

Master's thesis

**Growth and population structure of perch in relation to
diet in a small humic lake, Valkea-Kotinen**

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Afolabi Abideen Bolarinwa: Growth and population structure of perch in relation to diet in a small humic lake, Valkea-Kotinen.

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ABSTRACT

Lake Valkea-Kotinen is a long-term ecological monitoring site in the Evo region of southern Finland. The aim of this study was to investigate the growth and population structure of perch (*Perca fluviatilis* L.) in relation to diet in Valkea-Kotinen in order to provide reference data for a study investigating effects of increased loading of dissolved organic matter to nearby Lake Alinen Mustajärvi. Valkea-Kotinen was predominantly inhabited by small benthivorous perch. The growth relationship between opercular bone and total length of perch in the lake is similar to those earlier analysed for nearby lakes. Compared to wider growth rates, the growth of perch was slow and similar to those in similar lakes. Analyses of stable carbon and nitrogen isotopes and stomach content revealed that perch were mostly feeding on mayfly nymphs and did not undergo any clear ontogenetic dietary shifts. In summer and autumn, the perch population had more diverse diets than in spring. Zooplankton only contributes to the diet of <100 mm perch in summer, terrestrial insects and small prey fish were almost completely missing from the perch diet. Poor food condition and overall feeding behaviour are suggested to contribute to the observed slow growth and dominance of small individuals in the perch population.

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TIIVISTELMÄ

Valkea-Kotinen on Evon alueella sijaitseva pitkäaikaisen ekologisen seurannan kohdejärvi. Tämän pro gradu -työn tarkoituksena oli tutkia ahvenen kasvua ja populaatorakennetta suhteessa ravintoon. Tietoja käytetään Alinen Mustajärven kuormitustutkimuksessa vertailuaineistona. Valkea-Kotisen ahvenet olivat pääasiassa pienikokoisia pohjaeläinsyöjiä. Operculum-luusta takautuvasti arvioitu keskimääräinen pituuskasvu oli hidasta ja samaa luokkaa kuin muissa samantyyppisissä järvissä. Maha-analyysien ja hiilen ja typen vakaiden isotooppien analyysien mukaan ahvenet söivät pääasiassa päivänkorenon toukkia. Selvää ravintokohteen vaihtoa kehityksen myötä ei havaittu. Kesällä ja syksyllä ravinto oli monipuolisempaa kuin keväällä. Eläinplanktonia söivät vain alle 100 mm pituiset ahvenet keväällä. Terrestriset hyönteiset ja kalat puuttuivat ahvenen ravinnosta lähes tyystin. Huonot ravinto-olot olivat luultavasti syynä ahventen hitaaseen kasvuun ja pieneen kokoon.

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1. INTRODUCTION

The boreal region is characteristically dominated by numerous lakes with high concentration of allochthonous organic matter, a feature of flat landscapes with catchments dominated by forested areas (Salonen *et al.* 1993). Lakes in this region are an integral part of inter connected habitats some of which are rivers, valleys, wetlands, and peat lands. Boreal lakes are usually polyhumic, oligotrophic and have relatively low pH and naturally low oxygen in the hypolimnion during summer and winter (Eloranta 2004). The lakes are ice-covered (varies somewhat with latitude and between the years) from around November to April while surface water temperatures can be high (up to 28°C) in summer (Rask *et al.* 1992, Keskitalo & Eloranta 1999, Jarvinen *et al.* 2002). The littoral zones of boreal lakes in Northern Europe are narrow and their bottom often consists of soft mud and coarse woody debris. Fishes in small boreal lakes are no doubt adapted to harsh and changing environmental conditions (Olin *et al.* 2010).

Perch (*Perca fluviatilis* L.) is one of the most common and widespread fish species in Northern Europe. Perch is a food generalist fish species which often undergoes ontogenetic dietary shifts from zooplankton to benthic and fish prey. In many lakes, perch is the only fish species present or it can coexist with other species, most often with roach (*Rutilus rutilus* L.) and pike (*Esox lucius* L.). In small boreal lakes, perch populations are often affected by interspecific interactions from competing roach and predatory pike. The intensity of these negative interactions is regulated by several environmental factors like water temperature and light condition (Olin *et al.* 2010). In addition, perch populations are normally spatially segregated, size structured and characterized by a mixture of predator-prey and competitive interactions between conspecifics of different sizes (Persson & Eklöv 1995).

Perch undergo an ontogenetic dietary shift from zooplankton to larger prey food item such as benthic macroinvertebrates and can finally become piscivorous (Persson *et al.* 2000). After hatching, perch larvae move to the pelagic zone and remain there 1–2 months before returning to the littoral zone. The timing of this inshore and offshore migration may be rather flexible in terms of fish size both within and in-between populations (Wang & Ekman 1994). Perch is a generalist predator capable of shifting diets depending on spatial and temporal availability of different prey items. As a piscivore, perch can often forage broadly upon pelagic and benthic food (Svanbäck & Eklöv 2002) in addition to small prey fish. The diet of perch varies among populations in different lakes and is largely dependent on the availability of different food organisms (Elrod *et al.* 1981). Zooplankton is often the primary food source for small perch (Persson *et al.* 2000). Perch shift during the first summer from the pelagic zones, where they feed primarily on zooplankton, to the littoral zone where they feed mainly on benthic macroinvertebrates. After reaching a certain size (usually at total length of 130–200 mm), perch can become piscivorous and even consume smaller conspecifics (Persson & Eklöv 1995).

However, the size and timing of the piscivorous stage varies in different lakes and habitats depending on the availability and properties of prey fishes (Olin *et al.* 2010). Perch are capable of being piscivorous between 50–185 mm total length (Svanbäck & Eklöv 2002, Urbatkza *et al.* 2008). Feeding behaviour is also commonly a major contributor to the size divergences. There are individual differences in feeding behaviour such that some may shift to piscivory while others of the same size may continue feeding on invertebrates. Generalist feeding behaviour of perch may be particularly prevalent in boreal lakes for

several reasons. There are rather few fish species and their densities fluctuate from year to year due to climatic variability and unpredictable disturbances like winter kill. Fluctuating prey fish availability coupled with high invertebrate biomass and available energy may result in normally piscivorous fish regularly feeding at lower trophic level (Beaudoin *et al.* 1999). In many small lakes where perch are the only fish species, fish populations are usually dense and slow growing probably due to poor nutrition (Raitaniemi *et al.* 1988). Conversely, environments in large lakes and brackish water of the Baltic Sea are more complex and perch populations are less dense with access to abundant prey varieties including invertebrates and fish prey which can enhance better growth. This is probably the reason for the great differences in the growth rates of perch in large lake or Baltic Sea (Raitaniemi *et al.* 1988). In some cases, the growth of perch has been observed to speed up when the population size has decreased due to increased fishing pressure and/or predation. The more rapid growth has been possible because of increased food resources, better growth and thus higher potential to shift to piscivory (Raitaniemi *et al.* 1988). A higher abundance of invertebrates per individual fish probably enables the few fish to grow faster in acid lakes especially during the first year of their life. However, feeding on small prey animals with low individual energy content becomes an unprofitable strategy for the fish as they grow.

Previous studies on perch population structure, diet and growth in boreal lakes have seldom used stable isotope analysis, although, stable isotope analysis is now an important technique for characterizing food web structure following the patterns of energy flow through ecosystem (Fry 2006). While stomach content analysis reveals information about the short-term feeding behaviour of organisms, naturally occurring stable isotopes provide information about the long-term feeding behaviour (Persson & Hansson 1999) and thus reveal features of the foodweb that otherwise would not be detectable. Stable isotope values of carbon can help identify food sources assimilated by consumers over longer-term periods (e.g. weeks) while nitrogen stable isotope values can reveal the trophic position of an organism in the foodweb (Fry 2006).

1.1. Relevance of the study

About two-thirds of total Finnish lake catchment area is forested and almost 80% of this is under forestry management. In some areas, forestry management, including clear cutting, ditching, scarification and other manipulations, is the most widespread land use. However, impacts of forestry on boreal lakes and rivers are only recently being studied. More attention still needs to be paid to forestry-induced changes in Finnish lakes and running waters. This is because manipulation of silviculture in catchments of lakes and rivers can affect the loads of organic matter into waters thus changing the physiological and biological properties of aquatic ecosystems and thereby the conditions of the plankton, zoobenthos and fish (Gregory *et al.* 1987). A previous study (Rask *et al.* 1998a) of limnological responses of small forest lakes in Eastern Finland to forest clear cutting and soil scarification observed changes in zooplankton and zoobenthos community composition, and this was also reflected in the population structure and growth of perch and the entire food web structures of the lakes.

Characterization of pre-disturbance of food webs should provide a baseline for assessing impacts of future disturbances. Lake Valkea-Kotinen is a long term ecological monitoring site and hence studies of its food web structure can provide an important reference for many potential studies, including various manipulations of other small forest

lakes nearby. The area has long had a special value in terms of long term ecological research. The lake catchment area was protected as a part of Kotinen State Forest Reserve in 1955 and the protected area was enlarged in 1987, and at the beginning of 1994 the area was made a nature reserve area within the Finnish Long-Term Socio-Ecological Research network (FinLTSER) established to provide long-term monitoring of representative ecosystems. Lake Valkea-Kotinen is a FinLTSER site representing small humic lakes in southern Finland. The lake was also one of those being limnologically monitored in the Finnish Integrated Monitoring catchment area which started in 1994.

1.2. Specific objectives of the study

The work for this thesis contributes to the long-term monitoring data for Lake Valkea-Kotinen as well as providing reference data for an Academy of Finland funded project investigating the effects of increased loading of dissolved organic matter to nearby Lake Alinen Mustajärvi. The specific objectives of the thesis were:

- (1) To determine the growth of perch in Valkea-Kotinen and compare it to that of perch in other boreal lakes.
- (2) To determine the relative contributions of benthic, pelagic and terrestrial food sources to perch diet in Valkea-Kotinen, and to study seasonal and ontogenetic dietary differences.
- (3) To evaluate the extent to which diet determines growth and population structure of perch in Valkea-Kotinen.

2. MATERIALS AND METHODS

2.1. Site description

Lake Valkea-Kotinen (61° 14' N 25° 04' E) is a small humic lake located in a boreal coniferous forest area in the Evo region about 140 km north from Helsinki, Finland (Fig. 1). The lake has a catchment area of 30 hectares with annual mean precipitation of 618 mm and annual mean temperature of 3.1°C. The surface area of the lake is 4.1 ha, the maximum depth is 6.5 m (mean depth 3.0 m) and the estimated volume is 103,000 m³ (Bergström *et al.* 1995). Due to the brown water colour and restricted light penetration, the littoral zone is narrow, reaching only to a depth of around 2 m, and the vegetation is dominated by sparse stands of *Nuphar lutea* (L.) and submerged *Sphagnum* sp. (Kankaala *et al.* 2006).

Due to its sheltered position and high concentration of allochthonous humic substances, the lake is normally stratified with respect to temperature and oxygen. The spring turnover is usually short or incomplete and anoxic conditions in the hypolimnion usually prevail from June until the autumn turnover in October (Kankaala *et al.* 2006). The lake is covered by ice for 5.5 – 6 months each year. The lake becomes thermally stratified very soon after the ice melt in the middle of May. The epilimnion remains < 2 m thick until the autumn. In mid-summer, the temperature gradient between epi and hypolimnion is usually up to 15°C. The lake water is brown (colour 130–140 g Pt m⁻³) and acid (pH 5–5.5). Between 1990 and 1996, the mean concentration of dissolved organic carbon varied between 800–1000 mmol m⁻³, and mean concentration of total nitrogen and phosphorous in the epilimnion ranged from 31 to 40 and from 0.5 to 0.7 mmol m⁻³ respectively (Kankaala *et al.* 2006). Secchi depth is generally 1.4–1.6 m, and the euphotic zone reaches to a depth of 2.2 m. More information on the lake can be found in Salonen *et al.* (1993).

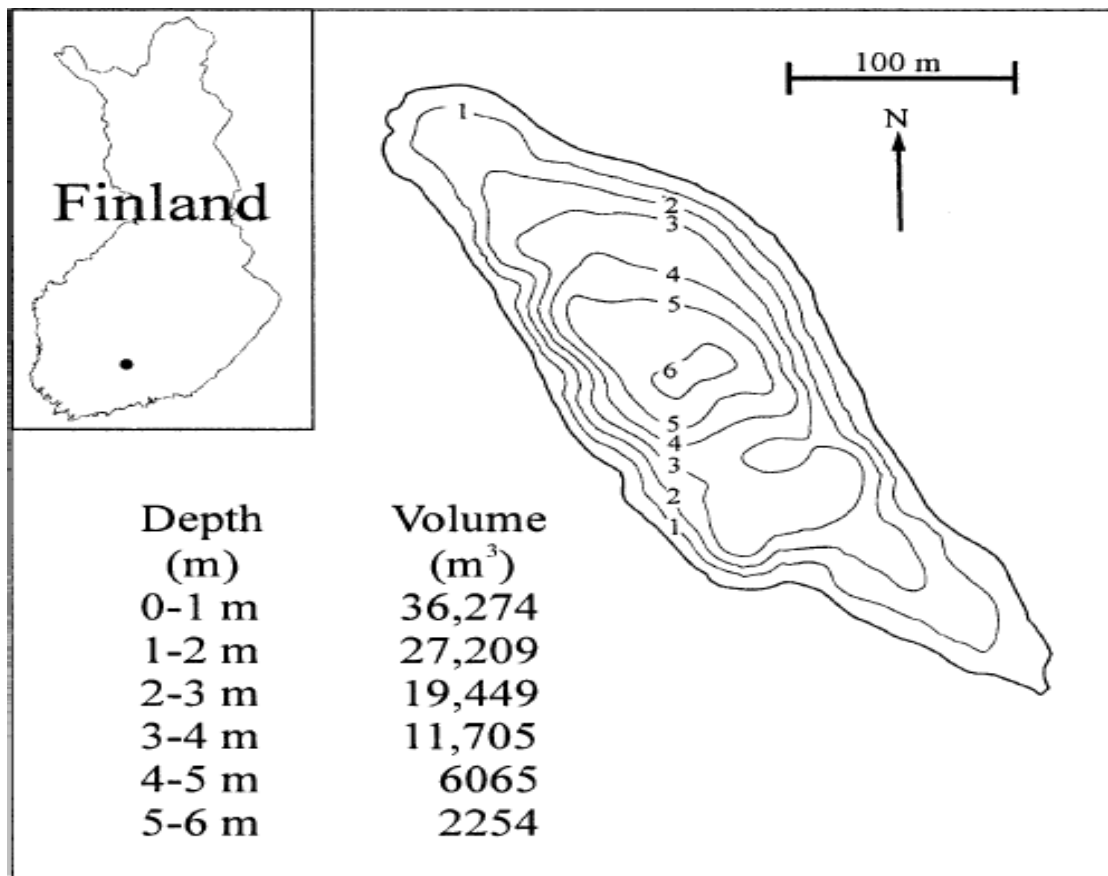


Figure 1. Location and bathymetric map of Lake Valkea-Kotinen (Kankaala *et al.* 2006).

2.2. Sample collection and analyses

Sampling of fish and benthic macroinvertebrates was carried out by the staff of Evo research station during 2008. Fish samples were collected using a Nordic-multi mesh gillnet series and 8 mm mesh size steel traps during overnight fishing for an average 12 hour period. The gillnet is composed of 12 different mesh-sizes ranging between 5 and 55 mm knot to knot (30 m long 1.5 m deep). The mesh size combination is expected to be able to target different sized individuals with approximately equal efficiency (Kurkilahti *et al.* 1998).

Fish for determination of perch population density and size structure were caught from the end of April through end of May. Fish for consideration of seasonal variations in perch diet and growth analysis were caught in spring (May), summer (July) and autumn (October). Invertebrates representing potential food for perch were handpicked from collected moss vegetation and from other benthic materials collected using sweep-net during the day time. Benthic macroinvertebrates (i.e. Waterlouse (Isopoda *Asselus aquaticus*), dragonfly nymphs (Odonata Anisoptera) ,damselfly nymphs (Odonata Zygoptera), caddisfly (Trichoptera) mayfly nymphs (Ephemeroptera), midge (Chironomidae Diptera), and water mites (Acariformes, Hydrachnidia) were collected only in spring and autumn).

The perch population density and size structure was determined by mark-recapture techniques (Krebs 1989) and Schnabel (1938) and Schumacher & Eschmeyer (1943) methods for males and females separately. Total catch was 1387 perch, of which 1255 were marked and 122 were recaptured. Recapture was conducted from 29 of April to 15 of May 2008. The estimated perch population represents perch caught based on the size selectivity of the gears. The total length of perch ranged between 70mm and > 200 mm. A total number of 63 individuals representing a perch sub-population were randomly selected from the catches based on the three different seasons, and measured to accuracy of 5 mm and 1g. In order to observe ontogenetic dietary shift, the perch were divided into three classes: <100 mm, 100–149 mm and >150mm with 7 individuals per size class per season. Fish sexing, gut content removal and opercula bones preparation were carried out in Evo research station laboratory by the staff. The opercular bones were removed, cleaned with water, dried and each put in a separate labelled envelope. Fish were dissected and gut contents were preserved in ethanol in labeled bottles. For stable isotope analysis, a small sample of dorsal white muscle was cut from each fish and placed in a labelled tube before being stored frozen at -20 °C.

2.3. Age determination and back-calculation of fish length

Age determination and back calculation of length of fish were carried out in the University of Jyväskylä using opercular bones of perch (Monastyrsky procedure, Bagenal & Tesch (1978). This was based on counting of opercular bone annuli viewed under microscope at magnification of $\times 6$. Each opercular bone was moistened with clean water to enhance readability of the annuli. Some annuli were difficult to read after the age of two years because they were either half formed along the radii or completely blurred. Because allometric relationship exists between the growth of opercular bone and the fish length, the back calculations of the growth from each bone had to be corrected with coefficient of allometry between the bone and fish length. The bone radius was measured as recommended by Le Cren (1947) and the relationship between opercular bone radius (S) and fish length (L) was estimated by power function between S and L (Fig. 2) in order to determine the regression coefficient for allometric growth (i.e. b value) for perch population in Valkea -Kotinen. According to Monastyrsky's (1926, 1930) method, a relationship between S (radius) and L (Length) is assumed obeying:

$$L = a * S^b, (0 < b < 1)$$

The length at age i (L_i) can be estimated from the equation

$$L_i = L * (S_i/S)^b$$

where L = Total length of fish

S = Total opercular bone radius

S_i = Opercular bone radius at age i

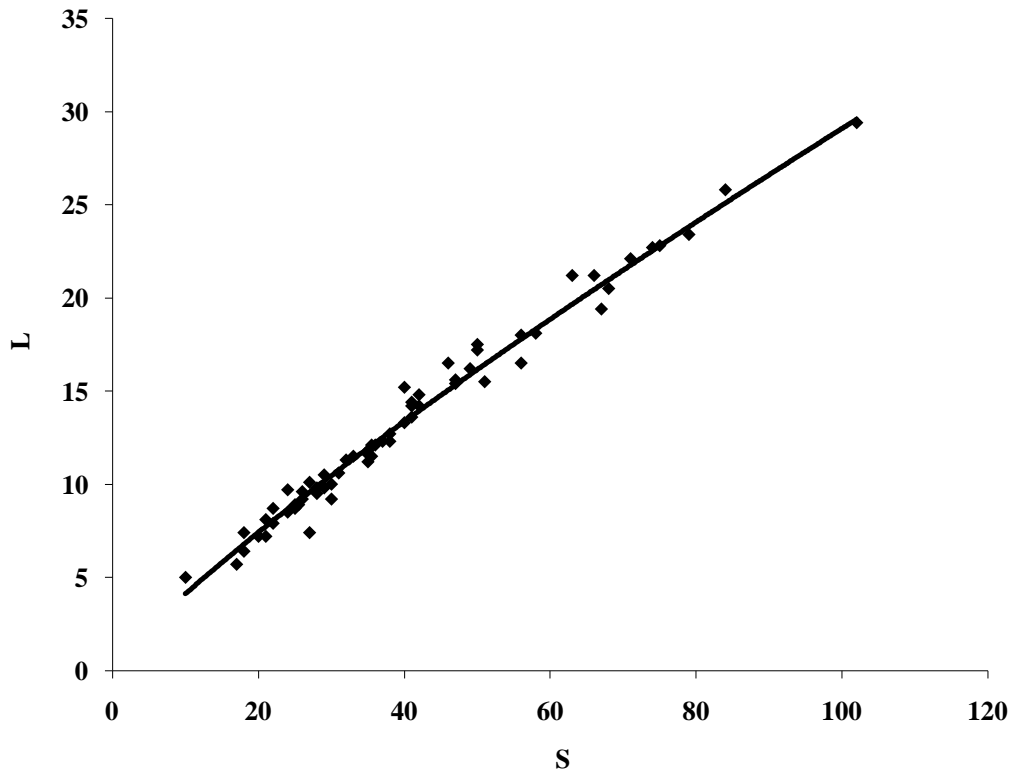


Figure 2. Regression between L and S for perch from Lake Valkea-kotinen in 2008. The power function is represented by $y=0.5835x^{0.8489}$.

The linear regression coefficient (i.e. b value) for allometric growth relationship between opercular bone and fish length for perch was 0.8489 and does not significantly deviate from the values used by Le Cren (1958) in Lake Windmere (0.876) and Kokko (1980) in Lievestuoreenjärvi (0.879). Therefore, (b= 0.8489) was used in back-calculating the length at age for perch in this study.

2.4. Stomach content analyses

In order to get information about the diet of perch in Lake Valkea-Kotinen, each preserved fish stomach was dissected using a scalpel and the contents emptied into a Petri dish filled with diluted ethanol and viewed under a dissecting microscope at the magnification of $\times 6$ – 8. The prey items were identified to order, family or species level and grouped into 8 categories: frog (Anura), waterlouse, dragonfly nymphs, midge, caddisfly larvae, mayfly nymphs, adult insects (Insecta), and zooplankton (cladocerans and the copepod). Stomach fullness was estimated by scoring on a scale from 0 (empty) to 10 (full) while relative contribution of each prey item was estimated by allocating a portion of the fullness value (Hynes 1950).

2.5. Stable isotope analyses

Preparation of fish muscle samples and prey items for stable isotopes analysis were carried out at the University of Jyväskylä. Because no zooplankton samples were available from the study period, isotope values for zooplankton were taken from previous studies

conducted on the lake (Jones *et al.* 1999). Fish muscle and prey samples were oven dried in clean glass vials at 60°C for 24 hours. All samples were ground to homogeneous powder using a mortar and pestle. Between 0.5 to 0.6 mg of ground tissue was then weighted into separate tin cups sealed, rolled into balls and each placed in a separate well in micro titre tray. Stable isotope analysis of carbon and nitrogen in the samples were conducted between 17th and 18th of March 2009 at the Institute for Environmental Research, University of Jyväskylä using a FlashEA 112 elemental analyzer coupled to Thermo Finnigan DELTA^{plus} Advantage mass spectrometer.

Pike white muscle tissue was used as an internal working standard, and replicates of standards were run in every sequence. Stable isotope ratios are expressed as parts per thousand (‰) delta values ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$), referred to the international standards for carbon (Pee Dee Belemite) and nitrogen (atmospheric nitrogen) (Peterson & Fry 1987). Internal precision for standards was always less than 0.7 ‰ for carbon and 0.3 ‰ for nitrogen in each run (usually both < 0.1 ‰).

2.5.1. Dual isotope three-source mixing model for food source partitioning

To estimate the relative contribution of benthic, pelagic and terrestrial food sources in the diet of perch, the Iso-source dual isotope three-source mixing model (Phillips and Gregg 2003) was used. The isotopic value for fish muscle was calculated using isotopic fractionation of carbon ($\Delta\text{N}=3.46\text{‰}$) and nitrogen ($\Delta\text{N} = 0.346\text{‰}$) between fish muscle tissue and a whole fish prey (Vander Zanden & Rasmussen 2001). In this study, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for pelagic baseline were assigned as the mean isotope signatures of cladocerans and copepods (Jones *et al.* 1999). Isotope value of water skater (*Gerridae* sp.) was used to represent the value of terrestrial insect because *Gerridae* feed on terrestrial insects. The mean value of several groups of benthic macroinvertebrates collected on two sampling occasions was used for benthic macroinvertebrates isotopic values.

2.6. Data analyses

The perch population in Valkea-Kotinen in 2008 was analysed according to size and weight distributions. Perch were divided into three length categories : <100 mm, 100–149 mm and >150 mm. Perch diets were analysed based on their total stomach contents and the proportion of each of the 8 recognised diet categories. Linear regression was used to analyse relationship between Ln (L) and Ln (S) of perch and to also analyse relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of perch muscle and fish length. Analysis of covariance (ANCOVA) was used to analyse the relationship between ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values and fish length with respect to each season. Both regression analysis and ANCOVA were carried out through SPSS software.

3. RESULTS

3.1. Population estimate

During the 2008 catching period, the mean values obtained using the Schnabel (1938) and Schumacher & Eschmeyer (1943) methods for perch population size above 70mm total length from Valkea-Kotinen in 2008 were quite similar. Mean population size obtained from Schnabel (1938) was 5687 ± 1531 S.E. (95 % c.l.) while 5646 ± 1554 S.E. (95 % c.l.) was obtained from Schumacher & Eschmeyer (1943) method. For the purpose of this study, the mean value from Schumacher & Eschmeyer (1943) method shall be upheld. Since the area of the lake is 4.1 ha, the estimated mean total population is 1377 ± 373 S.E. (95 % c.l.) ha^{-1} . Average male and female population densities were 1203 ± 416 S.E. (95 % c.l.) and 244 (95% c.l.) perch per hectare respectively. Based on average weight of the randomly selected sub-population (approximately 40 g) the total perch biomass in the lake was around 55 kg ha^{-1} . Based on gillnetting and mark-recapture, the length of perch in Valkea-Kotinen ranged from 70 mm to >200 mm. The frequency distribution shows the perch population was dominated by individuals of between 90–110 mm total lengths (Fig. 3). In the randomly selected sub-population for this study, perch length ranged from 50 mm to 294 mm and was dominated by individuals of between 75–124 mm total length (Fig 4a). The weight ranged from 1g to 327 g and the dominant weight class was individuals of around 25g weight (Fig. 4b). Age of perch ranged from 0+ to 16± years and the dominant age class was individuals between 2± and 3± years (Fig. 4c).

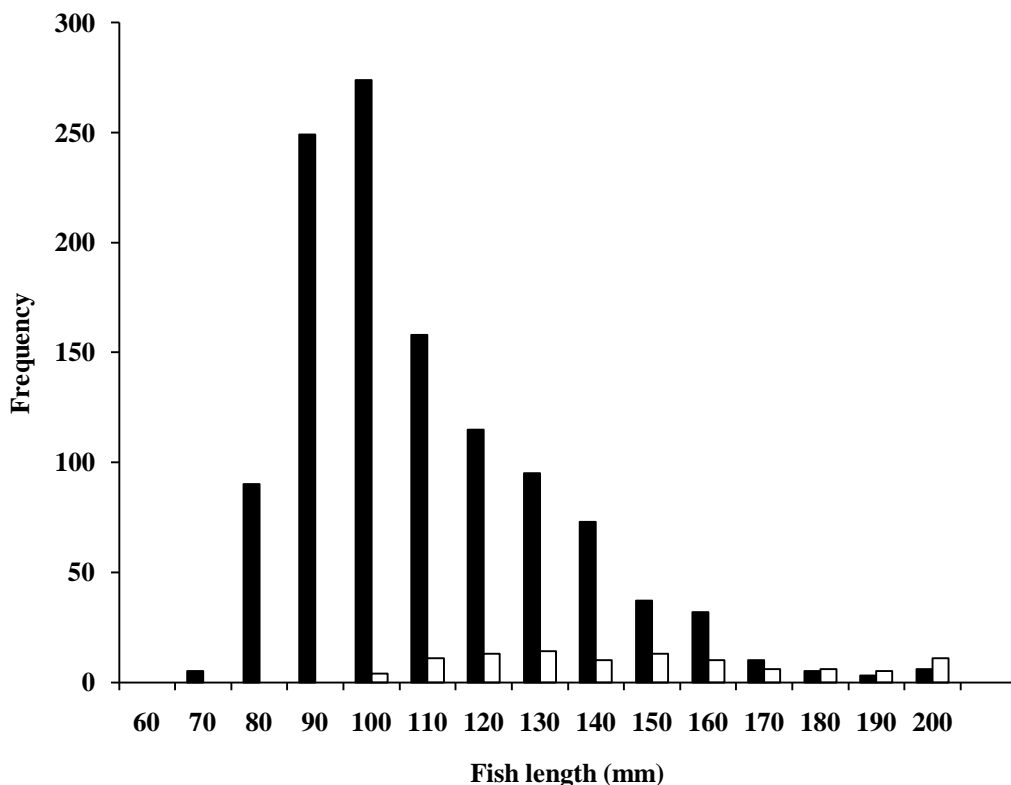


Figure 3. Length frequency distribution of perch from gillnets and steel trap catches from Valkea-Kotinen in April and May 2008. The black columns indicate males and white columns indicate females.

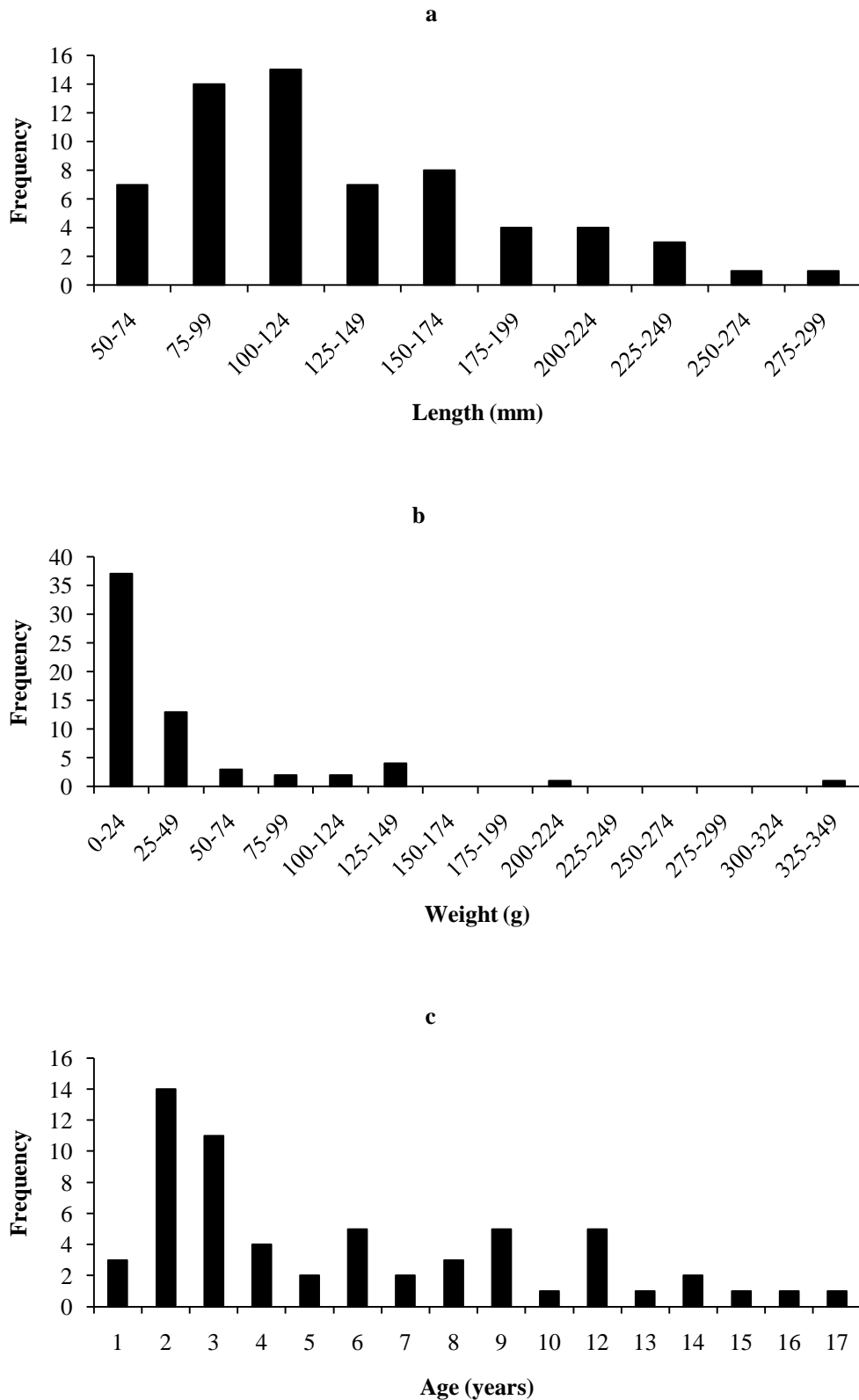


Figure 4. (a) Length, (b) Weight, and (c) age frequency distributions of randomly picked perch sub-samples caught from Valkea-Kotinen in May, July and October 2008.

3.2. Growth of fish

There was a positive relationship between $\ln(L)$ and $\ln(S)$ of perch in Valkea - Kotinen (Regression analysis $p < 0.001$, $b=0.8489$, 95 % c.i.). However, according to the back calculated length at age data, the growth of perch in Valkea-Kotinen was relatively slow (Fig. 5). The mean length of age group 3 years is less than 160 mm. The growth rate is observed to be rapid between ages 0+ to 2 years after which the growth rate declined. The fish reached the mean length of 150 mm at age between 7–8 years. The mean length at age 10 years was 184 mm whereas, it took between 11–12 years to reach total length of 200 mm.

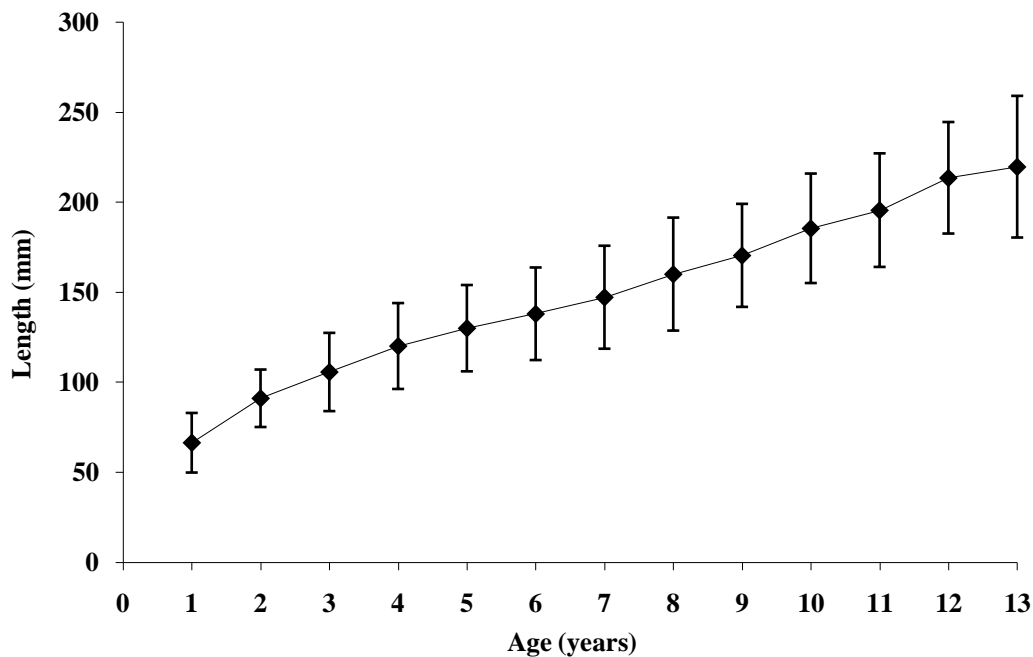


Figure 5. Mean back-calculated length at age for perch captured from Valkea-Kotinen in 2008. Error bars show standard deviations.

3.3. Stomach content analysis

In all, 63 perch stomachs were examined, of which 51 contained prey suggesting inadequate prey items in the lake. A total of 8 different prey categories were identified which are: frog (Anura), waterlouse, dragonfly nymphs, caddisfly larvae, midge larvae, mayfly nymphs, adult insects and zooplankton. However, mayfly nymphs appear to be the dominant prey item in the diet of perch in Lake Valkea-Kotinen. Perch did not clearly undergo ontogenetic diet shift except a temporary diet shift observed in <100 mm perch in summer. In the spring, mayfly nymphs were found dominating the diet of all fish size classes (Fig. 6). In summer, <100 mm perch were mostly feeding on zooplankton (cladocerans and copepods). There was a progressive decline of zooplankton proportion in the diet of perch with increase in fish length (Fig. 6). 100–149 mm perch were mostly feeding on dragonfly nymphs, whereas >150 mm perch were mostly feeding on mayfly nymphs. Both 100–149 mm and >150 mm perch showed markedly more diverse diet in

summer than in spring. In autumn, mayfly nymphs appeared to be the dominant prey for all perch size classes (Fig. 6) but not in the same magnitude as observed in the spring.

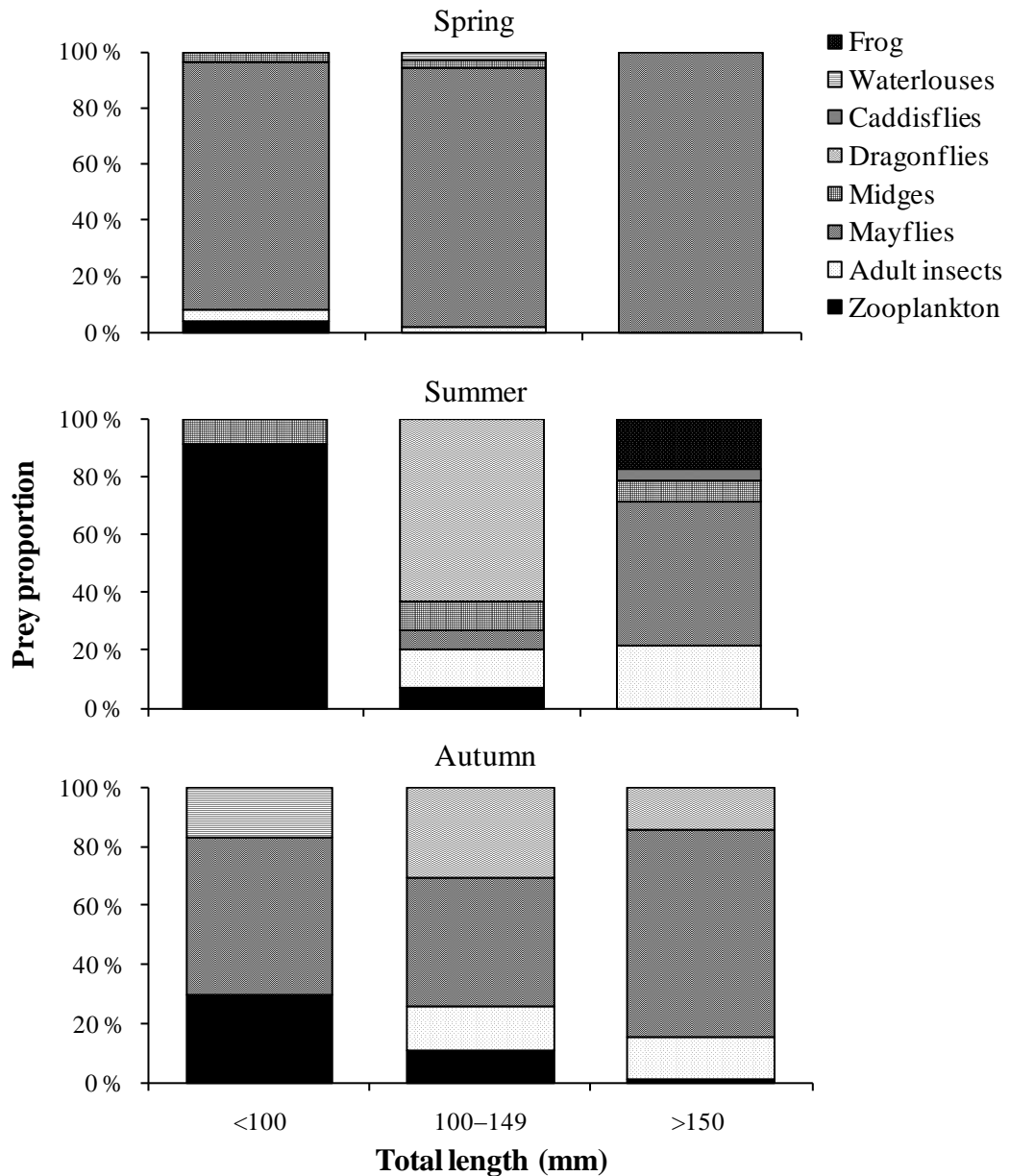


Figure 6. The diets of perch <100 mm, 100–149 mm and >150 mm in spring, summer and autumn in Valkea-Kotinen in 2008.

3.4. Stable isotope analyses

The linear regression between the stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and fish lengths indicated no statistically significant ontogenetic dietary shift (Linear regression $n=63$, $p > 0.05$). In general, the isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from perch muscle suggested no statistically significant dietary differences between the stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of all perch size classes throughout the seasons: $\delta^{13}\text{C}$ (ANCOVA, $n=63$, $p > 0.05$) and $\delta^{15}\text{N}$ (ANCOVA, $n=63$, $p > 0.05$).

In spring, all the perch size classes had similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig.7) indicating a homogenous diet. In summer, the wide variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values (Fig.7) suggests perch were probably feeding on different kinds of food sources. Furthermore, there is a difference of approximately 1‰ observed for the > 150 mm perch $\delta^{15}\text{N}$ signatures above the nitrogen isotope values of smaller size classes (<100 mm and 100–149 mm) (Fig. 7). This suggests that >150 mm perch were probably feeding on young perch in addition to other prey items in the summer. In autumn and spring, the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggest perch were mostly feeding on benthic invertebrates (Fig.7).

3.4.1. Three-source mixing model

Outputs from the Iso-source mixing model suggest that perch were mostly feeding on benthic macroinvertebrates except in summer when zooplankton contributed significantly to the diet of small size (<100 mm) perch (Table 1). Surface insects were not a significant food source for perch in any seasons. Perch were probably feeding on surface insects sparingly particularly in spring and summer.

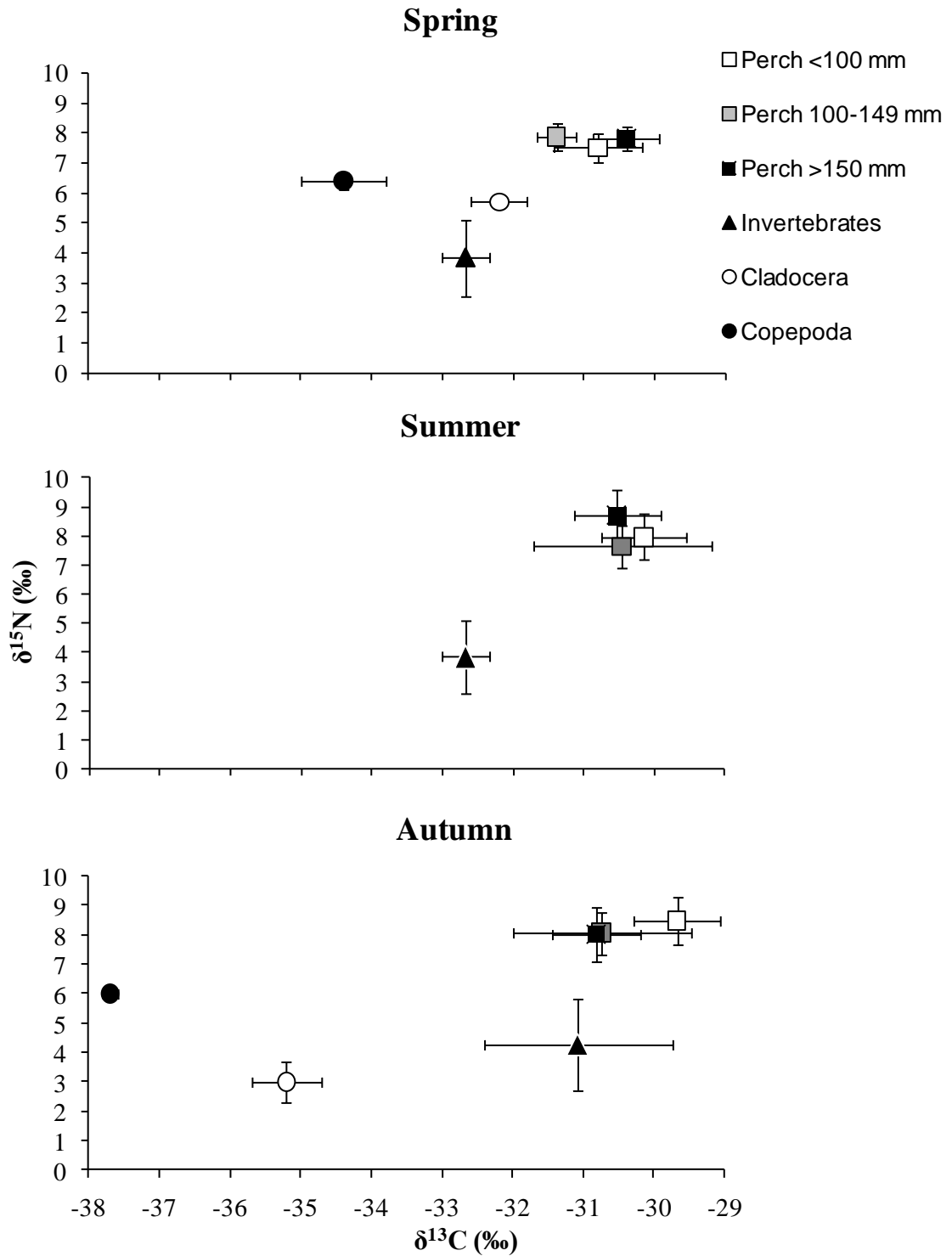


Figure 7. Isotope biplots showing the mean (\pm standard deviation) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of perch of three size classes, benthic macroinvertebrates and zooplankton in spring, summer and autumn in Valkea-Kotinen in 2008.

Table 1. Relative contribution (%) of major food sources in the perch diet according to the Iso-source mixing model. Values are means \pm SE.

Season	Zooplankton Mean \pm S.E.	Macroinvertebrates Mean \pm S.E.	Terrestrial insects Mean \pm S.E.
Spring	35 \pm 7	60 \pm 5	5 \pm 7
Summer	51 \pm 7	45 \pm 7	3 \pm 6
Autumn	22 \pm 4	92 \pm 4	-13 \pm 2

4. DISCUSSION

4.1. Population structure and growth

Lake Valkea-Kotinen is dominated by slow growing, benthivorous, small sized perch, suggesting a possible strong intraspecific food competition and lack of appropriate prey fish. Similar population densities of perch have been reported from other small humic lakes in the Evo region (Rask 1983, 1984, Rask & Arvola 1985, Rask & Hiisivuori 1985) as well as in eastern Finland (Rask *et al.* 1998a), in central Europe (Ronnberger & Anwand 2000) and elsewhere Jellyman (1980). The very similar growth pattern of perch in Lake Valkea-Kotinen reported earlier (Rask *et al.* 1998b) suggests that over time, probably little change has taken place.

The perch population analysed in this study is a sub-population vulnerable to the size selectivity of the gears used and underrepresentation of the females at the time of spawning. Compared to the population densities of 18 humic lakes in southern Finland (Olin *et al.* 2010), the population density of perch in Valkea-Kotinen is intermediate. Overall, the population size from 2008 study falls within the values obtained from the lake between 1991-1996 (Rask *et al.* 1998b) (Table 2.). Their estimates of the perch population density varied between 680 to 1370 perch individuals per hectare larger than 90 mm total length. Taking away individuals below this length category from the 2008 study figure (1377 ± 373 S.E. , 95 % c.l.) gives a population size within their reported range. In fact, fluctuations of population size are typical of perch in humic forest lakes in Scandinavian (Lappalainen 1988). In terms of biomass, perch in Valkea-Kotinen have demonstrated significantly higher biomass compared to those earlier reported by Rask *et al.* (1998b) (Table 2). The estimated biomass of perch in this study was 55 kg ha⁻¹ which is probably due to higher average fish weight approximately 40 g. The reason for the marked difference in biomass is not totally clear. Total number of 63 individuals ranging from 50–294 mm total length were analysed in this study as against between 50 and 84 individuals of > 90 mm total length analysed annually between 1991–1996 (Rask *et al.* 1998b).

Table 2. Population estimate, population density (ind. ha⁻¹) and biomass (kg ha⁻¹, wet weight) of perch of > 90 mm total length in Valkea-Kotinen during 1991–1996 (Rask *et al.* 1998b).

Year	Population estimate	95% c.l.	Population density (ind. ha ⁻¹)	Biomass (kg ha ⁻¹)
1991	3130	2 675–3 585	870	23
1992	2733	2 527–2 951	760	23
1993	4930	4 352–5 686	1370	37
1994	4500	3 960–5 210	1250	36
1995	3194	2 744–3 821	890	30
1996	2455	2 162–2 814	680	31

Perch in Valkea-Kotinen indicated an allometric growth relationship between opercular bone and total length that is similar to those earlier analysed in Lake Windmere (Le Cren (1958) and in Lievestuoreejärvi (Kokko 1980). The perch grow slowly with a growth pattern closely similar to the pattern earlier reported for perch in this lake (Rask *et al.* 1998b). They had taken 11–12 years to reach a total length of 200 mm. On average, the size distribution and growth of perch in the lake seems to largely correspond to previously studied perch populations in nearby lakes such as Alinen Mustajärvi and Horkkajärvi (Rask & Arvola 1985). In those two lakes, perch never grew to 150 mm, whereas in Valkea-Kotinen, perch grew to 240 mm (Fig. 5). Similarly, in Fushskuhle, a German acid lake, younger perch grew well while the growth of the older perch was poor (Ronnerberger & Anwand 2000).

Overall, the growth of perch in Valkea-Kotinen was similar and comparable to growth of perch in other humic lakes in southern Finland. On the contrary, faster growth has been recorded for perch in lakes with relatively different conditions. For example, perch in Lake Mumajärvi, Majaslampi and Orajärvi exhibited a better growth comparable to those in Baltic Coastal waters or large lakes (Rask & Raitaniemi 1988). This is probably due to lower population density and better food supply for individual fish as a result of thinning of the perch population due to acid induced reproduction failures (Rask & Raitaniemi 1988).

4.2. Ontogenetic diet shift

Perch in Valkea-Kotinen did not show any clear evidence of ontogenetic diet shift. In summer, <100 mm perch were mostly feeding on zooplankton and the significance of which declined with fish size (Fig. 6). This means that they do undergo some kind of ontogenetic dietary shift (although this was not evident in the stable isotope signatures). Similarly, stable isotope signatures of >150 mm perch showed that they were feeding at a higher trophic level relative to <100 mm and 100–149 mm perch. Fish larvae were not found in the gut of any fish. A frog found in the gut of an individual in this size class

confirmed that they generally had capacity to forage on large prey items, potentially also small fish. Digestion time depends on hardness or size of the prey (Persson 1981). Probably, some individuals in >150 mm perch opportunistically foraged on fish larvae in summer. Moreover, lake water is usually relatively warm in summer and thus the metabolic rate of fish is higher causing rapid digestion of fish larvae in the perch stomach. Overall, the main results from the gut content and stable isotope analysis were similar since they both suggest that perch at all size categories were mostly feeding on macroinvertebrates. Similarly, the result from gut content analysis and from the Iso-source mixing model confirmed significant contribution of zooplankton to diet of smaller perch in summer.

However, perch in some nearby lakes, Horkkajärvi and Alinen Mustajärvi (Rask & Arvola 1985), showed similar feeding behaviour to perch in Valkea-Kotinen. For example, perch of 85–120 mm total length in Alinen Mustajärvi mostly foraged on benthic food items whereas zooplankton formed > 50 % diet of <120 mm perch in Horkkajärvi and there was no evidence of piscivory. This is probably due to lack appropriate prey and high fish population densities in the lakes. On the contrary, perch from other humic lakes within Evo region showed different feeding behaviour. For instance, perch in lakes Haarajärvi and Horkajärvi were planktivorous at <120 mm and <160 mm respectively while the benthic invertebrate phase was short at the size of 140 mm and 160 mm respectively and > 50 % were already piscivorous. Whereas in Majajärvi and Haukijärvi, perch shifted to benthic invertebrates at larger size and did not clearly shift to piscivory (Eslander *et al.* 2010). The difference is probably due to availability of prey. Availability of appropriate prey appears to play a major role in perch feeding habits. For example, in Fushskuhle, a German acidic lake, perch from age 1+ to 3+ were mostly feeding on benthic macroinvertebrate while the older perch could not change from benthic feeding to piscivory as they normally do at certain size because the lake lacked small prey fish species (Ronnerberg & Anwand 2000).

4.3. Seasonal diet shift

It appears perch in Valkea-Kotinen undergo some temporary seasonal diet variations probably due to increased pelagic food production in summer and simultaneous decrease in density of benthic macroinvertebrates (particularly mayfly nymphs) which may have mostly emerged towards the end of spring through summer. Hence, zooplanktons are probably most abundant and possibly contribute to perch diets in higher magnitudes than in other seasons. Both results from gut content and stable isotope analyses suggest a shift towards a more diverse diet of perch from spring to summer and autumn. This is probably due to limited availability of prey variety at the beginning of the season and high productivity of the lake in summer. In the spring, both gut content and stable isotope analyses showed that perch at all size classes were mostly feeding on the same food source, evidently mayfly nymphs. In summer and autumn, perch showed a wider prey spectrum. For example, <100 mm perch fed on zooplankton whereas dragonfly nymphs was the dominant prey item for 100–149 mm perch. A similar trend was observed in the diet of >150 mm perch but mayfly nymphs were still the dominant prey. In autumn, perch were still foraging on diverse preys but with a narrower spectrum than in summer. Throughout

the ice-free period, there were dynamic variations in the mean $\delta^{13}\text{C}$ values of all perch size classes. This confirmed the diverse prey items observed from the gut contents. Individual dietary variation within a fish population can be detected as the degree of variation in consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Syväranta & Jones 2008). Here, the variation in $\delta^{13}\text{C}$ of all perch size classes was wider in summer than in spring or autumn. This suggests that perch individuals were feeding on different kinds of food sources.

However, it is also possible that <100 mm perch were mostly feeding on zooplankton probably due to strong intraspecific food competition for larger preys at this period. Rapid growth observed in perch age 0+ to 2 (Fig.5) is probably a reflection of available food. Growth above this stage is recruitment to benthivorous phase. Recruitment into this phase appears to be rapid, hence explaining the dominance of individuals in this length category (> 100 mm) (Fig.3). This probably further leads to increased competition for benthic macroinvertebrates and the declined growth rate. Benthivorous stage of perch is often the bottleneck for the recruitment to the piscivorous stage due to intraspecific competition for benthic resources (Persson & Greenberg 1990). Seasonal diet shift resulting from simultaneous reduction of benthic macroinvertebrate and increased pelagic production and intraspecific food competition could have possibly contributed to the existing perch population size structure.

Intra-specific food competition for larger prey items may be stronger in summer than spring and autumn in Valkea-Kotinen due to two possible reasons: (1) usual oxygen and temperature stratification and (2) limited availability of certain macroinvertebrates like mayfly nymphs which mostly emerge towards the end of spring through summer. In shallow highly productive lakes, low oxygen concentration during winter and summer stratification may be detrimental to many fish ((Rask *et al.* 1998b). Oxygen stratification tends to restrict the fish foraging area towards littoral zone which is narrow in Valkea-Kotinen reaching to around 1.5 m depth. In Valkea-Kotinen, the spring turnover is usually short or incomplete and the anoxic conditions in the hypolimnion usually prevail from June until autumn turnover in October (Kankaala *et al.* 2006). This probably increases the density of perch along the limited littoral zone and makes competition for larger prey to be more difficult for smaller perch. This may also force them to forage on smaller or less consumed preys irrespective of their nutritional qualities. Availability of dragonfly nymphs at this period is probably due their tolerance for low oxygen level. Throughout the ice-free period >150 mm perch were almost exclusively feeding on mayfly nymphs more than <100 mm and 100 –149 mm except temporal diet shift to pelagic food source in summer. Perch in this lake may be following this dietary cycle on annual basis if there is no major change in the community composition of benthic macroinvertebrates, perch population density and size structure which may potentially affect the trophic niche and growth.

Perch diet varies among populations and is probably largely dependent on the availability of different prey items (Elrod *et al.* 1981). Perch in Valkea-Kotinen exhibited a similar seasonally varying dietary pattern in previous studies. In 1991, there was a change in zooplankton and zoobenthos community composition in the lake which was also reflected in the diet of perch throughout the season (Rask *et al.* 1998b). The diet of <150 mm perch was dominated by mayfly nymphs in May by (*chaoborus* sp.) larvae in June and

July, by crustacean zooplankton in August and by amphipods in September (Rask *et al.* 1998b).

The reason for the dominance of mayfly nymphs and their seasonal variation in perch diet is not completely clear. Either mayfly nymphs are preferred by perch or they were simply the most abundant prey item in the lake. Mayfly nymphs are highly nourishing and thus a good substitute for fish protein in fish food (Tamale *et al.* 2010). This probably accounted for the marked increase in biomass of perch recorded in this study. The high level of productivity of the lake in summer may be responsible for the observed seasonal change in perch diet. There is currently no available information about the abundance of mayfly nymphs in Valkea-Kotinen. Overall, among the dominant benthic macroinvertebrates in perch diet, mayfly nymphs were the most dominant followed by dragonfly nymphs which contributed to the diet of >100 mm perch. They are perennial and thus are assumed to be available for perch through the growing season but still made no contribution to diet in spring and autumn. Dragonfly nymphs prefer habitats with macrophytes and more abundant in less humic lakes than in darker lakes (Eslander *et al.* 2010). They were probably most abundant and available for perch at the period of summer stratification compared to other invertebrates that cannot readily tolerate low oxygen level.

4.4. Correspondence of gut content and stable isotope analyses

The results of gut contents and stable isotope analyses were similar and complementary. The methods confirmed that the major food source of perch in Valkea-Kotinen was benthic macroinvertebrates, whereas terrestrial insects contributed to the summer-time diet of <100 mm perch. Stable isotope analysis was particularly helpful, especially in providing information about the diet of perch with empty guts. Iso-error estimated larger dietary contribution of zooplankton than the gut content. Gut content analysis reveals only the recent prey items ingested, while the stable isotopes in muscle reflect the long-term assimilated food of perch. The shift to zooplankton was probably temporal and fish muscle has relatively slow isotopic turnover rate and thus low temporal resolution for dietary changes (Persson & Hansson 1999, Eloranta *et al.* 2010). Fish liver tissue could be used for future study, due to its higher resolution compared to muscle and may provide a better match with the results of stomach content and Iso-error. Future study should include sampling of zooplankton and other possible prey items for stable isotope analysis to obtain a more comprehensive view of the foodweb structure in Valkea-Kotinen. In addition, a larger number of fish samples might provide more reliable general conclusions, if a relatively small subsample of the total population as had to be used in this study, is not adequately representative.

5. CONCLUSIONS

Lake Valkea-Kotinen is dominated by slow growing benthivorous perch. The growth of perch reported in this study is similar to those in other small humic lakes in Evo region. Mayfly nymphs were the major diet of perch with zooplankton only contributing to the diet of <100 mm perch in summer. Terrestrial insects and fish prey were almost completely

missing from the perch diet. Lack of appropriate food and also a lack of piscivorous perch or other species, which could control the population density, probably accounts for the poor growth and for the population structure of perch in Valkea-Kotinen.

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REFERENCES

- Bagenal T.B. & Tesch F.W. 1978. Age and growth. In: Bagnold T. (ed.), *Methods for assessment of fish production in fresh waters* IBB Handbook 3, Blackwell Scientific Publications, Oxford, pp. 101-136.
- Beaudoin C. P., Tonn W.M., Prepas E.E. & Wassenaar L.I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox Lucius*): an isotope and dietary analysis. *Oecologia* 120:386-396
- Bergström I. Mäkelä k. & Starr M. (Eds). 1995. *Integrated Monitoring Programme in Finland*. Ministry of the Environment. Environment policy department. Report 1, 138 pp.
- Eloranta P. (Ed) 2004. *Inland and Coastal Waters of Finland*. Helsinki: University of Helsinki.
- Eloranta A.P., Kahilainen K.K. & Jones R.I. 2010. Seasonal and ontogenetic shifts in the diet of Arctic charr *Salvelinus alpinus* in a subarctic lake. *Journal of Fish Biology* 77: 80-97.
- Elrod J. H., Busch W.-D.N., Griswold B.L., Schneider C.P. & Wolfert D.R. 1981. Food of white perch, rock bass and yellow perch in eastern Lake Ontario. N.Y. *Fish Game J.* 28: 192-201.
- Estlander S., Nurminen L., Olin O, Vinni M., Immonen S. Rask M., Ruuhijarvi, J., Horpila J. And & Lehtonen H. 2010. Diets shift and food selection of perch *Perca fluviatilis* and roach *Rutilus rutilus* in humic lakes of varying water colour. *Journal of Fish Biology* 77: 241-256.
- Fry, B. 2006. *Stable Isotope Ecology*. Springer, New York, 308 pp.
- Gregory S.V., Lamberti G.A., Erman D.C., Koski K.V., Murphy M.L. & Sedell J.R. 1987. Influence of forest practices on aquatic production. In: Salo E.O. & Cundy T.W. (eds.) *Stream side management: Forestry and fishery interactions*, University of Washington, Institute Forest Resources, pp. 233-255.
- Hynes, H.B.N. (1950). The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* 19: 37-58.

- Järvinen M., Rask M., Ruuhijarvi J. & Arvola L. 2002. Temporal coherence in water temperature and chemistry under the ice of boreal lakes (Finland). *Water Research* 36: 3949-3956.
- Jellyman D.J. 1980. Age, growth and reproduction of perch *Perca fluviatilis* L. in Lake Pounui. *N.Z. Journal of Marine and fresh water Research* 14: 391-400.
- Jones R. I., Grey J. Sleep D., Arvola L. 1999 Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos* 86:97-104.
- Kankaala, P.2006. Methanotrophic activity in relation to methane efflux and total heterotrophic bacterial production in a stratified, humic boreal lake. *Limnol. Oceanogr.* 51: 1195-1204.
- Keskitalo J. & Eloranta P. (Eds). 1999. *Limnology of Humic waters*. Leiden: Backhys publishers.
- Kokko, H. 1980. Taanehtivat Kasvunmäärittämenetelmät kaloilla (Back-calculating methods of growth of fish. In Finish). –Hydrobiologian Lisensiaattiseminaariesitelmä, tiivistelmä. Jyväskylän yliopisto, 4 pp.
- Krebs C.J. 1989. *Ecological Methodology*. Harper & Row, New York, 12 + 654 pp.
- Kurkilahti M., Appelberg M., Bergstrand E. & Enderlein O. 1998. An indirect estimate of biomodal gillnets selectivity of smelt. *Journal of Fish Biology* 52: 243-254.
- Lappalainen A., Rask M. & Vuorinen P. 1988. Acidification affects the perch, *Perca fluviatilis* L., populations in small lakes of southern Finland. *Envi. Bio. Fish* 21: 231-239.
- Le Cren E.D. 1947. The determination of the age and growth of perch (*Perca fluviatilis* L.) from the opercula bone. -*J. Animal Ecol.* 16:188-204.
- Le Cren E.D. 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. *J. Anim. Ecol.* 27: 287-334.
- Monastyrsky G. N., 1926. *K metodike opredeleniya rosta ryb po izmerenijam cheshui.* (Methods of determining fish growth from scale measurements) In *Sbornik statej po metodike opredelenija vozrasta i rosta ryb*, Krasnojarsk.
- Monastyrsky G. N. 1930. *O Metodakh opredeleniya lineigono rosta po cheshue ryb po* (Methods of determining the growth of fish in length by their scales). *Trudy nauch. Ryb Khozy* 5:5-44.
- Olin M., Vinni M. Lehtone H., Rask M., Ruuhijarvi J. Saulamo K & Ala-Opass P.2010. Environmental factors regulate the effects of roach *Rutilus rutilus* and pike *Esox lucius* on perch *Perca fluviatilis* population in small boreal forest lakes. *Journal of Fish Biology* 76: 1277-1293.
- Persson A. & Hansson L.-A. 1999. Diet shift in fish following competitive release. *Can. J. Aquat. Sci.* 56: 70-78.
- Persson L. 1981. The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. *Fresh water Biology* 11:131-138.
- Persson L. & Greenberg L. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. *Ecology* 71: 44-56.
- Persson L. & Eklöv P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76: 70-81.
- Persson L., Byström P. & Wahlsteröm E. 2000. Cannibalism and competition in Eurasian Perch: population dynamics of an ontogenetic omnivore. *Ecology* 81:1058–1071.
- Peterson B.J. & Fry B.1987. Stable isotopes in ecosystem studies. *Annual Review in Ecology and systematic* 18: 239-320.
- Phillips D.I. Gregg J.W. 2003 Source partitioning using stable isotopes: Coping with too many sources. *Oecologia* 136: 261-269.

- Raitaniemi J., Rask M. & Vourinen P.J. 1988. The growth of perch, *Perca fluviatilis* L., in small Finnish lakes at different stages of acidification. *Ann. Zool. Fennici* 25: 209-219.
- Rask M. 1983. Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. - *Hydrobiologia* 101: 139-144.
- Rask M. 1984: The effects of low pH on *Perca fluviatilis* L. III. The perch population in a small, acidic extremely humic forest lake. *Ann. Zool. Fennici* 21: 15-22.
- Rask M., & Arvola L. 1985. The biomass and production of pike, perch and white fish, in two small lakes in Southern Finland. *Ann. zool. Fennici* 22:129-136.
- Rask M. & Hiisivuori C. 1985 the predation of *Asellus aquaticus* (L.) by perch, *Perca fluviatilis* (L.) in a small forest lake. *Hydrobiologia* 121: 27-33.
- Rask M. & Raitaniemi J. 1988. The growth of perch *Perca fluviatilis*, in recently acidified lakes of southern Finland-a comparison with unaffected waters.-Arch. *Hydrobiol.*1123: 387- 397.
- Rask M., Arvola L. Salonen k. & Ruuhijarvi J.1992. Limnological studies on the lakes in Evo forest area- a historical perspective. *Aqua Fennica*. 22:185-192.
- Rask M., Nyberg K. Markkanen S.-L. & Ojala A. 1998a. Forestry in catchments: Effects on water quality, plankton, zoobenthos and fish in small lakes. *Boreal Env. Res.*3: 75–86.
- Rask M., Holopainen A.-L., Karusalmi A., Niinioja R., Tammi J., Arvola J., Keskitalo J. Blomqvist I., Heinimaa S., Karppinen, C., Salonen K. & Sarvala J. 1998b. An introduction to the limnology of Finnish integrated monitoring lakes. *Boreal Env. Res.* 3: 263-274.
- Ronneberger D. & Anwand K. 2000. Food preference of perch (*Perca fluviatilis*) stocked previously fishless, Acid Bog Lake and development of the fish population in absence of piscivory. *Internat. Rev. hydrobiol.* 85: 423-431.
- Salonen k., Arvola L. & Rosenberg M. 1993. Diel vertical migration in a small steeply stratified humic lake with low nutrient concentration. *Verh. In verh. Internationat. Verein. Limnol.* 25: 539-543.
- Schnabel, Z.E. 1938. The estimation of the total fish population of a lake. *American Mathematician Monthly*: 45:348-352.
- Schumacher, F.X. & R.W. Eschmeyer. 1943. The estimation of fish populations in lakes and ponds. *Journal of the Tennessee Academy of Sciences*: 18:228-249.
- Svanbäck R. & Eklöv P. 2002. Effects of habitats and resources on morphology and ontogenetic growth trajectories in perch. *Oecologia* 131: 61-70.
- Syväranta J. & Jones, R.I. 2008. Changes in feeding niche widths of perch and roach following biomanipulation, revealed by stable isotope analysis. *Fresh water Biology* 53: 425-434.
- Tamale A., Mayendende T.S., Mwangi K. G., Ayieko M., Ndonga M.F.O. & Otude T. 2010. Use of mayflies (Ephemeroptera) as total replacement of *Rastrineobola argentea* in diets of catfish (*Clarias gariepinus*) in Lake Victoria Basin. *African Journal of Animal and Biomedical Sciences* 5: 1819-4214.
- Urbatzka R., Beeck, P., van der Velde G. & Borcharding J. 2008. Alternative use of food resources causes intra-cohort variation in the size distribution of young-of-the year perch (*Perca fluviatilis*).*Ecology of fresh water Fish* 17:475-480.
- Vander Zanden M.J.& Rasmussen J.B. 2001. Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic fractionation: implications for aquatic food web studies. *Limnological and oceanography* 46:2061-2066.
- Wang N. & Eckman, R. 1994. Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. *Hydrobiologia* 277: 135-143.