

Hydroacoustic monitoring of the distribution, density and the mass-removal of pelagic fish in a eutrophic lake

Juha Jurvelius¹ & Ilkka Sammalkorpi²

¹Finnish Game and Fisheries Research Institute, FIN-58175 Enonkoski, Finland

²University of Helsinki, Lahti Research and Training Centre, Box 26, FIN-00014 University of Helsinki, Finland

Received 16 December 1993; in revised form 6 December 1994; accepted 15 February 1995

Key words: mass-removal, biomanipulation, hydroacoustics, roach, smelt

Abstract

A large scale biomanipulation of pelagic fish by trawling was started in the eutrophic Enonselkä basin (26 km²) of Lake Vesijärvi to improve the water quality which had remained poor in spite of the termination of nutrient loading. The distribution and density of the fish were studied by hydroacoustics before and during the removal. The initial annual fish density varied between 13 000–21 000 fish ha⁻¹ in the study area in August 1984–89. The mass-removal of the fish by pelagic trawling took place in 1989–1992. The catch varied annually between 64 and 92 kg ha⁻¹. Roach (*Rutilus rutilus* (L.)) and smelt (*Osmerus eperlanus* (L.)) accounted for c. 85% of the weight of the catch. The mass-removal decreased the pelagic fish density in the Enonselkä basin during the trawling. An increase in the density was observed after the trawling ceased in these years, and the initial density level was reached within one month. The density level after mass-removal remained high compared with oligotrophic lakes. The pelagic fish had a diurnal ascending trend with the decreasing light intensity in August, and the fish were significantly ($p < 0.01$) higher in the water mass in temperature non-stratified water in autumn than in stratified water in summer. The fish were somewhat deeper in the years of mass-removal than before it. Mass-removal did not affect the individual length of the echosurveyed fish. Fish smaller than c. 15 cm (TS < -44 dB; mainly smelt) were numerically dominant throughout the whole study period.

Introduction

Eutrophication increases the standing crop and changes the species composition of lacustrine fish communities (Hartmann, 1977; Hanson & Leggett, 1982). The high density of small planktivorous and benthivorous fish may be of great importance for the water quality of eutrophic lakes (c.f. Hrbacek *et al.*, 1961; Andersson *et al.*, 1978; Reinertsen & Olsen, 1984; Keto & Sammalkorpi, 1988, several case studies in Gulati *et al.*, 1990; Gliwicz, 1992). Reduction of these fish has consequently become an important method in lake management. For their mass-removal, information on densities and migrations is of crucial importance. Effects of large scale fishing on lacustrine fish populations have been studied either by depletion methods (Helminen *et al.*, 1992; Backx & Grimm, 1994) or by an application of virtual population analysis (VPA) (Peltonen

& Horppila, 1992). Monitoring with hydroacoustics has so far been infrequent.

The pelagic fish stock in the Enonselkä basin of Lake Vesijärvi has been echosurveyed since 1984. This paper deals with the effects of an intensive trawling on fish distribution and density in the Enonselkä basin. The length distribution, seasonal and diurnal migrations of pelagic fish were also studied.

Material and methods

Research area

The center (10 km², depth > 10 m) of the Enonselkä basin in Lake Vesijärvi was the research area (Fig. 1). The Paimelanlahti bay was a shallower and a more eutrophic part of the area (Table 1). Lake Vesijärvi was

Table 1. Hydrological properties and water quality in the Enonselkä basin (A) and the Paimelanlahti bay (B) of Lake Vesijärvi in the 1980's (I) and the 1990's (II) (Keto & Sammalkorpi, 1988 and 1993).

Area (km ²)	Depth		Tot. P (μg/l)		Tot. N (μg/l)		Transparency (m)	
	max.	mean						
			I	II	I	II	I	II
A. 26	33	6.8	45	35	650	600	1.6	2.1
B. 4	14	6	45	45	650	650	1.5	1.5

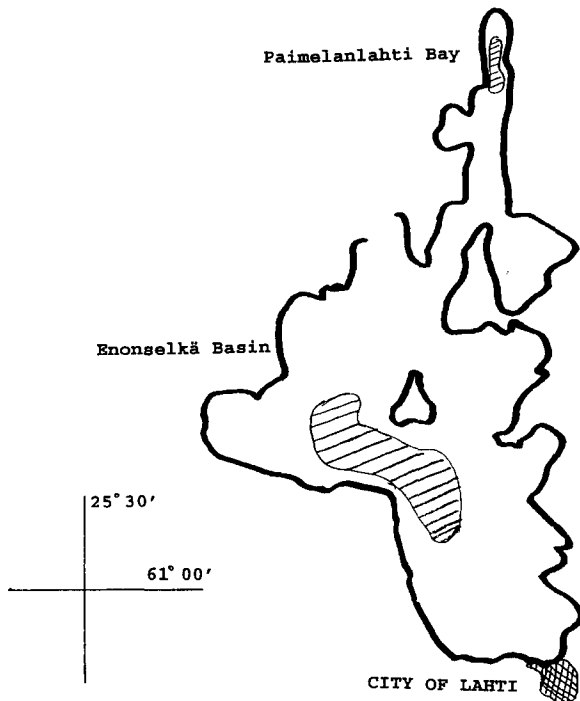


Fig. 1. The Enonselkä basin and the Paimelanlahti bay of L. Vesijärvi. ▨ = trawling and echosurvey area.

fertilized with municipal sewage until 1976. It became the largest heavily eutrophicated lake basin in Finland. Blooms of blue-green algae, poor stocks of predatory fish and a replacement of valuable fish species with coarse fish e.g. roach (*Rutilus rutilus* (L.)), small perch (*Perca fluviatilis* L.), ruffe (*Cymnocephalus cernua* (L.)), smelt (*Osmerus eperlanus* (L.)) and stunted bream (*Abramis brama* (L.)) characterized the lake. As a result of these changes commercial and recreational fishing had almost ceased (Keto & Sammalkorpi, 1988).

Table 2. Trawl catch (kg ha⁻¹ a⁻¹) calculated for the whole area of Enonselkä basin in 1987–1992 (J. Keto, unpubl., Peltonen & Horppila, 1992).

Species	1987	1988	1989	1990	1991	1992
Smelt	2.3	1.7	23.4	22.9	17.2	18.4
Roach	5.4	1.6	29.1	33.3	59.3	43.5
Others	1.1	1.8	3.0	7.7	27.2	19.1
Total	8.8	5.1	64.4	63.9	103.7	81.0

The management of the lake shifted after 1984 from hypolimnetic aeration and stocking of planktivorous whitefish to biomanipulation, stocking with predatory fish and attempts at selective fishing of roach. The Enonselkä basin was annually stocked with 50 yearlings of zander (*Stizostedion lucioperca* (L.)) ha⁻¹ in 1987–91.

Mass-removal of fish

The start of the fish removal was laborious since fishermen and their gear were not 'adjusted' to the fishing of unwanted roach and smelt. The first attempts made in 1987 and 1988 thus gave poor results. Intensive fishing with pair trawling started in 1989 and trawling was the most important method employed in the mass-removal of fish in this study (Table 2). The annual roach catch varied between 900 and 1700 fish ha⁻¹ in 1990–92 (J. Horppila, unpubl.). The corresponding figure was about 11 000 for smelt (T. Turunen, unpubl.). There were usually 2–3 pair trawlers fishing in the Enonselkä basin at the same time. The vertical trawl opening varied between 6 and 12 m and the mesh size of the cod end was from 8 to 10 mm depending on the trawl. The trawling began annually in May–June and it ended by September. Only water areas deeper than 10 m

were trawled in 1989–90 (Fig. 1). The corresponding depth was 7 m in 1991–92. Mainly surface hauls were used.

Echocounting

The acoustic data were collected with a Simrad EY-M echosounder. The data were later analysed by HADAS PC program to get a target strength (TS) distribution and the areal density (fish ha⁻¹) of the echoes. The technical properties of the echosounder and the transducer (70 kHz) are described by Bayona (1984) and the echocounting method by Lindem (1983) and Jurvelius (1991).

The target strengths (TS) obtained in this study ranged from –56 to –38 dB. The length of individual fish (L) in centimetres was estimated with $\log L = (TS + 67)/20$ (e.g. Bagenal *et al.*, 1982). The TS-distribution of the echoes obtained provided the basis for fish length estimates. All single-fish echoes greater than –38 dB were truncated and shifted into the –38 dB size group. Thus the minimum estimated fish size was about 4 cm, and the maximum 28 cm.

Echocounting was started c. 2 m from the surface and stopped one metre above the bottom. For the vertical analysis of fish distribution, the water mass was divided into 2 or 5 m depth layers. For TS distribution and areal fish density estimates, the fish were analysed in one depth layer.

The precision – defined as the difference from the mean between two successive 15 min runs over the same area – for the estimates of areal fish density has varied between 1 and 10% in several studies with this method (Jurvelius, 1991). The precision of the TS-distribution has been c. 1% (Jurvelius & Auvinen, 1989).

Methane bubbling from the sediments of the lake occurred during summer stratification in limited areas. We assumed that the bubble density in the oxygenated epilimnion was the same as the one observed in the anoxic hypolimnion. Strictly speaking this was not the case. However, the error caused by the splitting or dissolving of methane bubbles in surface layers has no practical importance in this study. In the fish density estimates, the number of hypolimnetic bubbles was thus subtracted from the echo number of the epilimnion.

Echosurveys

To study the effects of trawling on the vertical fish distribution we first tested the significance of diurnal vertical fish migrations in August. An echosurvey was completed over the same area at 12, 18 and 22 h. Secondly, seasonal variation between July, August, September and October was studied. The time for density estimation surveys was based on vertical fish migration results.

The boat speed was 5 knots (3 ms⁻¹) in the surveys. Because of the small boat, the wind conditions had to be taken into account in the survey design. In the estimates of the areal fish density we surveyed one transect through the middle of the study area from north to south, and then we zig-zaged the same area from south to north. Hansson (1993) found no consistent differences between these types of transects. The degree of coverage was 3 in our study.

To estimate the density variation (95% CL) the survey was segmented into horizontal samples. The variance of the samples was usually greater than their arithmetic mean, i.e. the fish had an aggregated distribution. In such cases a logarithmic transformation can be used (Elliott, 1983). This transformation stabilises the mean.

The number of single fish echoes was always more than 100 in each sample, and the percentage of single fish echoes was usually more than 75%. Echosurveys were not done in areas shallower than 10 m and the surveys concentrated on the central pelagic area, which was approximately the same as the trawling area (Fig. 1).

Echosurveys made in August 1984, 86, 88–90, 92, in April and October 1990, and in September and October 1992 were used in this study. The diurnal vertical fish migrations were studied in August 1989. Echosurveys in August 1985, 1987 and 1991 were excluded because of technical problems. Only one recording from the end of July was available in 1991. It was made during a very intensive trawling period.

The variation in the vertical migrations and in the TS-distribution of fish was tested with the Kolmogorov-Smirnov-test.

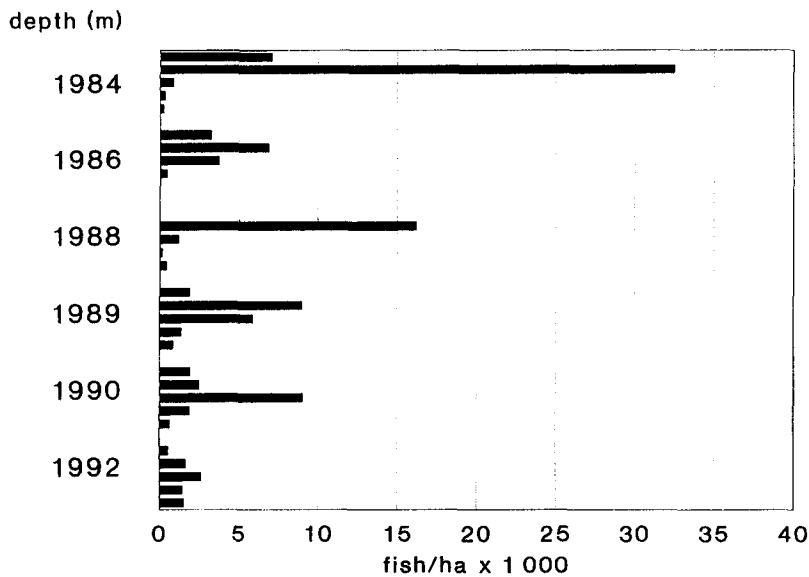


Fig. 2. The August vertical fish distribution before (1984–88) and during (1989–92) the mass-removal of fish by trawling in the Enonselkä basin. Depth layers are 3–5, 5–10, 10–15, 15–20 and 20–25 m.

Results

The vertical distribution of fish

The pelagic fish were significantly ($D_a = 0.02$, $p < 0.001$) higher in the water mass at night than at noon in August. About 20% of the fish were always found below 14 m depth. The total density of echosurveyed fish was smallest in the darkness. This together with the ascending trend indicates that a considerable proportion of the fish may have migrated into the surface layer where their echosounding was not possible. An increase (from 55 to 70) in the percentage of single fish echoes showed that fish schools dispersed somewhat during the night. According to these diurnal fish migrations, early evening was the most suitable time for the hydroacoustic estimation of pelagic fish. It was also obvious that the time of the day should not affect the surface trawl-catches in August.

The pelagic fish were significantly ($D_a = 0.03$, $p < 0.001$) higher in the water mass in October than in the beginning of August. About 20% of the echosurveyed fish were between 3 and 7 m depth in the thermally stratified water in summer. The corresponding figure was more than 50% in unstratified water in autumn. This, in addition to the increased fish density, indicates that the catch per unit of effort in surface and midwater trawling could be higher in late autumn than in summer.

Before the mass-removal of fish in the years 1984–88 the maximum fish density was between 5 and 10 m depth (Fig. 2). A very distinct peak in this depth layer was found in 1988. The maximum density was between 10 and 15 m in 1990–92. The first year of trawling (1989) was a year of transition in this respect. The vertical fish distribution differed very highly ($D_a = 0.002$, $p < 0.001$) between all these years. However, a descending trend in the fish distribution could be seen after the beginning of the trawling.

Areal density and length of the echosurveyed fish

The largest and densest fish aggregation – 45 000 fish ha^{-1} – was 3.5 km long between 5 and 9 m depth in August 1984. The lowest fish density in the study area, less than 300 fish ha^{-1} , was observed on July 27th 1991 when 180 tons (69 kg ha^{-1}) of fish had been removed in the preceding four weeks. In the densest areas in August there were about 21 000 fish ha^{-1} in the years before the trawling, the respective figure was 12 000 during the trawling.

The average density estimate of pelagic fish in the research area in August was highest in 1984 (Fig. 3). In the other studied years the corresponding estimate was about 45% lower. The trawling took place in 1989–92 and it seemed to have no effect on these densities. However, the density was very low during the trawling season in June–July in the years of mass-removal.

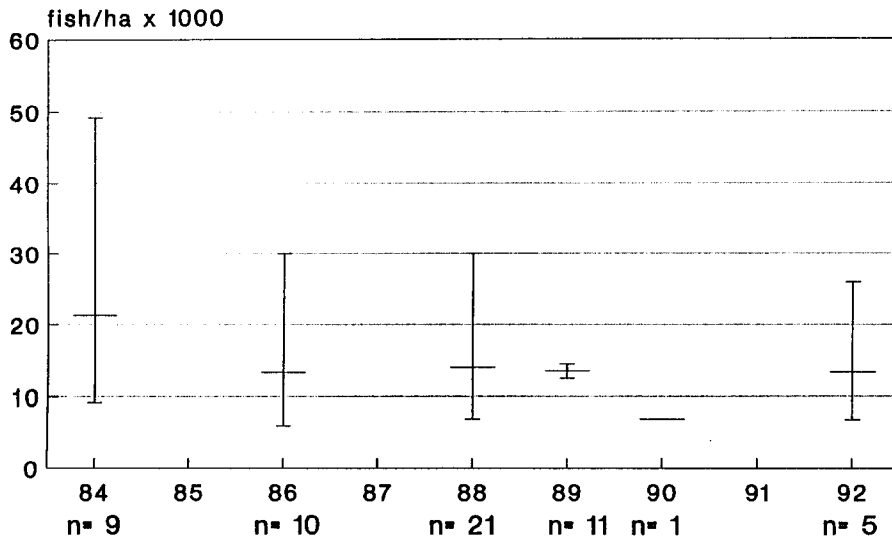


Fig. 3. The relative density (geometric mean and its 95%CL) of pelagic fish in the deepest area of Enonselkä basin in August 1984, 1986, 1988–1990 and 1992. Echosurveys in 1985, 1987 and 1991 were excluded because of technical problems.

After the trawling period the density increased e.g. it nearly doubled from 7500 to 13 300 fish ha⁻¹ in one month in 1992. Thus a replacement of the trawled fish took place from the littoral into the central area of the Enonselkä basin. After becoming aware of these migrations attention was also paid to trawling in the shallower (< 10 m) areas of the Enonselkä basin.

Large fish schools and a high number of single-fish echoes were echosurveyed in a restricted area (c. 15 ha) close to the spawning areas in the Paimelanlahti bay after the thaw at the end of April. The fish density in this area decreased from 30 000 to 2 000 fish ha⁻¹ in one month after the spawning. An increase to 5 000 fish ha⁻¹ took place by September.

According to the TS distributions, the percentage of fish under 10 cm (≤ -47 dB) length were dominant in all surveys except in Paimelanlahti bay in spring (Fig. 4). Fish longer than 15 cm (≥ -44 dB) were rare in the Enonselkä basin. Since the trawl catch in the Enonselkä basin area has mainly consisted of adult roach (length 14–20 cm) and smelt (length 5–9 cm) it is evident that the echosurvey has concentrated mainly on smelt.

The echosurveyed fish in the Paimelanlahti bay were significantly ($D_a = 0.02$, $p < 0.001$) larger in spring than in summer (Fig. 4). These fish preparing for spawning in the bay were also significantly larger ($D_a = 0.02$, $p < 0.001$) than the ones living in

the central basin. This difference between the areas was smaller in August. The relative frequency of TS-groups -56 and -54 dB increased in both areas by August. This indicated a higher abundance of small fish in comparison to April. The species in Enonselkä was almost entirely smelt according to the trawl catches in August (Peltonen & Horppila, 1992). Small roach, bream (*Abramis brama* L.) and bleak (*Alburnus alburnus* L.) were numerically dominant according to seine catches in the Paimelanlahti area in winter (I. Sammalkorpi, unpubl.).

Discussion

It is generally known that certain pelagic fish ascend and disperse in the darkness (e.g. Dembinski, 1971; Hamrin, 1986; Jurvelius *et al.*, 1988). Obviously the low oxygen concentration in the hypolimnion together with the species composition caused the vertical migration pattern in the Enonselkä basin to differ from that of more oligotrophic lakes. For instance, we never saw fish rising from the lake bottom, which is often the case in shallow oligotrophic lakes. The slight vertical descent which occurred after the mass-removal could have some connection with the increased water transparency.

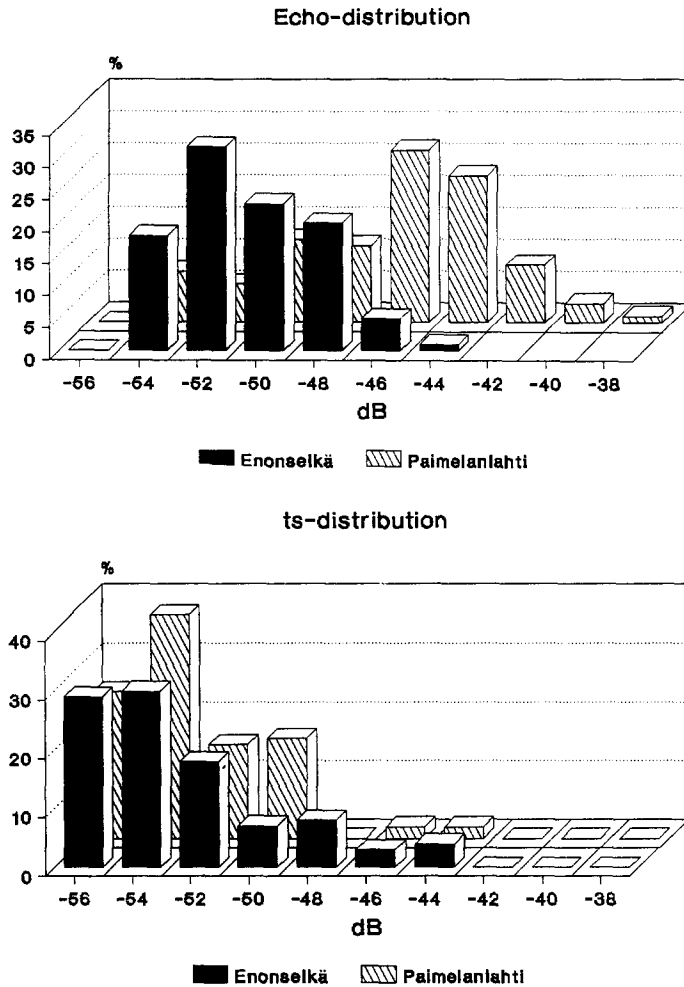


Fig. 4. The target strength distribution of fish in the pelagic area of the Enonselkä basin and near the littoral spawning areas in the Paimelanlahti bay in spring (A) and summer (B) 1990.

The majority of the published hydroacoustic density estimates are from lakes with commercially exploited coregonid stocks. The estimates in these oligotrophic lakes are roughly an order of magnitude lower than in the Enonselkä basin (Jurvelius *et al.*, 1984, 1988; Rudstam *et al.*, 1987). The density of 1-year-old vendace in L. Pyhäjärvi – the most productive Finnish vendace lake – has never been higher than 2 000 fish ha^{-1} (Helminen *et al.*, 1992).

In eutrophic lakes the species composition and fish density differ from that in oligotrophic lakes. In a hydroacoustic study in two eutrophic Norwegian lakes dominated by roach, the density was up to 11 000–20 000 fish ha^{-1} (Bjerkeng *et al.*, 1991). Hansson & Rudstam (1990) estimated that the fish density could even amount to 40 000 fish ha^{-1} in a eutrophic bay of

the Baltic Sea. This was almost an order of magnitude higher than in the nearby reference area.

In July–August 1988 there were thousands of surface-feeding gulls and terns (Laridae) in the Enonselkä basin. Their fish consumption in July–August was estimated at 16 tonnes (Sammalkorpi & Lammi, 1995). Such high numbers of gulls were not found in any other year. This suggests that yearlings of smelt etc. were particularly abundant in 1988 which was a very favorable year for spring spawning fish species e.g. perch (Böhling *et al.*, 1991).

The large sedimentation caused by the eutrophication may favor the spring spawning fish species at the expense of autumn spawning species (Nissinen, 1972; Müller, 1992). In the Enonselkä basin the annual sedimentation rate has been c. 1.5 cm (Liukkonen *et*

al., 1993). This is obviously one very important reason for high smelt, roach and perch density, and low vendace (*Coregonus albula* (L.)) and whitefish (*Coregonus lavaretus* (L.) *s.l.*) density in the study area.

The bottom-up and top-down regulation

Increased productivity caused by the moderately high nutrient concentration and supported by internal phosphorus loading in the growing season (Keto & Sammalkorpi, 1988; Horppila & Kairesalo, 1990) raises the densities of crustacean zooplankton (cf. Hrbacek & Hrbackova, 1966; Langeland, 1982; Mills & Scivone, 1982; Hanson & Peters, 1984) and probably explains a major share of the positive correlation observed between the phosphorus concentration of water and fish biomass (Hanson & Leggett, 1982; Pavlov *et al.*, 1986). The concentration of crustacean zooplankton in the epilimnion varied between 50 and 200 ind.l⁻¹ in L. Vesijärvi in summer 1985 and 1989 (I. Sammalkorpi, unpubl.). The densities of cladocerans have gradually decreased in the 1990's (E. Luokkanen, unpubl.). This is a very abundant food supply for smelt, the numerically dominating pelagic fish species. Crustacean densities in the neighbouring oligotrophic Lake Päijänne have been an order of magnitude lower (Hakkari, 1978). The abundant food supply has increased the survival of smelt fry in the Enonselkä basin from average conditions. This explains partly the very high density of the species.

The phosphorus concentration in the trophic layer of the Enonselkä basin declined after the first summer (1989) of effective trawling. The average summer concentration since 1990 has been c. 80% of that in the 1980's (Keto & Sammalkorpi, 1988, 1993). The predictions of fish biomass calculated from the equation of Hanson & Leggett (1982) have been 93 kg ha⁻¹ for the latter half of the 1980's and 75 kg for the years 1990–1992. This indicated that the potential fish biomass of the 1990's was c. 80% of the value in the 1980's. This trend could not be seen in the hydroacoustic estimate because a heavy migration happened from the littoral to the pelagic zone to replace the trawled fish. A significant positive correlation between epilimnetic phosphorus concentration and the density of perch and roach in the epilimnion was observed by Jurvelius *et al.* (1987) in Lake Päijänne. However, the varying eutrophication did not affect the fish density in the hypolimnion.

The top-down regulation in L. Vesijärvi is probably too weak to exert a considerable influence on smelt.

Zander was extinct in the lake in the last century (Keto & Sammalkorpi, 1988), and the proportion of introduced zander and predatory perch was very low in the trawl catches. The avian predators, although very abundant, did not consume more than 17 kg ha⁻¹ a⁻¹ in the 1990's (Sammalkorpi & Lammi, 1995). Fishing in the basin was very weak before the trawling started; the catch was only c. 5 kg ha⁻¹ a⁻¹ (Keto & Sammalkorpi, 1988). Both natural and fishing mortality were thus very low in the 1980's.

The role of quantitative echocounting

The nocturnal ascent of fish close to the surface may result in an underestimate in hydroacoustic fish density estimation (Jurvelius, 1991; Auvinen & Jurvelius, 1994). A precise echocounting of fish should coincide with the time of their maximal dispersion but a so far unknown and probably varying share of the fish targets may be in the surface layer. Vertically segregated test fishing in the pelagial area of L. Vesijärvi has shown that roach and particularly bleak stay in the uppermost 4 metres (J. Ruuhijärvi, unpubl.) which was reported also by Dembinski (1971) in Polish lakes. The mean length of roach has been 14–17 cm and that of bleak 12–15 cm in the pelagic trawl catch and gill-net test-fishing (J. Ruuhijärvi & I. Sammalkorpi, unpubl.). The roach and bleak living close to the surface may be the reason for the continuously rather low share of larger size classes in hydroacoustic fish length estimates in the Enonselkä basin. These size classes were more abundant in the estimates in the Paimelanlahti bay in April.

The roach in the trawl catches were age 3+ and older fish, whereas 2+ were very rare (Peltonen & Horppila, 1992; Horppila & Peltonen, 1994). Analysis of the trawl data suggests that there has been a reduction of roach density to c. 30% of the density in 1990 (Horppila & Peltonen, 1994). We could not confirm this since an unknown part of roach has probably 'escaped' the echosurvey to the uppermost two meters of the epilimnion.

A major proportion of the pelagic fish in the Enonselkä basin were spring spawners which had their spawning migration to the littoral areas in April–May. Many of these fishes migrated to the central and deepest areas of the Enonselkä basin later in spring and summer. To achieve good results in the mass-removal of these fish, considerable effort should be made to intervene in their reproduction by catching the fish in winter

and spring before their spawning. Attention should be paid also to the catching of subadult yearclasses.

Conclusions

1. Early evening was the best time for hydroacoustic assessment of the pelagic fish stock in August.
2. The catch per unit effort of smelt in trawling of the Enonselkä basin should be higher in autumn than in spring and summer.
3. Fish were slightly deeper in the water mass after the beginning of the mass-removal than before it.
4. The trawling in summer did not have a permanent effect on the fish density on the studied pelagic area. Replacement from shallower areas or surface layers took place in autumn.
5. The rather stable level of smelt densities in the 1990's indicated that the mortality of 0+ smelt in the trawling was low.
6. A decrease of nutrient concentration of the water took place. Part of the reduction in the fish density may have been caused by bottom-up regulation since young (0+ and 1+) smelt respond rapidly to a change in productivity.
7. Our data was not suitable for analyzing the effects of trawling on roach.

Acknowledgements

We thank Juha Keto for practical help and constructive discussions. This study was financially supported by the City of Lahti.

References

- Andersson, G., H. Berggren, G. Cronberg & C. Gelin, 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia* 59: 9–15.
- Auvinen, H. & J. Jurvelius, 1994. Comparison of pelagic vendace (*Coregonus albula*) stock density estimation methods in a lake. *Fish. Res.* 19: 31–50.
- Bagenal, T.B., E. Dahm, T. Lindem & P. Tuunainen, 1982. EIFAC experiments on pelagic fish stock assessment by acoustic methods in Lake Konnevesi, Finland. Rome. EIFAC Occas. Pap. 14: 1–16.
- Backx, J.J.G.M. & M.P. Grimm, 1994. Mass removal of fish from Lake Wolderwijd, The Netherlands. Part II: Implementation phase. In I.G. Cowx (ed.), *Rehabilitation of freshwater fisheries*: 401–414. Fishing News Books.
- Bayona, J.D.R., 1984. Comparison of acoustic survey systems for use in developing countries. In R.B. Mitson (ed.), *Acoustic systems for the assessment of fisheries*. Rome. FAO Fish. Circ. 778: 1–19.
- Bjerkeng, B., R. Borgström, Å. Brabrand & B. Faafeng, 1991. Fish size distribution and total fish biomass estimated by hydroacoustic methods: a statistical approach. *Fish. Res.* 11: 41–73.
- Böhlting, P., R. Hudd, H. Lehtonen, P. Karås, E. Neuman & G. Thoreson, 1991. Variations in year-class strength of different perch (*Perca fluviatilis*) populations in the Baltic sea with special reference to temperature and pollution. *Can. J. Fish. Aquat. Sci.* 48: 1181–1187.
- Dembinski, W., 1971. Vertical distribution of vendace *Coregonus albula* L. and other pelagic fish species in some Polish lakes. *J. Fish Biol.* 3: 341–357.
- Elliott, J.M., 1983. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwat. Biol. Ass. Sci. Publ.* 25: 1–158. (3rd Impression).
- Gliwicz, Z.M., 1992. Can ecological theory be used to improve water quality? *Hydrobiologia* 243/244 (Dev. Hydrobiol. 79): 283–291.
- Gulati, R.D., E.H.R.R. Lammens, M.-L. Meijer & E. van Donk (eds), 1990. *Bio-manipulation. Tool for Water Management. Developments in Hydrobiology* 61. Kluwer Academic Publishers, Dordrecht, 628 pp. Reprinted from *Hydrobiologia* 200/201.
- Hamrin, S.T., 1986. Vertical distribution and habitat partitioning between different size classes of vendace, *Coregonus albula*, in thermally stratified lakes. *Can. J. Fish. Aquat. Sci.* 43: 1617–1625.
- Hanson, J.M. & W.C. Leggett, 1982. Empirical prediction of fish biomass and yield. *Can. J. Fish. Aquat. Sci.* 39: 257–263.
- Hanson, J.M. & R.H. Peters., 1984. Empirical prediction of zooplankton biomass and profundal macrobenthos biomass in lakes. *Can. J. Fish. Aquat. Sci.* 41: 439–445.
- Hansson, S., 1993. Variation in hydroacoustic abundance of pelagic fish. *Fish. Res.* 16: 203–222.
- Hansson, S. & L.G. Rudstam, 1990. Eutrophication and Baltic Fish Communities. *Ambio* 19(3): 123–125.
- Hartmann, J., 1977. Fischereiliche Veränderungen in kulturbedingt eutrophierenden Seen. *Schweiz. Z. Hydrol.* 39: 243–254.
- Hakkari, L., 1978. On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland. *Biol. Res. Rep. Univ. Jyväskylä* 4: 3–87.
- Helminen, H., A. Hirvonen & J. Sarvala, 1992. Impact of fishing on vendace (*Coregonus albula*) population in Lake Pyhäjärvi, SW Finland. *Pol. Arch. Hydrobiol.* 39: 779–787.
- Horppila, J. & T. Kairesalo, 1990. A fading recovery: the role of roach (*Rutilus rutilus* L.) in maintaining high phytoplankton productivity and biomass in Lake Vesijärvi, southern Finland. *Hydrobiologia* 200/201 (Dev. Hydrobiol. 61): 153–165.
- Horppila, J. & H. Peltonen, 1994. The fate of a roach *Rutilus rutilus* (L.) stock under an extremely strong fishing pressure and its predicted development after the cessation of mass removal. *J. Fish Biol.* 45: 777–786.
- Hrbacek, J., M. Dvorakova, V. Korinek & L. Prochakova, 1961. Demonstration of the effect of fish stock on the composition of zooplankton and the intensity of metabolism of the whole planktonic association. *Verh. int. Ver. Limnol.* 14: 192–195.
- Hrbacek, J. & M. Hrbackova, 1966. The taxonomy of the genus *Daphnia* and the problem of biological indication. *Verh. int. Ver. Limnol.* 16: 1661–1667.
- Jurvelius, J., T. Lindem & J. Louhimo, 1984. The number of pelagic fish in Lake Paasivesi, Finland, monitored by hydro-acoustic methods. *Fish. Res.* 2: 273–283.
- Jurvelius, J., T. Heikkinen, P. Valkeajärvi & T. Lindem, 1987. Fish density and fish species composition in relation to the phosphorus

- concentration in some pelagic areas of Lake Päijänne. Biol. Res. Rep. Univ. Jyväskylä 10: 189–199.
- Jurvelius, J., T. Lindem & T. Heikkinen, 1988. The size of a vendace (*Coregonus albula* L.) stock in a deep lake basin monitored by hydroacoustic methods. J. Fish Biol. 5: 679–687.
- Jurvelius, J. & H. Auvinen, 1989. Fish echo-sounding in a large lake: a systematic and unsystematic sampling of pelagic fish stocks. Aqua Fennica 19: 123–127.
- Jurvelius, J., 1991. Distribution and density of pelagic fish stocks, especially vendace (*Coregonus albula* (L.)), monitored by hydroacoustics in shallow and deep southern boreal lakes. Finnish Fish. Res. 12: 45–63.
- Keto, J. & I. Sammalkorpi, 1988. A fading recovery: A conceptual model for Lake Vesijärvi management and research. Aqua Fennica 18 (2): 193–204.
- Keto, J. & I. Sammalkorpi, 1993. Vesijärven veden laatu vuoden 1992 tutkimusten perusteella ja veden laadun kehitys vv. 1989–92. (Water quality in L. Vesijärvi in 1992 and its trend in 1989–92). City of Lahti. Series A, 3: 1–27. (in Finnish).
- Langeland, A., 1982. Interactions between zooplankton and fish in a fertilized lake. Holarct. Ecol. 5: 273–310.
- Lindem, T., 1983. Successes with conventional in situ determinations of fish target strength. In O. Nakken & S.C. Venema (eds), Symposium on fisheries acoustics. Selected papers of ICES/FAO Symposium on fisheries acoustics. Bergen, Norway, 21–24 June 1982. Rome. FAO Fish. Rep. 300: 104–111.
- Liukkonen, M., T. Kairesalo & J. Keto, 1993. Eutrophication and recovery of Lake Vesijärvi (south Finland): diatom frustules in varved sediments over a 30-year period. Hydrobiologia 269/270 (Dev. Hydrobiol. 90): 415–426.
- Mills, E.L. & A. Sciavone, 1982. Evaluation of fish communities through assesment of zooplankton populations and measures of lake productivity. North Am. J. Fish. Mgmt 2: 14–27.
- Müller, R., 1992. Trophic state and its implications for natural reproduction of salmonid fish. Hydrobiologia 243/244 (Dev. Hydrobiol. 79): 261–268.
- Nissinen, T., 1972. Mätitiheys ja mädin eloonjääminen muikun (*Coregonus albula* L.) kutupaikoilla Puruvedessä ja Oulujärvessä. (Summary: The egg density and the survival of eggs on the spawning grounds of the vendace (*Coregonus albula* L.) in lakes Puruvesi and Oulujärvi. Finnish Game and Fish. Res. Inst., Rep. 1: 1–114. (in Finnish with English summary).
- Pavlov, D.S., A.G. Gusar, A.I. Pyanov & A.N. Gorin, 1986. The results of hydroacoustic observations on roach in Lake Glubokoe in winter. Hydrobiologia 141 (Dev. Hydrobiol. 36): 125–132.
- Peltonen, H. & J. Horppila, 1992. Effects of mass removal on the roach stock of Lake Vesijärvi estimated with VPA within one season. J. Fish Biol. 40: 293–301.
- Reinertsen, H. & Y. Olsen, 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. Verh. int. Ver. Limnol. 22: 649–657.
- Rudstam, L.G., C.S. Clay & J.J. Magnuson, 1987. Density and size estimates of cisco (*Coregonus artedii*) using analysis of echo peak PDF from single-transducer sonar. Can. J. Fish. aquat. Sci. 44: 811–821.
- Sammalkorpi, I. & E. Lammi., 1996. The trophic role of piscivorous birds in the eutrophicated Lake Vesijärvi, southern Finland. Hydrobiologia (in press).