instead, decrease in PPR with pikeperch size was significant (I). Decreasing PPR with pikeperch size has been often reported (Popova & Sytina 1977, Willemsen 1977, Zivkov & Raikova-Petrova 1991, Turesson et al. 2002, Dörner et al. 2007). A constant relationship in the Baltic Sea has been found by Hansson et al. (1997) who considered it evidence of good feeding conditions for predatory fish. The results in paper I indicate, that in the study lakes small pikeperch have to consume larger prey than preferred and large pikeperch smaller prey than preferred.

The importance of smelt decreased and that of roach increased with pikeperch size. This phenomenon has been suggested to be a consequence of

habitat selection by small roach, which usually inhabit the littoral zone, whereas pikeperch usually forage in open water (Peltonen & Horppila 1992, Jepsen et al. 1999, IV). After introduction of pikeperch, roach have been reported to change their behaviour avoid the pelagic zone (Brabrand & Faafeng 1993, Hölker et al. 2002). Even roach too large to be potential prey, avoided predators (Schulze et al. 2006a). This kind of behaviour decreases the encounter rate and potential risk of being eaten by pikeperch. These results are important in respect to biomanipulation by predatory fish. If a goal in management is a predation focusing on roach, it is important that the pikeperch stock includes large individuals, which are able to consume roach. This usually means restricted fishing. On the other hand, a dense pikeperch stock induces behavioural changes in roach population, which can lead to reduced growth (e.g. Wootton 1990) and thus changes in food web dynamics. It is also possible that other predators, mainly pike, can consume more roach in the littoral zone. However, Skov & Nilsson (2007) and Søndergaard et al. (2007) concluded that in general stocking of age 0+ pike is not an effective method in biomanipulation projects.

No pikeperch were found in over 500 stomachs of pikeperch analysed, which indicates that cannibalism was not a common phenomenon in the studied lakes (I). Cannibalism generally increases with density (Smith & Reay 1991), and Lappalainen et al. (2006) have shown this for pikeperch in L. Hiidenvesi in southern Finland, where cannibalism of pikeperch was connected to high abundance of 0+ pikeperch. According to the results of Lappalainen et al. (2006) and the absence of pikeperch in stomach samples (I), it seems that the effect of cannibalism on pikeperch population dynamics is negligible.

Although total phosphorus concentration seemed to explain differences in growth rate between lakes, the effect of water colour could not be excluded (II). Lappalainen (2004) stated that lakes with pikeperch stocks typically had high turbidity, low Secchi disk depth and are shallower than average. In contrast to the results in paper I, Ruuhijärvi et al. (1996) found no association between growth and water colour, which was possibly due to the smaller variation in water colour than in paper I. Pikeperch yield, however, correlated positively with water colour (Ruuhijärvi et al. 1996).

Summer temperature has been observed to be positively correlated with pikeperch growth (Svärdson & Molin 1973, Lehtonen et al. 1996, Ruuhijärvi et al. 1996, Lappalainen 2001, Lappalainen et al. 2005). The observed temperature sum of two previous summers did not correlate with observed total length of 3-year old pikeperch, indicating that differences in growth rate are mostly consequences of differences in lake characteristics (II). In laboratory experiments (V), temperature showed a clear effect on instantaneous growth rate of pikeperch, being at 22 °C more than double that at 10 °C (Fig. 2). However, variation between years in temperature sum in the lake was about 10 %, while in laboratory experiments the variation was larger. These results indicate that pikeperch have a high growth capacity at high temperatures if food is not a limiting factor.

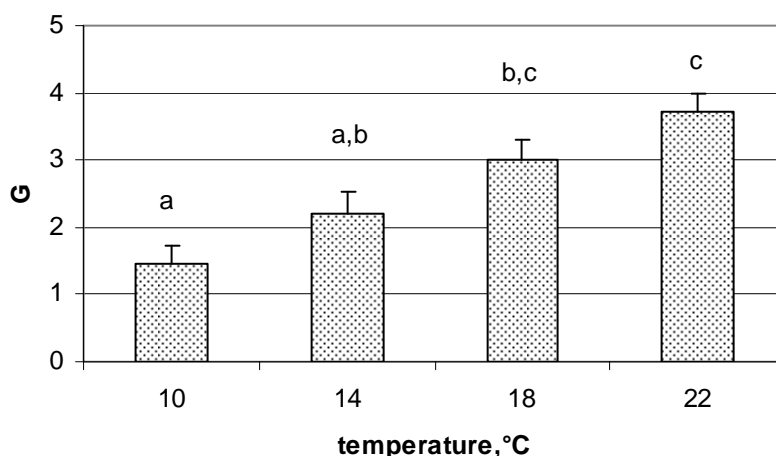


FIGURE 2 Average instantaneous growth rate ( $G$ ) ( $\pm$  s.e.) of pikeperch reared at 4 different temperatures during four weeks. Temperatures with same letter above bars do not differ statistically significantly.

Water colour has two possible ways to affect growth of pikeperch. First, pikeperch is usually considered a predator foraging in low light (Jepsen et al. 1999). It has a *tapetum lucidum* in the eye, which makes it sensitive to low levels of light (Ali et al. 1977). In turbid and also high water colour polyhumic lakes, foraging can be more effective than in clear water lakes. Ryder (1977) reported that walleye were more active during day in turbid than clear water lakes. The second possible explanation is connected to temperature and also morphometry of the lake. Shallow lakes with high water colour have a higher temperature sum during the open water season and thus potential for higher growth rate of pikeperch (II).

#### 4.2 Pikeperch behaviour and migrations in a lake system (III, IV)

In general, fish try to select habitats which maximise their fitness (Dodson 1997). The quality of the habitat depends on suitable prey, competition, risk of predation and physical and chemical characteristics of the water (e.g. Kramer et al. 1997). In many boreal lakes, temperature and oxygen create vertical habitat gradient. Migrations of fish between habitats occur from a large scale, (i.e. thousands of km) to a smaller scale (i.e. a few cm) (Kramer et al. 1997). Features of the preferred habitat can change with ontogeny and season (Wootton 1990, Vehanen & Lahti 2003, Nykänen et al. 2001, 2004). Separate fish stocks of the same species living in partly the same area can have separate seasonal feeding or spawning habitats (Kristiansen & Døving 1996, Saulamo & Thoresson 2005), while the foraging tactics within same species can also differ between habitats (Hart 1997).

Pikeperch in L. Päijänne migrated between separate summer and winter habitats (IV). Summer habitats were typically sites where the water is thermally unstratified because of continuous flow. According to ADCP measurements maximum water velocity was  $10 \text{ cm s}^{-1}$ , but near the bottom the velocity was  $0 \text{ cm s}^{-1}$ . The winter habitats were thermally stratified and more open lake basins. In contrast, pikeperch in L. Jyväsjärvi used mainly the same habitats during summer and winter.

On an annual time scale, the maximum linear distance between locations was over 20 km (IV). The average distance was longer for pikeperch overwintering in L. Päijänne (15.7 km) than in L. Jyväsjärvi (1.5 km). Although it was impossible to move long distances within the small lake, it was possible to move to the larger lake, and in the large lake to stay in a restricted area. Thus, the results indicated different migratory behaviour of pikeperch on an annual time scale between lakes. However, the area of the seasonal home range did not differ between these two lakes in summer, or between summer and winter in L. Jyväsjärvi. Daily home range was larger during summer than winter in L. Jyväsjärvi and during summer larger in stratified than in unstratified areas.

Migrations of pikeperch between seasons in the studied lake system (IV) show some similarities with earlier results from rivers (Koed et al. 2000, 2002) and reservoirs (Jepsen et al. 1999, Vehanen & Lahti 2003). In a Danish river, pikeperch had distinct summer habitats in the upper part of the river and winter habitats in the lower part of the river (Koed et al. 2000, 2002). The reason for these migrations was dense prey stocks during summer in the upper part. Pikeperch in L. Päijänne showed the same kind of migrations, aggregating during summer in flowing areas near lake inlets. Unfortunately, monitoring of prey fish density was not possible in these areas, but high prey density was a probable reason for the observed behaviour. Another potential benefit for pikeperch in these areas was the unstratified water column, which makes it possible to forage simultaneously in dark and warm water. Vehanen & Lahti (2003) observed that pikeperch preferred the lowest available water velocities during winter, whereas during summer and autumn, a wide range of velocities were used. In streams salmonids migrate to areas of lower velocity for overwintering (Cunjak 1996, Nykänen et al. 2004). In L. Päijänne, the unstratified areas offered a good feeding habitat during summer for pikeperch, whereas during winter lower numbers of prey and cold water decreased the value of the habitat and made large lake basins a more profitable habitat. In L. Jyväsjärvi pikeperch did not have separate summer and winter habitats, which is in accordance with studies in reservoirs (Jepsen et al. 1999).

The results of swimming speed indicated that pikeperch used different foraging tactics in thermally stratified and unstratified habitats (IV). In the former it was an actively moving predator and in the latter more stationary. These observed differences are consistent with earlier studies of pikeperch behaviour. Koed et al. (2000) found that in a lowland river pikeperch were stationary for long periods, whereas in reservoirs pikeperch has been classified as an actively moving predator (Jepsen et al. 1999, Vehanen & Lahti 2003). Here (III, IV), pikeperch were studied in a lake system which included both habitats

types. As Hart (1997) has shown, a predator can adapt their searching tactics in different environments. Both sedentary and active searching tactics were recorded (IV), but each individual exhibited almost exclusively only one tactics suggesting coexistence of two different phenotypes. The preferred tactics were probably a consequence of different prey availability. The density of prey fish in unstratified foraging areas was probably high and there was no need to search large areas. In pelagic areas of the lake, prey fish are usually in schools and unevenly distributed, which makes it necessary for a predator to patrol large areas. Thus, different foraging tactics were preferred in different habitats by pikeperch. This difference between these two types of environments was also evident in the areas of daily home range.

According to data for the selected temperature of tracked pikeperch and observations of the water column temperature, pikeperch preferred the warmest available water during summer (IV). In unstratified areas temperature did not limit the selection of depth and illumination. This also confirms that pikeperch did not migrate vertically across the thermocline because time of a day had no effect on the selected temperature. The most important prey species, smelt, makes vertical migrations and usually occurs in the epilimnion only during night (Dembinski 1971) and is only at that time available prey for pikeperch in stratified lakes. The temperature selected by individual fish in a lake is a compromise between specific physiological preference (Hokanson 1977), age and feeding status (Wootton 1990) and interspecies interactions (Brett 1971). According to Hokanson (1977), pikeperch has an optimum temperature for growth of 28-30 °C. The maximum temperature of the epilimnion in the study lakes never exceeds 28 °C, which means that pikeperch can never find the optimum thermal habitat. Thus, it is logical that pikeperch stay in the warm epilimnion. Related walleye also prefer the warm epilimnion (Kelso 1978), despite having a lower optimum temperature for growth of 22-25 °C (Hokanson 1977).

Pikeperch is usually considered as a predator foraging in low light (Jepsen et al. 1999, Poulet et al. 2005a). Results of activity in IV are not in full accordance with these earlier studies because activity during summer showed no differences between times of day. Poulet et al. (2005a) suggested that one reason for an activity peak at dusk is the avoidance of large avian predators. However, these are lacking or rare in Finnish lakes. The lakes in the study area are deeper than the reservoir (Jepsen et al. 1999) or channel (Poulet et al. 2005a) studied in the earlier papers. In these studied lakes pikeperch can occur during day in deeper waters (above the thermocline) where the light level is low and hence there is no need for activity peaks at dusk. Moreover, in the study area during summer the time between sunset and sunrise is at minimum only 4 h, limiting the dusk time.

Based on the results of transplantation experiments (III) and other tagged pikeperch (IV), it seemed evident that several pikeperch stocks lived in the study area, at least with respect to migration behaviour. Results of homing behaviour were in accordance with transplantation experiments done with pikeperch in Lake IJssel (Willemsen 1977) and other species (e.g. Ridgway &

Shuter 1996, Richardson-Heft et al. 2000). The pikeperch stock in L. Jyväsjärvi could be considered a fixed stock, which did not randomly migrate between lakes.

Even though there was inter-individual variation in migratory behaviour, those individuals tracked for more than a year showed similar behaviour in consecutive years (IV). Large individual variation in migration behaviour has also been observed by Fickling & Lee (1985) and Poulet et al. (2005b). The areas used were identical and the movements between them were almost at the same time of year (IV). This kind of homing behaviour has been previously observed in spawning behaviour (Nyberg et al. 1996, Jepsen et al. 1999, Lappalainen et al. 2003, Saulamo & Thoreson 2005) but seems to cover also the habitat use in other seasons.

A limit value often used for tag:fish mass ratio is smaller than 2 % (Winter 1983). Here, the maximum value was 1.7 % (III, IV). However, Brown et al. (1999) showed that tagging had no effect on critical swimming speed of rainbow trout even if this ratio was 6-12 %. Koed & Thorstad (2001) reported that tagging had no effect on critical swimming speed of pikeperch when the tag:fish mass ratio was < 0.5 %. Jepsen et al. (2008) found no differences in survival between a control group and tagged brown trout in the wild, but growth of tagged fish was lower indicating that tagging has some harmful effects. All the tagged pikeperch in the present study survived and started moving actively after operation. In recaptured fish the incisions were well healed. Thus, the results can be considered reliable in describing the behaviour of pikeperch in a boreal lake system.

The fate of four tagged individuals remained unknown and 17 were reported caught by fishermen. Nine fish survived over one year after tagging and three over two years. Instantaneous fishing mortality (F) during the first year after tagging was 0.8 in L. Jyväsjärvi and 0.5 in L. Päijänne, if fish with unknown fate are considered as surviving. This reflects the high fishing pressure on pikeperch stocks. The size structure and abundance of pikeperch stocks are mainly a consequence of fisheries (Lehtonen et al. 1996, Eero 2004, Lappalainen et al. 2005), which in turn affect the predation of pikeperch stocks on their prey species populations.

### **4.3 Bioenergetics model for pikeperch (V)**

In the application of bioenergetics models, parameter values are often borrowed from related species, if there is no specific model available. However, Trudel et al. (2004) have shown that this practise is questionable even in related species or size-classes. Moreover, a model should be validated with independent data (Bajer et al. 2003). A revised model for walleye has been used for pikeperch (Salonen et al. 1996, Vehanen et al. 1998, Wysujack & Mehner 2002), but this model had not actually been validated for pikeperch. Thus, there was a clear need for a specific and validated bioenergetics model for pikeperch.



In verification, the model I (Wisconsin-type) underestimated consumption at high rations, which was improved using model II (Elliot-type). Thus, the model II was used in experimental validation and field evaluation.

In laboratory validation with independent data, model II had high modelling efficiency and predicted well the observed food consumption. However, it had a tendency to underestimate consumption at high rations. This phenomenon is widely known in bioenergetics models (Bajer et al. 2003, 2004a, Trudel & Rasmussen 2006), and has been corrected afterwards by regression between growth rate and absolute error in consumption estimator (Bajer et al. 2004b). However, this correction is only a technical operation and does not address the ultimate reason for the error. Uncertainty in parameters U, F and SDA has been suggested to be the ultimate reason for this underestimation error (Bajer et al. 2004a), although Trudel & Rasmussen (2006) discussed how the activity parameter in bioenergetics models can be a large source of error assuming that activity increases with consumption. SDA is usually assumed to be independent of temperature, but some results are contradictory (Beamish & Trippel 1990, Tarvainen et al. 2008). If SDA increases with temperature, it offers a logical explanation for the underestimation by the models.

In the field evaluation, when observed and predicted Hg concentrations of individual pikeperch were compared, model II predicted the observed concentrations very well. Field evaluation of models using contaminants as a marker has been done previously by Madenjian et al. (2000, 2006), Trudel & Rasmussen (2001) and Pääkkönen et al. (2005). Mercury is a good marker because intake other ways than as food is negligible and the elimination process in fish has been modelled earlier (Trudel et al. 2000, Trudel & Rasmussen 1997). Based on the validation with laboratory data and field evaluation, model II was able to predict food consumption of pikeperch based on observed growth. The revised model for walleye (Salonen et al. 1996) and the original walleye model both underestimated food consumption in the field evaluation.

Sensitivity analyses of bioenergetics models give information about the uncertainty in the parameters; in other words it helps to identify in which parameters any connected uncertainty will most affect the uncertainty in output parameters. Traditionally this has been done by changing one variable with fixed relative width while keeping the others constant (Kitchell et al. 1977, Rice et al. 1983, Stevens et al. 2006). The method used in this thesis has two advantages over compared that approach. First, every input parameter has its own distribution, which is based on general knowledge about this input parameter. Secondly, all the parameters were varied simultaneously instead of changing only one. The results of uncertainty evaluation indicate that the activity parameter in bioenergetics models is the critical point, because it was the most important input variable determining both Hg concentration and food consumption.

In the evaluation of uncertainty, the 80 % probability range was narrow, both for Hg concentration and food consumption estimates. In Hg concentration it was typically  $\pm 25$  % of the median value and in food consumption  $\pm 20$  %. The activity coefficient was the most important input

parameter affecting values of both output variables. Both the earlier models (Kitchell et al. 1977, Salonen et al. 1996) underestimated consumption more than the uncertainty of input parameters affected the 80 % probability ranges.

The activity multiplier is traditionally set to 1-2 in bioenergetics models (e.g. Whitley et al. 2003, Chipps & Wahl 2004, Tarvainen et al. 2008) or uses functions based on estimated swimming speed (Stewart et al. 1983, Rice et al. 1983, Madenjian & O'Connor 1999). In many cases this activity parameter value or function has been reported to be able to predict food consumption or growth in laboratory (Karjalainen et al. 1997, Pääkkönen et al. 2003, Whitley et al. 2006) or in field evaluations (Worischka & Mehner 1998, Madenjian et al. 2000, Stevens et al. 2006). However, Boisclair & Leggett (1989) and Post (1990) showed that activity vary greatly in yellow perch (*Perca flavescens*) populations. Trudel & Rasmussen (2006) have criticized using a constant activity multiplier because it has large variations.

In the bioenergetics model for pikeperch presented in this thesis, the level of activity seems to be valid, because both laboratory validation and field evaluation indicated good ability to predict food consumption based on observed growth. In this study, the routine respiration rate was measured in the laboratory and it seems to correspond well to activity in the field over a period of one or more years. Thus, the presented model is a useful tool for estimating food consumption of pikeperch in lakes and gives more realistic values than models used earlier.

#### **4.4 Food consumption by the pikeperch population in L. Jyväsjärvi estimated by a bioenergetics model**

Stocking and fishing restrictions of piscivory fish have been widely used in biomanipulation projects to decrease the planktivorous fish populations (e.g. Jeppesen et al. 2007). The intensive fishing of coarse fish decreases their populations, change size structure and increases the potential for regulation by predators. The food consumption of the pikeperch population, size of the perch population and perch catch during the fish removal project were compared in L. Jyväsjärvi to evaluate the effect of pikeperch on their prey populations. The consumption estimates are based on several assumptions, but provide information on the proportional consumption of perch population by pikeperch and how this proportion is affected by age of recruitment of pikeperch to the fishery.

The perch population of age 1 and older was 3 million individuals before biomanipulation in 2004 (Fig. 4), and consisted mainly of year classes 2000-2003. In 2006 the year-class 2005 dominated and the perch population was about 1.5 million individuals after the intensive fishing season. The estimated size of the 0+ perch population at the beginning of July was 4.5 million in 2004 and 3.0 million in 2006.

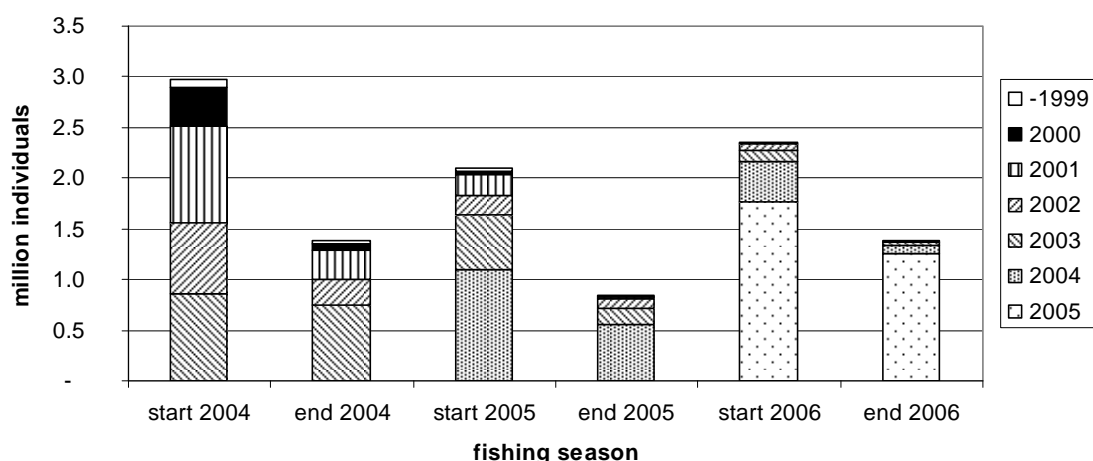


FIGURE 4 Estimated size of perch population (age-group 1 and older) in L. Jyväsjärvi at the start and the end of every intensive fishing season 2004-2006. Estimates are based on cohort analysis.

When the constructed bioenergetics model for pikeperch (V) was applied to situation before biomanipulation in L. Jyväsjärvi with age of recruitment 4, the estimated yearly consumption by pikeperch was 0.6 million perch with an initial pikeperch population density of 15 individuals  $\text{ha}^{-1}$  (5055 individuals in the whole lake) (Table 2). The consumption by the pikeperch cohort increased to age 4 years, when pikeperch biomass was highest, and then declined sharply (Fig. 5a).

TABLE 2 Estimated number of perch consumed by pikeperch and biomass of pikeperch population in L. Jyväsjärvi in 2004 (before biomanipulation) and 2006 (after biomanipulation) with age of recruitment 4 and 6. Consumption and biomass values of pikeperch were calculated with initial densities of 15 and 30 individuals  $\text{ha}^{-1}$  at age of one year. These densities correspond to 5055 and 10110 individuals in the whole lake. Proportions (%) of 0+ and 1+ perch in pikeperch diet are also given.

Year	Age of recruitment	Density at age 1	Pikeperch biomass	Consumption			Proportion in diet	
				kg	$10^6$ ind.	% of perch population	0+	1+
		ind. $\text{ha}^{-1}$	kg $\text{ha}^{-1}$					
2004	4	15	1.6	2500	0.6	8	59	25
2004	4	30	3.2	5000	1.2	16	59	25
2004	6	15	4.2	6000	1.1	15	43	29
2004	6	30	8.4	12000	2.2	29	43	29
2006	4	15	1.6	2700	0.9	21	49	47
2006	4	30	3.2	5400	1.8	41	49	47
2006	6	15	4.2	6500	1.3	30	43	50
2006	6	30	8.4	13000	2.6	59	43	50

With the age of recruitment of 6 years, the consumption was 1.1 million individuals (Table 2). Maximum consumption by the cohort was during the 6<sup>th</sup> growing season, when the pikeperch biomass was highest (Fig. 5b). When the initial pikeperch population was 30 individuals ha<sup>-1</sup>, the estimated consumption doubled, because no density-dependent effects were assumed (Table 2).

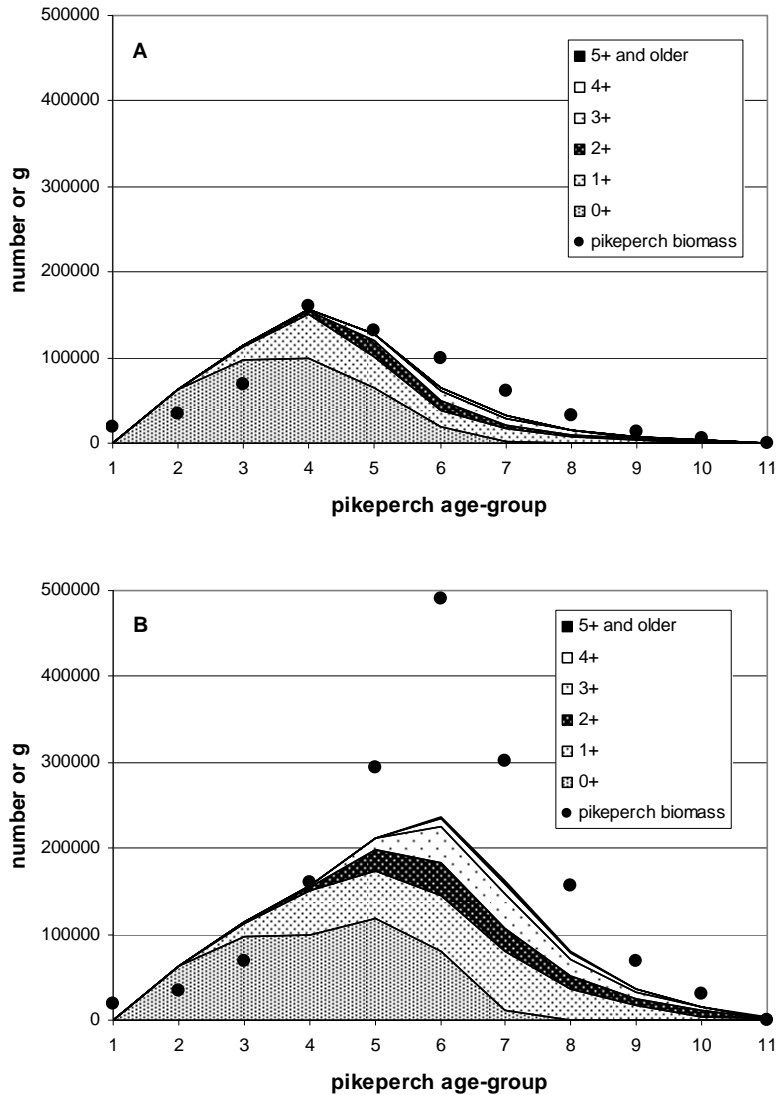


FIGURE 5 Estimated consumption of perch (in numbers) of different age-groups by the pikeperch population and mean annual biomass of the pikeperch population (g) in L. Jyväsjärvi before fish removal in 2004. The initial pikeperch density was 15 individuals ha<sup>-1</sup> and age of recruitment was A) 4 years and B) 6 years.

At the beginning of the biomanipulation in L. Jyväsjärvi, the estimate of total perch population was about 7.5 million individuals including 4.5 million 0+ individuals. The maximum consumption by pikeperch was 29 % in the case with an initial pikeperch density of 30 ha<sup>-1</sup> and a recruitment age of 6 years. Natural mortality of the perch population (1+ and older) was estimated to take 1.0 million individuals in a year with an M value 0.4. According to the

assumptions made, predation by pikeperch can alone cause the estimated natural mortality from age 1 onwards.

In the first year of biomanipulation, 2004, a total yield of 45000 kg of perch was removed from the lake causing a dramatic decrease in the perch population (Fig. 4). Since this was about fourfold the maximum simulated consumption by pikeperch, it is unrealistic to expect that the pikeperch population could be abundant enough to produce the same kind of effect in the perch population.

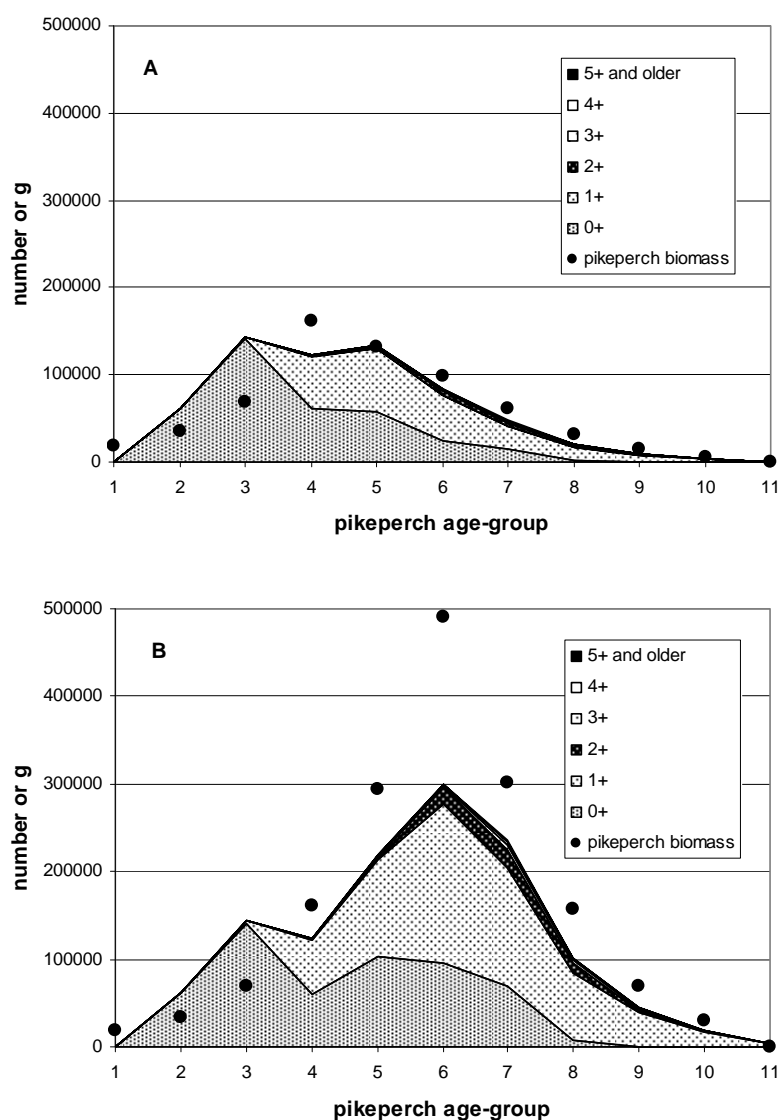


FIGURE 6 Estimated number of perch consumed by the pikeperch population and mean annual biomass of pikeperch population (g) in L. Jyväsjärvi in 2006 after fish removal. The initial pikeperch density was 15 individuals ha<sup>-1</sup> and age of recruitment was A) 4 years and B) 6 years.

By the end of the biomanipulation project in 2006 the perch population consisted mainly of age-groups 0+ and 1+ and these were also dominant in the simulated consumption of pikeperch (Table 2). With a recruitment age of 4 years, the consumption was highest in the 3<sup>rd</sup> growing season although the

pikeperch biomass was highest at age 4. In that period almost the whole consumption consisted of 0+ perch and after that 1+ became the dominant age-group in the diet of pikeperch (Fig. 6a). When the recruitment age was 6, the consumption was highest in the 6<sup>th</sup> growing season with the highest pikeperch biomass (Fig. 6b).

The age of recruitment to the fishery has a strong effect on estimates of consumption by pikeperch. The delay of two years from 4 to 6 more than doubled the consumption as biomass (Table 2). The consumption as numbers of perch depended on the structure of perch population. In 2004, the perch population consisted mainly of age-groups 0+ to 4+; thus, pikeperch older than 4 years consumed perch age-groups 2+ and older. In 2006, the consumption by pikeperch concentrated mainly on perch age-groups 0+ and 1+; thus, in 2006 the number of perch consumed was higher than in 2004.

The assumed number of pikeperch has a large effect on consumption estimates. The studies (III, IV) showed that pikeperch in L. Jyväsjärvi are resident at least during summer, when most of the consumption takes place. There are no estimates of the pikeperch population in L. Jyväsjärvi and thus the estimates of food consumption were made for two population levels. In standard gill net fishing in 2001-2006, the average CPUE of pikeperch was 157 g and 0.6 individuals day<sup>-1</sup>. An extremely dense pikeperch population in L. Sahajärvi in Southern Finland had a biomass of over 10 kg ha<sup>-1</sup> in the pelagic areas with gillnet CPUE of 1230 g and 14 individuals day<sup>-1</sup> (T. Malinen, University of Helsinki, unpublished). The estimated mean biomass of pikeperch in L. Jyväsjärvi ranged from 1.6 to 8.4 kg ha<sup>-1</sup> depending on recruitment age and starting density. Biomass estimates of boreal pikeperch populations are scarce. In L. Köyliönjärvi, pikeperch biomass was 1.2 kg ha<sup>-1</sup> (Salonen et al. 1996). Although catch is a function of fish stock and fishing effort, it gives some information about the biomass. Ruuhijärvi et al. (1996) reported that the maximum catch was 1 kg ha<sup>-1</sup> in a stocking experiment in lakes with no previous pikeperch population. In northern L. Päijänne (Fig. 1), the estimated pikeperch catch was 0.9 kg ha<sup>-1</sup> in 2001 according to a fishing questionnaire (Salo 2002). In the case of L. Jyväsjärvi, the fishing mortality was set based on telemetry studies (IV). The age of fisheries was about 4 years, because the size limit was 37 cm. Thus, the densities used in calculations are representative of Finnish lakes with efficient fishing because a size limit of 37 cm is generally used.

Several studies have estimated the effect of pikeperch predation on prey populations, some also as a biomanipulation tool. Dörner et al. (1999, 2007), concluded that pikeperch and perch predation have a major impact on the population dynamics of perch in Bautzen Reservoir in Germany. Salonen et al. (1996) concluded that the total mortality of pikeperch should be decreased in order to create a possibility for regulating coarse fish populations in L. Köyliönjärvi. Moreover, fish removal was more economical by fishing than by stocking pikeperch. In a German lake, pikeperch is regarded as an efficient predator of zooplanktivorous fish, but stockings are needed in order to maintain large enough population (Wysujack et al. 2002). Also in a lake in

Germany, stocking of pikeperch increased the consumption by piscivorous fish 1.7 times (Schulze et al. 2006b). In Turkey, introduction of pikeperch caused a collapse of prey species (Campbell 1992). The related walleye has also been documented to regulate the abundance of its prey species. Nielsen (1990) concluded that walleye were able to consume a large proportion of a yellow perch cohort and Olson et al. (2001) reported accelerated growth rate of yellow perch after walleye stockings. Changes in the prey fish community after increase in abundance of walleye have also been reported (Knight & Vondracek 1993). Thus, these examples from Europe, America and Asia indicate that pikeperch is an effective predator with a considerable ability to regulate prey species populations.

The model used in this thesis simplifies the predator-prey relationship, which in nature is a complex phenomenon. The functional response of pikeperch to the abundance of different size-classes of perch was assumed to be linear; i.e. the number of prey eaten increases linearly in relation to the prey density. At high densities of pikeperch, when the number of perch decreases dramatically, the selection of alternative prey, including cannibalism (Lappalainen et al. 2006), increases. From a biomanipulation perspective, this is not important, because the target (i.e. decrease in perch population) has in that case already been achieved. The growth rate of pikeperch was assumed equal in 2004 and 2006, because data were sufficient only for determining the average growth of pikeperch in L. Jyväsjärvi. The model does not include any density-dependent parameters in the perch population dynamics. Even though cannibalism and competition are important factors in the population dynamics of perch (Persson et al. 2000). Moreover, perch can have an important role in regulating self sustaining pikeperch populations (Dörner & Wagner 2003). Introduction of pikeperch has also been reported to cause behavioural changes in prey populations (Brabrand & Faafeng 1993, Hölker et al. 2007). Strengthening existing pikeperch population with stockings and fishing restrictions, have the same effect as introductions, i.e. an increase in predation pressure on prey fish. Thus, stockings of pikeperch can also induce behavioural changes. The behavioural changes could expose prey fish to other predators and limit their growth rate. In the future, a more sophisticated model including behavioural parameters is needed to assess more precisely the interactions between predator and prey populations.

Intensive fish removal has often led to high recruitment of young-of-the-year fish and young fish dominance in fish populations (Romare & Bergman 1999, Olin et al. 2006). Regarding biomanipulation, the key question is how to prevent the recovery of unwanted fish populations. In L. Jyväsjärvi, unlike case of perch, the roach population remained at a low level after biomanipulation, possibly by strong predation pressure from abundant perch year-class of 2005. This possibility is also supported by data of Syväranta (2008) showing that perch shifted to piscivory at a smaller size after biomanipulation than before. Pikeperch did not seem to be an efficient predator of roach in L. Jyväsjärvi (I. J. Syväranta, University of Jyväskylä, unpublished). Urho (1994) has suggested that predation pressure should be towards young individuals to limit the

biomass of coarse fish populations. In the case of L. Jyväsjärvi, the estimated predation by pikeperch on the perch population after biomanipulation was higher in numbers than before and focused on young age-groups. Based on the consumptions estimates, a pikeperch population with a density of 15 ind. ha<sup>-1</sup> at age 1 year and a recruitment age of 6, is able to consume about half of the age 1+ perch after biomanipulation. Although these numbers are only rough estimates, the present calculations indicated that pikeperch has high potential to regulate perch populations and that intensive pikeperch stocking could be an efficient tool for sustaining the effects produced by fish removal.



## 5 CONCLUSIONS

The results of this thesis illustrate the importance of pikeperch as a top predator in boreal lakes. Pikeperch is an economically valuable species and management of pikeperch populations by stocking and fishing restrictions is very common in Finland. Together with fisheries management, a question concerning a role for pikeperch in biomanipulation has risen. Several studies concentrating on pikeperch have been published, but few have focused on the effects on prey fish stocks.

The trophic state of the lake affected the diet of pikeperch. This suggests the importance of encounter rate and capture success in the prey selection process. However, these processes are complex and depend on the characteristics of both prey and predator. Studies concerning prey selection have usually been done in aquaria or small ponds and applying them to the lake scale is not always straightforward. Growth rate was highest in eutrophic lakes and/or those with highest water colour. Although the ultimate reason for this is not clear, the observation provides information for planning stocking. Because fast growth usually increases survival and production of a fish population, the best yield from stocking is predicted from eutrophic lakes and from lakes with high water colour. The importance of temperature for growth of pikeperch has been documented in earlier studies, but data collected experimentally give possibilities to model the effect of temperature on growth. These kinds of models are needed for aquaculture (Koskela et al. 2007) and to predict effects of climate change.

The telemetry studies showed different stocks living in the Päijänne lake system with respect to migratory behaviour. Such possible differences should be taken into account in fisheries management. Because the origin of different stocks is unknown, a study of genetic differences is needed, from which it would be possible determine the existence of original stocks compared to stocked fish. Especially important would be the behaviour of stocked fish and their offspring.

The bioenergetics model constructed for pikeperch was more accurate than those used previously which were based on a model for walleye. This

stresses the need for specific and validated models instead of using model for some related species. The bioenergetics model for pikeperch is a useful tool for estimating food consumption in applications concerning biomanipulation, prey resources or aquaculture. Because the activity was found to be the most important parameter creating uncertainty in the bioenergetics model, future research should focus on this parameter in the field.

The application of the bioenergetics model to L. Jyväsjärvi showed that a realistic pikeperch population is not alone able to consume the number of prey fish equivalent to that removed by intensive fishing. However, after intensive fishing the simulated consumption by pikeperch focuses on young age-groups and would be able to control the number of prey fish. In economical view, the cost of perch removed by pikeperch was 0.2-0.5 € kg<sup>-1</sup> when the initial density was 15 ind.ha<sup>-1</sup> and age of recruitment to fishery 4 or 6 years. This is below the cost of intensive fishing. However, the ability of the pikeperch population to consume bream and large roach is low.

The method used to estimate the pikeperch predation in L. Jyväsjärvi was quite simple and, because predation is a complex process, a more sophisticated model including behavioural aspects is needed to estimate better the effect of predation by pikeperch. On the other hand, the data requirements of more complicated models are high, so in practical applications simpler models based on less data, are used. It is possible to increase pikeperch populations by stocking and thus increase the predation pressure. However, the fishing management also has an important effect on the consumption by pikeperch. A high age of recruitment to the fishery leads to a population including large individuals, high consumption including also roach, high yield and increased public interest in lake management and protection.

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My wife Johanna and daughters Venla and Alina have reminded me that there are much more important things in the world than some thesis. On the other hand, they have reminded me that “try to stay there in the work to get something ready”.

## YHTEENVETO

### **Kuhan (*Sander lucioperca* (L.)) ravinnonkäyttö ja käyttäytyminen boreaalisissa järvissä**

Kalakantojen hoidossa ja hyödyntämisessä tarvitaan tietoa yksittäisten lajien ekologiasta sekä lajienvälisistä vuorovaikutuksista. Yleensä tavoitteena on kalakantojen hoito kalastuksen tavoitteiden mukaisesti, mutta viime vuosina myös kalakantojen hoito rehevöityneiden järvien kunnostuksessa on noussut esiin. Petokalojen saalistuksen aiheuttama kuolleisuus on merkittävä kalakantoja muokkaava tekijä. Suorien vaikutusten (kuolleisuus) lisäksi pedon läsnäolo voi aiheuttaa saalislajien käyttäytymisessä epäsuoria muutoksia, jotka saattavat heijastua koko kalayhteisöön. Kuha esiintyy lähes koko Euroopassa makeissa vesissä ja murtovesissä. Levinneisyys Suomessa kattaa lähes koko maan pohjoisimpia osia lukuun ottamatta, mutta vahvimmat kuhakannat ovat Etelä- ja Keski-Suomessa. Rehevien järvien kalayhteisössä kuha on merkittävä petokala, jonka kotiuttamisen on havaittu aiheuttavan muutoksia sekä ravintokalayhteisöjen koostumuksessa että käyttäytymisessä.

Tässä väitöskirjatyössä tutkittiin kuhan ravintoa ja kasvua erityyppisissä järvissä perustuen maha- ja suomunäytteisiin. Näiden perusteella arvioitiin järven ominaisuuksien vaikutusta ja vaikutusmekanismeja kuhan ravintoon ja kasvuun. Telemetrialähtetimestä merkityistä kuhista saatujen havaintojen perusteella selvitettiin kuhien vaelluksia ja elinpiirin laajuutta Päijänteessä ja siihen yhteydessä olevassa Jyväsjärvessä. Kuhapopulaation ravinnonkulutuksen arvioimista varten rakennettiin bioenergeettinen malli. Tätä mallia sovellettiin Jyväsjärven kalayhteisöön ja arvioitiin kuhapopulaation kuluttamaa ahvenmäärää (*Perca fluviatilis* L.). Bioenergeettistä mallia voidaan soveltaa arvioitaessa kuhapopulaation merkitystä ravintoketjukurunostuksissa, ravintovarojen riittävyyden arvioinnissa ja vesiviljelyssä.

Kuore (*Osmerus eperlanus* (L.)) oli tärkein kuhan ravintokohde tutkituissa järvissä ja ahven toiseksi tärkein. Särjen (*Rutilus rutilus* (L.)) osuus ravinnossa kasvoi kuhan koon ja järven rehevyydestä mukana. Vaikka suuret kuhat söivät hieman suurempia saaliskaloja kuin pienet, pieneni saalis-peto -pituussuhde (PPR) kuhan koon mukana. Samoin järven rehevyyden kasvaessa PPR pieneni. Kuhan kasvu oli nopeinta rehevissä ja tummavetisissä järvissä. Koska rehevyys ja tummavetisyys korreloivat keskenään, ei yksiselitteistä syytä pystytty osoittamaan. Selityksenä havaituille kasvueroilte voi olla ravinnon suurempi määrä rehevissä järvissä, jolloin kuha pystyy valikoimaan ravintoa, joka tuottaa suuremman nettohyödyn. Tähän viittaa havaittu PPR:n ero rehevyydestään erilaisissa järvissä. Vaihtoehtoinen selitys liittyy veden väriin, joko saalistusmenestyksen tai tummavetisten järvien nopeamman lämpenemisen kautta. Kuha on sopeutunut saalistamaan heikoissa valaistusoloissa, joten tummavetisissä järvissä saalistusmenestys voi olla kirkkaita parempi. Tummavetiset järvet lämpiävät kirkkaita nopeammin, joten kuhan kasvu saattaa näissä järvissä olla nopeampaa myös tästä syystä.

Telemetriatutkimuksissa kuhista erottui kaksi ryhmää suhteessa vaellukseen vuodenaikojen välillä. Päijänteestä pyydyt kuhat vaelsivat säännöllisesti kesä- ja talvihabitaattien välillä. Kesällä kuhat suosivat alueita, joilla jatkuva virtaus esti lämpötilakerrostuneisuuden syntymisen. Talvihabitaatit olivat puolestaan avoimia ja syviä selkävesiä. Jyväsjärven kuhat pysyivät pääsääntöisesti samoilla alueilla ympäri vuoden. Uimanopeuden ja päivittäisen elinpiirin perusteella kuhan saalistustaktiikka kesäaikaan vaihteli riippuen habitaatista. Virtaavilla alueilla kuhat pysyivät pienellä alueella, kun taas lämpötilakerrostuneella alueella elinpiiri oli laajempi ja aktiivisuus uimanopeudella mitattuna suurempaa. Tämä saattaa johtua eroista saalis-kalatiheyksissä, mikä suosii erilaisia kuhan saalistustaktiikoita. Päijänteestä Jyväsjärveen siirretyt kuhat palasivat nopeasti takaisin alkuperäiselle pyyntipaikalle. Päijänteen järvisysteemissä elävät kuhat eivät siis ole käyttäytymisen perusteella yhtenäistä populaatiota. Geneettisiä menetelmiä tulisi jatkossa käyttää populaatioiden alkuperän selvittämiseen. Erityisen tärkeitä kuhakantojen hoidon kannalta olisi tietää, eroaako istutuksista peräisin olevien kuhien käyttäytyminen luonnossa kuoriutuneista.

Bioenergeettiset mallit perustuvat energiabudjettiin, jossa eliön syömä energia jakaantuu kasvuun, hengitykseen ja eritystuotteisiin. Mallin parametrien tulisi olla lajikohtaisia ja ainakin yhdellä menetelmällä validoituja. Kuhalle sopivaa mallia varten hapenkulutusta mitattiin erikokoisilla kuhilla eri lämpötiloissa (12, 16, 18 ja 24 °C). Maksimiravinnonkulutuksen määrittämistä ja mallin validointia varten kuhia kasvatettiin akvaarioissa ahvenella ruokittuna neljässä eri lämpötilassa (10, 14, 18 ja 22 °C). Hapenkulutus- ja maksimiravinnonkulutusmittausten perusteella iteroitiin bioenergeettisen mallin parametrien estimaatit. Saatua mallia testattiin akvaariokokeista saadulla riippumattomalla aineistolla ennustamalla havaitun kasvun perusteella mallilla ravinnonkulutusta ja vertaamalla tätä ennustetta havaittuun ravinnonkulutukseen. Tämän testauksen perusteella malli näytti ennustavan hyvin kuhan ravinnonkulutusta. Koska elohopean (Hg) kertymis- ja eliminoitumisprosessit tunnetaan hyvin, voitiin mallia testata myös kenttäolosuhteissa ennustamalla kuhan elohopeapitoisuutta kahdessa eri järvessä. Myös tässä kenttätestauksessa malli näytti toimivan hyvin ja kykeni ennustamaan elohopeapitoisuudet luotettavasti.

Kuhalle tehtyä bioenergeettistä mallia sovellettiin Jyväsjärven kuhapopulaation ravinnonkulutuksen arviointiin. Koska kuhapopulaatiosta ei ole luotettavaa runsausarviota, tehtiin arviot kahdella 1-vuotiaiden kuhien alkutiheydellä (15 ja 30 kpl ha<sup>-1</sup>) ja kahdella kalastuksen aloittamisiällä. Jyväsjärvessä kuhan ravinto koostui isotooppimääritysten mukaan lähes täysin ahvenesta. Ahvenpopulaation kohdistuvaa saalistusta arvioitiin ennen tehokalastusta (vuonna 2004) ja sen jälkeen (vuonna 2006). Ahvenpopulaation runsautta arvioitiin tehokalastuksen saaliiseen perustuvan populaatioanalyysin avulla. Ahvenpopulaation kooksi ennen tehokalastusta arvioitiin 3,5 miljoonaa yksilöä (ikäryhmät 1+ ja vanhemmat) ja lopputilanteessa 1,5 miljoonaa. Tehokalastusta edeltävässä tilanteessa ahvenpopulaatio ja kuhan ravinto koostuivat neljästä ikäryhmästä (0+ - 3+). Tehokalastus nuorensi ahven-populaation

ikärakennetta, minkä jälkeen kuhan ravinto koostui pääosin ikäryhmistä 0+ ja 1+. Riippuen alkutiheydestä ja kuhan kalastuksen aloittamisiestä kalastukseen kuhapopulaation arvioitu ravinnonkulutus oli vuonna 2004 0,6–2,2 miljoonaa ahventa ja vuonna 2006 0,9–2,6 miljoonaa. Kuhan kalastuksen aloittamisiän nosto 4 vuodesta 6 vuoteen lisäsi ahvenkantaan kohdistuvaa saalistusta 1,4–1,8-kertaiseksi riippuen ahvenkannan ikäjakaumasta. Kalastuksen säätelyllä voidaan siis vaikuttaa kuhapopulaation ravinnonkulutuksen määrään ja kohdentumiseen eri ikäryhmiin ja lajeihin. Ravintoketjukurunostuksen kannalta kuhan aiheuttamalla saalistuksella on suurin merkitys tehokalastuksen jälkeisessä tilanteessa, jolloin tiheä kuhakanta voi rajoittaa saalislajiensa populaatioiden toipumista tehokalastuksesta.

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