

Limnological responses to the collapse of the perch population in a small lake

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Several limnological responses were recorded after an almost total collapse of the population of perch, *Perca fluviatilis*, in the control basin of the limed Lake Iso Valkjärvi in autumn 1992. Increases in hypolimnetic concentrations of dissolved organic carbon and ammonium-nitrogen were the most striking changes in water chemistry. After a few months, high densities of ciliates were recorded in the hypolimnion, suggesting an increased microbial activity in the decomposition of fish carcasses. Correspondingly, hypolimnetic bacterial biomasses in summer 1993 were higher than earlier. In crustacean zooplankton: the densities of planktonic cladocerans were lower in the fishless side of the lake in summer 1993 than before the fish kill in the previous summer. The decline in cladocerans was probably due to predation by the rapidly increased numbers of *Chaoborus* larvae and corixids after the disappearance of fish. The mean biomass of zoobenthos also increased following the fish kill. The remaining perch in the control basin started to grow very rapidly. Instead of the normal length increase of 1–2 cm per year, they grew 5–7 cm in the summer of 1993 and their weight increased ten times more than that of perch of the limed basin of the lake. The mercury concentrations and radioactivity of the perch showed a 50% decrease, probably due to the growth dilution. A behavioural change in the golden-eye, *Bucephala clangula*, was also recorded. The breeding individuals continued to use both basins of L. Iso Valkjärvi, but the brood clearly preferred the control basin after the collapse of the perch population.

1. Introduction

Besides resource based (bottom-up) factors, more attention has recently been paid to consumer based

(top-down) factors as controlling mechanisms in the structure and function of aquatic ecosystems (Hrbáček *et al.* 1961, Carpenter *et al.* 1987). The increased understanding of trophic cascade theory

and top-down effects has been widely applied in connection with the restoration of eutrophicated water bodies by means of biomanipulation (Shapiro 1990, Horppila & Kairesalo 1992).

The importance of top-down control has also been shown in oligotrophic lakes (Langeland 1982). In small Finnish forest lakes with dense perch populations, small cladocerans like *Bosmina longispina* and *Ceriodaphnia quadrangula* often dominate the crustacean zooplankton (Rask 1986, Salonen *et al.* 1990) whereas in ponds with no fish predation, the large-sized *Daphnia longispina* is often the dominating cladoceran (Salonen *et al.* 1990, Salonen & Lehtovaara 1992). A similar connection between the existence of fish populations and the biomass of benthic fauna has been shown in small, rotenone treated lakes (Tuunainen 1970). A good example of the significance of top-down control in oligotrophic lakes has been the acidified lakes that have lost their fish populations. After the disappearance of fish, the number of invertebrates has increased and macroinvertebrate predators have replaced fishes as top predators (Eriksson *et al.* 1980, Stenson *et al.* 1993).

In the Lake Iso Valkjärvi Liming Experiment, an acidified mesohumic lake was divided into two parts of similar size by a plastic curtain in order to record the effects of liming on the structure and functioning of the ecosystem and on the contents of mercury and caesium in aquatic biota (Rask 1991). Liming of one half of the lake resulted in typical changes in water quality: increases in pH, alkalinity, conductivity, dissolved inorganic carbon, calcium and magnesium and decreases in total aluminium (Järvinen & Rask 1992).

The overall hydrobiological responses to the liming were quite small. Some changes were recorded in the species composition and dominance relations of phytoplankton as well as in the production of the cladoceran *Bosmina longispina* (Järvinen *et al.* 1995). In the zoobenthos community, a short term increase in *Asellus aquaticus* in the year of liming and the appearance of the mayfly *Cloeon dipterum* were related to the neutralization (Rask *et al.* 1995). Minimal effects of liming were recorded in the perch population as well. Both the growth and diet of perch remained quite similar after liming in both basins of the lake (Rask *et al.* 1993). However, the symptoms of failure in reproduction, such as increased mortality of fertilized eggs, disappeared. Liming did not change the concentrations of mer-

cury or the radioactivity of the perch. Mild responses to liming in the food web of L. Iso Valkjärvi have been explained by several reasons (Rask *et al.* 1995, Järvinen *et al.* 1995) which together fulfil two essential factors. Firstly, the lake was not very strongly acidic before the liming (pH 5.0–5.5, labile aluminium 20–30 µg/l, dissolved organic carbon (DOC) 6–8 mg/l). Secondly, the dense population of perch controlled the zoobenthos and zooplankton communities both before and after the neutralization. This, in turn, has probably resulted in more or less stable zooplankton grazing pressure on phytoplankton (Järvinen *et al.* 1995).

In September 1992, an almost complete (> 95%) killing of the perch population took place in the control basin of L. Iso Valkjärvi. The most probable reason for this was the mixing zone effect, which means interactions of acidity, calcium and labile aluminium in certain concentrations, detrimental to fish (Rosseland *et al.* 1992), possibly connected to the polymerization of aluminium (Poléo 1995). In this study, redox conditions and iron may also have been factors in the fish kill because it occurred during the autumn turnover. Higher hypolimnetic concentrations of total aluminium in the winter following the fish kill supported our speculation that it was due to altered Al chemistry during the autumn turnover.

The fish kill severely disturbed our original experimental design. On the other hand, it offered us an opportunity to study the various responses of the entire ecosystem to the disappearance of top predators and thereby to assess the role of perch in structuring the lower trophic levels of the system. In this paper we describe the chemical and biological changes that were recorded in the control basin of L. Iso Valkjärvi following the collapse of the perch population.

2. Material and methods

Lake Iso Valkjärvi is an acidified mesohumic lake (area 4 ha, maximum depth 8 m) located in southern Finland. It is a seepage lake with a small catchment area of glacial fluvial origin. Scots pine forest is the dominating vegetation of the catchment. The aquatic vegetation is mainly composed of *Nuphar lutea* and *Warnstorfia* moss at the bottom of the lake. A survey of water chemistry and hydrobiology was carried out in 1990 (Rask 1991). The lake was divided into two parts of equal size in spring 1991, one basin of which was limed at the end of May 1991 (Table 1, Järvinen & Rask 1992). Chemical

and hydrobiological responses to the liming were monitored and the observations were compared to those from the untreated basin until the autumn of 1992 (Rask 1991, Järvinen & Rask 1992, Rask *et al.* 1995) and the occurrence of the fish kill. Monitoring of the limed basin is still ongoing although the observations from the control basin can no longer be used as a reference. Instead, the chemical and biological changes in the control basin recorded after the fish kill are compared both with the records before the fish kill and those from the limed basin.

Samples for water chemistry and the plankton community have been taken at an interval of two weeks to one month since 1990. For details, see Järvinen *et al.* (1995). Quantitative samples for zoobenthos were taken from five permanent sampling points (one sample = five lifts) with a 64 cm² Kajak-type tube sampler once a month from May to September. Free swimming aquatic invertebrates were sampled with activity traps (Pöysä *et al.* 1994). The perch population have been sampled monthly from May to September each year since 1990. Fifty perch were caught from each basin with wire traps (1 cm square mesh), measured to the nearest millimetre and gram, sex determined, and sampled for growth (operculum) and diet (stomach). Each spring the size of the catchable perch (> 8.5 cm) population was estimated by the Schnabel method (Krebs 1989). The fish were caught with traps (six traps per basin), measured to the nearest cm for length frequency distribution (Table 2), fin clipped, and released immediately. Total mercury concentrations of perch were determined in the laboratory of the Finnish Environment Agency. Samples were taken from the dorsal axial muscle and the analyses were conducted according to Armstrong and Uthe (1971). The radioactivity of the perch was analyzed in the Finnish Centre for Radioactivity and Nuclear Safety using gamma-spectrometric methods (Saxén 1990). Waterfowl censuses have been made since 1989 every second week between early May and mid August (Pöysä *et al.* 1994).

3. Results and discussion

3.1. Water chemistry

The decay of fish carcasses in the control basin of L. Iso Valkjärvi in late autumn and winter 1992–93 remineralized high amounts of nutrients near the bot-

Table 1. Morphometric and hydrological characteristics of the two basins of Lake Iso Valkjärvi.

	Control basin	Limed basin
Surface area (km ²)	0.0157	0.0221
Catchment area (km ²)	0.0724	0.0976
Maximum depth (m)	5.5	8.0
Mean depth (m)	2.8	3.8
Volume (m ³)	45 070	83 810

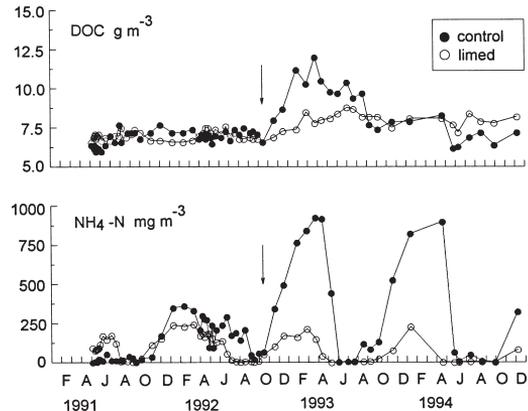


Fig. 1. The concentrations of dissolved organic carbon (DOC) and ammonium-nitrogen at 4–5-m depth in the control and limed basins of L. Iso Valkjärvi. Arrow indicates the time of the fish kill in the control basin.

tom of the lake. The concentrations of DOC increased in the hypolimnion from 6–8 mg/l to 9–12 mg/l during the winter 1992–93 (Fig. 1). The hypolimnetic concentrations of ammonium-nitrogen (NH₄-N) and phosphate also increased markedly during the stratification (Fig. 1). This was at least partly due to increased hypolimnetic anoxia and reduced redox potentials. The concentrations of NH₄-N were also higher in the epilimnion in 1993–1994. Beneath the ice the concentrations of total nitrogen and phosphorus were high in the winters 1992–93 and 1993–94.

The effects of fish decay on nutrient concentrations could mainly be found in the hypolimnetic water. Epilimnetic concentrations of nutrients remained more or less at the same level as before the fish kill. About two years after the fish kill, the hypolimnetic concentrations of nutrients had returned to the pre-fish kill levels. Decomposition resulted in low redox potentials, which were followed by increased concentrations of iron (Fe) in the hypolimnion. This, and increased DOC, resulted in higher water colour values in the hypolimnion in 1993.

3.2. Plankton community

Hypolimnetic densities and biomasses of bacterioplankton increased after the fish kill (Fig. 2). This led to increased densities of protozoans deeper in the water in the late autumn–winter of 1992–1993. For example, high densities (> 300 cells/ml) of ci-

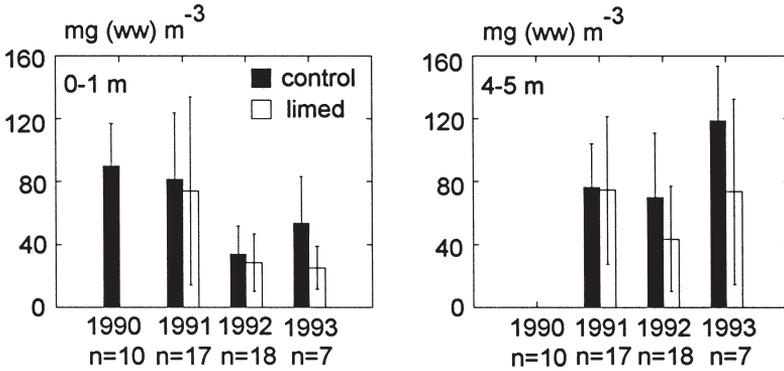


Fig. 2. Bacterial biomass (mean ± S.D.) at 0–1 and 4–5 m depth in the control and limed basins of L. Iso Valkjärvi from 1990–1993.

liates were recorded in the hypolimnion one month after the fish kill. Before the fish kill hypolimnetic densities of ciliates averaged 20–30 cells/ml (range 1–80 cells/ml). Choanoflagellates and many unidentified protozoans were also abundant following the fish kill. Although competition and predation by metazoans or oxygen depletion may markedly regulate the population size of protozoans (Stenson 1984) it implies that in the hypolimnion of the control basin of L. Iso Valkjärvi, the increase in the densities of protozoans could mainly be related to increased bacterial numbers.

Biomass and primary production of phytoplankton was very low in the summer of 1993 if compared to the period 1990–1992 before the fish kill (Fig. 3). Epilimnetic biomass of phytoplankton has also remained low after 1993. The decrease in algal biomass was mostly due to a decreased abundance of the large-sized flagellate *Gonyostomum semen*,

which has dominated the phytoplankton biomass since the 1980's. After the fish kill, other large mainly colonial species (*Uroglena sp.*, *Chrysostephanosphaera globulifera*), increased their proportion in the total algal biomass. In planktivore-dominated lakes, excretion by fishes may dominate phosphorus recycling through algae (Schindler *et al.* 1993). One possible explanation for the decreased algal biomass in the control basin could be a decreased availability of P after the disappearance of perch. Since the nutrients released in the hypolimnion by decomposition did not enrich the surface layers of the lake, the epilimnetic phytoplankton community may have been strongly nutrient limited.

During the two years following the fish kill, the crustacean zooplankton densities of the ice-free season were lower in comparison with the preceding years (Fig. 4) and the limed side of the lake. This was mainly due to a collapse of the dominating

Table 2. The length frequency distribution of perch in caught during the marking and recapturing Lake Iso Valkjärvi in the period 1990–1995. L = limed basin, C = control basin.

Year L/C	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
1990		36	578	813	1 003	150	80	65	35	15	6	4		2 785
1991 L		37	400	388	100	39	22	8	1					995
1991 C		39	414	455	110	44	31	9	4	4				1 110
1992 L			31	497	359	97	40	18	11	1	4			1 058
1992 C			1	114	688	318	75	36	11	3	4	1		1 251
1993 L				1	53	460	371	175	108	40	18	9	3	1 238
1993 C				2	9	13	6	2	2			1		35
1994 L		3	10		7	116	253	85	51	16	10	1	4	556
1994 C		89	103	14				4			1	2	6	219
1995 L		1	4	35	83	103	217	256	95	48	12	11	2	867
1995 C		3	88	388	290	106	30	9	5	3	2	1	2	927

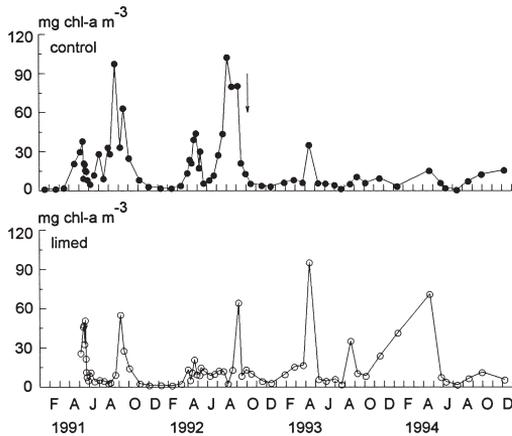


Fig. 3. Algal biomass at 0–1-m depth in the control and limed basins of L. Iso Valkjärvi from 1991–1994.

cladoceran *Ceriodaphnia quadrangula* and the copepod *Mesocyclops leuckarti*. Densities of another dominating cladoceran, *Bosmina longispina*, and the copepod *Cyclops strenuus* remained at the same level, whereas reduced predation by fish apparently allowed the large cladoceran *Holopedium gibberum* to increase in abundance. With the exception of the winter months, rotifers (mainly *Kellicottia bostoniensis*, *Keratella cochlearis* and *Polyarthra* spp.) were numerous after the fish kill, probably as a result of reduced food competition by cladocerans and reduced predation by *Mesocyclops*.

Increased predation by invertebrate predators was probably initially responsible for the altered zooplankton composition. The vulnerability of small zooplankton to invertebrate predation is well documented (e.g. Zaret 1980). Larvae of phantom midges were abundant the first year following the fish kill (Fig. 4) in zooplankton samples taken with a tube sampler. There was also a clear increase in the number of corixids in the catches of activity traps (Fig. 5). Predaceous corixids are known to colonize limnetic habitats when the fishes disappear (Henrikson & Oscarson 1985) and, together with chaoborids, prey on crustacean zooplankton (Nyman et al. 1985). In L. Iso Valkjärvi the invertebrate predators probably preyed heavily on small crustaceans, especially *Ceriodaphnia*, leaving rotifers to dominate over most of the ice-free season. Stenson *et al.* (1978) found an increase in invertebrate plankton predators after fish removal from a small lake and consequently a shift from a dominance of small cladocerans to a dominance of large calanoid

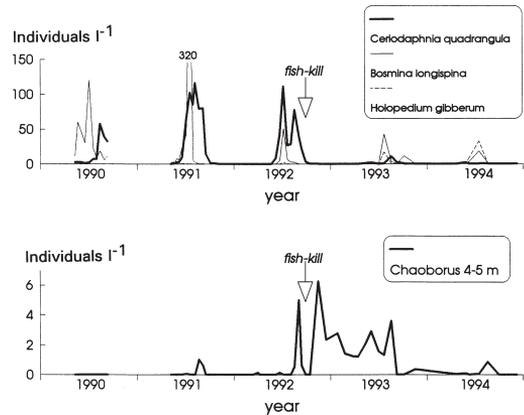


Fig. 4. The densities of the most abundant cladocerans (top) in the epilimnion and *Chaoborus* larvae in the hypolimnion (bottom) of the control basin of L. Iso Valkjärvi from 1990–1994.

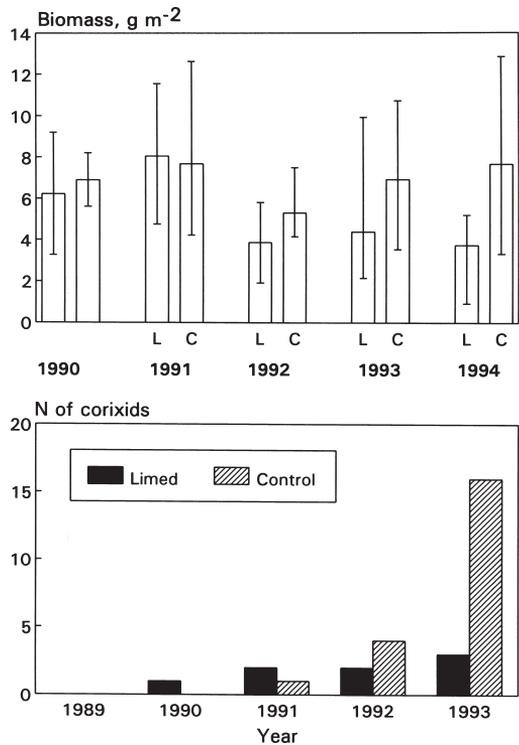


Fig. 5. The mean total biomasses of zoobenthos in L. Iso Valkjärvi in September 1990–1994 (top, L = limed basin, C = control basin, error bar = range) and the number of corixids per 100 trap days in the activity traps of L. Iso Valkjärvi from 1989–1993 (bottom).

copepods. In L. Iso Valkjärvi, however, no corresponding increase in the amount of calanoid copepods was recorded.

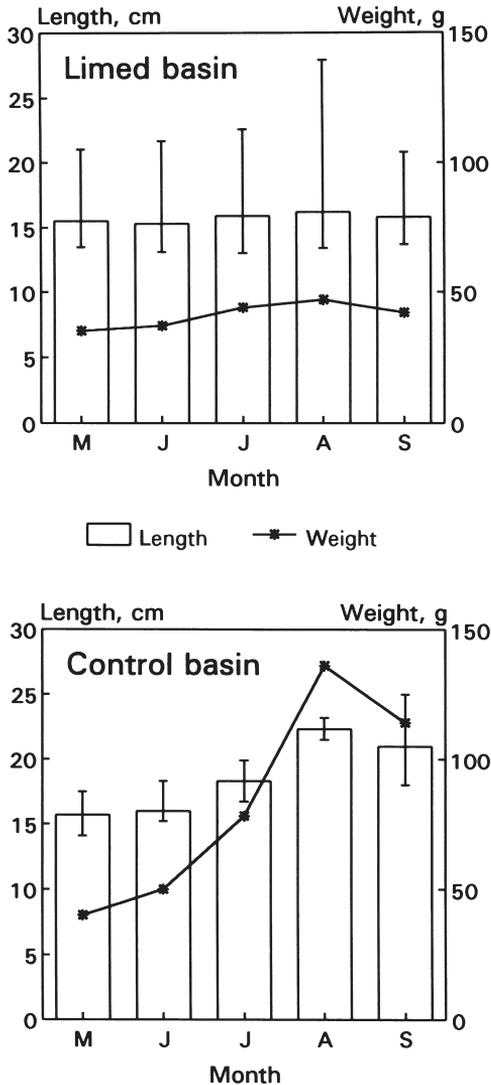


Fig. 6. The mean length and mean weight of perch in the limed and control basin of L. Iso Valkjärvi in the 1993 growing season. The number of fish in monthly samples was 50 in the limed basin and 5–13 in the control basin. Error bars = range of length.

3.3. Macroinvertebrates

According to samples taken with a tube sampler in September of 1990 and 1991, the total biomasses of zoobenthos in both basins of Lake Iso Valkjärvi averaged between six and eight grams (fresh weight) per square metre (Fig. 5). In 1992, the biomasses were lower, due perhaps to an increase in the mean size of perch and their subsequent shift to a predomi-

nantly zoobenthos diet rather than zooplankton. In the limed basin, there has been no trend in the zoobenthos biomass since 1992 although variation between sampling points has been wide. However, after the fish kill, the zoobenthos biomass of the control basin showed an increase and was twice as high as in the limed basin in September 1994 (Fig. 5). Due to wide variation in both basins, the differences between the basins were not statistically significant (t -test, $P > 0.1$).

Based on the material collected with the activity traps, a number of responses to the fish kill were also recorded. For example, the number of littoral cladocerans as well as of caddis larvae (Trichoptera) increased. The clear increase in corixids (Fig. 5) could also be recorded visually. These kinds of responses have been commonly recorded in lakes that have lost their fishes due to acid precipitation (Eriksson *et al.* 1980, Stenson *et al.* 1993).

3.4. Perch

In 1990, the population was estimated at 11 500 perch of catchable size (> 8.5 cm) with the corresponding density 2 900/ha (Rask 1991). The fish were mostly from the abundant 1988 year-class. In spring 1992 the same year-class still dominated and the density of perch was 1 800/ha in both basins of the lake. After the fish kill, there were very few perch left in the control basin (Table 2) and their density was less than 50 per hectare (Pöysä *et al.* 1994).

The disappearance of more than 95% of the perch population in the control basin resulted in a dramatic change in food availability for the remaining perch. This, in turn, caused a very clear growth response. While almost no changes took place in the mean length or weight of perch in the limed basin during the 1993 growing season, the few perch left in the control basin grew very well (Fig. 6). Their mean length increased from 15 to 20 cm and their mean weight at the end of the growing season was more than twice as high as in the spring.

Mercury concentrations in perch from L. Iso Valkjärvi were first measured in 1983 (Metsälä & Rask 1989). Since then, there has been some decrease in concentrations and the level has been 0.2–0.3 $\mu\text{g/g}$ in recent years (Fig. 7). In 1991 and 1992 no essential differences appeared between the limed and the control basin. In 1993 and 1994 the Hg concentrations of perch

in the control basin were, however, about half of those recorded earlier or those in the limed basin (Fig. 7, Rask & Verta 1995). This was interpreted as a consequence of the increased growth of the fish, the so called growth dilution (Göthberg 1983, Verta 1990).

A response similar to that recorded with Hg concentrations took place in the radioactivity of the perch. After the Chernobyl accident, the radioactivity of perch due to ^{137}Cs in Lake Iso Valkjärvi was close to 10 000 Bq/kg (Fig. 7) which was three to ten times higher than levels recorded in larger lakes in the same county (Saxén 1990). The values decreased over the years to levels at 4 000 Bq/kg and there were no differences between the limed and the control basin until, after the fish kill, the radioactivity of perch in the control basin dropped to half of the former levels. We suppose that the reason was growth dilution.

3.5. Waterfowl

In small headwaters insectivorous water birds like the common golden-eye may compete for food with fish and especially with perch. High overlap in diet and observations from acidified lakes with sparse fish populations support the existence of these kinds of interactions (Eriksson 1979, McNicol & Wayland 1992, Pöysä *et al.* 1994). In L. Iso Valkjärvi no changes were recorded in the behaviour of adult golden-eyes after the fish kill whereas the broods clearly increased use of the control basin and decreased use of the limed basin (Pöysä *et al.* 1994). The liberation of competition between perch and the common golden-eye after the perch crash is the most evident explanation for the change. The fact that the remaining few perch in the control basin grew so well is direct evidence of food limitation before the collapse of the population. Data from other lakes in the study area also indicate that food abundance is important in lake selection by common golden-eye broods (Pöysä & Virtanen 1994, Pöysä *et al.* 1994, see also Eriksson 1978).

4. Conclusions

Our observations emphasized the role of a perch population in regulating the structure and function of the entire ecosystem of a lake. Some of the re-

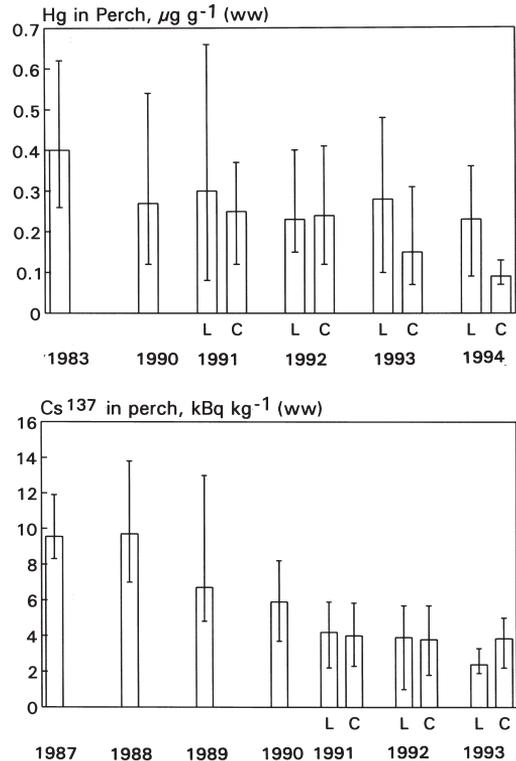


Fig. 7. The mean mercury concentrations from 1983–1994 (top) and the mean radioactivity from 1987–1993 (bottom) of perch in L. Iso Valkjärvi. L = limed basin, C = control basin, error bars = range.

sponses, like those recorded in macroinvertebrates, were clearly consumer based due to the disappearance of fish predation. On the other hand, the increased growth of the perch remaining after the fish kill clearly demonstrated the resource limitation (intraspecific food competition) of the perch population at “normal” densities. This is further emphasized by food competition with the common golden-eye. At lower trophic levels, distinguishing between the effects of resource based and consumer based factors was more difficult.

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