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The vendace stock and fisheries in Lake Inari

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Vendace (*Coregonus albula*) has a short history (30–40 year) in Lake Inari, being introduced into the watercourse in the 1950s and 1960s. The growth of the stock was slow at the beginning, but increased rapidly in the 1980s due to three strong, successive year classes in 1983, 1984 and 1986. All these years, and also in 1989, summers were quite warm and the water temperature favourable after the ice-break. The peak stock size was recorded 1987, and after that, there was a slump. In the middle of the 1990s, the stock size had stabilized to a very low level compared with the situation in the end of 1980s, and the vendace stock concentrated mostly in the southern parts of the lake. The vendace fishery flourished for less than five years. The peak year concerning fisheries and catches was 1989 with a vendace catch of nearly 3 kg ha^{-1} and a total catch of about 5 kg ha^{-1}, rather high figures in subarctic northern regions. After 1989, the vendace catch decreased rapidly. It seemed that the fishing effort of some years (1989 and 1990) was so heavy that the spawning stock size gradually decreased to a level, where the revival was difficult. Unfavourable weather conditions with cold summers at the beginning of 1990s, and, at the same time, quite hard pressure of predation by abundantly stocked salmonids on vendace contributed together to the fact that only very scanty year-classes were born. This, in turn led to a collapse of the vendace stock in the 1990s.

Introduction

Vendace (*Coregonus albula* L.) was introduced into Lake Inari (around 69°N) and the Paatsjoki system in Finland — north of its natural distribution area — in the 1950s and 1960s. Elsewhere, the north distribution border of the species reaches Nuorttijärvi (68–69°N), a part of the Russian Tuloma river system bounded in the west by the Paatsjoki system. The aim was to stock vendace fry only into the tributary river systems in the Inari area, not into Lake Inari itself. However, the species spread accidentally into the southern parts of the lake from the west, via rivers Juutuanjoki and Ivalojoki (Fig. 1). Vendace was first found in Lake Inari in 1973, and the test fishings of 1983–84 showed that the species had already spread throughout the lake (Sergejeff 1985, Mutenia and Salonen 1992). Thus, the history of vendace is very short in the area, only 30–40 years.

With a growth in the vendace population, fishing for this species began in the middle of the 1980s when fishermen started to buy special vendace gillnets. Prior to that, only fine-meshed nets were

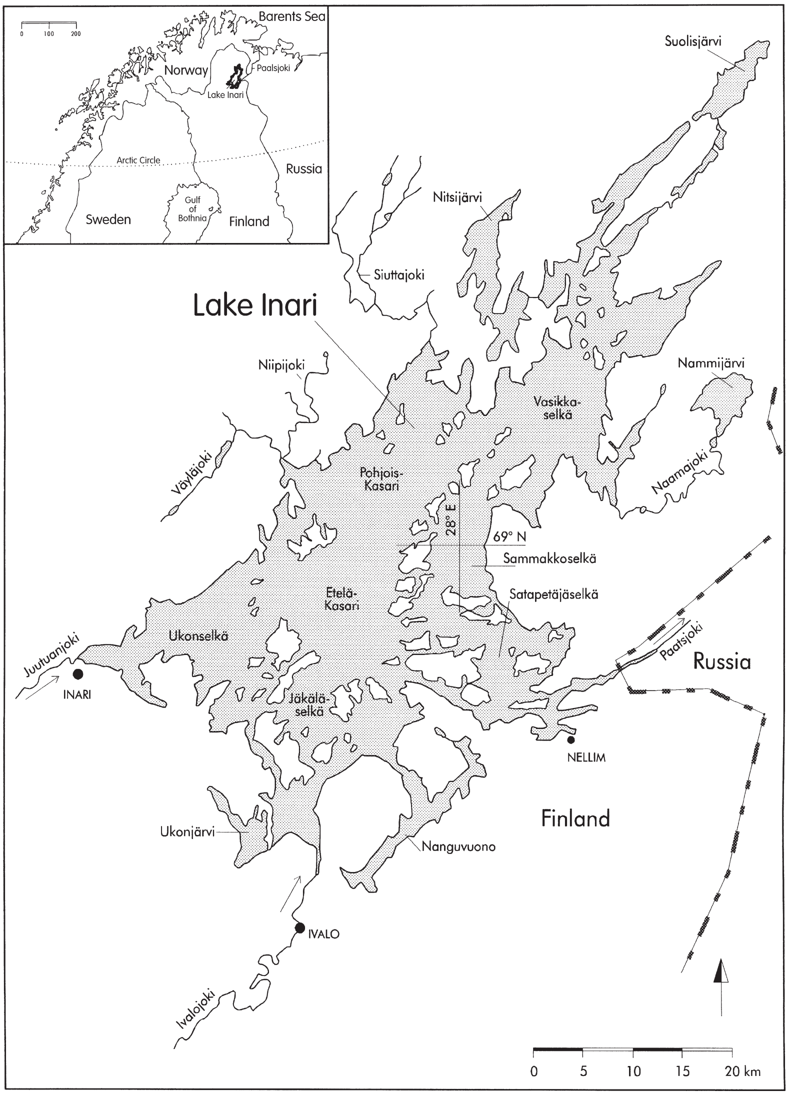

Fig. 1. Map of Lake Inari with the most important inflowing rivers and the outflow (Paatsjoki).

used for catching dwarf whitefish. More extensive fishery for vendace began in 1987 when new fishing methods were, after a testing period, taken into use in Lake Inari (Mutenia and Ahonen 1990). Modern, professional fishery with winter seines, trawls and large trapnets developed surprisingly fast due to a loose fishing permit policy, an economic upswing, and a generous subsidy policy in the end of the 1980s. The vendace catch had been, however, very high (over 300 tonnes at its highest) only for a few years, and dropped to 10 tonnes by 1994–96.

No research was conducted on the development of the vendace stock until the mid 1980s, but apparently the strongest population growth took place quite rapidly in the 1980s because of a few strong year classes. There has been a lot of discussion on the growth, and especially on the drastic decrease of the vendace population in the area. A common argument has been that the slump was caused by excessive fishery, especially trawling. On the other hand, vendace stocks have fluctuated very strongly even elsewhere in Finland where vendace is a native species. In such areas, fluctuations in vendace year classes was mainly caused by environmental factors, especially temperature, by interaction with other fish species, by predation, and by competition, including intraspecific competition (according to e.g., Auvinen 1994, Salojärvi 1987). In this article, I present the development of the vendace stock and fisheries on Lake Inari on the basis of a reasonably short research period from 1980s until 1996, and I also examine some factors, like temperature, spawning population, fisheries and predation which are presumed to have had a major impact on the drastic changes in the recruitment and population size of vendace.

Material and methods

Study area

Along with Lake Saimaa and Lake Päijänne, Lake Inari is one of the largest lakes in Finland with a surface area of approx. 1 100 km^2 (Raatikainen and Kuusisto 1988). It is a very diverse and ragged lake with 3 318 islands and a 2 776-km-long shoreline. Lake Inari is located in the northernmost part of Finland (69°N, 28°E) (Fig. 1). It is a relatively deep and clear oligotrophic lake (mean depth 14.4 m, max. depth 95 m). The water quality in the lake varies so that in the south, the transparency is about 4 m and the total phosphorous content 6–7 μg l^{-1}. In the northern parts, however, the transparency is over 7 m, even 10 m, and the total phosphorous content only 3 μg l^{-1} (Marttunen *et al*. 1997). Its water level has been regulated since the 1940s (max. amplitude 2.36 m) for the production of hydroelectric power in Russia and Norway in the Paatsjoki system which drains into the Arctic Ocean. The lake is covered with ice 6–8 months a year.

There are 10 native fish species living in Lake Inari of which some species, e.g. whitefish (*Coregonus lavaretus*), include several forms. Besides these, four other fish species have been introduced into the area, and of these, the vendace has had the most significant influence on the catches and the whole ecosystem of the lake. The other important species are nowadays especially whitefish and also brown trout (*Salmo trutta m. lacustris*).

Data on fisheries and catches

The data on the fisheries and catches of the vendace are gathered every year by the Finnish Game and Fisheries Research Institute in connection with the obligatory observation procedure concerning Lake Inari. Since 1987, fishery surveys have been based on the uniform permit registers of the Finnish Forest and Park Service, and from then on, the data on fisheries and catches are quite comparable to each other. The surveys have been made in the form of mail inquiries which have usually had a reply percentage of 50%–75% among local fishery groups. The data on fishing efforts and catches of gillnet fishing are based on the fishery surveys.

Regarding trawling and trapnet fishing, the fishing permits require keeping a catch record, and the data on the fishing efforts, catches, and CPUEs have been calculated from these records. The data on trawling catches were also compared to the data given by the fish purchasers. Wintertime fishing with seines does not involve any special permits, so the catch data are based on fishery surveys or on interviews with those fishing with seines.

There are also catch records on gillnet fishing of vendace from 1985 on. The CPUEs based on these records vary a lot, and the data are only suggestive, as there have only been 1–5 gillnet fishers per year who have kept records. On the other hand, the CPUEs of gillnet fishing calculated from the fishery surveys are based on a large material. The number of fishermen who fished vendace with gillnets for their own use and answered the inquiry varied from 91 to 209 in 1987–96.

Catch samples

Since 1987, vendace samples have been collected regularly from the catches with different gear (Table 1). The aim has been to get samples from all the parts of Lake Inari where considerable vendace fishery has taken place. In recent years, vendace have only been fished for in certain areas in the southern part of the lake. A majority of the vendace samples have been collected from this area. The ages of the sampled fish were determined from the scales. This was mostly done by the same persons. In 1996, the sample-collecting period aiming at an assessment of the vendace stock had lasted for ten years.

Stock assessment with virtual population analysis (VPA)

The vendace samples were used for calculating the mean weights and age distributions by different gears. Relying on the catch data and sample material, we counted the annual catches for each age group (number of fish) and used these as the basic data for population analysis (VPA, *see* e.g. Pope 1972). The catches were also assessed by the year class, calculating the catch and accumulative catch of each year class throughout the life of the fish. The catches in kilograms by each year classes were achieved by multiplying the number of fish by the mean weight of fish in each gear and age group and then by adding the catches of the different gears.

A software program based on EXCEL (S. Kuikka, unpubl.) was used to assess the vendace stock with VPA analysis for 1–8 year old fish. In the sample material of over 32 000 vendace, there were only approx. 20 fish older than eight years, the oldest ones being 12+ years.

For the preliminary VPA run, the total mortality (Z) was assessed from the survival estimate of the year classes of 1986 and 1989, which were well represented in the material throughout the study period. It was estimated that the natural mortality (M) of each age group was 0.3. Elsewhere in Finland, at least values $M = 0.2$ (Auvinen and Jurvelius 1994) and $M = 0.3–0.7$ (Salojärvi 1992) have been used in the VPAs of vendace. The fishing mortality of the age groups of the last material year 1996 was adjusted after the first VPA runs to a level which corresponded with the fishing mortality of the previous years (Pope and Shepherd 1985). During the last years, the total fishing effort of vendace fishery was estimated to have stayed approximately on the same level. The stock assesment of the first years is based on the presumption that the population was only diminished by natural mortality ($M = 0.3$). Recruitment figures are based on the number of 1-year-old fish. Since the first catch samples were collected in 1987, the fish number of the year classes older than 1986 were assessed as if they had only died of natural causes in 1983–86. Fishing mortality was still in those days so low that it is of no importance e.g., when assessing the recruitment of the year classes of 1983 and 1984. The recruitment assessments are most accurate for the year classes of 1986–93, and at their most inaccurate in the case of both the oldest year-classes (due to restricted sample material) and the youngest year classes of 1994–95 (due to the characteristics of the VPA analysis).

The VPA analysis was also used for calculating the size of the spawning stock. The analysis gives the stock size in the beginning of the year, before the fishing of that year starts. Vendace spawns in the end of October, sometimes in November, at a time when vendace fishing ends for the year. Therefore, the stock size in the beginning of the year given by VPA was adjusted to correspond to the spawning stock of the previous year so that young fish not able to reproduce were deducted from the stock given by VPA. When assessing the spawning stock, the data on the sexual maturity of sampled fish (mostly female) caught in October before or during spawning were used (Table 2). In the 1990s, the vendace turned ripe faster than before, due to more rapid growth. The spawning stock size in tonnes by each year-class was achieved by multiplying the number of fish by the mean weight of fish in each age group in the gill net catch samples (caught in autumn). The estimates of the mean weigthts of 1982–86

Table 1. Number of sampled and aged vendace (*C. albula*) for different gears in Lake Inari in 1987–96.

Year	Trawl	Trapnet	Winter seine	Gillnets	Total
1987	1 682	78			1 760
1988	1 541	1 073	1 720	161	4 495
1989	5 852	1 148	1 423	200	8 623
1990	995	1 230	2 108	156	4 489
1991	1 882	636	1 497	397	4 412
1992	925	162	1 119	105	2 311
1993	298	13	534	279	1 124
1994	460	67	316	838	1 681
1995	485	13	289	687	1 474
1996	493	269	521	545	1 828

Table 2. Share of sexually mature vendace in catch samples from October in 1987–1990 and 1991–1996. The percentages are roundings based on yearly data for estimating the spawning stock. Fish with a maturation rate 4–6 (Nikolsky) were interpreted as mature in the same autumn.

Age group	1987–1990	1991–1996
1+	50%	75%
2+	85%	100%
3+	100%	100%

were based on the first sample years 1987–88.

When interpreting the fluctuations in the recruitment of vendace, the impact of the temperature in Lake Inari was examined. We used material from the Hydrological Observation Station in Nellim to calculate, on the basis of daily surface temperatures of the open-water season, the heat sum from the break-up of ice to the time of freezing. In addition, we also examined graphically the temperature trend of the different years especially as regards the beginning of the summer.

Results

Fisheries, catches and CPUEs of vendace

For the first time, the catch of vendace was included in statistics in 1983, when the total catch was 380 kg. At its heighest (over 300 tonnes) the catch was in 1989. After that, it slumped. In recent years, the catch level has stayed around 10 tonnes (Fig. 2A). In 1983–86, vendace was caught with gillnets. Then, more efficient fishing methods were brought into the area and developed further here. In 1987, vendace was fished by three trawling teams (trawl pairs) and two winter seine teams. In addition, some vendace was caught with the large trapnets meant for whitefish fishing. Gillnet fishing for vendace increased strongly, and an increasing number of local fishermen bought special vendace gillnets to be used during the spawning season. In 1988–89, vendace fishery was quite intensive taking the scanty population of the area and the distant location of the lake from population and consumption centers into account. In 1989, vendace was trawled by 16 trawling teams and 7 winter seine teams (Table 3). In recent years, no actual trawling has taken place, with the exception of some experimental trawlings.

In vendace fishery, the combined fishing effort of the different gear types was at its peak in 1989. In 1990, fishing had been still intensive, but after that especially the fishing effort of trawling declined to almost zero by 1996. In gillnet fishing, the fishing effort has stabilized since 1991 on a level clearly below the peak years (Fig. 2B). The number of winter seine teams was highest in the late winters of 1989–90 (Table 3). In 1991, there were two winter seine teams fishing actively

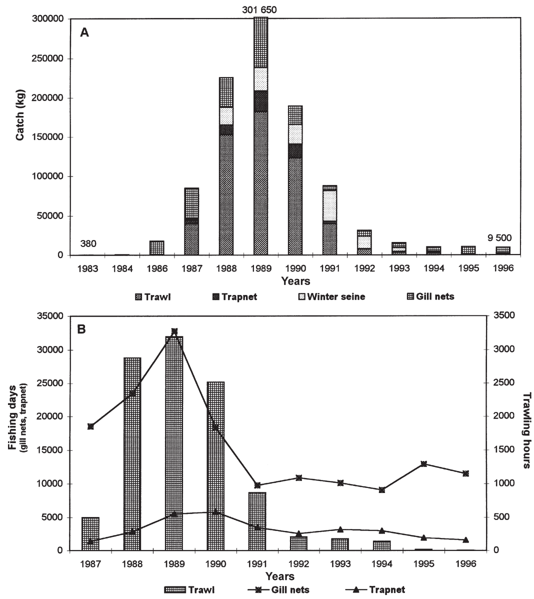

Fig. 2. Vendace catch by different gears (A) and the fishing effort with trawling, gillnetting and trapnetting (B) in Lake Inari in 1983–1996.

on Lake Inari, and the catch of their seines accounted for almost half of the vendace catch. Vendace was also caught with large trapnets especially during the peak years of trapnet fishing in 1989–90. Later, the trapnet catches of vendace have been occasional and of no real importance in terms of the overall development (Fig. 2A).

CPUE of trawling was highest right in the beginning, in the test year 1987 (Ahonen 1987). The rich catches of the three trawling teams al-

Table 3. Number of gear suitable for vendace fishery used in Lake Inari in 1987–1996.

Year	Trawl pair	Trapnet	Winter seine	Gillnet
1987	3	21	2	1 400
1988	11	41	6	1 900
1989	16	82	7	2 500
1990	16	89	5	1 624
1991	15	68	3	1 061
1992	11	53	3	913
1993	7	57	3	967
1994	5	59	2	1 107
1995	3	37	2	1 293
1996	2	43	1	1 383

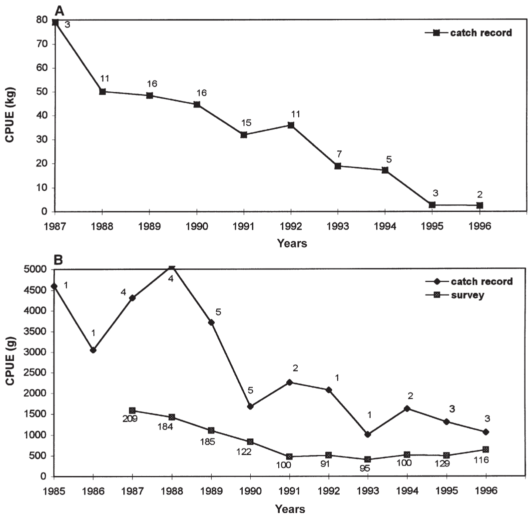

Fig. 3. Development of the mean vendace catch per unit of effort (CPUE) (kilograms per trawling hour) (A) and (grams per fishing day) (B) based on catch records and surveys. Numbers of operating trawl pairs (A) and number of fishermen (B) used in calculation of CPUE are presented in figures.

lured many new enterprisers into fishery. Mean CPUE of the following year, 1988, was approx. 50 kg/trawling hour which was already less than in 1987. After that CPUE has declined steadily (Fig. 3A) reaching rapidly a level where trawling is no longer economicly profitable. Mean CPUE levels in Lake Inari in 1988–89 (48–50 kg/trawling hour) have in some studies been considered the limit of profitable trawling (e.g., Ylitalo 1990).

In the gillnet fishing of vendace, CPUEs also declined, although not as steeply as in trawling. Mean CPUEs based on fishery surveys (mail inquiries) by subsistence fishermen are much smaller than CPUEs based on catch records by professional fishermen. Among those fishing for own use, there are many who only fish with vendace gillnets once or twice an autumn, and not necessarily anymore during the spawning season when the lake are freezing but the catches are highest. In 1991–96, typical CPUE of these fishers was 500 g/vendace gillnet/day, while during the first years it was around 1 500 g. According to catch records, mean CPUEs declined from the level of 3 000–5 000 g to the level of 1 000–1 500 g in last years (Fig. 3B).

Development, recruitment and year-class fluctuations of vendace stock

The vendace that ended up in Lake Inari in the 1950s and 1960s "took its time" to spread in the lake without anybody really knowing about it before the turn of the 1980s. The dwarf whitefish, a fish the size of vendace, was only sligthly fished at that time with small-meshed gillnets. Not very many people knew how to distinguish between the vendace and dwarf whitefish. Relying on observations, test fishings, catch statistics and sample material, the strong growth of the vendace population took place in the 1980s. Vendace also spread to the adjacent fairly large lakes Ukonjärvi and Nitsijärvi (Sarjamo *et al.* 1989), and descended from Lake Inari to Paatsjoki which flows into the Arctic Ocean. As a result, the first observations of the vendace on the Norwegian side were made in 1989 (Amundsen and Staldvik 1993). By 1995, the vendace had already spread to most lakes of Paatsjoki and started to reproduce there (Bøhn *et al.* 1996). As the population in Lake Inari diminished in the 1990s, the vendace now seems to live in areas which are apparently more favourable in terms of temperature and food, mostly in the southern parts of the lake, the areas where it is still fished.

The vendace catches of the year 1987, in terms of kilograms, mostly consisted of quite old and large (3–4 years, weigth 30–50 grams) vendace from the year classes of 1983 and 1984. These apparently first strong year classes of vendace yielded by the turn of the 1990s approx. 7 million fish, or over 300 tonnes. The year class of 1982 and those older than it were subject to very little fishery. In 1986, the vendace year class was extremely strong. This year class was subjected to fishery already when it turned 1–2 years (from 1987–88 on), and had, by the age of 7 (1993), yielded a total catch of approx. 13 million fish, or over 360 tonnes. The total catches of the year classes of 1985, 1987 and 1988 were considerably smaller. The year class of 1989 was again strong. By 1996, it had yielded the fisheries over 8.5 million fish, or over 126 tonnes, significantly less kilograms in relation to number of fish than the older strong year classes. The vendace of the year class of 1989 were subject to intensive fishery right from the beginning, age 0+, in the trawlings of the late summer and autumn. The catches of the year class of 1990 and younger dropped rapidly as compared with the year-class catches of the previous decade despite the fact that the accumulative catches of the year classes of the 1990s are still unfinished and that vendace fishing has declined. The catch of year class of 1991 appears to be particularly low (Table 4).

The population analysis VPA showed that, due to two successive strong year classes (1983–1984), and the year class of 1986, the size of the vendace stock increased very rapidly to its peak in 1987, when the number of 1–8 years old vendace was over 40 million. At the highest, there were thus almost 400 vendace per water hectare in Lake Inari. By 1994–96, the population slumped to a level below 1 million fish (5–7 fish ha^{-1}) according to the VPA analysis (Fig. 4).

The vendace of the 1983–84 year classes became a target of fishery only when old and large. In 1988, these year-classes still had rather low fishing mortality rates (F = 0.3–0.5), and their abundances were declining slowly. The year class of 1986 as well as the year classes of 1987–89

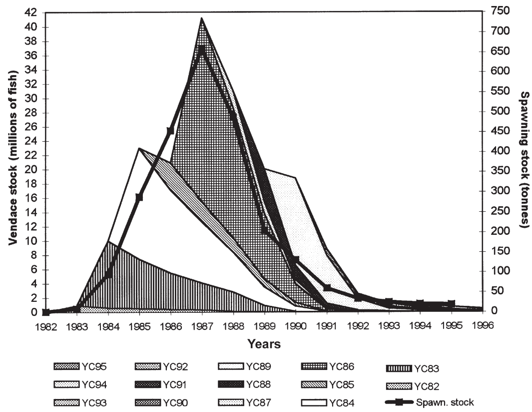

Fig. 4. Development of the estimated vendace stock size (1–8 year old fish) of different year classes (YC) (millions of fish), and the estimated spawning stock size (tonnes) according to population analysis (VPA) in Lake Inari in 1982–1996.

Table 4. Vendace catches by year classes in 1987–1996 and the cumulative catch of different year classes 1983–1995 (YC83–YC95) up to 1996 in numbers (× 1000) (A) and in kilograms (B).

Year	YC83	YC84	YC85	YC86	YC87	YC88	YC89	YC90	YC91	YC92	YC93	YC94	YC95
A. Catch (× 1000) in numbers													
1987	757	872	130	894	16	–	–	–	–	–	–	–	–
1988	792	1 796	460	5 104	176	119		–	–	–	–	–	–
1989	721	1 299	344	4 867	687	1 627	698	–	–	–	–	–	–
1990	58	617	352	1 840	287	1 055	2 738	283	–	–	–	–	–
1991	–	62	53	276	72	240	3 928	209	1	–	–	–	–
1992	–	–	7	11	20	83	850	209	40	5	–	–	–
1993	–	–	–	2	6	39	191	68	26	52	3	–	–
1994	–	–	–	–	3	11	57	13	12	95	39	8	–
1995	–	–	–	–	6	16	44	5	5	16	29	33	0
1996	–	–	–	–	–	0	8	15	12	14	30	73	17
Total	2 328	4 646	1 346	12 994	1 273	3 190	8 514	802	96	182	101	114	17
B. Catch (kg)													
1987	30 670	29 919	2 308	9 480	97	–	–	–	–	–	–	–	–
1988	36 667	76 849	14 977	94 277	1 393	547	–	–	–	–	–	–	–
1989	35 560	59 491	14 534	158 994	12 623	19 042	2 496	–	–	–	–	–	–
1990	3 308	33 481	18 190	83 957	10 165	19 698	27 829	1 497	–	–	–	–	–
1991	–	3 437	2 787	13 073	2 822	6 831	57 318	2 125	8	–	–	–	–
1992	–	–	344	726	1 031	2 871	20 662	4 475	461	17	–	–	–
1993	–	–	–	253	345	2 332	8 511	2 426	599	668	9	–	–
1994	–	–	–	–	274	812	3 648	813	576	3 462	475	46	–
1995	–	–	–	–	716	1 848	4 537	402	429	951	1 070	395	1
1996	–	–	–	–	–	6	1 095	1 656	1 100	1 285	1 826	2 306	223
Total	106 205	203 177	53 140	360 760	29 466	53 986	126 096	13 395	3 173	6 383	3 380	2 747	224

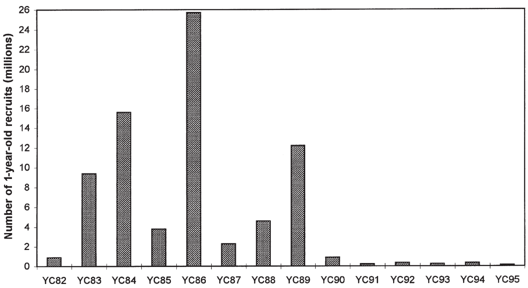

Fig. 5. Number of vendace recruits by the year classes (YC) of 1982–1995. The estimates are based on VPA analysis.

were a target of intensive fishery, which shows as high fishing mortality figures in 1989–91, and further as a rapid drop in the year-class strength (Table 5 and Fig. 4).

We can say roughly that, in terms of the number of fish, the spawning stock was reasonably big in 1984–90, at least around a few million fish (100 tonnes). The spawning stocks of 1983 and prior to that were small, as were also those of the autumns in 1993–95 (around 0.5 million fish and 10–20 tonnes). The spawning stock of the autumn in 1987 was very big, due to the large number of young vendace of the year class of 1986 (age 1+). The biomass of spawning stock in 1987–88 were estimated to around 500–600 tonnes (*see* Fig. 4).

The recruitment rate of the year class of 1986 (1-year old), over 25 million fish, was clearly the highest during the study period. The recruitment figures of the year classes of 1983, 1984 and 1989 were also high, approx. 10–15 million fish. In 1985, 1987 and 1988; a reasonably high number of vendace hatched. In the 1990s, all the year classes have, however, been very scanty. The recruitment rates of the year classes of 1991–95 were only around a few hundreds of thousands (Fig. 5). The difference between the recruitment of the weakest year classes of 1991 and 1993, and the strongest one, 1986, was almost hundredfold. According to preliminary information, the year class of 1996 was also very weak. One-summer-old fingerlings of the year class of 1997 were, however, caught in somewhat greater numbers than such fish in the fingerling studies of the previous autumns (E. Salonen, unpubl.). Such fingerling studies were carried out in 1994–97, during a period which coincides only partly with the study period of this research. The aim is to conduct further studies which compare the results of the fingerling studies and the VPA analysis.

As regards the heat sums of Lake Inari, especially the years 1987, 1993 and 1996 stick out as cold summers, or open water seasons. Warm ones were the years 1986 and 1989, that is the years when strong vendace year classes were born (Figs. 5 and 6). In the whole material, the heat sum and recruitment figures correlate weakly, but in the case of the 1980s, warm summers did produce bigger year classes than cold summers. On the other hand, all the year classes of the 1990s were very weak although there were also open water seasons that were warmer than average in the decade (Fig. 6B). All the strong year classes were born in a year when the break-up of ice took place earlier than on average, in May (15–25 May), and when the water temperature rose quite rapidly to an adequate level, like in 1986 (Appendix). The rapid rise in temperature is favourable for the fast development of zooplankton, the food of vendace (e.g., Helminen and Sarvala 1994). The rise of temperature was quite slow after the break-up of ice in 1987, 1990–91 and 1993. After the cold growing season of 1987, the 1-year-old vendace of the

Table 5. Fishing mortality (*F*) of vendace by different age groups according to the population analysis (VPA) in 1987–1996.

Age	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
1	0.04	0.09	0.53	0.30	0.31	0.22	0.19	0.20	0.11	0.18
2	0.05	0.39	0.72	0.93	1.14	0.66	0.23	0.74	0.25	0.45
3	0.13	0.31	0.96	0.89	0.64	0.98	0.52	0.19	0.30	0.50
4	0.26	0.47	0.46	1.73	0.66	0.55	0.70	0.19	0.13	0.50
5	0.55	0.55	0.86	1.64	2.77	0.43	0.62	0.52	0.12	0.50
6	–	0.37	2.32	2.13	1.86	1.51	0.26	0.39	1.26	0.70
7	–	–	–	–	–	–	–	0.23	3.43	1.00
8	0.50	0.50	1.50	1.80	1.80	1.00	1.00	1.00	1.00	1.00

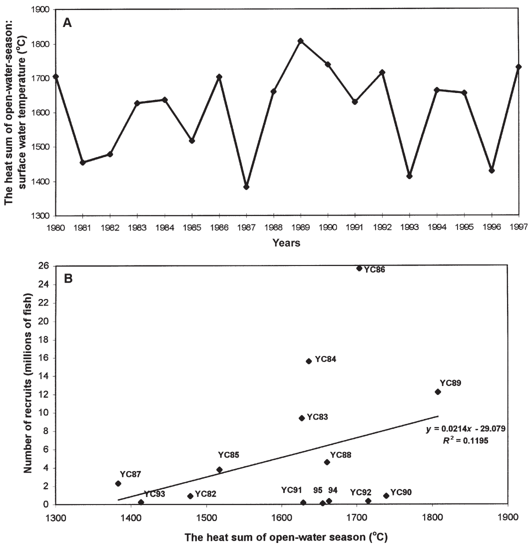

Fig. 6. Cumulative heat sum of water during the open-water season, from the break-up of ice to the time of freezing by shoreline in Nellim, Lake Inari in 1980–1997 (A) (Source: Hydrological observation station, Nellim) and the relationship between this heat sum and the number of recruits (year-class size) of vendace in Lake Inari (B).

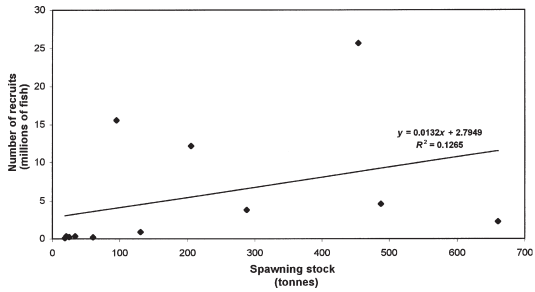

Fig. 7. Relationship between the estimated spawning stock size and the number of recruits (year-class size) of vendace in Lake Inari.

next winter were smaller (mean length ca. 7 cm) than those of other years (mean length 8–9 cm).

There was also no clear correlation between the spawning stock and the recruitment figures of the year-class hatching from it, which is very often the case with other fish stocks, too (e.g., Hilborn and Walters 1992). On the other hand, almost all strong year classes have developed from reasonably large spawning stocks. The year class of 1984 showed as an exception, as it was very hard to estimate the size of its spawning stock in 1983. The examination of the spawning stock 1982/year class 1983 was not included in Fig. 7. On the basis of fish stock estimates, the strong year classes of 1983 and 1984, however, developed from small spawning stocks. At the other end, we had the very large spawning stock of fall 1987 which produced only a reasonable number of recruits (the year class of 1988).

Discussion and conclusions

By the middle of the 1980s, the vendace population had grown so strong that test fishing brought high catches and CPUEs. High CPUEs rapidly attracted the interest of fishermen to the fishing of vendace, a species so far unfamiliar in the area. There seemed to lie great potentialities in vendace fishery, and people started to see the great Lake Inari as being "full of vendace". At the time, there was no knowledge of the vendace and its populations in the area, as the first research examining the state of vendace stock was finished only in 1989 (Kolari *et al.* 1989). A new fishing equipment was bought in rapid succession, and the fishing effort of all the gears suitable for vendace fishing increased strongly in 1987–89. As a result of the trawling permits granted to 17 teams in 1988, there were 16 trawling teams fishing on the lake already in 1989. The permit policy, legislation, and economic boom in the end of the 1980s brought ample subsidies and loans to fishery and also helped to create homesteads relying on nature-based occupations (Salminen and Mutenia 1991, Salonen 1992). The good markets of vendace also contributed to the growth of fishery, as very little vendace was caught at that time elsewhere in Finland and as the demand for the rather large vendace of Lake Inari was great in southern Finland. The collection and transport system financed by public funds, and run by a wholesale fish enterprise in Sodankylä worked well, and it was even possible to market and forward substantial vendace catches at the time. Small-scale commercial fishery had already long traditions in the area, and a great number of fishermen, even young ones, became recruited to vendace fishery. All these factors contributed to the extremely fast development of the vendace fishery in Lake Inari.

At the same time as the fishery turned more intensive, CPUEs already started to decline, although the total catch grew very high with the increase in fishing effort. However, the total catch also started to drop rapidly by the 1990s. The fishing effort still stayed on a reasonably high level for some time, as great capitals invested in e.g., trawling gave rise to a great need to go on fishing. The same thing happens almost always when fishing for a species not exploited before starts (e.g., Gulland 1983, Hilborn and Walters 1992). The drop of CPUEs and then also total catches to an unprofitable level together with the general recession, and a decrease in demand of vendace in the first half of the 1990s created an unbearable situation for numerous fishermen. It has been shown that granting ample state subsidies to fishery leads more certainly to economical overfishing than when no subsidies are granted (Kuikka 1996).

According to general ecological knowledge, population fluctuations are often very big in the extremities of the distribution area. The impact of environmental factors, particularly climate and water temperature, on fish populations can be greater in such areas than closer to the center of their distribution area. As regards the vendace in Lake Inari, strong year classes were born only during warm or reasonably warm summers, whereas during cold summers, 1987 and 1993 for example, the year classes were weaker than those of the surrounding years. It has been estimated that the first weeks after the hatching are critical in terms of the survival of vendace fry (Helminen and Sarvala 1994, Auvinen 1994). The exact hatching time in Lake Inari is not known, but experience from elsewhere gives reasons to estimate that hatching happens around the break-up of ice (Helminen and Sarvala 1994). The year 1986 when the ice broke up somewhat earlier than usually and the water warmed up rapidly was obviously favourable in Lake Inari, as the year class of 1986 turned out especially strong. The growing season of vendace is shorter in Lake Inari than in the more southern vendace lakes, and the fingerlings are usually 7–9 cm long by its first winter. Thus, the warmth of the growing season (open water season) has an impact on whether or not a fingerling reaches a size adequate for surviving through the first winter. The mortality of smaller fingerlings is higher than that of larger ones both due to predation (e.g., Post and Prankevicius 1987) and starvation which is, however, hard to show (Heath 1992). After the cold summer of 1987, the 1-year-old vendace of the next winter were smaller than those of other years. On the other hand, the size of the vendace population was also at its heighest at that time, so the slower growth may be a result of both abiotic and biotic factors. Elsewhere in Finland, the growth rate of the vendace in the first summer has been found to depend mainly on population density (Valkeajärvi *et al*. 1997a).

It was problematic to estimate both the total and spawning stock sizes in the beginning of the 1980s. Very probably the stock in the first years of VPS was somewhat bigger than has been estimated on the basis of the material available (Fig. 4). The total stock size (density) in Lake Inari even at its highest was estimated to be under 400 fish per water hectare, which is less, or at most at the same level, than in other studied lakes in Finland. The same estimation method (VPA analysis) for example in Lake Paasivesi produced density estimates from 37 to 949 vendace per water hectare (Auvinen and Jurvelius 1994). In Pyhäjärvi (south-western Finland), the highest number of recruits alone (the majority of the total stock) was around 2 000 vendace per water hectare (Helminen *et al*. 1997).

The spawning stock in Lake Inari was in any case relatively large for only a short period from the mid 1980s to the turn of the 1990s, and at least the strong year classes of 1986 and 1989 developed from rather large spawning populations. There are many factors of uncertainty linked with the estimates on the size of the spawning stock. When looking at this size, we must note for example that if there are many mature fish, the number of potential spawners is high and the spawning area is larger than with a small spawning population (e.g., Radovich 1979). On the other hand, the production of roe and amount of roe per spawner increases strongly as the size, especially the weight, of the fish increases (Jensen 1981, Auvinen 1994). In Pyhäjärvi in Karelia, the fecundity values of vendace rose from a few thousand eggs to over 20 000 eggs when the weight of a female vendace grew from under 50 grams to approx. 150 grams (Auvinen and Auvinen 1994). The reproductive contribution of larger vendace may indeed be markedly bigger than that of smaller ones, because not only the amount but also the quality of roe may be better (Auvinen 1994, Helminen and Sarvala 1994). In the case of Lake Inari, the reproductive contribution of vendace age group 1+ (mean weight at most around 30 grams) may be much smaller than that of bigger and older fish.

The slump of the spawning stock in the 1990s to a fraction of what it was earlier, took place at a time when the already declining stock had been subject to quite intensive fishery, also according to the fishing mortality figures of the VPA analysis. Less intensive fishery could have slowed down the slump in the population of vendace in Lake Inari; a long-lived vendace compared to those in other Finnish lakes. This way, the period of good catches might also have been prolonged. The spawning stock has been so poor in the 1990s that even during summers with reasonably favourable temperature conditions, only extremely weak year classes have developed. When the spawning stock is scanty, the chance of ample year classes being born — a chance influenced simultaneously by several factors — most probably diminishes (Myers *et al.* 1995). The vendace population trends in Lake Inari and Pyhäjärvi in Säkylä, southern Finland, are also similar to that in Pyhäjärvi; the spawning stock slumped in the beginning of the 1990s. The recruitment figures also stabilized on a lower level than during the earlier 2-year-long cycles. Apparently unfavourable temperatures in some years had an impact on the decline in the recruitment of vendace in Pyhäjärvi, too (Helminen *et al.* 1997).

Predation, probably plays also an important role in regulating the strength of the vendace year classes in Lake Inari. The stockings of salmonid predatory fish into Lake Inari were still carried out in the beginning of the 1980s, i.e. at a time when vendace was not yet being fished, at the level of 1–1.5 fish ha^{-1}, but have later increased to about 2–3 fish ha^{-1} (Mutenia and Salonen 1994). These stocking consisted of the brown trout (*Salmo trutta*), land-locked salmon (*Salmo salar m. sebago*), arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*). From these, the two last ones probably feed more on other species than on vendace; especially on dwarf whitefish "reeska" which is, in addition to vendace, an important alternative prey species for all those salmonids. On the other hand, there are also naturally reproduced brown trout and arctic chars in the area, which further increases the pressure of predation on vendace in Lake Inari. There were several studies published in the 1990s which demonstrate that predators, especially brown trout, may eat up a considerable portion of a vendace year class already at an early stage (e.g., Valkeajärvi *et al.* 1997b, Helminen *et al.* 1997, Marttunen and Kylmälä 1997). All these studies recommend that abundant stockings of brown trout should be avoided when the vendace population is scanty. Thus, the preconditions for a rise of the vendace population in Lake Inari in the beginning of the 1980s were good compared to later years, as the pressure of predation was reasonable and the impact of fishery still minimal. Impact and role of predation in Lake Inari is also subject to further studies.

In conclusion, it needs to be noted that very many factors may have caused the great fluctuations of the vendace stock and, above all, the recruitment rate of vendace. During the early, critical stages of life, many factors have to coincide in order for a strong year class to develop (Cushing 1982). Several successive failures, as a result of the above-mentioned factors, may lead to a disappearance of vendace (Valkeajärvi *et al.* 1997a). In case of the vendace in Lake Inari, such factors include at least the temperature conditions of the first summer, the size of the spawning stock, fisheries, and predation, and possibly also interactions with potential competitors like dwarf whitefish and large sparsely rakered whitefish. In future, if the revival of the vendace stock is the common goal, the stocking level of predatory salmonids should be limited preferably to less than one predatory salmonid fish per hectare in the lake (*see* Valkeajärvi *et al.* 1997b). Anyway, the vendace has turned to be out a profitable addition to the fish community of Lake Inari, both as a prey species for predatory salmonids and in terms of the catch itself. If vendace fishing still increases, the fishing effort should be limited with caution so that the spawning stock may have a chance to revive.

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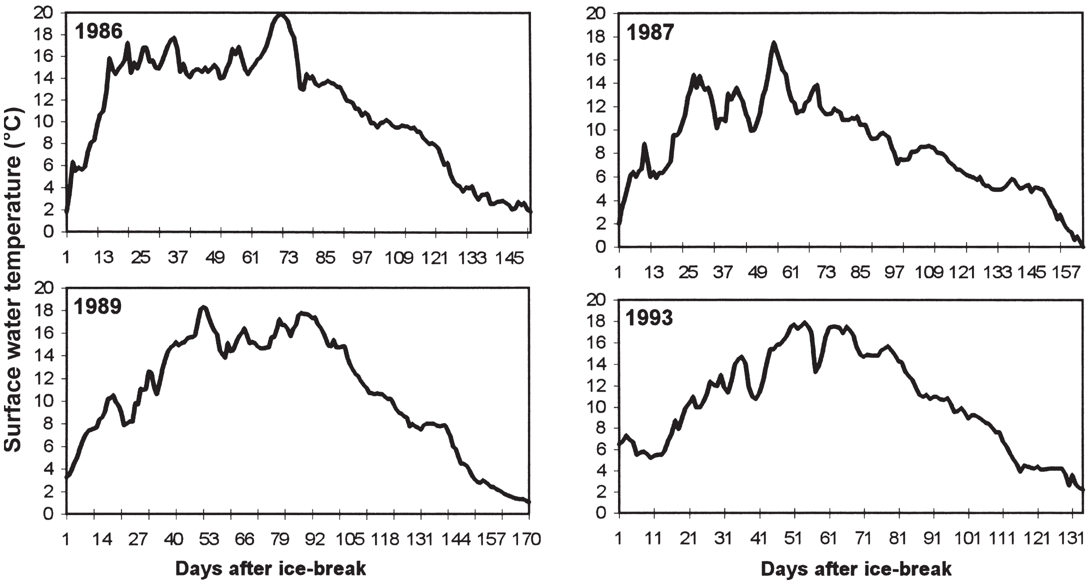

Appendix. The development of the water temperature in Lake Inari in two warm open water seasons 1986 and 1989 an two cold seasons 1987 and 1993. The day of ice-break was 24 May 1986, 2 June 1987, 15 May 1989 and 1 June 1993.

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