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Year-class fluctuations of perch (*Perca fluviatilis*) in Lake Pyhäjärvi, Southwest Finland

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Year-class variation of perch (*Perca fluviatilis*), a potentially important predator of larval and juvenile vendace (*Coregonus albula*), was assessed in Lake Pyhäjärvi, based on a two-stage sampling of the winter seine net catches in 1989–1995. From these data, we could estimate relative abundances of perch year-classes for the years 1986–1993. During this period, the year-classes of 1988 and possibly 1992 were strong. The year-class 1988 dominated numerically in catches from 1990 to 1993 and the year-class 1992 in 1994 and 1995. Year-class strength of perch was positively associated with the June–August temperature sum.

1. Introduction

Lake Pyhäjärvi in southwest Finland is known for its flourishing fisheries, mainly based on the coregonids vendace (*Coregonus albula*) and whitefish (*C. lavaretus*), introduced into the lake during this century (Sarvala *et al.* 1994). Most of the annual fish catches arise from winter seining for vendace in the ice-covered lake.

Fish data from Lake Pyhäjärvi are available since the start of this century. A regular monitoring scheme for vendace and whitefish was initiated in the early 1970s. In the 1980s these studies developed into more comprehensive whole-ecosystem research programs (Sarvala *et al.* 1984), which are being continued through the 1990s in connection with a program to combat eutrophication.

During the 1990s the previously relatively stable vendace stock has declined and, at the same time, increasing amounts of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernuus*) and smelt (*Osmerus eperlanus*) have been landed as a by-catch of the fishery for the more valuable coregonids (Helminen *et al.* 1995). Recent population analyses suggest that the final year-class strength of vendace in Lake Pyhäjärvi is to a large extent determined through the predatory mortality of the early larvae (Helminen & Sarvala 1994), with the two-year-old perch the most likely predator affecting vendace larvae in this lake (Helminen & Sarvala 1994). Therefore, a more detailed study into the year-class formation and fluctuations of perch was initiated. Here we describe the recent year-class fluctuations of perch in Lake Pyhäjärvi, and try to link these to environmental variation, mainly to varying temperature conditions.

2. Study area, materials and methods

Lake Pyhäjärvi is a fairly large (area 154 km^2), shallow (mean depth 5.4 m) and mesotrophic (total phosphorus level

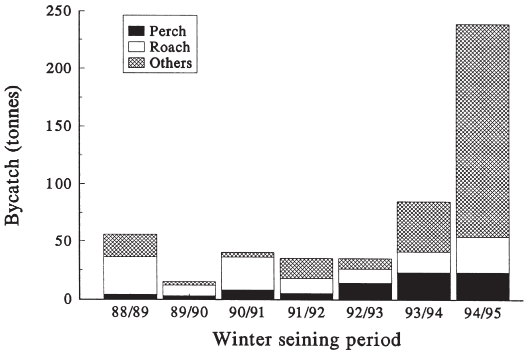

Fig. 1. Non-coregonid by-catches in the winter seine fishery for vendace in Lake Pyhäjärvi 1988–1995. The group 'others' consists mainly of smelt and ruffe.

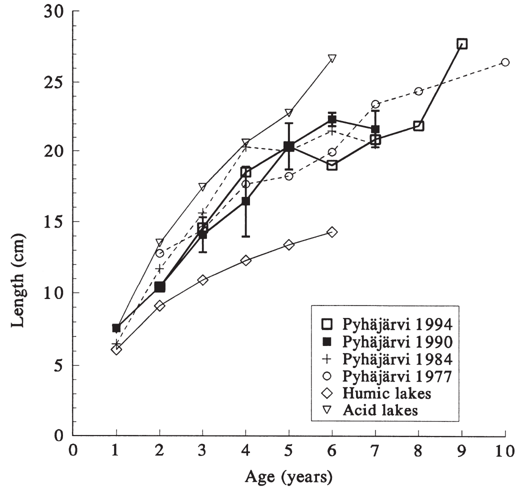

Fig. 2. Length at age of perch in Lake Pyhäjärvi in the autumns of 1977, 1984, 1990 (± *S.D.*) and 1994 (adjusted from Sarvala *et al.* 1994; year 1994 added). Average length at age in the dense populations of small humic forest lakes and in the sparse populations of acidified lakes (Rask & Raitaniemi 1988) indicate the lowest and highest growth rates of perch in southern Finland.

in water 12–19 mg m^{-3}, chlorophyll 4–6 mg m^{-3}, phytoplankton primary production 26–56 g C m^{-2} a^{-1}) lake in southwestern Finland (60°54–61°06'N and 22°09'–22°25'E). There is no permanent temperature stratification during summer, and maximum temperatures may exceed 24°C. Owing to the simple morphometry of the lake, seine net fishing is relatively easy over a large part of the lake (Helminen *et al.* 1993b).

Catch statistics for all fish species are reported annually by the Pyhäjärvi fisheries management association. For the commercially most important species, vendace, usually at least 70% of the total catch occurs during the winter seining period. In the 1970s and 1980s, until 1993, vendace and whitefish accounted for over 70% (Sarvala *et al.* 1994, Helminen *et al.* 1995), and perch for under 10% of the total catch.

In connection with studies on the population dynamics of vendace, since winter 1988–1989, we have applied a two-stage sampling strategy to work out the age and size composition of the winter seine net catches of vendace and whitefish (Helminen *et al.* 1993a). From 1989–1990 we have also recorded more detailed information on the by-catch species, including perch, roach, ruffe, smelt and bream. The sampling dates were distributed throughout the winter seining period, which extends from November–January to late March or April, depending on the ice cover (Table 1). On each date, the primary sampling units were sleigh loads of unequal size and the secondary units were 12-kg fish boxes. The number of primary units varied from two to four and the number of secondary units from one to three. All fishes in each box were sorted into species, age or size groups, weighed, and subsampled for individual measurements.

Sampled perch were subjectively sorted into homogeneous size groups, which were weighed and counted separately. The mean individual mass in each lot was compared to observed growth curves to work out the probable age of the group. Unsorted samples for age and growth determinations (age from opercula and otoliths) were taken in two winters, 1990–1991 ($n = 51$) and 1994–1995 ($n = 211$).

The total catch of perch was inferred from the known catches of vendace during the winter seining period and from the proportion of perch observed in the catch samples. In winter 1994–1995, fishing of the less valuable fish species was financially subsidized to attempt to improve the fish community structure and existing water quality. The collection and transport of these fish was arranged by one local company, which provided an accurate figure for the total subsidized fish catch. This figure (191.6 tonnes) was satisfactorily close to the estimate based on our routine catch sampling scheme (216.5 tonnes; without large perch, because they were not included in the subsidized catch), indicating that the latter gave an acceptable description of the fishery.

The numbers of each age group in the catch were calculated by dividing the total perch catch estimate between the age groups according to biomass distributions in the catch samples, and dividing these age-specific catches by the mean individual mass of the respective group. Relative year-class strength was assessed from the numbers caught at ages 2, 3 or 4, or from the cumulative numbers of the year-class caught during the whole study period.

Water temperature data for the years 1970–1992 were obtained from weekly measurements made by the power station of Ahlstrom Oy near the outflow and from our own more frequent measurements as described in Helminen & Sarvala (1994). Temperature data for 1993–1994 were recorded in connection with water quality sampling by the Turku Water and Environment District Laboratory.

3. Results

Winter seine catches of perch increased from 4 and 3 tonnes in winters 1988–1989 and 1989–1990, respectively, to 23 tonnes in winters 1993–1994 and 1994–1995 (Fig. 1). Smelt and ruffe catches showed an even steeper increase in the last-mentioned two winters.

Perch in Lake Pyhäjärvi grow moderately well, reaching a length of 20 cm after five growing seasons (Fig. 2). Utilizing an age-length key, the youngest age groups, up to the age of 4, could be relatively easily discerned from the size distribution (Fig. 3). The separation of older age groups was more uncertain because of the large size overlap between adjacent age groups and the small number of big fishes in the samples. Perch recruited to the winter seine fishery after two growing seasons, when they were about 10 cm long and weighed 11–14 g, but they seemed to be fully recruited after three growing seasons at a length of 12–16 cm and mass of 25–30 g (Figs. 3 and 4). At older ages the numbers in the catch declined (Fig. 5); the oldest perch aged was 10 years old.

From the winter 1989–1990 to 1992–1993 the interpretation of the catch data was straightforward, because the 1988 year-class contributed the majority of the catches (85–96% of total numbers; Fig. 4). The steadily increasing average individual mass of perch during these four years (26, 36, 46, and 77 g, respectively) also reflected the total dominance of a single year-class. In 1993–1994 and 1994–1995 the catches divided more evenly among several year-classes, and reliable separation of the adjacent groups became more difficult. Fortunately, the age groups 2–4, which made up the major part of the catches, were the most readily identifiable.

The numbers of fish caught at the ages 2, 3 and 4 indicated strong year-classes in 1992 and 1988, moderate in 1991 and 1993, and weak in other years (Fig. 6). However, such catch-at-age figures are sensitive to between-year variation in the effectiveness

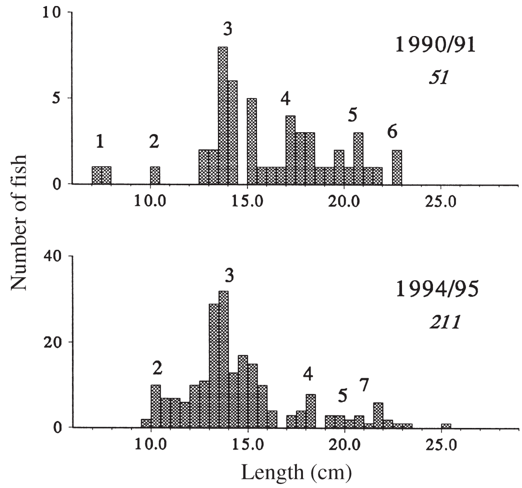

Fig. 3. Length distributions of perch in the winters 1990–1991 and 1994–1995. Sample sizes shown in italics below the year. Numbers above bars indicate age groups based on operculum and otolith readings.

of fishing, and there were significant qualitative changes in the fishery during the study period. The number of seine net licences was 10 in 1988 and 7–8 in all other years, but actually only six of the seining crews were actively fishing each winter. Judging from the constant number of active crews, there were probably no major changes in the total fishing effort. However, when commercial markets for perch started to develop in the 1990s, seine nets and seining techniques were adjusted to enable more efficient catching of perch, when earlier it was being avoided. There was a good market for big perch for the first time in winter 1993–1994, and in winter 1994–1995 there was also a demand for small perch. Finally, in winter 1994–1995, all non-coregonid catches were subsi-

Table 1. Data on perch samples obtained in 1988–1995 from the winter seine net fishery in Lake Pyhäjärvi, southwest Finland. The length of the sampling period, the number of sampling dates, the total number of sleigh loads sampled, the total mass and numbers of perch sampled for generating the size distributions, and the mass proportion of perch in the total winter seine catch are shown for each winter.

Winter	Sampling period	No. of dates	No. of sleigh loads	Total sample size g	Total sample size Indiv.	Perch in total catch%
1988–1989	11 Jan–16 Mar	6	17	–	–	1.0
1989–1990	18 Dec–02 Mar	5	13	862	33	0.9
1990–1991	26 Nov–28 Feb	9	25	23 223	644	5.6
1991–1992	11 Jan–23 Mar	9	16	7533	164	2.6
1992–1993	26 Nov–24 Mar	7	11	21 605	280	8.9
1993–1994	30 Nov–07 Apr	5	8	13 530	194	12.7
1994–1995	11 Jan–05 Apr	6	13	11 949	309	7.0

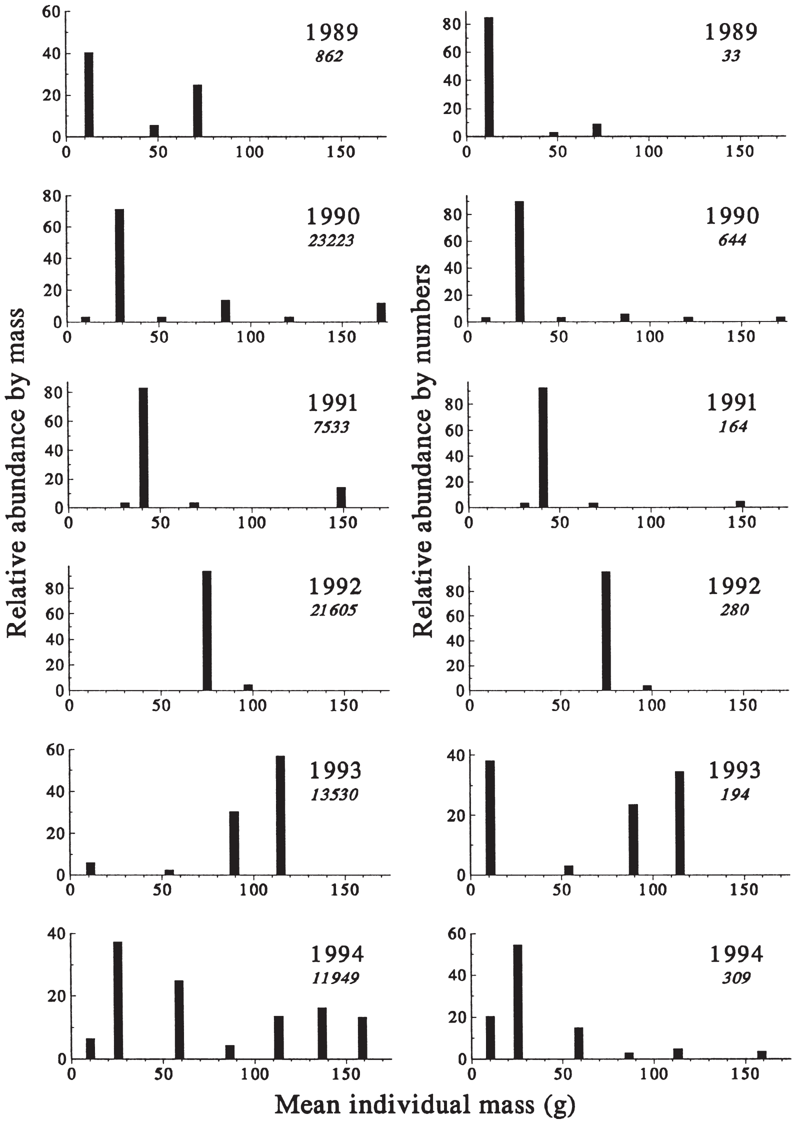

Fig. 4. The contribution of different size groups to the total catch samples of perch in Lake Pyhäjärvi from 1989–1990 (= 1989) to 1994–1995 (= 1994), based on mass (left) or numbers (right) (for clarity, the smallest percentages have all been rounded upwards to 3%).

dized for one month (March), and this increased the total non-coregonid by-catch to about 240 tonnes. This was mainly composed of smelt, but also perch catches peaked. These qualitative changes in fishery were likely to bias our catch-at-age data. The total numbers of perch caught during the winter, which varied between 110 000 and 220 000 in 1989–1993, increased to 330 000 in 1993–1994 and to 640 000 in 1994–1995. Accordingly, the numbers of the 1992 year-class caught almost tripled from age 2 (winter 1993–1994) to age 3 (winter 1994–1995), yet accounted for only 54% of the total numbers caught in 1994–1995. Unexpectedly large numbers of big old perch probably belonging to the 1986 year-class were caught in both 1993–1994 and 1994–1995. The influence of the behaviour of the fishermen was most clearly seen for the 1991 year-class, which was absent from the catch samples of previous winters, but appeared abundantly in the samples in 1994–1995. Thus, it seems clear that our catch-at-age data overestimate the strength of the year-classes 1991, 1992 and 1993 compared to the earlier year-classes.

The cumulative numbers of a year-class caught during the whole study period suggested strong year-

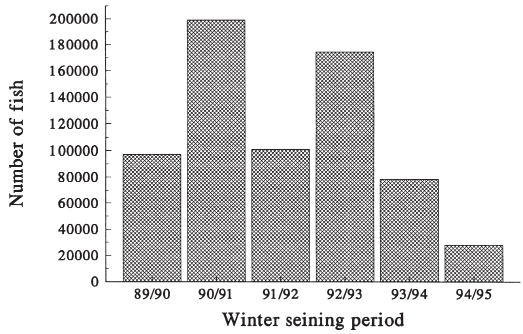

Fig. 5. The numbers of the 1988 year-class of perch caught in seine net fishery in successive winters.

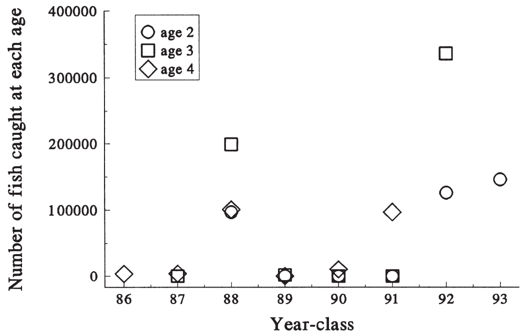

Fig. 6. Perch year-class strength for the year-classes 1986–1993, expressed as numbers caught in the winter seine fishery at ages 2, 3 or 4 years. High catches of the year-classes 1991–1993 partly reflect the intensified fishery in winter 1994–1995.

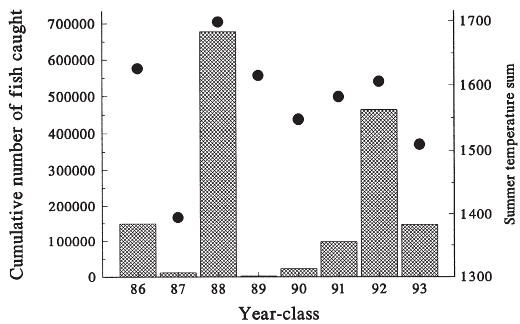

Fig. 7. Perch year-class strength for the year-classes 1986–1993, expressed as the cumulative numbers of each year-class caught in the winter seine fishery during the whole study period. Dots show the June–August temperature sum (over zero).

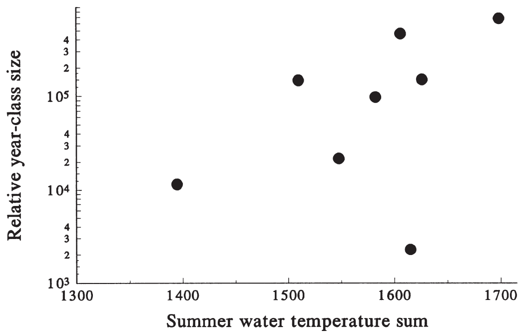

Fig. 8. The relative year-class strength (as cumulative numbers in catch) of perch in Lake Pyhäjärvi plotted against the June–August temperature sum (year-classes 1986–1993).

classes in 1988 and 1992, moderate in 1986, 1991 and 1993, and weak in other years (Fig. 7). Although the cumulative numbers underestimate the strength of the youngest year-classes, which are still to be caught in future years, they effectively smooth out chance variation and varying fishing effort.

Allowing for the bias caused by fishery changes, both catch-at-age and cumulative catch measures thus gave roughly similar results: the year-classes 1988 and 1992 were strong, those of 1986 and 1993, and perhaps 1991, were moderate, while the year-classes of 1987, 1989, and 1990 were very weak. The year-class 1988 numerically dominated the catches from 1990 to 1993. The year-class 1992 dominated the following two winters and may continue to dominate for two–three more years.

In Pyhäjärvi, perch spawn soon after the ice-out, and the larvae appear in net samples usually in late May. They reach their final size for the first season by the end of August. Therefore, the conditions during June–August can be considered most important for the success of a perch year-class. Accordingly, the relative strength of the perch year-classes 1986–1993 in Pyhäjärvi (measured at the age of 2, 3, 4 or as the cumulative numbers caught) seems to be associated with the temperature sum (over zero) for June–August (Fig. 7; because only eight year-class estimates were available, we refrain here from any statistical analyses). The relationship seemed to be curvilinear, and could be linearized by taking logarithms of the year-class strength (Fig. 8). In the linearized figure, the year-class 1989 clearly deviates downwards from the general trend.

The seasonal temperature course may differ in significant ways even between favourable summers

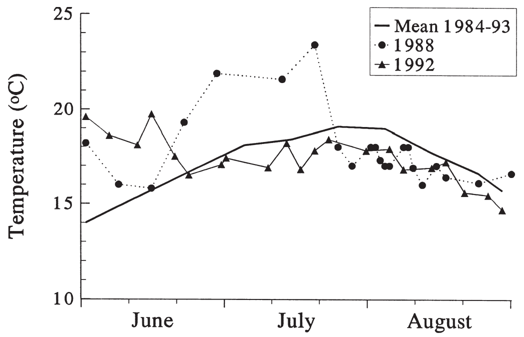

Fig. 9. The development of summer temperature in Lake Pyhäjärvi in 1988 and 1992, compared with the mean course of temperature in 1984–1993.

(Fig. 9). In general, the largest differences appear in spring and early summer, while the late summer temperatures show much less between-year variation. In 1988, when the exceptionally strong perch year-class was born, early and late June and the whole of July were particularly warm; in 1992, only June was warmer than average (Fig. 9).

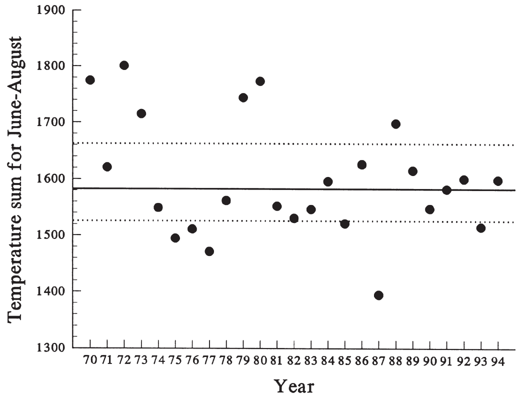

Fig. 10. Summer temperature variation in Lake Pyhäjärvi in 1970–1994, as seen in the temperature sum for June–August. Median for the whole period shown with a solid horizontal line; dotted lines indicate the first and third quartiles.

4. Discussion

Strong year-class variations are typical for perch populations (LeCren 1987, Mills & Hurley 1990, Buijse *et al.* 1992). In our study, perch year-class strength varied over more than two orders of magnitude during a period of eight years. The assessment of the absolute size of perch populations is always difficult, especially in moderately large lakes, such as Lake Pyhäjärvi. However, when there are large differences in recruitment among years, the relative year-class strengths can be determined. In Lake Pyhäjärvi, we had to rely on data from winter seine fishery, which certainly includes only a part of the total perch population. Yet it was possible to establish the relative strength of the individual year-classes with acceptable confidence. The uncertainties inherent in our data had least influence on the strongest and weakest year-class estimates.

Our data suggest a positive correlation between perch year-class size and summer temperature. A similar relationship has been well established in several studies (LeCren 1987, Mills & Hurley 1990, Böhling *et al.* 1991, Lehtonen & Lappalainen 1995). The actual mechanisms translating high summer temperatures into year-class success are, however, less well documented. Temperature exerts a direct physiological influence on metabolism and growth, but it also has indirect effects on growth via food production. First-year growth is known to be positively associated with survival (e.g. Mills & Hurley 1990, Karås & Thoresson 1992), but the relationship between temperature and mortality is more complex. All biotic interactions, such as competition and predation, are in many ways dependent on temperature, as was clearly shown by Mills and Hurley (1990). It is perhaps noteworthy that in Pyhäjärvi also the vendace year-class hatched in 1988 was exceptionally strong; yet the late summer crustacean zooplankton biomass remained moderately high (Sarvala & Helminen 1995). This suggests that, at least during warm summers, such as summer 1988, food competition between the planktivorous perch and the young-of-the-year vendace does not limit their success. The situation may be different in cold summers, however, because zooplankton production is highly dependent on temperature.

Using the relationship with the June–August temperature sum, it is possible to hindcast perch year-class sizes from the historical temperature data in Lake Pyhäjärvi (Fig. 10). Especially strong perch year-classes should have been born in 1970, 1972, 1973, 1979, 1980, and 1988. Temperature conditions were moderately favourable for perch recruitment in 1971, 1984, 1986, 1989, 1991, 1992, and 1994. The weakest year-classes were anticipated for 1975–1977, 1985, 1987, and 1993. For 1987 and 1988 this pattern was corroborated in the present study; for 1991–1993, further data are needed for the final evaluation of year-class strength. The year 1989 clearly deviated from the pattern: temperature conditions predicted a moderately strong perch year-class, while the realized year-class was the weakest during the whole study period. The poor success of the 1989 year-class might be due to predation on newly-hatched larvae in spring by the one-year-old perch of the preceding very strong 1988 year-class. Cannibalistic suppression of perch recruitment by large perch has been reported several times earlier (e.g. Craig 1982), and the potential for cannibalism on larvae by perch yearlings was recently suggested by H. Schultz, F. Wieland and M.-G. Werner (unpubl.). On the other hand, owing to strong winds, the break-up of ice in 1989 was exceptionally early (partial ice-out in late March and complete ice-out by mid-April), and the temperature increase in April–May was very slow. A similar situation prevailed in spring 1990. The unfavourable temperature development may have contributed to a poor survival of perch larvae.

Earlier data also contain some indications of the strong perch year-classes. In experimental gill net fishing with 12–75 mm mesh nets (knot to knot) in Pyhäjärvi in 1984, the peak in perch size distribution was around a mass of 100 g, a size to be then expected for perch born in 1979 or 1980 (total sample size about 2 000 perch; own unpublished data). A similar situation as regards the potentially strong 1972 and 1973 year-classes prevailed in 1977 (P. Ahlfors, unpublished data). A corresponding climatically driven pattern of year-class variation seems to apply throughout southern Finnish perch populations: along the Baltic coasts of Finland and in Lake Lohjanjärvi, between 1971 and 1986, the perch year-classes of 1972, 1973, 1979 and 1980 were noted as being strong, in complete agreement with our hindcasts for Lake Pyhäjärvi, and those of 1974, 1977 and 1981 were weak (Lehtonen & Lappalainen 1995).

In the multiple regression model describing vendace population dynamics in Lake Pyhäjärvi during 1972–1990, we used the water temperature sum for June–August to indicate the year-class strength of perch (Helminen & Sarvala 1994). In the present study we could confirm that summer temperature sum can indeed be used to forecast perch abundance in Pyhäjärvi. Further refinements of the temperature-dependence of perch year-class formation may be possible by applying higher threshold values for the temperature sum (e.g. degree-days over 14°C as used for perch in lakes Windermere and Ijssel; LeCren 1987, Buijse *et al.* 1992), or including the effect of daylength (Karås & Thoresson 1992).

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