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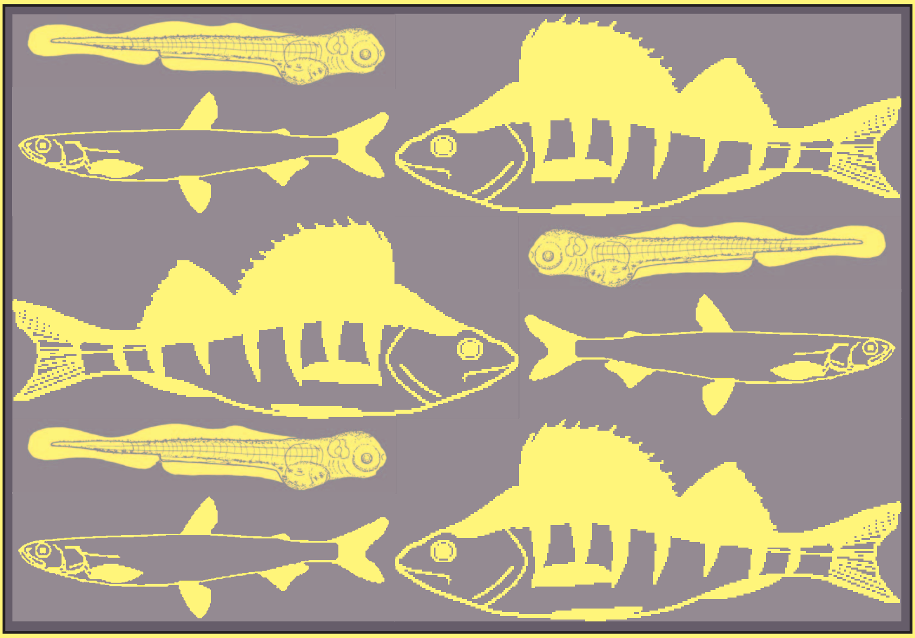
Effects of predation and fish stock management on the abundance of larval vendace: experimental and field evidence in a large oligotrophic lake

by
Helena Haakana



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Effects of predation and fish stock management on the abundance of larval vendace: experimental and field evidence in a large oligotrophic lake

ACADEMIC DISSERTATION

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Keywords: *Coregonus albula*, diet, intensive fishing, *Osmerus eperlanus*, *Perca fluviatilis*, piscivory, population dynamics, predation, predator-prey relationship.

Lake Höytiäinen in eastern Finland has suffered from several prolonged vendace (*Coregonus albula* (L.)) recessions during last few decades. In 2000 the low spawning stock was strengthened by stock transfer from Lake Suvasvesi. The success of the transfer was studied by determining the genetic origin of the larvae after the transferred vendace had reproduced. Of the vendace larvae, 69% were assigned to the indigenous Lake Höytiäinen population and 11% to the Lake Suvasvesi population, and thus stock transfer seemed to have some effect on the population structure of vendace. However, the contribution of the stocked fish to the 2001 year class was lower than expected, most likely due to high mortality associated with the transfer.

Predation on vendace larvae can prevent the recovery of vendace stock from a state of low density. It has been suggested that especially perch (*Perca fluviatilis* L.) may be a significant predator of larval vendace. In the 1990s the density of the perch population in Lake Höytiäinen increased, and the population was intensively fished in 2001-2004 to reduce the predation pressure on vendace larvae. According to the results of test fishing with multi-mesh gillnets and the Leslie depletion method, the population size clearly diminished and the mean weight of perch increased during the intensive fishing period.

The diet of perch and smelt (*Osmerus eperlanus* (L.)) was studied to reveal their possible predation on vendace larvae. No predation on vendace larvae by smelt was found, but perch fed on vendace larvae at the sampling site, where the densities of larvae were high. Overall, mean vendace larvae abundance was low in all studied years, and possibly under the threshold limit where the prey item is included in the diet. Bioenergetics modelling estimated that the perch population consumed 18% of the vendace larvae in Lake Höytiäinen in 2001. However, the present data do not enable conclusions about the effect of perch predation on larval vendace abundance. The estimated total number of smelt in Lake Höytiäinen was 12-22% of the total number of vendace larvae. Hence, the smelt population has potential to affect the recruitment of vendace in Lake Höytiäinen.

Since the spawning time of perch and smelt and the larval period of vendace overlap, feeding activity differences between spawning and non-spawning individuals were studied. The feeding activity of both sexes of smelt decreased during spawning time, whereas in perch only females were found to reduce their feeding activity during spawning time. Because only a small proportion of the female perch are spawning at a time and some of the females have omitted spawning completely, the spawning period of perch can represent only a minor refuge for the vendace larvae. The spawning time of smelt may provide a temporary refuge against predation, but its duration depends strongly on the warming of the water in spring.

The effects of predation on larval fish populations may be underestimated due to the rapid rate at which the larvae are digested. According to the aquarium tests coregonid larvae were still identifiable and countable after 2 hours' digestion, suggesting that a two-hour sampling interval is suitable for studying predation on larval coregonids.

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Contents

List of original publications

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Huuskonen, H., Haakana, H. & Aho, T. 2004: Stock transfer in vendace: an evaluation using microsatellite markers. Annales Zoologi Fennici 41: 69-74.

II Haakana, H., Huuskonen, H. & Karjalainen, J. 2007: Predation of perch on vendace larvae: diet composition in an oligotrophic lake and digestion time of the larvae. Journal of Fish Biology 70: 1171-1184.

III Haakana, H. & Huuskonen, H. 2008: Predation of smelt on vendace larvae: experimental and field studies. Ecology of Freshwater Fish (in press).

IV Haakana, H. & Huuskonen, H. 2008: Effects of intensive fishing on the perch population in a large oligotrophic lake in eastern Finland. Fisheries Research 91: 144-150.

The publications are reprinted with permission from the publishers. Some unpublished results are also presented.

Author's contribution:

I. The author participated in writing the article.

II.-IV. The idea and design of the study was joint. The author had the main responsibility for the sampling, the data analyses and for writing the article.

1. Introduction

Large variation in year-class strength is typical for vendace (*Coregonus albula* (L.)) stocks. The variation can be cyclic fluctuation caused by density-dependent processes or more irregular, density-independent, alternation of strong and weak year-classes (e.g. Viljanen 1986, Salojärvi 1987, Helminen & Sarvala 1994, Marjomäki 2003). During the last few decades, prolonged recessions in the vendace stocks have been reported in several Finnish lakes (Valkeajärvi & Bagge 1995, Karjalainen et al. 2000, Heikinheimo 2001). One of these lakes is Lake Höytiäinen which has suffered from several recessions in the last few decades. The most recent of them has extended to 20 years; the latest strong year class hatched in 1988 (Korhonen & Turunen 1995).

Predation, too small spawning stock and/or environmental conditions have been suggested as factors preventing the recovery of vendace stock from a prolonged state of low density (Auvinen 1994, Helminen et al. 1997, Heikinheimo 2001, Marjomäki 2003). The relationship between the abundance of larval vendace and subsequent year-class strength is strong, implying the importance of the larval stage to vendace stock dynamics (Viljanen 1988). According to Karjalainen et al. (2000), the average larval mortality of vendace during the first 3 weeks was 65% in Finnish lakes. The spawning stock of vendace can theoretically be strengthened by stock transfer, but the success of transfers is difficult to assess reliably (Lahti 1987, Jurvelius et al. 1995). In Lake Höytiäinen, the low spawning stock was strengthened between 1978 and 1980, and again in 2000. A few years after the earlier transfer, the vendace stock recovered, but whether this was due to the transferred fish is not known (Korhonen & Turunen 1995).

Several fish species have been found to feed on vendace larvae and juveniles (Huusko & Sutela 1992, Huusko & Sutela 1997, Vehanen et al. 1998), but it has been suggested that perch (*Perca fluviatilis* L.) is the most important predator of vendace in many Finnish lakes (Helminen & Sarvala 1994, Heikinheimo 2001, Valkeajärvi & Marjomäki 2004). Smelt (*Osmerus eperlanus* (L.)) has been observed to prey on vendace larvae in Lake Säämäjärvi, Russia (Sterligova 1979). Also rainbow smelt *Osmerus mordax* (Mitchill), a close North American relative, has been found to cause recruitment failure by predation on the larvae of *Coregonus* sp. (Loftus & Hulsman 1986, Hrabik et al. 1998) and other species (Mercado-Silva et al. 2007) in several lakes in North America.

In addition to stock transfers, fish stock management can affect the recovery of the vendace stock by reducing stocking of predator species and decreasing the population densities of predators by fishing. In Lake Höytiäinen the stocking of salmonids was restricted for several years. The density of the perch population in the lake increased during the 1990s (Korhonen & Turunen 1995). To reduce the density of the perch population and hence the predation pressure on vendace larvae, intensive fishing of perch was started in Lake Höytiäinen in 2001.

The aim of the present study was to assess the success of stock transfer by determining the genetic origin of the hatched year class after the transferred vendace had reproduced in Lake Höytiäinen (I). Furthermore, the objective was to collect diet samples of perch and smelt to reveal their possible predation on vendace larvae (II, III). Newly hatched vendace larvae were sampled every spring during the study period in order to obtain abundance estimates of the larvae and effect of management practices on vendace abundance. Since the spawning time of perch and smelt and the early larval period of vendace overlap, the aim was to study whether feeding activity differs in spawning and non-spawning individuals (II, III). Experimental studies were conducted to study the digestion time of larvae in the alimentary tract of perch, and hence validate the sampling interval used in field sampling (II). Also, the capacity of smelt to prey on vendace larvae of different sizes and at different densities was assessed by experimental studies (III). Finally, the effects of intensive fishing of perch on the size and structure of the perch population in Lake Höytiäinen was studied (IV).

2. Study area, materials and methods

2.1 Study area

Lake Höytiäinen is an oligotrophic lake situated in eastern Finland. Its total area is 293 km^2, mean depth 11.8 m and maximum depth 56 m. Mean total phosphorus content is 7 µgl^{-1} and colour value 26 mg Ptl^{-1} (Niinioja et al. 2005). The study area (154 km^2) in the southern part of the lake was divided into four sub-areas (Fig. 1). The deepest area is found in the southern part of the lake, where the slope of the littoral zone is steep. Water transparency is higher and total phosphorus content is lower in the southern part than in the northern part of the study area.

Vendace has traditionally been the most important target of fishing in Lake Höytiäinen (Lappalainen 1998). During the vendace stock recessions, perch, bream (*Abramis brama* (L.)), pike (*Esox lucius* L.), and recently especially pikeperch (*Sander lucioperca* (L.)) have become more important.

Fig 1. Lake Höytiäinen. Study area with sub-areas 1-4 and sampling areas A and B are indicated.

2.2 Sampling of larval vendace

The abundance of newly hatched vendace larvae was estimated using a stratified random sampling design. The study area (Fig. 1) was divided into 2 x 2 km squares,

Table I. Summary of the materials, study years, sampling areas (Fig. 1) and original publications.

Materials	Year(s)	Area	Article
Sampling of larval vendace	1999-2008	1-4	I, II, III
Stock transfer of vendace	2000	1-4	I
Genetic analysis of vendace larvae	2001	1-4	I
Intensive fishing	2001-2004	2	IV
Population samples of perch	2001-2004	2	IV
Population samples of smelt	2003, 2005	1-4	III
Gillnet test fishing	2001-2004, 2006	1-4	IV
Diet samples, perch	2001-2002	A, B	II
Diet samples, smelt	2003, 2005	1-4	III

from which sampling areas were randomly selected. The sampling procedure and equipment are described in detail by Karjalainen et al. (1998). The sampling was conducted one week after ice break in 1999 and twice each spring in 2000-2008: one week and three weeks after ice break. Each sampling occasion consisted of 20 littoral and 20 pelagic sampling squares. Samples were collected from five depth zones (0-0.5 m, 0.5-1 m, 1-2 m, 2-4 m and >4 m; two samples from each zone). In the shallowest zone samples were gathered with a tube net pushed by a wader parallel to shore. In the other zones samples were collected with two Bongo nets pushed at the front of the vessel 0-0.6 m below the water surface. In all zones, the volume of each sample was measured with a flowmeter and catches were converted to sample abundances. In the original publications, the total number of larvae was calculated according Karjalainen et al. (1998) and expressed as individuals per hectare (I) or as individuals per m^3 (II) or per 100 m^3 (III). New calculation method by Urpanen et al. (2008) for the abundance estimates for coregonid larvae was used in this thesis. This method produced annual larval abundance estimates which were on average 42% of the estimates produced by the method of Karjalainen et al. (1998), because the vertical distribution of larvae was taken more precisely into account. The new calculation method affects only area-specific estimates (individuals per hectare), not volume-specific values (individuals per m^3 or per 100 m^3).

2.3 Genetic analysis of vendace stocks

A genetic analysis was made to assess the success of stock transfer of vendace to Lake Höytiäinen. Genetic differences between original and stocked (Lake Suvasvesi) vendace were analysed using microsatellite DNA markers (details in I). Newly hatched larvae were collected in 2001 after the first reproduction of the transferred fish in Lake Höytiäinen. Microsatellite DNA variation of the larvae was assessed, and the genotypes were compared with the genotypes of the two original populations and known hybrids of these two populations.

2.4 Intensive fishing of perch

Intensive fishing targeted at perch was conducted by professional fishermen with a paired bottom trawl, seine net, hoop net and small fish traps (IV). Fishing was restricted to sub-area 2 (3850 ha, Fig. 1), starting in 2001 and finishing in 2004. To encourage recreational fishermen to catch perch, 160 fish traps were given to local fishermen in spring 2002 (Salonen et al. 2004). The catch statistics of intensive fishing were obtained from the bookkeeping of the professional fishermen and from recreational fishermen who fished with fish traps.

The Leslie catch-depletion method (Leslie & Davis 1939), modified by Braaten (1969) was used to estimate the size of the perch population at the end of October 2001 - 2003 in Lake Höytiäinen. The estimation is based on the regression between the yield per unit effort of trawling (kg perch min^{-1}) and the cumulative yield. The intercept with the abscissa gives an estimate of the initial population size, and the absolute of the slope of regression is the catchability (q), i.e. the fraction of the perch population caught by a unit of trawling time.

2.5 Population samples of perch and smelt

The average weight, length distribution and growth of perch were annually estimated by samples taken randomly from trawl catches from sub-area 2 in October, when 0+ perch had been recruited to the fishery (IV).

The population samples of smelt were collected in 2003 and 2005 in Lake Höytiäinen at the same time as the smelt diet samples. Samples were taken randomly from the total catch (III).

2.6 Gillnet test fishing

Relative abundance and population structure of perch and pikeperch were studied by test fishing with multi-mesh gillnets. The fishing was carried out using a stratified random sampling design. The study area was divided into four sub-areas (Fig. 1), each of which was sampled monthly from June to September in all sub-areas in 2001 - 2004 (IV) and in sub-areas 1 and 2 in 2006. The average yield per unit effort (YPUE, kg net^{-1} $night^{-1}$) and catch per unit effort (CPUE, number net^{-1} $night^{-1}$) of both species (mean ±95% C.I., calculated after log-transformation according to Krebs 1989) were calculated by weighting with the area of the depth strata. In addition, the gillnet-specific mean weight of perch in the catch of different sub-areas was calculated annually.

2.7 Diet samples

Perch

The diet sampling was conducted in 2001 in both sampling areas A and B, and in 2002 only in sampling area A (Fig. 1) (II). The perch were caught in 2001 using gillnets and in 2002 using fish traps. The sampling was carried out during one 24-hour fishing period weekly in May and June and the gears were examined every two hours. The stomach fullness was estimated on a scale of 0-5. The ingested zooplankton, invertebrates and fish were identified, counted and measured. The reconstructed carbon biomass of the ingested food items was calculated and used in the analysis (details and references in II). Food items were separated into four categories: zooplankton, benthic invertebrates, fish and others. Differences in feeding activity between spawning and non-spawning perch were examined using stomach fullness as a proxy for feeding activity. The sampled perch were divided into five size classes: <100 mm (total length), 100-130 mm, 131-160 mm, 161-190 mm, >190 mm. The stomach fullness dataset contained 690 perch in 2001 and 601 perch in 2002. The stomach contents of 508 perch in 2001 and 515 in 2002 were analysed.

Bioenergetics modelling by computer software Bioenergetics 3.0 was used to quantify the food consumption of perch and especially its predation pressure on vendace larvae. Parameter values for computations and references are given in II. The diet of perch used in computations was based on samples from sampling site B in 2001, where perch had fed on vendace larvae. The estimate of larval density for the computation (year 2001) was calculated according to Urpanen et al. (2008).

Smelt

The diet samples of smelt were collected in 2003 and 2005 in Lake Höytiäinen. During the sampling period in 2003, part of the smelt population was at spawning grounds and part in the pelagic area, whereas in 2005 the smelt spawned after the sampling period as a result of a colder spring. The sampling was carried out at nightfall. At the spawning ground smelt were caught with a beach seine, whereas in the pelagic area smelt were caught by pair trawling, which lasted for one hour and was hauled at 0-8 m from the surface. Samples were taken randomly from the total catch and the dissected stomachs preserved in 70% ethanol. For the diet analysis each fish was measured for total length to the nearest mm, and sexual maturity was assessed according to Nikolsky (1963). The maturity stage I was assessed as immature, III-IV as reproducing and VI and II as spent. Stomach fullness was estimated on a scale of 0-5. Stomach fullness was used as a proxy for feeding activity. Stomach contents were divided into three categories: zooplankton, other invertebrates and fish, and the volumetric proportions of each category were estimated. In total, the stomach contents of 1113 smelt in 2003 and 1247 in 2005 were determined.

2.8 Aquarium experiments

Digestion rate of perch

Aquarium experiments were carried out to determine the time when it is possible to count and identify larval coregonids in the stomach of perch (II). Perch were starved in trial aquaria (40 l) for 20 hours before the experiments to empty the stomachs. Two water temperatures (8 ºC and 12 ºC) were used in the experiments. Perch were fed either vendace (total length 10 mm) or whitefish (13 mm) larvae. Prey availability was adjusted to allow *ad libitum* (150-250 larvae per aquarium) feeding of the perch. After 15 minutes' feeding time the perch were removed from the aquaria and allowed to digest the larvae 0.5 to 6 hours. Immediately after the experiments, the degree of digestion of larvae was classified into five categories: (0) no digestion, species identification possible, (1) digestion started, length measurement possible, (2) counting of larvae possible, (3) structure of fish flesh found, counting of larvae not possible, and (4) homogeneous mass. The stomach contents of 130 perch were examined.

Feeding capacity of smelt

The capacity of smelt to prey on vendace larvae was studied by aquarium experiments (III). The feeding of the smelt was studied in 40 l aquaria. Water temperature during the experiments was 10 ºC and light intensity imitating dusk. Before the experiments the smelt were starved for 20 h and acclimated to trial aquaria for half an hour, one smelt per aquarium. After acclimation, vendace larvae were added to the aquaria. Three different densities (2, 10 or 50 larvae per aquarium) and six different size groups of vendace larvae were used in the experiments: 1 = 8.2 ±0.4 mm (mean total length ±S.D.); 2 = 13.0 ±0.9 mm; 3 = 16.7 ±0.7 mm; 4 = 18.9 ±1.0 mm; 5 = 21.4 ±2.1 mm; 6 = 25.5 ±2.2 mm. The size range of the smelt was 54 - 141 mm (total length). The smelt were divided into two size categories: ≤100 mm (mean total length ±S.D. 75.9 ±6.6 mm) and >100 mm (118.1 ±7.0 mm). The experiments were replicated 8 times with each density, larval size group and smelt size group, except with the smaller smelt and larval size groups 5 and 6, because the smelt were not able to eat these largest larvae at all. The smelt were allowed to feed for one hour. The number of ingested larvae was counted from stomach contents.

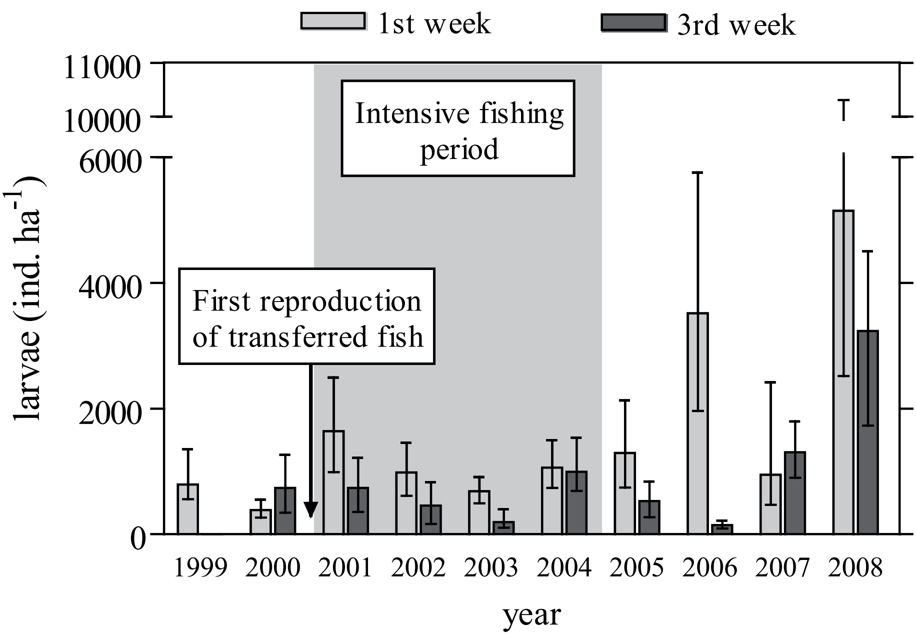

Fig. 2. Density of vendace larvae (ind. ha^{-1}, ±95% C.I.) in Lake Höytiäinen in 1999-2008. Abundances at the first and third week after hatching are given separately. In 1999 there was only one sampling occasion. The time of the first reproduction of transferred fish and the intensive fishing period is indicated.

3 Results

3.1 Abundance of vendace larvae

According to larval sampling, the abundance of vendace larvae was low (<2000 ind. ha^{-1}) in most sampling years 1999 - 2008 (Fig. 2). The abundance stayed at the low level after first reproduction of the transferred fish and during the intensive fishing period. At the end of the study period, however, higher densities were observed in 2006 and 2008. In 2006, the so far highest density of larvae decreased rapidly soon after hatching due to high mortality possibly caused by unfavourable weather conditions. Instead, in 2008 larval density remained at a higher level until the third week after ice break.

3.2 Genetic analysis of vendace

An exact differentiation test between the reference populations (Lake Höytiäinen, Lake Suvasvesi, known hybrids) showed that the populations were genetically different: four out of five loci showed significant differentiation in allele frequencies (I).

Of 88 vendace larvae sampled after the first spawning of the transferred vendace, the majority (69%) were assigned to the original Lake Höytiäinen population and 11% to the Lake Suvasvesi population. 4.5% were assigned to the reference group of known hybrids and 15% could not be assigned to any of the groups. The assignment probabilities were quite low: 10 individuals exceeded a probability level of 0.5, 34 exceeded a level of 0.1 and 13 could not be assigned to any of the groups using a probability threshold of 0.01.

3.3 Catch of the intensive fishing and population size of perch

The total yield of intensive fishing in four years (2001 - 2004) was ca. 79 500 kg, of which 84% consisted of perch (IV). Intensive fishing by professional fishermen was conducted in sub-area 2, where the total yield was 16 kg ha^{-1} and the perch yield was 12.5 kg ha^{-1}. The most effective professional fishing gear in terms of total yield was the trawl, giving 62% of total yield. The fish trap yield by local fishermen was ca. 17 600 kg, of which 94% consisted of perch. The local fishermen fished all around Lake Höytiäinen. Recreational fishermen caught 60 kg of perch per fish trap in a year (Salonen et al. 2004) and 22% of the total yield.

Autumn trawling in Lake Höytiäinen began at the end of August, when perch started to move into deeper waters for overwintering. In 2001-2003, perch yield per trawling time declined linearly with cumulative yield from the beginning of September (IV). It was assumed that the main part of the perch population had reached the overwintering area at the beginning of September, when the YPUE was highest, and that catchability was constant from September to October. In addition, it was assumed that natural mortality was negligible, growth was slow at low and decreasing water temperatures (Le Cren 1958) and migration from other areas was of minor importance (IV). This allowed the use of the Leslie method in the estimation of the perch population size in sub-area 2. In 2004, fishing was not intensive enough to allow any estimation. The estimated population sizes of perch in 2001, 2002 and 2003 were 22 600 kg (95% C.I. 19 080 kg – 31 760 kg), 13 220 kg (11 690 – 16 300) and 9 350 kg (7 189 – 25 750), respectively. The catchability

(q) in trawl fishing was 1.8% h^{-1} in 2001, 3.9% h^{-1} in 2002 and 2.5% h^{-1} in 2003. The estimated perch biomass in sub-area 2 decreased during the intensive fishing period by ca. 60%.

3.4 Population samples

Perch

The growth rate of perch was moderate (IV) compared to the growth rate of perch in other Finnish lakes (Auvinen 1987, Sarvala & Helminen 1996), where the total length of perch exceeded 100 mm after 2 years and 150 mm after 4-5 years. In Lake Höytiäinen the mean total length of a 2-year-old perch was 104 mm and of a 5-year-old perch 158 mm.

According to the samples taken from the trawl catch in sub-area 2, the average weight of perch clearly increased during the intensive fishing period (Fig. 3). In 2001 and 2002 the length frequency distributions of perch in the trawl samples were practically identical and the majority of the fish belonged to the smallest size class (IV). In 2003 and 2004 there was a shift towards larger length classes, indicating a relative increase of larger fish.

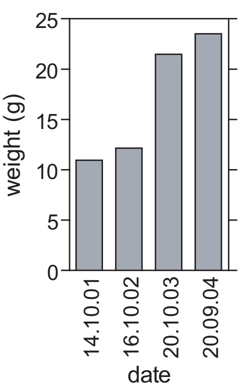

Fig. 3. The mean weight (g) of perch in samples taken from trawl catches in autumn 2001-2004.

Smelt

The size range of the smelt in population samples was 32-168 mm, and the distributions were bimodal (III). The ages of the smelt were not determined, but it is obvious that the first mode represented age 2 fish and the second mode age 3 and older fish. Age 1 fish were clearly underrepresented in the samples due to the mesh size of the trawl cod end. In Lake Höytiäinen the smelts were clearly smaller in 2005 compared to those in 2003.

3.5 Gillnet test fishing

According to gillnet test fishing, the proportion of perch in the total YPUE ranged between 44 and 79% (II). Both perch CPUE and YPUE were highest in sub-area 2 in 2001 (Figs. 4 and 5). After the fishing period in 2004, YPUE in this area was ca. 30% lower (Fig. 5) and the decrease in CPUE was even more prominent (Fig. 4). In the other areas, changes in YPUEs were smaller. The decrease in perch CPUE also continued in 2006.

The CPUE of pikeperch clearly increased in the study years (Fig. 6), especially in the northern sub-areas 1 and 2. In sub-area 1 the increase was as high as 20-fold from 2001 to 2006. Also, the YPUE of pikeperch increased in sub-area 1 (Fig. 7). In sub-area 2 YPUE increased until 2004, but in 2006 YPUE decreased reflecting smaller mean size of pikeperch.

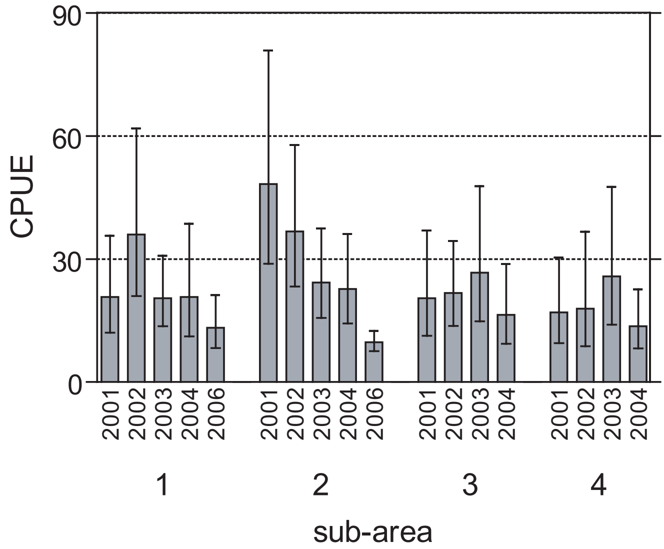

Fig. 4. Mean CPUE (ind. net^{-1}night^{-1}) (±95% C. I.) of perch in test fishing with multi-mesh gillnets in Lake Höytiäinen in 2001-2006.

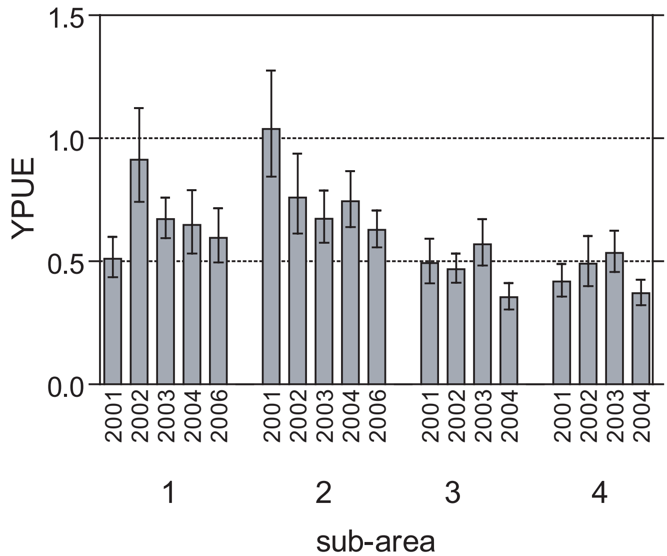

Fig. 5. Mean YPUE (kg net^{-1}night^{-1}) (±95% C. I.) of perch in test fishing with multi-mesh gillnets in Lake Höytiäinen in 2001-2006.

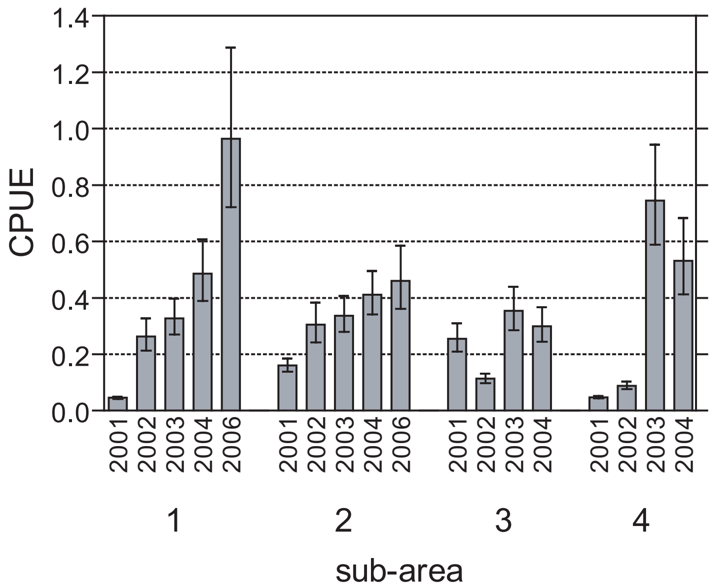

Fig. 6. Mean CPUE (ind. net^{-1}night^{-1}) (±95% C. I.) of pikeperch in test fishing with multi-mesh gillnets in Lake Höytiäinen in 2001-2006.

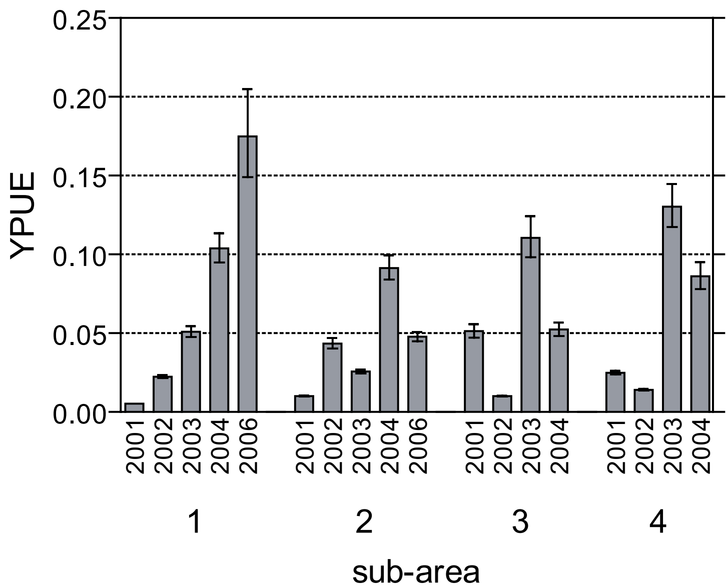

Fig. 7. Mean YPUE (kg net^{-1}night^{-1}) (±95% C. I.) of pikeperch in test fishing with multi-mesh gillnets in Lake Höytiäinen in 2001-2006.

The gillnet-specific mean weight of perch in the catch of test fishing was significantly higher in 2004 compared to 2001 in sub-area 2 (Mann-Whitney, P=0.008), whereas there were no differences in the other sub-areas (Mann-Whitney, P>0.364) (IV).

3.6 Diet

Perch

In 2001 11% and in 2002 14% of the perch stomachs sampled from Lake Höytiäinen were empty. Overall, the diet of small perch was dominated by zooplankton, shifting more towards benthic invertebrates and fish in larger perch (II). There were no clear differences in the diurnal feeding activity of perch.

At sampling site B, 23% of the perch were piscivorous, whereas at sampling site A only 8% (2001) and 11% (2002) of the perch were piscivorous. The smallest piscivorous perch was 82 mm long. Predation on vendace was found only in sampling area B. Three perch individuals had eaten 2, 18 and 40 vendace larvae.

The bioenergetics model simulation predicted that the perch population consumed ca. 4.5 million vendace larvae, which constituted 18% of the total number in the study area of Lake Höytiäinen in 2001 (about 25.2 million individuals). In article II, the percentage value was 7% due to different calculation method of larval vendace abundance used (see 2.2).

The diets of spawning (maturity stages III – VI; Nikolsky 1963) and non-spawning (maturity stages I and II) males and females were compared. In sampling area A, the proportion of spawning perch was higher in 2002 than in 2001, and it was also higher in sampling area B in 2001. Females differed significantly in stomach fullness (Mann-Whitney, n=716, P=0.004), so that food intake was reduced in spawning females. The median of stomach fullness was 2 in spawning females and 3 in non-spawning females. No significant differences were found in the stomach fullness between spawning and non-spawning males (median of stomach fullness = 2).

Smelt

In the pelagic area, 4 - 56% of smelt were immature on different sampling days, while in the spawning area in 2003 only 1% of the smelt were immature (III). In 2003, the majority of the mature males had already spawned at the first sampling day at the end of May. At the time of the last sampling most females had also spawned. In 2005, only a few smelt had spawned during the sampling period.

Feeding activity was reduced in spawning smelt, while both immature and spent fish fed actively. In spawning fish, the proportion of empty stomachs was 35% in 2003 and 18% in 2005, while in immature fish the corresponding proportions were only <1% and 3%, respectively. After spawning in 2003, smelt started to feed intensively, and only 2% of their stomachs were empty. In 2005, there were too few spent smelt to draw any conclusions.

The diet of smelt on all sampling occasions and in all areas consisted mainly of zooplankton, making up 88 - 99% of the stomach content (III). The proportion of fish in the diet was only 0-1% on different sampling days. All identified prey fish were smelts. The total length of the smallest piscivorous smelt was 113 mm.

3.7 Aquarium experiments

3.7.1 Digestion rate of perch

The digestion rate of ingested larvae was high, but coregonid larvae were still identifiable and countable after 2 hours' (sampling time in the field) digestion at both water temperatures used (II). During the experiments, perch had eaten 1 to 87 larvae. The digestion rate was dependent on the size of the larvae and on temperature. On average, smaller vendace larvae were still countable after 3.5 hours and larger whitefish larvae after 4 hours.

3.7.2 Feeding capacity of smelt

In the aquarium experiments, smelt >100 mm ate vendace larvae of all size groups, while smelt ≤100 mm could eat only size groups 1-3 (III). The larvae in size group 4 were too large for these small smelt, and hence experiments with largest size groups were not conducted at all. Smaller smelt were barely able to consume vendace larvae, since 83% of their stomachs were totally empty, and those that had eaten had only a few larvae in their stomachs. Larval density and size had no effect on the number of ingested larvae in smaller smelt. In larger smelt, both larval density and size affected the number of ingested larvae. At the lowest prey density, all size groups were eaten evenly, whereas at the medium and especially the highest density, larvae in size group 2 were preyed most.

4. Discussion

4.1 Predation on vendace larvae

The diets of both perch and smelt were studied from the field samples taken during the first weeks after ice break, i.e. soon after the hatching of vendace larvae. In Lake Höytiäinen small perch fed mainly on zooplankton, and their diet shifted more towards benthic invertebrates and fish as the perch grew larger. The present findings are in accordance with those of previous studies (e.g. Allen 1935, Rask 1986, Bergman 1991, Huusko et al. 1996). The smelt is also zooplanktivorous at younger ages and can shift to feed on larger invertebrates and fish as they grow (Nilsson 1979, Karjalainen et al. 1997, Horppila et al. 2000, Vinni et al. 2004). In Lake Höytiäinen the smelt was mainly zooplanktivorous in spring and was only occasionally found to feed on amphipods or fish.

Both smelt and perch can be piscivorous and potential predators on vendace larvae. In Lake Höytiäinen no predation on vendace larvae by smelt was found, but perch ate vendace larvae at the sampling site B (II). According to optimal diet theory, foragers obey a quantitative threshold rule that determines whether specific prey types are included or excluded in the diet (Begon et al. 1990). The mean abundance of vendace larvae was low in Lake Höytiäinen in all years when diet sampling was carried out and hence possibly under the threshold limit. However, at sampling site B, where perch predation on vendace larvae was observed, the densities of larvae were clearly higher than at sampling site A. The differences in the diet of fish can usually be explained by seasonal prey vulnerability and the availability of alternative food items (perch: e.g. Craig 1978, Rask 1986, Huusko et al. 1996, Dörner et al. 2003; smelt: e.g.

Vinni et al. 2004). In Lake Lentua, perch increased their predation rates on vendace larvae only when the relative abundance of alternative, more preferred zooplankton was low (Huusko et al. 1996). In Lake Puruvesi, perch predation on vendace was strong in pelagic area in July, but the mean size of the perch was substantially larger (170-184 mm) than in Lake Höytiäinen (Jaatinen et al. 1999). Predation on newly hatched larvae in littoral area was not found. In Lake Hiidenvesi, smelt shifted from larger invertebrates (*Chaoborus flavicans* and *Mysis relicta*) back to zooplankton in autumn, when the availability of these larger invertebrates was low (Vinni et al. 2004).

In Lake Höytiäinen the vendace larvae hatch during the ice break, usually in the middle of May. The spawning of smelt normally begins in Finnish lakes when the water temperature reaches 4-7 °C, and it lasts only few days. The spawning of perch begins when the temperature reaches 5 °C and may last up to several weeks (Karels & Oikari 2000). Because food intake is usually restricted prior to spawning (Jobling 2001), the overlapping spawning time of the above-mentioned species and the vendace larval period may serve as a refuge for the larvae. Vinni et al. (2005) found the increased frequency of empty stomachs in smelt during the spawning period in May in Lake Hiidenvesi. In Lake Höytiäinen the feeding activity of both sexes of smelt decreased during spawning time, whereas in perch only females were found to reduce their feeding activity. Reduced food intake by females has also been observed in pike, and Tammi & Kuikka (1994) suggested that the size of the developing ovaries prevents maximal filling of the stomach in spawning females. Because only a small proportion of perch females are spawning at a time, and some of the females omit annual spawning completely (Holmgren 2003), the spawning period of perch can represent only a minor refuge for the vendace larvae. The spawning time of smelt, for its part, may provide a temporary refuge against predation, but its duration depends strongly on the warming of the water in spring. The growth rate of coregonid larvae (Huuskonen & Karjalainen 1993) and the spawning time of smelt are strongly temperature-dependent (Nellbring 1989). In Lake Höytiäinen, there was a large difference in temperature development between the sampling years 2003 and 2005 (III). In the colder spring of 2005, when smelt spawning was delayed and smelt fed actively during the larval stage of vendace, the larvae were under predation risk for a clearly longer period than in 2003. The immature smelt fed actively all the time, but according to aquarium experiments (III), they are too small to eat vendace larvae.

According to Heikinheimo (2001), the role of perch as a predator of vendace is significant because perch is much more abundant than larger predators, such as brown trout (*Salmo trutta* L.). According to the results of gillnet test fishing, perch was the most abundant fish species in Lake Höytiäinen (IV), and smelt clearly dominated the pelagic area during the vendace recession period (Jurvelius et al. 2005). To estimate the significance of perch predation on vendace larvae as well as the overall capacity of smelt predation, some calculations were made (II, III). Bioenergetics modelling revealed that the perch population consumed 18% of the vendace larvae present in Lake Höytiäinen in 2001 (II). However, the present data do not enable conclusions about the effect of perch predation on larval vendace abundance. This would require more data at different larval densities (see Heikinheimo 2001 and references therein). The total number of smelt in Lake Höytiäinen was estimated to be 22% and 12% of the total number of vendace larvae in 2003 and 2005, respectively. Thus the smelt population has the potential to affect recruitment of vendace in Lake Höytiäinen, although no evidence of predation was obtained during the study years. The estimations are fairly rough, but they give an idea of potential significance of predation by perch and smelt on the vendace population when the density of larvae is low. Furthermore, it should be noted that there is high uncertainty in some parametres of the bioenergetics model (e.g. mortality) and the computations are based only on samples from sampling area B in 2001. The interannual variation in abundance of vendace larvae and availability of alternative food items will certainly affect perch predation in the wild.

The effect of predation on larval fish populations may be underestimated due to the rapid rate at which the larvae are digested. When the fish diet is studied by field sampling, a 1-4 hour sampling period is commonly used (e.g. Tolonen et al. 2000, Dörner & Wagner 2003), sometimes even a longer period (Horppila et al. 2000). According to Shirobokov (1992), ingested coregonid larvae became uncountable in 25-150 minutes (temperature 8-12 ºC), depending on the predator. The digestion time depends on predator species and size, the amount and size of the ingested food items and on water temperature (Persson 1981, Shirobokov 1992). In the present study, the diet sampling of smelt was conducted by seining or trawling for one hour, and the stomachs were preserved immediately after sampling (III). The perch were sampled by gillnets or small fish traps using a two-hour sampling period (II). The aquarium tests demonstrated that the two-hour sampling interval is short enough for studies of perch predation on larval coregonids. In Lake Höytiäinen the surface water temperature during the last sampling week was higher (17 ºC) than in the laboratory tests, but otherwise the temperatures (6-14 ºC) corresponded to temperatures used in the laboratory (II). Given that the surface water temperatures measured in the field were inevitably higher than at the depths where the perch were caught, it can be concluded that larval predation was not underestimated as a result of the sampling interval.

4.2 Fish stock management

4.2.1 Stock transfer

Even a relatively small spawning stock of vendace can produce a strong year class (Viljanen 1988), but in the lowest spawning stocks a clear decrease in recruitment has been observed (Helminen et al. 1997, Karjalainen et al. 2000). For this reason a precautionary fisheries management policy aiming at the conservation of at least moderate spawning stocks is recommended (Marjomäki 2003). Stock transfers have been used in Finland to strengthen low spawning stocks, and hence also the forthcoming year class (Jurvelius et al. 1995). In Lake Höytiäinen stock transfers were carried out between 1978 and 1980, and in 2000. The vendace stock recovered after the earlier transfer, but whether this was due to the transfer is not known (Korhonen & Turunen 1995).

In 2000, the transferred vendace reproduced successfully in Lake Höytiäinen, and therefore stock transfer had some effect on the population structure of vendace (I). However, the microsatellite DNA assignment test showed that the majority (69%) of the larvae sampled originated from the indigenous Lake Höytiäinen population and only 11% from the stocked Suvasvesi individuals, 4.5% being most likely hybrids between the two populations. Although the assignment probabilities were quite low and the sample size of the larvae was small, the results give a clear indication that the majority of the larvae actually originated from the Lake Höytiäinen population. The spawning stock in autumn 2000, i.e. in the first autumn after stock transfer was very small. According to an echo survey conducted in August 2000, the estimated vendace biomass was well below 0.5 kg ha^{-1} (Jurvelius et al. 2005). The stocked biomass was about 1 kg ha^{-1}, so that the mortality associated with the transfer was very high. According to results obtained by experimental caging of transferred fish, the mortality ranged between 61 and 97% (Huuskonen et al. 2001). The contribution of the stocked fish to the 2001 year class was lower than expected, and this was most likely due to high mortality associated with the transfer.

4.2.2 Intensive fishing

The reduction of potential predators in a lake is another possible action that can be taken to enhance the size of the vendace population. It has been suggested that introduced salmonids, such as brown trout, predate on vendace, maintaining a low-density state of the vendace population, and hence recommendations have been made to restrict stocking of salmonids (Helminen et al. 1997, Vehanen et al. 1998, Heikinheimo 2001). Accordingly, no brown trout or landlocked salmon (*Salmo salar* m. *sebago* L.) were stocked in Lake Höytiäinen after stock transfer, in order to reduce predation on juvenile and adult vendace.

There are several possible reasons for the increase of the perch population in the 1990s in Lake Höytiäinen. Water temperature has positive effects on the growth of perch and hence, due to decreased mortality, year class strength (Böhling et al. 1991, Lehtonen & Lappalainen 1995, Sarvala & Helminen 1996, Tolonen et al. 2003). According to length frequency distributions of perch in Lake Höytiäinen, the youngest year classes (2000, 2001 and 2002) were very strong at the beginning of the intensive fishing period. The summer temperatures were high in 2001 and 2002 (Environmental Information System HERTTA, 14.10.2008), but the effect of temperature on perch growth was not studied here. Food competition with vendace may affect perch growth and year class strength. When the vendace population is sparse, the perch is assumed to disperse to the pelagic zone and broaden its feeding areas (Heikinheimo 2001). This was found in Lake Höytiäinen, too. Apparently, the vendace stock recession increased the availability of zooplankton and enabled the perch population to increase. On the other hand, there has been no increase in the nutrient levels of Lake Höytiäinen from the 1960s to 2007 (Environmental Information System HERTTA, 14.10.2008), so this can be excluded from the possible factors behind changes in the fish community.

To reduce the density of the perch population and hence the predation pressure on vendace larvae (Helminen & Sarvala 1994, Heikinheimo 2001, Valkeajärvi & Marjomäki 2004), intensive fishing of perch was started in Lake Höytiäinen in 2001 and finished in 2004 (IV). Compared to several earlier studies of the effects of intensive fishing on the fish population, the total yield per hectare (16 kg ha^{-1} in 4 years) in sub-area 2 of Lake Höytiäinen was small. According to Olin et al. (2006), the yields in intensive fishing projects in several Finnish lakes ranged between 44 and 472 kg ha^{-1} in 3 years, but these projects were conducted in eutrophic lakes and aimed at improving water quality by removing mainly cyprinids. In the eutrophic Lake Vesijärvi, the average yearly catch was 65 kg ha^{-1} during the intensive fishing period (Peltonen 1999). Lake Höytiäinen is an oligotrophic lake, and the target species for intensive fishing was perch. Not many studies with similar aims can be found in the literature. However, in the mesotrophic Lake Windermere, intensive fishing of perch was conduced in the 1940s (Le Cren et al. 1977). The annual catch in the North Basin of Lake Windermere was 2 - 24 kg ha^{-1} during the 7-year intensive fishing period. In the oligotrophic and acidic Lake Munksjøen in Norway, the total yearly catch of perch ranged between 1.4 and 16.0 kg ha^{-1} (Linløkken & Seeland 1996).

According to the results of gillnet test fishing and theoretical population size estimated by the the Leslie depletion method, the size of the perch population diminished in the intensive fishing area from 2001 to 2004 (IV). However, the latest gillnet test fishing results demonstrate that the decrease continued after the fishing period in 2006 (Fig. 4 and 5). Hence, fishing was not the only factor involved in the changes in the perch population. During the study period, the abundance of pikeperch increased sharply (Fig. 6 and 7) throughout the study area. In the intensively fished sub-area 2 the increase in numbers was three-fold from 2001 to 2006. Since perch is usually an important species in the pikeperch diet (Peltonen et al. 1996, Vehanen et al. 1998, Keskinen & Marjomäki 2004), also in Lake Höytiäinen (Puolakka 2008), pikeperch could have reduced the perch population. This is especially true for the end of the study period, when pikeperch population increased. Small perch may be an important prey item, also for piscivorous perch (Mehner et al. 1996, Horppila et al. 2000, II), and it has been found that YOY perch abundance is controlled by piscivorous conspecifics (Claessen et al. 2000, Claessen et al. 2002, Dörner and Wagner 2003). In Lake Höytiäinen, the strong perch year classes 2001 and 2002 may have controlled the abundance of subsequent year classes. To conclude, at the beginning of the study period, the perch population size was reduced by intensive fishing, whereas at the end of the period predation by pikeperch and piscivorous perch probably played an important role.

Intensive harvesting of the fish population produces compensatory reactions: faster growth of individual fish, increased reproductive output and/ or decreased mortality (Mills & Hurley 1990, Persson & Greenberg 1990, Hansson et al. 1998, Karjalainen et al. 1999, Peltonen et al. 1999, Romare & Bergman 1999). According to Le Cren (1958) the population density of perch has no effect on first-year growth, only minor effect on second-year growth and the strongest effect on older fish. Le Cren (1958) concluded that the density of prey animals (zooplankton) for 1- and 2-year-old perch was not significantly reduced by the size of the fish population, but that the density of benthic invertebrates, the prey animals of older perch, was the restrictive factor. In Lake Pyhäselkä, on the contrary, the density of the perch population correlated negatively to first-year growth (Huuskonen et al. 1999). In Lake Munksjøen the growth of perch was enhanced after biomass removal, but the growth response was suggested to be at least partly caused by water quality improvement due to liming (Linløkken & Seeland 1996). In a subarctic lake, density-dependent factors as well as summer temperature affected the growth rate of perch (Tolonen et al. 2003). In the intensively fished sub-area 2, the size of the perch increased. This was the only area where size changes were observed, and thus the removal of small-sized perch individuals may have resulted in the dominance of larger perch.

5. Concluding remarks

Besides being the most important target for professional fishermen, vendace is a valuable species for recreational fishermen, too. Prolonged recessions are particularly difficult for fisheries, and this raises a question about measures to enhance the size of the vendace population. Vendace has a high recruitment potential, but the emergence of a strong year class is dependent on the presence of several positive and the absence of many adverse conditions that can cause recruitment failure. Some of these conditions may be manipulated by stock management practices. In Lake Höytiäinen the vendace population was attempted to be improved by strengthening the spawning population of vendace and decreasing the size of a predator population.

The vendace stock stayed at the low level for several years after the stock transfer in Lake Höytiäinen, thus stock transfer eventually had no effect on recruitment of vendace population. The stocked biomass was c. 1 kg ha^{-1}, totally 15 000 kg, but the biomass of survived vendace was much lower due to high mortality related to transfer. The mortality can not be totally avoided in transferring vendace (Huuskonen et al. 2001), thus the transferred biomass should be much higher to increase remarkably the size of the spawning population. At a low-density state of vendace, transferred fish biomass should be multifold compared to native stock which often means high expenses of the transfer. In a large lake such as Lake Höytiäinen the stock transfer of vendace can not be recommended.

Although the perch population diminished during the intensive fishing period, there was no increase in the abundance of vendace larvae until 2006. In 2006 the mortality of the vendace larvae was high possibly due to unfavourable weather conditions in spring. Unfortunately no predator diet sampling was carried out in 2006. In 2008 a strong year-class of vendace hatched and mortality was low during the first three weeks. Hence, conditions affecting the larval mortality have been favourable, including the sparse populations of predators, also perch. Thus intensive fishing of perch may have contributed to the recovery of vendace population, although the role of pikeperch as a predator of perch is probably more prominent. Larval predation is only one of the factors affecting recruitment of vendace, hence the reduction of predators does not guarantee the recovery of vendace stock.

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