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Portrait of a flourishing freshwater fishery: Pyhäjärvi, a lake in SW-Finland

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Fish yields from Pyhäjärvi, a lake in southwestern Finland, (ca. 34 kg ha^{-1} a^{-1}) are much higher than expected from published relationships between yield and nutrient concentrations or primary production in lakes. The basis of this fishery has been studied since 1983 in a series of ecosystem and fisheries projects. Here we review the historical development and present state of this fishery, analyse its biological and economic basis, and speculate on its future in the changing world. The main targets of the commercial fishery have been the coregonids vendace and whitefish, both introduced into the lake during this century. However, in the 1990s, the vendace stock has declined, and the less valuable perch, roach, smelt and ruffe have become dominant in the catch. This change in the fish community seems to be primarily due to climatic factors. The main reason for the high fish yields in Pyhäjärvi is the very efficient fishery: the annual harvest approaches the total production of vendace. The simple morphometry of the lake and its short food chains contribute to the productivity of the fishery. The intensive fishing itself enhances the productivity of the vendace population. Under the prevailing food-limiting conditions, exploitation focusing on juveniles leads to faster growth and higher reproduction rates, allowing high harvest rates without a population collapse. However, the recent decline of the vendace population in Pyhäjärvi shows the vulnerability of a heavily exploited fish stock under adverse environmental conditions.

Introduction

The general level of fish production seems to be predictable from primary production (Downing *et al.* 1990). Fish yields are more variable because the proportion of fish production that is taken as catch depends on the fishing effort and fishery conditions. In addition, the level of sustainable yield is a function of the biological characteristics of the fish species involved, and the interactions between the fish and their prey and predators as well as potential competitors. In temperate lakes, the observed catches normally vary from 0.02% to 0.2% of primary production (Morgan *et al.* 1980). Pyhäjärvi, a lake in southwestern Finland, seems to form a prominent exception to this general rule: its fish yield is almost an order of magnitude higher than expected from published relationships between fish yield and nutrient concentrations or primary production (Oglesby 1977, Nixon 1988, Sarvala *et al.* 1984, 1994a, Sarvala and Jumppanen 1988). Mechanisms leading to such high sustained yields are of general interest and have been studied since 1983 in a series of ecosystem and fisheries projects (Sarvala *et al.* 1984, Helminen *et al.* 1993a, Helminen and Sarvala 1997). Here we review the historical development and present state of this fishery, analyse its biological and economic basis, and speculate on its future in the changing world.

Study area

Pyhäjärvi is relatively shallow (mean depth 5.4 m, maximum depth 25 m), but moderately large (area 154 km^2) north-temperate lake in southwestern Finland (60°54´–61°06´N and 22°09´–22°25´E), in an area of generally fertile soils, flat topography and few lakes. With its few islands and relatively straight shoreline, Pyhäjärvi is unusually open for a Finnish lake. As a result, there is no permanent stratification during the open water season; 94% of the lake area is less than 7 m deep. The lake is covered by ice from November to April. The lake is mesotrophic (average total phosphorus in summer 12–19 mg m^{-3}, primary production 26–56 gC m^{-2} a^{-1}; Sarvala and Jumppanen 1988), but known for its clear water (Secchi depth usually 3–4 m) (Sarvala *et al.* 1984, Sarvala and Jumppanen 1988, Helminen and Sarvala 1997). In phytoplankton, typical groups are diatoms, chrysophyceans, cryptophyceans, and, especially in recent years, cyanobacteria. Characteristic zooplankton crustaceans are the calanoids *Eudiaptomus graciloides* (Lilljeborg) and *Heterocope appendiculata* Sars, the cyclopoids *Mesocyclops leuckarti* (Claus), *Cyclops kolensis* Lilljeborg and *Megacyclops viridis* (Jurine), and the cladocerans *Bosmina coregoni* Baird, *Daphnia galeata* Sars, *D. cristata* Sars, *D. longiremis* Sars, *Ceriodaphnia pulchella* Sars, *Chydorus sphaericus* Müller and *Holopedium gibberum* Zaddach. Zooplankton biomass normally shows two seasonal peaks, in June and August. During the last decades, Pyhäjärvi has slowly eutrophicated, mainly due to diffuse loading from agriculture. Recently a specific Pyhäjärvi Protection Fund has been organized to promote the reduction of external loading (Mattila 1997).

Reviewed studies

Fish data from Pyhäjärvi have been available since the start of this century (Järnefelt 1921, Järvi 1940, 1953). A more regular monitoring scheme for vendace and whitefish was initiated in the early 1970s in connection with plans to use the lake as a municipal water reservoir (Helminen *et al.* 1993a), and these studies intensified during the 1980s into comprehensive ecosystem research (Sarvala *et al.* 1984, Sarvala *et al.* 1997, 1998a).

Estimates of the total fish catches as well as the numbers of licensed fishing gears have been available in the annual reports of the local fisheries management unit (originally founded in 1916 as a voluntary co-operative of the statutory fisheries associations around the lake, and since 1990 reorganized as a fisheries region based on the 1982 Fisheries Act: for the structure of Finnish fisheries system, *see* Sipponen 1995). The majority of the annual catch is taken in winter by seining through holes in the ice (Sarvala *et al.* 1994a). For vendace and whitefish, daily seine catch records from the winters 1980–1997 were obtained directly from each seine crew or the most important fish agent. Catch records from fyke nets in the autumn have been collected by the local fishery region since the year 1983. Summer gill net catches were estimated from personal interviews and book-keeping statistics of local fishermen (Helminen *et al.* 1992, Sarvala *et al.* 1994a). In addition, the size of the total catches by species and fishing gear were surveyed in 1976 and 1994 (commercial catches only) by the Finnish Game and Fisheries Research Institute (Sarvala *et al.* 1994a and P. Kummu and M. Naarminen, unpubl). In 1976, a catch inquiry was sent to all licensed professional, semi-professional and non-professional fishermen. About 63% (349 persons) of the non-professional fishermen answered the questionnaire; most professional (35 persons) and semi-professional (66 persons) fishermen were interviewed personally. When comparing fish catches to primary production we assumed that 1 g of fresh fish mass contains 0.1 g carbon (Oglesby 1977).

Data on growth and population structure of all species were derived from experimental gill net fishing in May–November 1984 (sets of 30 m long and 1.8 m high benthic nets, each with a mesh size of 12, 15, 20, 25, 35, 45, 60 or 75 mm bar measure; sets of 30 m long and 4.5 m high pelagic nets, each with a mesh size of 12, 15, 17, 20, 22, 25 or 27 mm bar measure; altogether 558 net periods of usually 1–2 hours). Gill net sampling of mainly vendace, whitefish and smelt was continued in 1987 and 1989, and some additional gill net data were available from 1977, 1980, 1982 and 1987–1991. Material was complemented with representative catch samples (a two-stage sampling strategy) from the commercial winter seine fishery (in 1983–1984 and 1987–1997 especially vendace, whitefish and smelt; from 1989 onwards also perch, roach, ruffe and bream) (Helminen *et al.* 1993a, Sarvala and Helminen 1996, Sarvala *et al.* 1998b).

Total length, mass and sex of each individual were recorded. Age determinations were based on scales (vendace, whitefish, roach, partly ruffe), otoliths (smelt, partly ruffe) or opercular bones (perch). In the case of vendace, whitefish, ruffe, perch and smelt the age determinations could be checked by following growth through at least one growing season and by comparing size distributions in successive years. The diets of vendace, whitefish and smelt were studied from stomach contents in 1983–1984, 1987 and 1989–1990. Perch, roach and ruffe diet data were available from 1980 (Rajasilta 1981), 1982 and 1984. Brown trout diet was studied throughout the summer 1995 (Helminen *et al.* 1997b).

For the period 1979–1997, vendace year-class sizes were estimated from the declining catch per unit effort in the seine net fishery during each winter (DeLury method, Helminen *et al.* 1993b, Helminen *et al.* 1997c), and for the period 1970–1978 from the correlation between first-year growth and year-class size (Helminen *et al.* 1993a). Minimum estimates for whitefish were obtained directly from the catch of each year class; the two youngest age groups were well represented in the winter seine catches. The proportions of each species in the winter seine catches relative to vendace could be used to derive approximate biomass estimates of the stock (Sarvala and Helminen 1996, Sarvala *et al.* 1997, 1998a).

Fecundity of vendace was assessed in 1978 and 1983 and annually in 1987–1997 (Sarvala *et al.* 1992, Sarvala and Helminen 1995); whitefish fecundity was also monitored during the 1990s (J. Sarvala *et al.*, unpubl.). The abundance of vendace and whitefish larvae was assessed in 1985–1997 using towed or (since 1992) pushed larval nets, in 1988–1997 according to a stratified sampling design (Sarvala *et al.* 1988, Helminen *et al.* 1997c).

Bioenergetic models were used to estimate daily food consumption of vendace, whitefish and smelt, combining field data on growth, population size, diet and temperature with laboratory information on the physiological energetics (Helminen *et al.* 1990, 1997a, Karjalainen *et al.* 1997).

Water quality (nutrients, chlorophyll, phytoplankton) in Pyhäjärvi was intensively monitored during 1980–1992 (as well as primary production during this period) by the Water Protection Association of Southwest Finland and in 1993–1997 by the Southwest Finland Regional Environment Centre, as described by Sarvala and Jumppanen (1988) and Sarvala *et al.* (1997, 1998a). Crustacean zooplankton was sampled in 1980 (Vuorinen and Nevalainen 1981), 1982, 1984, 1986, and 1987–1997, usually at weekly intervals (in 1984 partly daily). From 1984 onwards, samples were taken from surface to bottom at ten locations following a stratified random design (Sarvala *et al.* 1997, 1998a).

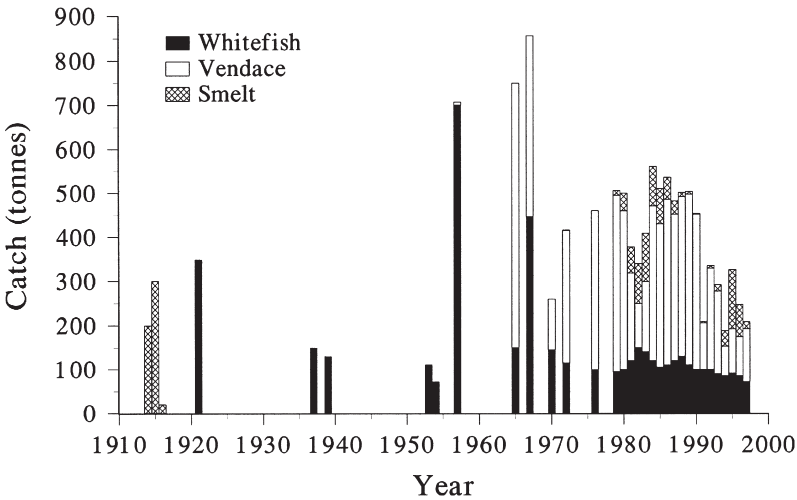

Fig. 1. Catches of whitefish, vendace and smelt from Pyhäjärvi during the 1900s according to the unpublished annual reports of the local fisheries region (and its predecessors, see text), published sources, and our own data.

History

Large-scale fishing in Pyhäjärvi started early this century and has undergone considerable changes through the decades, as is evident from the reported catches (Fig. 1). At first, Pyhäjärvi was a productive noble crayfish (*Astacus fluviatilis* L.) lake, but the crayfish catches collapsed with the arrival of the crayfish plague in 1906. The crayfish stock regained commercial importance after the initial crash, but new plague outbreaks followed, and the stock never recovered from the epidemic in the early 1940s. In hope of reviving the crayfish fisheries, a five-year program of signal crayfish (*Pacifastacus leniusculus* Dana) introductions was started in the late 1980s.

Winter seining of smelt began around the year 1908 and peaked in 1915, when there were ten seine crews (Hagman 1915). After the depletion of the smelt stock in winter 1916, seine nets were used to catch roach, perch and ruffe, which were caught in large quantities (largest catches per haul were > 5 800 kg; Hagman 1916). In the following years, a flourishing new fishery developed, based on the whitefish introduced since 1908. In 1921, this fishery yielded as much as 350 tonnes of whitefish (Olander 1922), and an estimated additional 210 tonnes of other species, mainly smelt; this total catch was equivalent to 36 kg ha^{-1}. From then until the 1960s, whitefish was the most important target of professional fishery.

Another coregonid species, vendace, was introduced into the lake in 1948–1952, after one unsuccessful attempt in 1925. Since the early 1960s, vendace has been the dominant species in the commercial catches. In 1976, the total catch was estimated at 34 kg ha^{-1}, which is high in comparison to the average in lakes of Finland (about 10–15 kg ha^{-1} yr^{-1}; e.g., Sjöblom 1983, Dill 1990) or other northern European countries (Dill 1993). Furthermore, this total catch was about 0.8% of the average phytoplankton production of the lake in the 1980s (44 gC m^{-2} a^{-1}, Helminen and Sarvala 1997). Vendace and whitefish catch statistics (Fig. 1) suggest that such total catch levels were sustained throughout the 1970s and 1980s.

Judging from the numbers of licensed fishing gear, the fishing pressure in Pyhäjärvi is high. Since the 1970s, the number of full-time professional fishermen participating in the fishery has been around 40, and the number of part-time fishermen around 140. In 1976, fishermen in Pyhäjärvi area had 9 860 benthic and 5 208 pelagic gill nets, 535 fyke nets and 133 traps plus a number of longlines, hooks etc. (P. Kummu and M. Naarminen 1978, unpubl.); in later years, the numbers of gill nets and fyke nets have declined. Most importantly, there were nine active winter seining crews in 1976, and later their number usually varied from 7 to 9 (maximum 12; Helminen et al. 1992, Sarvala and Helminen 1996). In the 1990s, only 5–7 seine crews have actually been fishing.

In recent decades, the commercial fishing in Pyhäjärvi has been mainly based on the planktivorous coregonids vendace and whitefish. Yet according to experimental gill-netting, the

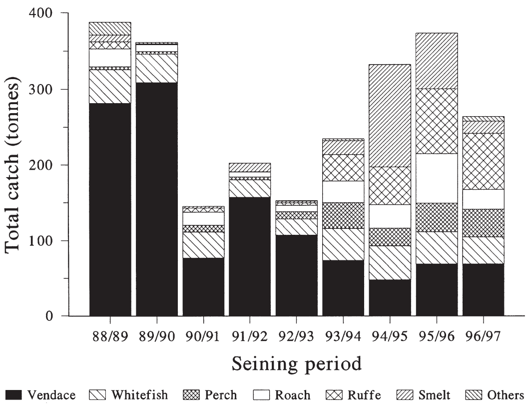

Fig. 2. Species composition of the winter seine catches from Pyhäjärvi in 1988–1997 (from Sarvala *et al.* 1998b, complemented).

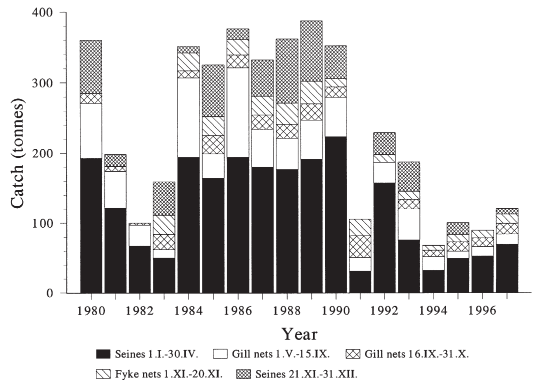

Fig. 3. Distribution of vendace catches in Pyhäjärvi in 1980–1997 by season and fishing gear (up to the year 1989 from Sarvala *et al.* 1994a).

most abundant fish species in Pyhäjärvi in 1984 was ruffe, followed by perch, roach, whitefish and vendace (benthic nets), or perch, vendace, roach and whitefish (pelagic nets) (Table 1). The discrepancy between these statistics may largely arise from the differing selectivity characteristics of the fishing methods. Gill net data not corrected for the different catchability of different species (as here) are known to give a biassed view of the fish community, strongly exaggerating the proportion of percids (M. Kurkilahti, pers. comm.). The average catch (± 95% confidence interval) obtained with a gill net set, calculated per hour and 100 m^2 net area, was 696 ± 159 g (benthic nets) or 451 ± 127 g (pelagic nets), night-time catch rates being twice as high as the daytime rates.

The present state of the fishery

Vendace

Vendace was the dominant species in the total fish catch from Pyhäjärvi in 1976 (Table 1) and remained so throughout the 1980s, but in the 1990s its role has diminished. Changing composition of the winter seine catches during the 1990s (Fig. 2) indicates drastic changes in the fish community. In the period 1980–1991, the annual catch estimates for vendace ranged from 100 to 389 tonnes or from 7 to 25 kg ha^{-1} (Fig. 3). The catch variation reflects vendace year-class fluctuations, but because vendace growth is strongly density-dependent (Helminen *et al.* 1993a), the catches vary less than the fish numbers. Part of the variation derives from changes in the fishery, caused by e.g., gear development and weather. Approximately 70% of the vendace catches were taken in winter with seine nets from under the ice (Fig. 3; Hirvonen *et al.* 1992). The winter catch consisted mainly (90%–95%) of fish hatched in the previous spring. Summer gill net catches of the one-year-old vendace were most important in years following an especially strong year-class, as in 1980, 1984 and 1986. In the summer gill net fishery and in the autumn fyke net fishery the proportion of older fish was higher. In 1992–1997, the winter catches of vendace declined to 50–150 tonnes. Assuming an unchanged relative seasonal distribution of catches, these figures translate into annual catches of 70–210 tonnes or 5–14 kg ha^{-1}. The decreased catches were due to diminished year-class sizes of vendace since the year 1990 (Fig. 4; Helminen *et al.* 1997c). Initially, this decline was caused by exceptionally unfavourable spring temperature development in two successive years, combined with an increased abundance of predators (the 1988 perch year-class) in the lake. The recovery of the diminished vendace population was later prevented by unfavourable combinations of weather conditions and predator abundance (perch, stocked brown trout; Helminen *et al.* 1997c) and partly also by the intensive fishery.

The fishing mortality of vendace is very high, although the exploitation rates have varied during the study period. About 8% of the vendace of

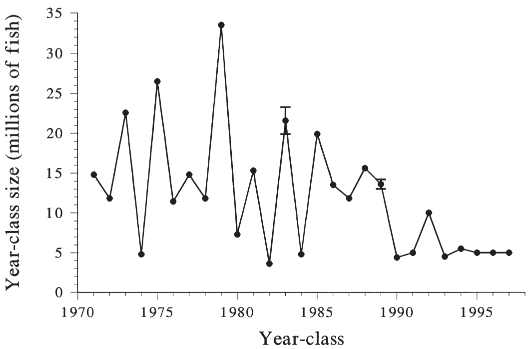

Fig. 4. Year-class variation of vendace in Pyhäjärvi in 1970–1997 (modified from Helminen *et al.*. 1997b). Vertical bars show 95% confidence limits of the estimate in two years (from Helminen *et al.* 1993b).

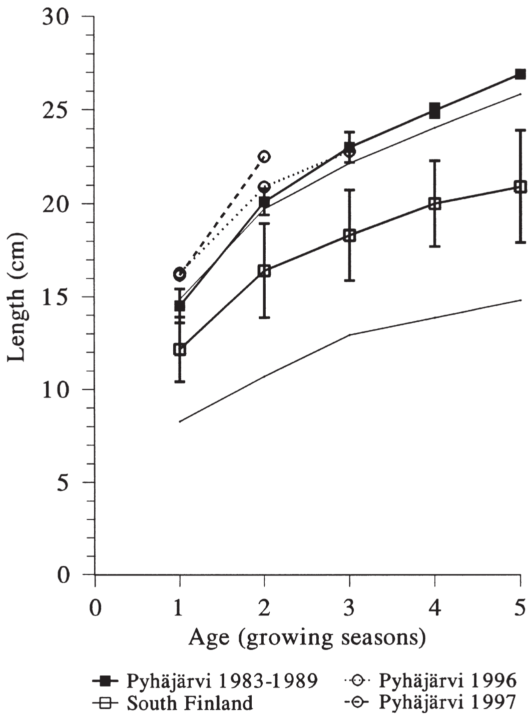

Fig. 5. Length at age for vendace in Pyhäjärvi (mean ± between-year SD, sexes combined; Sarvala *et al.* 1994a, complemented) compared with lake populations of southern Finland (average, SD and range [thin lines] shown; Viljanen 1986).

the 1983 cohort alive in the beginning of the winter fishing period of 1983–1984 survived until the next autumn (Helminen *et al.* 1993a). For the 1988 cohort the corresponding survival percentage was 1.2%, while for the 1989 cohort it was only 0.4% (the total instantaneous mortality rates Z were 2.6, 4.5 and 5.4 yr^{-1}; Helminen *et al.* 1992, 1993a). The growth is correspondingly very rapid (Fig. 5), fecundity is high (in 1983–1989 the average absolute fecundity of age 1+ females was 9 000–11 800 eggs $fish^{-1}$; Sarvala *et al.* 1992), and the age at first reproduction of males is lower than usual (Sarvala *et al.* 1992). In most lakes both male and female vendace mature in their second autumn, but in Pyhäjärvi a notable proportion of males and in some years even a small proportion of females mature in their first autumn (Sarvala *et al.* 1992, Sarvala and Helminen 1995). Although the total population density and biomass of vendace in Pyhäjärvi are comparable to other lakes (Helminen *et al.* 1992), the spawning population is very sparse, during recent years even less than 5 females per hectare. Therefore, in spite of the compensatory increase of individual fecundity, the population fecundity (21–36 eggs m^{-2} per spawning area; Sarvala *et al.* 1992) remains lower than in many other Finnish vendace lakes.

Whitefish

The whitefish catches during 1980–1991 were around 100 tonnes per year or 6.5 kg ha^{-1} yr^{-1} (J. Sarvala *et al.*, unpubl.). In terms of mass, the major part of the whitefish catch was derived from the gill net and fyke net fishery at ages from 2+ to 4+, but numerically about 70% were caught at ages 0+ and 1+ as by-catch in the winter seining for vendace (Fig. 6). Whitefish year-class variation is currently being evaluated, but the numbers were much lower than those of vendace. The abundance of 0+ whitefish in the winter catch suggests that, during recent years, stronger than average whitefish year-classes hatched in 1989, 1993, 1995 and 1996.

Whitefish growth has varied considerably during this century (Fig. 7), mainly as a response to variable population density. During the 1920s and 1930s, the dominant whitefish form in Pyhäjärvi was the river-spawning and plankton feeding northern densely rakered whitefish (Järvi 1940, 1953). In the early 1920s the population of the plankton whitefish was very dense (catch in 1921 was 350 tonnes; Olander 1922), and growth was correspondingly slow. During the 1930s growth of the same whitefish form was very rapid, but the rate declined during the 1940s, simultaneously with a shift in

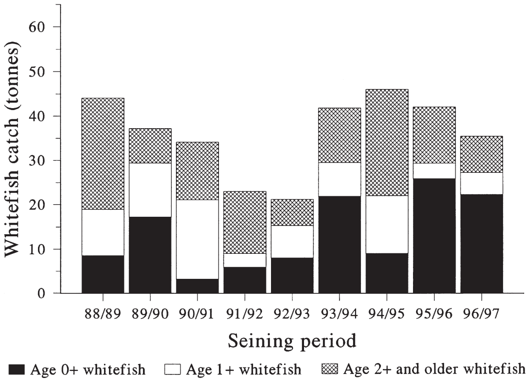

Fig. 6. Winter seine catches of whitefish from Pyhäjärvi in 1988–1997 (from Sarvala *et al.* 1998b, complemented).

the dominant whitefish form to the present lake-spawning southern densely rakered whitefish (Järvi 1953). In the dense population of the 1950s growth was very slow (Wikgren 1958), but it showed some improvement during the 1980s (Fig. 7), when the Pyhäjärvi whitefish had an almost identical growth curve to that of the corresponding whitefish forms in lakes Keitele (Fig. 7) and Päijänne in Central Finland (Valkeajärvi 1987). In the 1990s, after the decline of the vendace stock, whitefish growth seems to have improved (J. Sarvala *et al.*, unpubl.; Fig. 7).

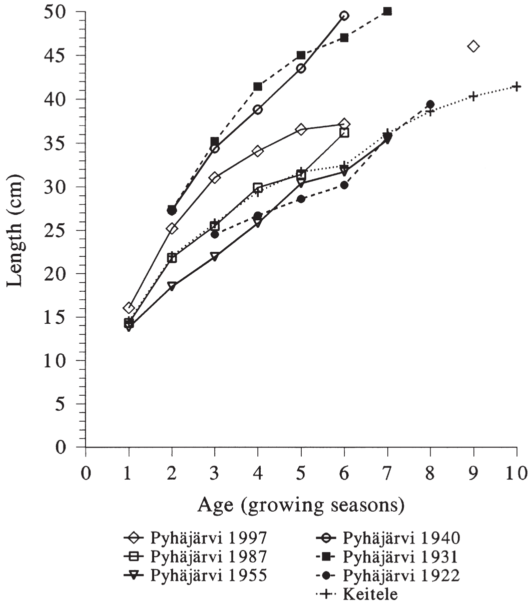

Fig. 7. Length at age of whitefish (sexes combined) in Pyhäjärvi (Järvi 1940, 1953, Wikgren 1958, J. Sarvala *et al.*, unpubl.) and in Lake Keitele (modified from Sarvala *et al.* 1994a).

Smelt

A major part of the smelt catch derives from winter seining. Smelt catches vary considerably between years. Very high smelt catches were reported early this century: the recorded catches of 204 907 kg in 1914 and 306 927 kg in 1915 were almost exclusively composed of smelt (Hagman 1915, 1916; the fishes were exported by rail and the local railway station officer kept precise mass records). In 1916 the stock was depleted and very few smelt were caught (Hagman 1916). In 1976 smelt catches (Table 1) were unusually small, but increased later to a peak in 1983 when they exceeded 100 tonnes. In 1986–1992 the smelt stock was again sparse, but the year-class 1993 was very strong (Karjalainen *et al.* 1997), and its development could be followed up to the winter 1996–1997 from winter seine catch samples (Sarvala *et al.* 1997, 1998a).

Other fish species

Roach is a typical by-catch species which is avoided during normal fishing operations. Yet considerable numbers are caught in connection with the winter seining and also in gill net fishery. Perch also appears as by-catch both in the winter seining and the gill net and fyke net fisheries, and in recent years bigger perch have themselves become commercial targets of fishing. Relative strength of perch year-classes was assessed for the years 1986–1993 from the catch samples (Sarvala and Helminen, 1996): strong year-classes were found in 1988 and 1992. More recent data indicate likewise strong year-classes for 1994 and 1997. Although ruffe is very abundant in the lake, there are no reliable data on its year-class variation. The fishermen try hard to avoid catching ruffe, but some (in 1976 more than 16 tonnes) are still hauled up as by-catch in the winter seining and in the gill net fishery. In 1995–1997, the fishing of smelt, roach, ruffe and small perch was subsidized to improve the water quality in the lake. This small financial incentive considerably increased the catches of these species

(Fig. 2), showing how selective even the winter seine fishery can be. Although seine nets are among the least selective gears, fishermen can affect the composition of catch by adjusting the hauling depth (e.g., ruffe can be avoided by keeping the net above bottom), by choosing suitable fishing sites based on previous experience or the use of hydroacoustic tools, or through seasonal distribution of effort (roach and ruffe catches are highest in late winter).

Discussion

Basis of the high fish catches

The total fish catch from Pyhäjärvi amounts to 0.8% of the phytoplankton primary production, an unusually high percentage relative to published relationships in lakes (e.g., Morgan *et al.* 1980, Nixon 1988). Several hypotheses have been presented to account for this anomaly (Sarvala *et al.* 1984, Sarvala 1991). The morphometric features of the lake favour high rates of nutrient cycling within the lake: non-stratified lakes usually have higher chlorophyll yields relative to phosphorus than stratified lakes (Mazumder 1994). However, the chlorophyll-phosphorus relationship in Pyhäjärvi is consistent with the general regressions for non-stratified lakes (Sarvala *et al.* 1998a). Since about 95% of the total bottom area in Pyhäjärvi belongs to the euphotic zone, the benthic primary production might be important (Sarvala *et al.* 1984). The measured phytobenthos production may indeed double the organic carbon available for consumers (J. Sarvala *et al.*, unpubl.), but this does not explain the discrepancy with data in the literature, because in most cases fish yields were compared to phytoplankton production only. Moreover, zooplankton production in Pyhäjärvi

Table 1. The species composition of the total annual fish yield to professional, semiprofessional and non-professional fisheries in Pyhäjärvi in 1976 (522.5 tonnes yr^{-1} or 33.9 kg ha^{-1} yr^{-1}; data from P. Kummu and M. Naarminen, unpubl. report in 1978; modified from Sarvala *et al.* 1994a), and the contribution of each species to the total catch in experimental fishing with benthic and pelagic gill nets in May–August 1984 (about 167 and 265 kg, respectively). Coregonid figures include vendace × whitefish hybrids that are common in the lake (Vuorinen 1988). Asterisks denote introduced species. In addition, grayling (*Thymallus thymallus* [L.]) have been stocked in the 1950s–1970s and a few rainbow trout (*Oncorhynchus mykiss* [Walbaum]) in the 1960s. Brook trout (*Salvelinus fontinalis* [Mitchill]) introduced into the river Pyhäjoki draining into Pyhäjärvi are also now and then caught in the lake.

Species	kg ha^{-1}	Total yield (%)	Catch in experimental fishing (%)	
			benthic	pelagic
Vendace*[a)], *Coregonus albula* (L.)	23.46	69.1	3.2	17.6
Roach, *Rutilus rutilus* (L.)	3.48	10.2	15.3	10.8
Whitefish*[b)], *Coregonus lavaretus* (L.)	2.96	8.7	3.8	3.4
Perch, *Perca fluviatilis* L.	2.08	6.1	28.8	20.0
Ruffe, *Gymnocephalus cernuus* (L.)	1.04	3.1	47.2	46.9
Pike[c)], *Esox lucius* L.	0.40	1.1	0.6	0.2
Burbot, *Lota lota* (L.)	0.23	0.67	0.0	0.38
Bream, *Abramis brama* (L.)	0.17	0.50	0.12	0.0
Smelt, *Osmerus eperlanus* (L.)	0.014	0.04	0.9	0.6
Brown trout*[d)], *Salmo trutta* L.	0.003	0.008	0.07	0.14
Pikeperch*[e)], *Stizostedion lucioperca* (L.)	0.006	0.016	0.0	0.0
Eel*[f)], *Anguilla anguilla* (L.)	0.09	0.26	0.0	0.0
Bleak, *Alburnus alburnus* (L.)	< 0.006	< 0.016	0.01	0.0

[a)] First introduction tried in 1925; successful introduction in 1948–1952.
[b)] Several forms introduced starting from 1908; later almost annual stocking of newly-hatched fry until 1987.
[c)] Native stock, but regular stocking of a few weeks old fingerlings.
[d)] Dependent on annual stocking of three summers old juveniles.
[e)] Adults stocked.
[f)] Latest stocking in 1968.

is not especially high relative to phytoplankton primary production, and the same applies to zoobenthos production (Sarvala 1991, J. Sarvala *et al.*, unpubl.). Thus, Pyhäjärvi is not especially productive at the phytoplankton level, nor is its fish food production unusually efficient.

Another hypothesis was based on the observation that the clear water and shallow depth of Pyhäjärvi together create very favourable conditions for predation by sight (Sarvala *et al.* 1984). Thus both planktivorous and benthivorous fish might be able to utilize a larger fraction than usual of the production of their prey. This would further require that the food organisms, zooplankton and zoobenthos, have special refuges enabling them to maintain their populations in spite of the presumably intense predation by fish (Sarvala 1991). In the shallow and unstratified Pyhäjärvi, diel vertical migrations do not provide any refuge for the zooplankton, and observations indicate that such migrations are indeed lacking (Sydänoja *et al.* 1995); only littoral zooplankton shows diel horizontal or microscale vertical movements, which seem to be tuned to the diel horizontal movements of fish larvae and young (Walls *et al.* 1990). Thus, in Pyhäjärvi, it is mainly the various life cycle adaptations that might rescue the zooplankton from excessive predation.

However, the total food consumption of vendace was estimated to be only 9%–14% of crustacean zooplankton production (Helminen *et al.* 1990, Helminen and Sarvala 1994a), and that of whitefish 2% (Sarvala 1992). These figures are roughly similar to those reported for other zooplanktivores in lakes (e.g. Gliwicz and Prejs 1977, Hewett and Stewart 1989) and thus the hypothesis of efficient predation is not corroborated. Yet at times the food consumption by planktivores exceeded the production of *Bosmina coregoni* and *Eudiaptomus graciloides*, the most favoured prey species, and could influence their population dynamics (Helminen *et al.* 1990). High densities of coregonid larvae were found to suppress the spring development of zooplankton (Sarvala *et al.* 1994b), and in the long-term time series there is a negative correlation between the planktivorous fish biomass and the crustacean zooplankton biomass (Helminen and Sarvala 1997, Sarvala *et al.* 1997, 1998a), indicating that fish abundance regulates zooplankton. On the other hand, the strong inverse correlation between the year-class strength and first-year growth of vendace (Helminen *et al.* 1993a) attests that food availability in turn is limiting planktivorous fish production. Indeed, in late summer, the total food consumption of the planktivorous fish reaches a plateau, and then age 1+ vendace stop growing (Helminen *et al.* 1990, J. Sarvala *et al.*, unpubl.), while the whitefish switch to alternative insect prey and continue their growth further (J. Sarvala *et al.*, unpubl.). Long-term data on whitefish growth also suggest food limitation (Järvi 1940, 1953, J. Sarvala *et al.*, unpubl.). Thus, it seems likely that the level of fish production in Pyhäjärvi is as finely tuned to the food production as is normal in other lakes (Downing *et al.* 1990).

Intensive fishing thus remains as the most likely explanation for the high fish catches. Indeed, the vendace fishery is taking an unusually large part of the vendace production: for the 1988 cohort, the commercial catches accounted for 87% of the production of the first year and 138% of the production of the second year (the percentage exceeds 100% because part of the biomass caught in the second year was produced already during the first summer) (Helminen *et al.* 1992). Normally only around 20%–25% of fish production can be taken as fisheries yield (Borgmann *et al.* 1984, Houde and Rutherford 1993). The resulting total mortality rates of vendace in Pyhäjärvi (2.6–5.4 yr^{-1}) are extremely high for a northern fish population, and higher than values for other intensively fished vendace populations in Finnish lakes: Pyhäselkä 1.6 yr^{-1} (Viljanen *et al.* 1982), Karjalan Pyhäjärvi 1.3–1.5 yr^{-1} (H. Auvinen, unpubl.), Onkamo 2.3 yr^{-1} (H. Auvinen, unpubl.), and other 0.4–1.8 (Viljanen 1986). The extremely high mortality rates result in relatively low population densities and imply high production to biomass ratios.

Even judged from fishing effort indices the fishing intensity in Pyhäjärvi is indeed exceptionally high for a northern lake. The total fishing effort is largely determined by the number of seines: in Pyhäjärvi, the average annual catch from a winter seine has equalled that from 4 667 gill nets or 172 fyke nets (one fyke net has thus been equivalent to 27 gill nets). Using these conversion factors between different fishing gear, the total fishing effort in Pyhäjärvi was in the 1980s about 3.0

gill net units ha^{-1}. Comparable calculations for other large Finnish lakes with seine net and gill net fishery yielded values of 0.3–0.8 gill net units ha^{-1}, except for Lake Onkamo in eastern Finland, in which intensive winter seining of vendace resulted in a total effort of 3.5 gill net units ha^{-1} (data from Finnish Game and Fisheries Research Institute). In seven large Finnish lakes with a developed trawl fishery, the total effort estimates varied between 0.5 and 1.7 gill net units ha^{-1}, but in Lake Paasivesi the effort was 3.0 gill net units ha^{-1} (conversion factor based on annual catches: one trawl = 7 000 gill nets).

Such high exploitation rates are partly made possible by the fact that the piscivorous fish stocks in Pyhäjärvi are weak, so that most of the vendace production remains to be harvested by fishermen. This situation is probably a consequence of the intensive fishery itself, because the large piscivores are more vulnerable to fishing than vendace. Consistent with this reasoning, large piscivorous perch and pike were more abundant early this century when the commercial fishery had just started (Sarvala *et al.* 1994a). Besides being caught by the professional fishermen, the piscivores are nowadays also subject to considerable recreational fishing pressure. The numbers of recreational fishermen in Pyhäjärvi have been estimated in different surveys at 1 000—2 000 persons (Salmi 1991, Hirvonen *et al.* 1992). Calculated per unit area, the number of recreational fishermen in Pyhäjärvi was highest, and the number of annual fishing days the second highest among Finnish lakes studied (H. Auvinen, unpubl., data from Leinonen *et al.* 1998).

The decisive importance of a well-developed fishery for the level of observed catches is confirmed by recently compiled data which show that catches may be high relative to primary production also in other intensively fished Finnish lakes (J. Sarvala *et al.*, unpubl.). In most such lakes, the major target of fishing is vendace, as in Pyhäjärvi. Recently published estimates of fish yield in some large northeast European lakes also imply high efficiencies (fish yield on an average 0.09%–0.29% of primary production; Lavrentyeva and Lavrentyev 1996).

Annual catches of 0.2–43 kg ha^{-1} were reported from 166 northern Finnish lakes by Ranta and Lindström (1998). Catch levels of 2–20 kg ha^{-1} a^{-1} were sustained for 9 years in 50 small, mostly relatively unproductive Finnish forest lakes with perch, pike and roach as their major species (Toivonen 1991). In another set of 50 similar lakes, the standing crop of fish varied between 5 and 112 kg ha^{-1} (Toivonen 1991). Based on these data, Toivonen (1991) suggested that in these lakes the sustained annual fish yield might be 20%–25% of the total fish biomass. Rough estimates of the total fish biomass in Pyhäjärvi can be obtained by comparing the experimental gill net catches to those from the shallow (mean depth 2 m) Littoistenjärvi, a lake in southwest Finland. In 1993–1997, the average catches from experimental gill nets in Littoistenjärvi varied between 0.6 and 2.2 kg 100 m^{-2} h^{-1} (J. Sarvala *et al.*, unpubl.), corresponding to total biomass levels of 31–73 kg ha^{-1} from mark-recapture experiments (M. Kurkilahti, unpubl., in Sarvala *et al.* 1998a). Assuming similar relationships between experimental catches and total fish biomass, the night-time catches from experimental benthic gill nets in Pyhäjärvi in 1984 (1.2 kg 100 m^{-2} h^{-1}) suggest total biomass levels of about 40–60 kg ha^{-1}. These figures sound realistic compared to the estimated biomass of planktivorous fish in Pyhäjärvi (5–28 kg ha^{-1}, where the upper bound is representative of fish stocks in 1984; Sarvala *et al.* 1998a), and are well within the range of other Finnish lakes. Using the yield to biomass relationship of Toivonen (1991), annual catches of 10–15 kg ha^{-1} would be expected from such fish biomass. The higher realized catches in Pyhäjärvi indicate either higher production to biomass ratio or higher exploitation of production, or both, compared to the small forest lakes.

When comparing fisheries yields, it should be noted that the lower the trophic position of the exploited species in the food web, the higher can be the efficiency of the fishery relative to primary production. Many of the productive marine fisheries listed by Nixon (1988) are based on relatively small-sized planktivorous or demersal species. The fisheries in Pyhäjärvi and other Finnish oligotrophic and mesotrophic lakes are mainly based on zooplanktivorous species (Sarvala *et al.* 1994a). Two thirds of the high catch rates from the African Lake Tanganyika likewise derives from zooplanktivorous clupeids (Sarvala *et al.* 1998c), while a large part of the traditionally reported fish catches in temperate lakes consisted of large-sized, often piscivorous species (Oglesby 1977).

Vendace as a key species

The commercial fishery in Pyhäjärvi is based on the coregonids vendace and whitefish. Vendace is a keystone species in the system, regulating zooplankton composition, biomass and size distributions, and thus indirectly the phytoplankton and water quality (Helminen and Sarvala 1997, Sarvala *et al.* 1997, 1998a). Larval vendace feed on cyclopoid nauplii and copepodids, and juveniles and adults consume in addition calanoids (especially *Eudiaptomus graciloides*) and cladocerans (especially *Bosmina coregoni*, *Daphnia galeata* and *Chydorus sphaericus*); adult insects from the water surface are occasionally used (Helminen *et al.* 1990, J. Sarvala *et al.*, unpubl.). As the most specialized zooplankton feeder in northern lakes, vendace is an effective competitor that during periods of strong stock seems to dominate over all other pelagic fish species (e.g., Svärdson 1976). In several Finnish lakes, whitefish growth rate has varied inversely with vendace stock strength (Huhmarniemi *et al.* 1985, Heikinheimo-Schmid 1992, Valkeajärvi 1992), consistent with our experiences from Pyhäjärvi. In some northern Norwegian lakes, recently invaded vendace has displaced the original plankton-feeding whitefish in the pelagic habitat (Bøhn *et al.* 1996), and similar habitat differences of whitefish depending on the presence or absence of vendace are known from Sweden (Svärdson 1976). In our experimental gill netting in the open lake of Pyhäjärvi in 1984, vendace used the whole water column, and was the only fish species that was consistently abundant in the upper and middle parts of the water column, while other species were usually caught close to the bottom. The recent decline of the vendace population in Pyhäjärvi has left space for whitefish (improved growth) and smelt (strong year-class hatched in 1993), and may have resulted in changed behaviour and habitat selection of juvenile perch that now migrate to the open lake already in early summer.

The population dynamics of both vendace and whitefish are to a large extent controlled by the fishery, although weather and climate fluctuations exert decisive influence, and competitive and other food web interactions are also important (Helminen and Sarvala 1994b). There is an important interaction between the fishery and the fish recruitment. Only a fish species with a short life cycle and rapid reproduction can withstand such a heavy fishing pressure: vendace has the shortest life cycle and highest rate of reproduction of commercially utilizable Finnish freshwater fishes (Koli 1984). Fishing reduces the populations of predatory fish, thus decreasing the natural mortality of vendace. However, the fishing mortality in Pyhäjärvi is so high that there is usually only one reproducing vendace year-class, and therefore a constantly high recruitment success is a prerequisite for the sustainability of the fishery. The rapid growth and ensuing high individual fecundity of the few fish surviving to maturity partly compensate for the low numbers of spawners. One factor also contributing towards a successful recruitment is that suitable spawning substrates are abundant: roughly 40% of the lake area can be classified as erosion bottoms (Salonen *et al.* 1997) with well oxygenated sandy sediments.

The majority of the vendace catch consists of juvenile fish. This kind of harvesting is not common in fisheries, and is at odds with the precautionary principle (Garcia 1994, Roberts 1997, Myers and Mertz 1998), according to which juvenile fish should be exploited sparingly in order to avoid recruitment overfishing, i.e. in order to guarantee a large spawning stock to ensure sustained reproduction. However, under conditions of limited food, such fishing focusing on the juveniles also theoretically allows much higher exploitation rates without a population collapse than fishing that is concentrated on adult fish (Begon and Mortimer 1981: p. 137). Intensive fishery keeps the fish populations small and rapidly growing. Fish are very plastic in their growth and reproduction, and heavily exploited populations respond with increased growth and earlier maturity, and thus compensate for fishing mortality (Hilborn *et al.* 1995). Besides vendace, most other fish species also grow faster in Pyhäjärvi than in Finnish lakes in general (Sarvala *et al.* 1994a). This pertains especially to the commercially important species, but to a certain extent to the bycatch species as well. The prerequisite here, strong intraspecific food competition, is consistent with the general observation that commercially important fish populations must have a high capacity to compensate for the fishing mortality through strong density-dependent responses (Garrod and

Horwood 1984).

Although vendace has many characteristics making it a suitable target for intensive fisheries, its exploitation in Pyhäjärvi seems to be approaching the limits of a sustainable fishery (Helminen *et al.* 1997c). Continuously high exploitation does not leave any buffers against environmentally induced recruitment failures (Lauck *et al.* 1998). Managing for ecological stability at higher target stock level would normally also guarantee better economic stability for the fishery (Roughgarden and Smith 1996). The influence of the predator-prey interactions between vendace and its major predators (perch, brown trout) should also be taken into account in the management (cf. Christensen 1996).

One of the strengths of the fishery in Pyhäjärvi has been the relatively unselective nature of the winter seine net fishing compared to, e.g. gill netting. Selective methods of fishing may bias the composition of the fish community. However, even in the seine net fishery it is possible to avoid some species and concentrate on the most valued ones by selecting seining areas and depths according to known species-specific aggregation patterns. Thus, in the late 1980s and early 1990s, each vendace year-class was decimated during its first winter, while each year-class of perch, roach or smelt remained in the fishery for several successive years. Later, when the vendace stock was low and subsidies were paid to the coarse fish fishery to improve water quality, these differences between species somewhat levelled off, and the 1993 year-class of smelt was practically fished out of the lake in two years.

Economic perspectives

Fishery is an important branch of economy in the local community. The value of the total fish catch from Pyhäjärvi was estimated at FIM 7 million in 1976, and about FIM 5 million in 1994. The winter seining methods have remained traditional, which means that the number of fishermen in each fishing crew is relatively high (4–6 men), while elsewhere in Finland crews using more developed techniques may be comprised of only two men (e.g., Turunen *et al.* 1997). This conservatism at least partly derives from natural causes: in the open Pyhäjärvi, wave action during freezing often results in a very uneven lower surface of the ice which seems to prevent the use of the new sophisticated devices for driving the seine ropes under the ice. Thus the winter fishery in Pyhäjärvi continues to provide earnings for more numerous fishermen than winter fisheries in other parts of Finland. In the Pyhäjärvi area, the total number of persons in households wholly or partly dependent on income from fishery was about 550 persons in the late 1980s (Salmi 1991). It is notable that until the 1990s this fishery did not require any economic subsidies.

There are several reasons for the success of this fishery. The bottom topography allows seine netting in a large part of the lake, and, owing to the shallowness, each haul can embrace the whole water column from bottom to surface. The fishing licence policy has been liberal (see below). The main fishing season is winter, which is favourable for marketing: it is easy to maintain the good quality of fish with little labour or investment, and there is less competition from other fisheries. The large size of vendace from Pyhäjärvi also improves both the demand and the price obtained. In summer, in contrast, the market situation is more difficult, particularly for the young vendace. In warm weather, the fish quality easily deteriorates, especially if the catches are not iced at the lake. There is much scope for improvement in the post-harvest treatment of the summer catches.

At present, the local fish markets in the Pyhäjärvi region are functioning well, and the surplus catches are exported to other parts of Finland, mainly as fresh (round) fish. Vendace is traditionally sold as fresh or smoked, and whitefish as fresh, smoked or filleted. Pike and burbot are sold as round fish. As in many other parts of Finland, special projects have recently investigated new ways of utilizing the less valued fish species (Partanen 1997). Market demand for filleted large or medium-sized perch developed in the early 1990s, giving thrust to the perch fishery. New smelt products were developed, but problems with steady availability and price hindered further progress. Roach was used for producing minced fish mass, but in spite of the good quality of the product, demand was limited. Highly variable catches from a single lake are a major problem for the utilization of all of the less valued fish species, and any commercial development would require an efficient regional collecting system. On the other hand, even the marketing of vendace is very sensitive to variations in catch levels. In the 1990s, the recovery of many South Finnish vendace stocks from a long-term decline phase (Valkeajärvi *et al.* 1997) immediately weakened the market situation for ungutted Pyhäjärvi vendace, while the demand for gutted vendace increased. As a response, the gutting machine capacity around the lake expanded fourfold (Partanen 1997), and ice machine capacity was likewise enlargened. Further development of local fish processing might better buffer the markets against catch and demand fluctuations. Technical improvements in the sorting of catches are also needed now when the proportion of coarse fish in the catches has increased.

Management possibilities

In Finland, the inland waters are privately owned. The owners can freely decide upon the fisheries management, within the framework of the Fisheries Act (from the year 1982, with later amendments; Sipponen 1995) that aims at an efficient use of the fish resources. The fisheries organization includes so-called fisheries regions, in which both water owners and fishermen participate in the administration. As regards Pyhäjärvi, a voluntary fisheries management association was established very early, in 1916. There were serious disputes about the fishing rights between interest groups around the mid-1800s, and renewed conflicts again early this century, following the successful introduction of whitefish into the lake. The high catches of big smelt in 1914–1915 aroused concern about the sustainability of the fishery, and the very establishment of the fisheries management association was a direct result of this dispute. Later, the management options included repeated introductions of fish fry (especially whitefish, but later also other species) and liberal licensing with only certain restrictions, e.g. lower limits to gillnet mesh sizes and limits to the sizes and types of fyke nets in whitefish fishery, a closed season during the autumn spawning period of whitefish, etc.

The ubiquitous problem of transforming scientific advice into practical fisheries management (e.g. Ludwig *et al.* 1993, Salmi and Auvinen 1998) has also been encountered in the Pyhäjärvi district. The final management decisions are made by local people with varying interests and educational background, and therefore it is often very difficult to implement any rational fisheries management. There is considerable resistance to external advice among the local fisheries managers. For example, it seems to be very difficult to give up fish stockings, even if they might be ineffective, as is stocking of newly emerged whitefish fry, or even harmful to the commercial fishery, as are brown trout stockings. Scientific advice tends to be accepted only as long as it agrees with the previous opinions of the managers.

Fortunately, the present winter seine fishery in Pyhäjärvi is (or at least was) to a large extent self-regulating, but the criteria are economic. Because the seine gangs fishing in Pyhäjärvi so far comprise 4–6 men, relatively high catches are required to keep the fishing economically profitable. In early winter, the daily coregonid catches of a seine gang may start from 800–1 000 kg, and they diminish with the depletion of the stock during the winter. When the daily catches fall below about 100 kg towards late winter, the fishermen stop fishing. The modern two-men gangs, nowadays common in eastern Finland, might continue fishing much longer and decimate the vendace stock to dangerously low levels. Even the present fishing practice has driven the vendace spawning stock to such low levels that some fishing restrictions could be contemplated. Besides climatic factors, one reason for this development may be the known, although undocumented, increase in the size of the seine nets during the 1980s. In most of the world's fisheries, technological development eventually tends to undermine sustainability (Whitmarsh *et al.* 1995). The obvious first control options in Pyhäjärvi might be to close the vendace fishery for the spawning period, or to agree on closed areas. A closed spawning season has been successfully applied in Pyhäjärvi in the whitefish fishery management. However, the vendace fishermen interviewed seemed to be more willing to accept closed areas than a closed season. Winter seining is already now forbidden in the eastern part of the lake (ca. 20% of lake area), and taking into account operational depth restrictions, seining is in practice confined to 55% of the lake area. Establishment of such "no-take" reserves seems elsewhere to be a socially accept-able and biologically successful route towards sustainable fishery (Botsford *et al.* 1997, Roberts 1997, Lauck *et al.* 1998).

Future prospects in the changing climate

Both of the economically most important species in Pyhäjärvi are coregonids that prefer cool or cold, oligotrophic waters. Their success in the non-stratified, mesotrophic lake Pyhäjärvi is thus somewhat surprising, although fishable coregonid (especially whitefish) stocks occur in some other shallow lakes in southern Finland. Maintenance of the coregonid stocks in Pyhäjärvi is favoured by the morphometry of the lake: due to the openness there are large areas of erosion bottoms that are suitable as spawning grounds for both species. However, the continuing eutrophication of the lake would eventually impair the reproduction of coregonids in the lake; there are ample examples of such development in other countries (Sterligova *et al.* 1988, Müller 1992). At present, there are serious attempts in the Pyhäjärvi area to curb the excess nutrient loading and to reverse the adverse development of the water quality (Mattila 1997).

However, even if the eutrophication can be stopped or even reversed, the ongoing climate change will have adverse effects, especially on the vendace recruitment. In a doubled carbon dioxide climate scenario, wet and mild winters would result in a one–two months earlier ice-out (Huttula *et al.* 1992). At the same time, winds would increase, and because temperatures would increase less in summer than in winter (e.g., Vehviläinen and Huttunen 1997), the warming of water after the ice-out in spring could become slower. These changes would have a pronounced negative effect on the growth and survival of vendace larvae (Helminen and Sarvala 1994b, 1995, Helminen *et al.* 1997c). Simultaneously, the elevated summer temperatures would increase the probability of strong perch year-classes (Böhling *et al.* 1991, Lehtonen and Lappalainen 1995, Sarvala and Helminen 1996), which would lead to higher predation pressure on larval and juvenile vendace. There are previous experiences with the effect of warm periods on vendace: long-term historical data on the year-class variation of vendace in Lake Keitele (Järvi 1942) indicate that year-classes were weak throughout the exceptionally warm decade in the 1930s. These changes, together with stockings of predatory fish, are likely to keep vendace recruitment low in the future, with serious negative effects on the fishery. On the other hand, whitefish larvae are not so sensitive to changes in the timing of ice-out or the abundance of predators, and, because the low vendace stock will diminish food competition, the whitefish population may be enhanced. It may be noted that in Europe, the various whitefish forms clearly have more southern distribution than vendace. Thus, it is likely that in a warmer climate the whitefish fishery in Pyhäjärvi would gain in importance again (for decades, the fisheries in Pyhäjärvi were mainly based on whitefish). Excessive warming would eventually harm the whitefish as well (Lappalainen and Lehtonen 1997).

Eutrophication and climate warming are likely to increase the stocks of several less valuable species, such as roach, bleak, smelt, small perch and ruffe, and this makes fishing more laborious, increasing the time needed to sort the catches. The warmer winters also restrict winter seine fisheries, and therefore fyke-net and gill-net fishing during the open-water season are likely to become more important. So far, open water seine netting has not been successful during the warm season, but late autumn trials have been promising, and it may develop as a feasible alternative. It may also be possible to broaden the basis of the fishery by strengthening the stocks of some other species, such as pikeperch (Helminen and Marjomäki 1995), especially if the eutrophication continues in spite of the attempts to reduce external nutrient loading. On the other hand, the stocking of brown trout, which is already not now economically viable (Helminen *et al.* 1997b), is bound to become even less profitable (increased temperature increases metabolic costs and leads to increased stress and impaired growth).

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