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Long-term decline of whitefish (*Coregonus lavaretus*) population in the boreal lake Pyhäjärvi, southwest Finland, relative to simultaneous abiotic and biotic changes

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Abstract – In recent decades many lake fish populations have faced complex pressures particularly due to climate warming and eutrophication. In Lake Pyhäjärvi, southwest Finland, profound changes have occurred in the commercial winter fisheries targeting the coregonids vendace, *Coregonus albula*, and whitefish, *Coregonus lavaretus*. The responses of vendace have been examined earlier, and here the detailed analyses are extended to the whitefish. In the 1970s and 1980s, the coregonid fishery was sustainable, but in 1991–1998, intense exploitation led to recruitment overfishing of vendace. Despite temporarily improved growth and recruitment of whitefish during vendace decline, whitefish population biomass declined throughout the study period, while perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernuus*) increased and vendace and smelt (*Osmerus eperlanus*) maintained their abundance. As many other northern lakes, Pyhäjärvi seems to be changing from coregonid to perch dominance due to climate warming and eutrophication. Whitefish decline was associated with decreases in fecundity, winter survival of embryos, and larval density. The spawning stock was kept small by intensive fishery. The decline of the relative fecundity was likely due to food competition with vendace and especially the perch and roach populations that increased with eutrophication and more frequent hot summers. The winter survival of whitefish embryos decreased when the introduced signal crayfish (*Pacifastacus leniusculus*) increased. Despite decreasing fishing effort in the 2000s the larval numbers continued to decline. In the prevailing circumstances in Pyhäjärvi, whitefish will with high probability remain as a minor and still declining species of the fish assemblage.

Keywords: Climate warming / intense fishing / larval abundance / population decline / eutrophication

1 Introduction

Contemporary lake fish populations have to cope with numerous simultaneous stressors, such as climate change, eutrophication, invasive species and commercial fisheries (Jeppesen *et al.*, 2012). Over the years these factors have caused profound changes in the fish assemblages, eurythermal species gaining higher importance, and stenothermal cold-water fishes declining, particularly in shallow lakes. An example of such changes is the development of fisheries in Lake Pyhäjärvi, southwest Finland. In this lake, the fishery was for hundred years based on the coregonids whitefish

Coregonus lavaretus (Linnaeus) and vendace *Coregonus albula* (Linnaeus), both initially introduced but now well established (Sarvala *et al.*, 1999). Starting from 1908, at least four different forms of whitefish have been introduced in Pyhäjärvi (Järvi, 1940; Järvi, 1953; Sarvala *et al.*, 1999). The first stockings consisted of a lake-spawning whitefish with a medium number of gill rakers (later "medium-rakered") that resembled the present form in the lake. Small numbers of another lake-spawning medium-rakered whitefish were later also introduced. River-spawning sparsely-rakered benthivorous and densely-rakered planktivorous whitefish were also stocked, but beginning from the 1940s, the present medium-rakered form (on an average 39–41 gill rakers) took over and became self-sustaining. The local fisheries managers continued stockings, mostly with newly-hatched larvae, originating

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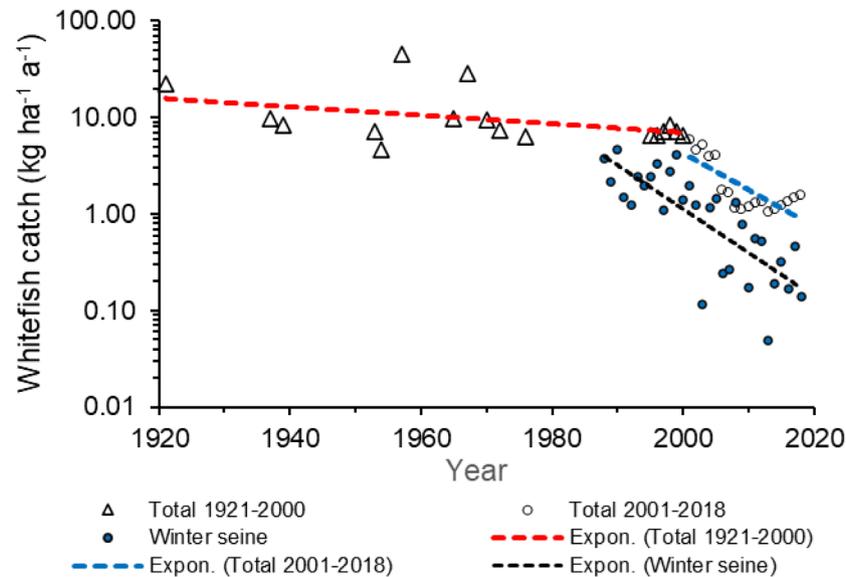
Fig. 1. Annual catches of whitefish (*Coregonus lavaretus*) from Pyhäjärvi, southwest Finland (Järvi, 1940,1953; Sarvala *et al.,* 1999; total catch estimates from the unpublished reports of the local fisheries management association; winter seine catches based on catch samples combined with the vendace catches reported by the fishermen).

from eggs of whitefish from Pyhäjärvi. In recent decades an average of 1.5 million larvae were stocked annually. A mark-recapture study by the Pyhäjärvi Institute in 2008–2013 showed that the proportion of stocked fish in the 0+ whitefish catch next winter was usually negligible (around 1%), but could be more important if natural reproduction failed. It has been suggested that the present whitefish in Pyhäjärvi evolved in the lake through hybridization of the various introduced forms (Svärdson, 1979). The existing data on the changes in the gill-raker numbers allow, however, another interpretation, namely that the lake-spawning medium-rakered whitefish, best pre-adapted to conditions in Pyhäjärvi, gradually replaced the other forms. The differences in spawning habitat between the introduced forms support this interpretation. Recent DNA-analyses of Austrian whitefish show that different ecotypes may maintain their integrity even when hybridisation with introduced forms occurs (Winkler *et al.,* 2011).

Whitefish fishery started in 1915, and since 1921 until the early 1960s whitefish was the most important target of commercial fishery (Fig. 1; Sarvala *et al.,* 1999). Whitefish were caught with seine nets in winter from under the ice and with fyke nets and gillnets in the open water season. Several published estimates of total annual catches and population structure exist from the decades before the regular monitoring of the coregonid fishery started in 1971. Catches and individual size of fish varied widely depending on the population density, irrespective of the whitefish form (Järvi, 1940, 1953; Sarvala *et al.,* 1999). At first, catches were high and whitefish individuals were big − a typical whitefish in catch weighed over one kilogram. Gradually the average weight of whitefish in the fyke net catches declined to about 200 g, initially because the whitefish stock became more abundant, but later probably because its major competitor vendace was successfully introduced in 1948–1952 and became the dominant planktivore. Vendace soon established a self-supporting population, which since the mid-1960s became the principal

target of the commercial fishery (Sarvala *et al.,* 1999). Vendace were mainly caught in winter with seine nets from under the ice.

The patterns of year-class fluctuations of vendace in Pyhäjärvi have been analysed earlier (Helminen *et al.,* 1993a; Helminen 1993b; Helminen and Sarvala, 1994; Helminen *et al.,* 1997; Sarvala *et al.,* 2020; Helminen and Sarvala, 2021; Sarvala and Helminen, 2021). Judging from similar winter seine catch levels for two decades, the coregonid fishery was sustainable in the 1970s and 1980s, with average catches per unit effort (CPUE) of 245 and 44 kg haul^{-1} for vendace and whitefish, respectively, corresponding to biomasses of 17 and 3 kg ha^{-1}. In 1990–1998, the intensive exploitation of vendace led to recruitment overfishing, from which the population recovered by the year 2000, although not quite to the earlier levels (Sarvala *et al.,* 2020; Appendix A). The whitefish population benefitted from this temporary decline of vendace, and the ensuing decline in fishing effort, but when the vendace population recovered, the whitefish catches showed a declining trend. No such trend was observable over long term in the vendace year-classes, although some years earlier the prospects were clearly weaker (Jeppesen *et al.,* 2012; Sarvala *et al.,* 2020).

Analyses of the population variability of vendace from a 50-year time series identified several possible factors affecting the abundance of coregonids (Sarvala *et al.,* 2020; Helminen and Sarvala, 2021), including intensive fishing (Sarvala *et al.,* 2020), inter- and intraspecific competition (Sarvala and Helminen, 2021), predation (Helminen and Sarvala, 1994), weather conditions, climate change (Jeppesen *et al.,* 2012), eutrophication and changing structure of the fish community (Helminen and Sarvala, 2021). It is evident that the fish and fisheries in Pyhäjärvi are currently subject to profound changes induced by eutrophication.

In the present study, the fluctuations of the whitefish population of Pyhäjärvi are related to recent changes in the lake

ecosystem. First, the trends in the whitefish population are confirmed and quantified. Then potential abiotic and biotic environmental factors affecting the various life stages of whitefish are identified and their possible roles examined, hoping to find ways to enhance the whitefish recruitment.

2 Material and methods

2.1 Study lake

Pyhäjärvi (Säkylän Pyhäjärvi, also known as Pyhäjärvi, southwest Finland) is a shallow but large boreal lake in southwestern Finland (61° 00' N, 22° 18' E, 45 m a.s.l.) (area 155 km^2, mean depth 5.4 m, maximum depth 26 m). Its characteristics have been described in numerous publications (Sarvala *et al.,* 1999; Ventelä *et al.,* 2011; Helminen and Sarvala, 2021), so only the most basic features are summarized here. There is no permanent stratification during the open water season; 94% of the lake area is <7 m deep. The ice-covered season, typically from November to April–May (average ± SE 139 ± 4 days in 1957–2014), is rapidly shortening with the warming climate (Ventelä *et al.,* 2011); exceptionally in winter 2019–2020 there was no permanent ice cover. According to the latest EU Water Framework Directive classification based assessment in 2019, the ecological quality ratio of Pyhäjärvi was satisfactory, with average June–September total phosphorus concentration of 20 µg L^{-1}, total nitrogen 444 µg L^{-1}, chlorophyll *a* 8.4 µg L^{-1}, and transparency 2.4 m (data from Centre for Economic Development, Transport, and the Environment of Southwest Finland). Phytoplankton, zoobenthos, zooplankton, and fish production have similar relationships with the physical and chemical environment as in other lakes (Sarvala *et al.,* 1999). The fish assemblage of Pyhäjärvi consists of 18 species, dominated by ruffe (*Gymnocephalus cernuus* (Linnaeus)), perch (*Perca fluviatilis* Linnaeus), roach (*Rutilus rutilus* (Linnaeus)), smelt (*Osmerus eperlanus* (Linnaeus)), whitefish and vendace (Sarvala *et al.,* 1999).

2.2 Methods: environmental data

Water quality of Pyhäjärvi has been monitored with standard methods since 1962 by environmental authorities, university researchers, and Pyhäjärvi Institute, and results are available from the open data service of Finnish Environment Institute (SYKE). Total phosphorus and chlorophyll *a* concentrations (µg L^{-1}) as well as temperature (°C), were recorded 6–24 times per year in the surface water (0–2 m) at the site *Pyhäjärvi Deep*. Daily data on air temperature for the nearest observation station (Kokemäki, Tulkkila, 20 km north of Pyhäjärvi) were obtained from the open data service of the Finnish Meteorological Institute. Littoral water temperature measurements were temporally intermittent, but they followed closely the air temperatures ($y = 0.86x + 3.6$, adj. $R^2 = 0.83$, $n = 32$, $p < 0.001$). Therefore the air temperature was used to calculate the average temperature for the first 28 days after the ice-out. Varying the period between 21 and 42 days did not change the between-year pattern.

For phytoplankton (data likewise available in the database of Finnish Environment Institute) and crustacean zooplankton, samples were taken from 0 to 5 m depth with a cylindrical sampler at ten locations selected using a stratified random design and combined into one composite sample per date 6–24 times per year). Zooplankton was concentrated with a 50 µm mesh net and subsamples were enumerated until 50–200 individuals of the dominant crustacean species had been counted and measured. Counts and measurements were converted to zooplankton biomass using carbon–length regressions (Sarvala *et al.,* 1998). For between-year comparisons, the water quality and plankton variables each year were averaged from 1 June to 30 September, following the EU Water Framework Directive practice adopted in Finland. The temporal patterns remained similar even if slightly different periods (*e.g.* May–September or June–August) were used.

2.3 Methods: whitefish data

2.3.1 Catch and biomass estimates

Local knowledge-based published estimates of the total whitefish catches were available for 11 years in 1921–1976 (Järvi, 1940, 1953; Sarvala *et al.,* 1999). Single annual samples of the size and age distributions of vendace and whitefish in the winter seine net and autumn fyke nets were collected by the Finnish Game and Fisheries Research Institute starting in 1971, and more extensive monitoring of the commercial winter seine fishery was initiated in the winter 1988–1989 by researchers from the University of Turku, in collaboration with Pyhäjärvi Institute. Then data on the species, size and age composition in the seine catches were derived from 11–95 (average 34) catch samples each winter taken on 5–21 (average 10) dates up to 2011 (data from Helminen and Sarvala (2021), complemented by Pyhäjärvi Institute with more recent years up to 2018/2019) (in all 1097 catch samples from 317 dates).

The use of catch records as indicators of fish stock abundance is confounded by temporal variability of fishing effort. Catch per unit effort (CPUE) used in Helminen and Sarvala (2021), is a better measure of the population size, but it is dependent on the fishing gear. In the present study, population biomasses were determined to provide the most reliable estimate of the total population abundance. The key here was the possibility to obtain reliable estimates of the year-class sizes of vendace. These were calculated from the declining catch per unit effort (CPUE, using a working day of a fishing crew as the unit effort) in the seine net fishery during each winter using the DeLury method (Helminen *et al.,* 1993). The year-class size N_0 was obtained from the equation

$$N_0 = T/(1 - q^k)$$

where T = total number of 0+ vendace caught in the winter, q = antilogarithm of the slope of the log-linear regression of CPUE against the cumulative effort through winter, k = total effort during the winter.

When the CPUE data were lacking or the decline was not significant, year-class numbers were estimated from the exponential regression between the average autumn mass of age 0+ vendace and year-class strength, obtained for the 28 years when the DeLury method was applicable (Sarvala *et al.,* 2020).

The 0+ vendace biomass density (kg per hectare) was obtained by multiplying year-class abundance estimates with the average individual mass at the end of the growing season, and dividing this with the lake area. Population biomass estimates for older vendace, whitefish and other species (perch, roach, bleak and smelt) were then calculated by relating their proportions in catch samples to those of age 0+ vendace. Each biomass estimate obtained from winter seine samples was assigned to the preceding calendar year (*e.g.*, winter 1990/1991 was assigned to 1990).

Because of short ice-covered period, seine-netting in 2007/2008 was possible only for a couple of weeks, resulting in insufficient catch sample size. In 2013/2014, age 2+ or older whitefish were completely lacking from the catch samples although their cohorts were present in the samples from adjacent years. Further, in 2011/2012, biomass estimates for whitefish were unrealistically high, exceeding other estimates for the decade by a factor of more than 15. This was because the catch samples for that winter included the highest ever catch of roach with a single seine net haul, some 20 metric tons, and samples from this haul did not contain any age 0+ vendace. Catch samples for other species for that date did not show any marked deviations from values on adjacent dates. The original biomass estimates for these three deviating years were considered outliers and substituted with the average of the estimates from the preceding and the following year.

2.3.2 Fecundity of whitefish

The egg size and various other reproductive indices affecting the population fecundity of whitefish were determined in 1995 and 1997–2004, using similar techniques as in assessing vendace fecundity (Sarvala *et al.*, 1993; Sarvala and Helminen, 1995). Mature females were sampled from the fyke-net catches in autumn just before spawning. Fresh ovaries were dissected onto a tared piece of nylon net and weighed, and a composite sample of 200 eggs picked from different parts of the ovary to another piece of nylon net. The subsample and the remaining gonads were dried at 60 °C for at least 16 h and weighed. Gonadosomatic index (GSI) was calculated as the percentage of the fresh ovary mass of female body mass including the gonads. Numerical fecundity was obtained by dividing the gonad dry mass with the dry mass of a single egg. The number of eggs per gram of female body mass (relative fecundity) was calculated for each fish and averaged for each year. The water content of eggs was recorded as an indicator of their lipid content (Lahti and Muje, 1991).

In Pyhäjärvi, whitefish reach sexual maturity and spawn for the first time typically in their third autumn at the age of 2+, and the majority of the spawning population consists of three age-groups (ages 2+–4+, or 3+–5+; Sarvala *et al.*, 1999; Forsman, 2015; Helminen and Sarvala, 2021). Because there were few whitefish older than 1+ in the winter seine net samples, separate estimation of the abundance of these age groups was not possible, and all whitefish of age 2+ and older were combined into a joint group for age 2+ and older fish. Because the spawning stock comprised several year-classes, the spawning stock biomass was estimated as the weighted average of the age ≥2+ biomass of the current year and three preceding years. The weights were 1.0 for the current year y,

0.7 for the years y-1 and y-2, and 0.25 for year y-3, mimicking the mortality of adult fish.

The estimate of population fecundity for every year was obtained by multiplying the estimate of the average number of eggs per gram of female mass (relative fecundity) with the estimated total female biomass of the spawning stock, assuming a 50:50 sex ratio. Sex ratio was examined in some samples, and the share of females varied between 40% and 60%. Relative fecundity values for 1995 and 1997–2004 were determined in this study. The mean relative fecundity, 31.4 eggs g^{-1} obtained for the period 1995–2000 was used for the years 1991–1994 and 1996 also, and the mean for 2001–2004, 24.9 eggs g^{-1}, for the years 2005–2018.

2.3.3 Whitefish larvae

Sampling of whitefish larvae started on an average 10 days after the ice-out using rectangular Bongo nets pushed in front of a boat equipped with a water-jet engine (Urpanen *et al.*, 2009). A stratified random sampling design was applied with three littoral (0–2 m depth zone), one sublittoral (2–4 m depth zone) and one pelagic strata. Larval samples were preserved in a 1:1 mixture of 70% ethanol and 1% formaldehyde.

The estimate of the total number of larvae for the study area in each lake was calculated by first multiplying the average density in each depth stratum by the volume of the stratum and then summing these products. Then, the estimate of the average larval density (individuals ha^{-1}) in the study area was calculated by dividing the total number of larvae by the study area. The 95% confidence intervals of the annual average densities in each lake were calculated by bootstrapping, involving the extraction of 5000 new random samples, with replacement, of 20 littoral and 10 pelagic plots from the annual plots (Urpanen *et al.*, 2009; Karjalainen *et al.*, 2021; Väänänen *et al.*, 2024).

2.3.4 Whitefish diet

Diets of whitefish were studied throughout the open-water season in 1989 and 1990, with additional small-scale surveys in 1984, 1987, and April and July–August 1997 (10 and 40 fish, respectively). The stomachs of 5–20 freshly caught fish per age group and date were dissected and preserved for microscopy. The mass reconstruction and relative fullness methods (Amundsen and Sánchez-Hernández 2019; Sarvala and Helminen, 2021) were used. Food items were identified to species level when possible and measured under a 100× magnification. The stomach fullness was estimated visually on a scale of 0–10. For plankton prey, subsampling was often necessary. Carbon-to-length regressions or tables of carbon mass per size group were used to convert the counts and measurements to carbon biomass (Sarvala *et al.*, 1998), taking into account that partly digested prey could appear in several pieces. The reconstructed biomass of prey at the moment of feeding was then obtained by adding all diet items. When dealing largely with plankton prey, differences in digestion rates did not cause severe bias in the reconstruction method.

To quantify the overall intensity of food competition, a food availability index (FAI; Appendix B) was calculated as the ratio between zooplankton biomass (converted to kg fresh mass per hectare, assuming that the carbon content of fresh

mass was 6%) and the total biomass of planktivorous fish (the sum of the whole biomass of vendace, whitefish, smelt and bleak, 50% of roach biomass and 20% of perch biomass). FAI indicates the relative availability of food resources for the planktivores, and it is assumed to be inversely related to the intensity of food competition.

2.4 Methods: predators of eggs, larvae and juveniles

A potential egg predator, the signal crayfish (*Pacifastacus leniusculus* Dana) (Karjalainen *et al.*, 2015b), was introduced in Pyhäjärvi starting from the year 1988. Before the crayfish plague invasion in 1906, Pyhäjärvi was very productive noble crayfish (*Astacus astacus* Linnaeus) lake. The noble crayfish recovered twice from a plague epidemic, but after the third collapse in the 1940s it did not recover any more, the disease became endemic. Therefore, fifty years later, the fishing right owners decided to try to re-establish the crayfish fishery using the alien signal crayfish. This happened before the EU forbid the introductions of signal crayfish. By the year 2000, the stock had reached a fishable size. The annual catches of signal crayfish ($ScfD_y$) in 2000–2021 were obtained from the local association Säkylän Pyhäjärven hoitoyhdistys (Appendix C).

Ruffe is a known predator of coregonid eggs (Mikkola *et al.,* 1979; Selgeby 1998). Annual estimates of its population biomass (Appendix D) were compared to the numbers of whitefish larvae in the following spring.

Potential predators of the larvae and small juveniles of coregonids are perch (Helminen and Sarvala, 1994; Vuorimies 1999; Haakana *et al.*, 2007) and smelt (Sandlund *et al.*, 2005), and their biomasses (Appendix D) were compared to the abundance and survival of 0+ whitefish. In Pyhäjärvi, strong year-classes of perch typically emerge in warm summers (Sarvala and Helminen, 1996) which are becoming more common with the climate change (Jeppesen *et al.,* 2012). In the 1990s and early 2000s there were several warm summers, implying high predation pressure on the whitefish. The predation pressure by perch on coregonid larvae in Pyhäjärvi is likely highest when perch are two years old, being still numerous and already starting piscivory (Helminen and Sarvala, 1994). Thus, June–September temperature at 1 m depth with a lag of two years was also used as a proxy for predation by perch (Appendix E).

2.5 Statistical methods

The development of the whitefish population and its recruitment-related characteristics were examined with linear regression and associated ANOVA. Variables with non-normal distributions were transformed to logarithms (ln or $\log_{10}$) before statistical analyses. The collinearities between the potential explanatory variables were examined with Pearson's correlation coefficient, and from each group of collinear factors only one variable was retained in the analyses at a time. Some factors in regression analyses were considered obligatory, and were always included. The collinearity problem of competing planktivores was solved by creating the composite planktivory variable Food Availability Index (FAI); benthivorous fish that are competitors or predators of whitefish were treated individually.

The effect of population fecundity (PF_y, eggs ha^{-1}) in autumn y on the density of newly hatched larvae (LD_{y+1}, individuals ha^{-1}) and further one-summer-old whitefish ($osoD_{y+1}$, individuals ha^{-1}) in year y+1 was analysed by regression analysis.

H_0-model was: survival (α) is not dependent on PF_y, *i.e.*, LD_{y+1} and $osoD_{y+1}$ (Y) are directly proportional to the PF_y

$$Y_{y+1} = \alpha\, PF_y \exp(\varepsilon_y),$$
$$\ln Y_{y+1} = \ln \alpha + \ln PF_y + \varepsilon_y,$$

where α = constant proportional survival, ε_y = annual value of normally distributed (*e.g.* Walters and Hilborn, 1976) random "error" consisting of the true variability in survival and random measurement error.

Alternatively (H_1), the survival depends on density, *e.g.* following the hump-shaped curve of Ricker (1954) model

$$Y_{y+1} = \alpha PF_y \exp(-\beta PF_y)\exp(\varepsilon_y)$$

$$\ln Y_{y+1} = \ln\alpha + \ln PF_y - \beta SB_y + \varepsilon_y,$$

where β = density dependent mortality term, with $\beta = 0$ matching with H_0-model or monotonously increasing Cushing (1971) model

$$Y_{y+1} = \alpha\, PF_y^{\gamma} \exp(\varepsilon_y)$$

$$\ln Y_{y+1} = \ln \alpha + \gamma \ln PF_y + \varepsilon_y,$$

where γ = density dependent mortality term (>0), with $\gamma = 1$ matching with H_0-model.

The significance of the increase in goodness of fit between nested models (H_0-model *vs.* Ricker and H_0-model *vs.* Cushing) was assessed using the F-test.

Additional variables (X_i) were included in the model if their correlation with the residuals from the models above was significant. For all X_i, a one-sided H_1-hypothesis was applied and the *p*-values calculated accordingly. Then the significant variables were added to the model

$$\ln Y_{y+1} = f(PF_y) + \varphi_i X_i, + \varepsilon_y,$$

where φ_i = the effect of variable X_i on Y.

When fitting the models to larval density of whitefish, the X_i hypothesized to affect survival in winter were the signal crayfish density index $ScfD_y$ = crayfish catch ha^{-1} in year y; the value of the total catch of 1 assumed for years 1992–1999 before the collection of catch statistics, ruffe biomass in year y and average FAI for years y and y–1.

When fitting the model to one-year-old whitefish density, the tested X_i variables, in addition to $ScfD_y$ and ruffe biomass in year y were perch, roach and smelt biomasses (Appendix D) and FAI in year y+1 (Appendix B).

The one-year-old whitefish density was not modelled as a function of larval density estimate because the precision of logarithmic larval density estimates (CV = 1.56) was not considered suitable for predictive regression analysis. Measurement errors were considered likely to induce considerable bias in the model parameter estimates (*e.g.* Walters and Ludwig, 1981).
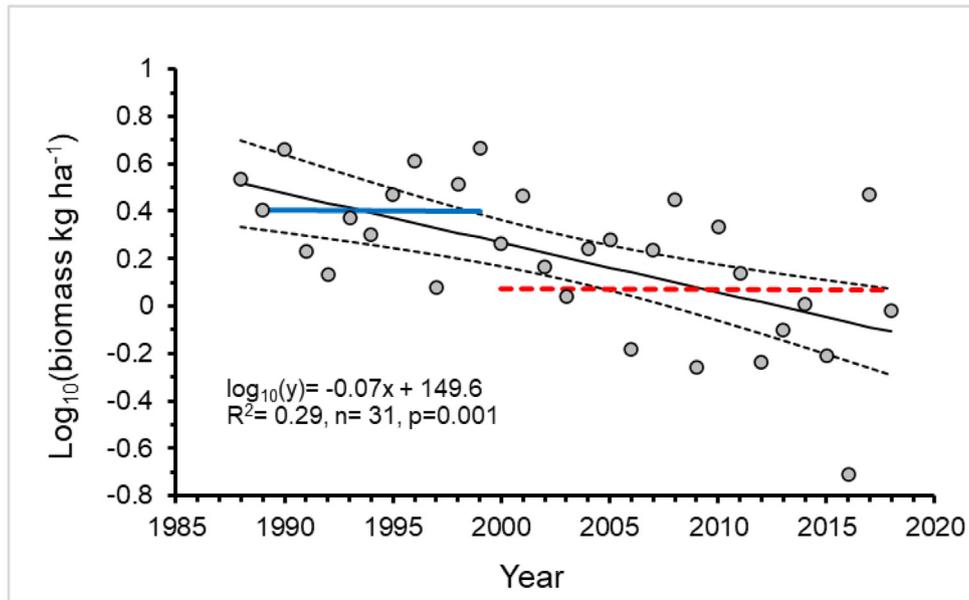
Fig. 2. Total whitefish population biomass in autumn in 1988–2018. Horizontal lines indicate the average biomass during the period of overfishing of vendace in 1989–1999 (blue), and after the vendace recovery in 2000–2018 (red dashed). The oblique trendline (black) indicates the general declining trend of whitefish biomass. The 95% confidence intervals are shown (dashed curves).

Standard predictive iterative minimum least squares fitting was applied in nonlinear model parameter estimation using SPSS (IBM statistics).

Piecewise linear regressions of the annual larval densities against year were fitted with the "segmented" package 1.3.0 in the R environment (Muggeo 2008, RStudio version 2023.03.0 and R version 4.2.3, R Core Team 2023). Correlations, linear regressions and ANOVA were calculated with Microsoft Excel 2016.

3 Results

3.1 Environmental changes

The lake environment varied with global change (Appendix E). From 1982 to 2018, climate warming increased the summer mean surface water temperature with 1.1 degrees to 18.3 °C. At the same time, eutrophication increased the average summer total phosphorus with $6\,\mu g\,L^{-1}$, and chlorophyll *a* with $5\,\mu g\,L^{-1}$, to 22 and $9\,\mu g\,L^{-1}$, respectively. These changes were accompanied by major alterations in the fish assemblage (Appendix D). Perch, roach, and ruffe increased significantly, while vendace and smelt did not show significant trends. Whitefish was the only species showing a significant decline. Although the overall trends in perch, roach and ruffe were all positive as were those of the water quality variables, at the level of annual averages, none of the correlations between fish and water quality were significant.

3.2 Population decline

The total whitefish catches reported from the 1920s to the 1990s indicated a fluctuating but moderately strong whitefish stock (Fig. 1). Annual biomass estimates that became available in 1988, still showed a strong whitefish population during the vendace overfishing period (1991–1999). But this was followed in the 2000s by a declining trend in whitefish larval numbers and in the biomass of the age groups 0+, 1+ and 2+, resulting finally in very sparse population (Figs. 1 and 2). Although the decrease in whitefish biomass after 2000 can be interpreted as a stepwise response to the recovery of the vendace population from overfishing, it looks rather as a gradual change throughout the study period (Figs. 1–3).

3.3 Population fecundity in autumn

The overall development of the whitefish population depends on numerous abiotic and biotic factors which affect in different ways the successive life stages (Tab. 1). The initial numbers of a new year-class are set by the population fecundity, *i. e.* the total number of eggs produced by the whole whitefish population in the autumn spawning period. In the spawning period in autumn, most of the reproductive indices of whitefish suggested unfavourable development from 1995 to 2004 (Figs. 4A–4E). Egg dry mass did not change (Fig. 4A), but the gonadosomatic index declined considerably, from about 20 % to 12 % (Fig. 4B), as also the numerical fecundity, from 12000 to 5000 eggs per female (Fig. 4C). The water content of eggs increased (Fig. 4E), indicating a decrease in lipid content and thus egg quality. The relative fecundity is linked to gonadosomatic index and egg size, which can also be related to egg quality. Population fecundity showed a significant decline during the study, roughly from 12000 to 2500 eggs ha^{-1} (Fig. 5). The relative fecundity also declined from 35 to 25 eggs g^{-1} (Fig. 4D), but yet a larger part of the drop in population fecundity was due to reduced size and number of spawners. The average population fecundity of whitefish in the years 1991–1999 when the vendace population was sparse, was significantly higher than in 2000–2018, when the vendace had recovered from overfishing (8795 *vs.* 4739 eggs/individual, $F_{9,19} = 39.2$, $p < 0.001$).
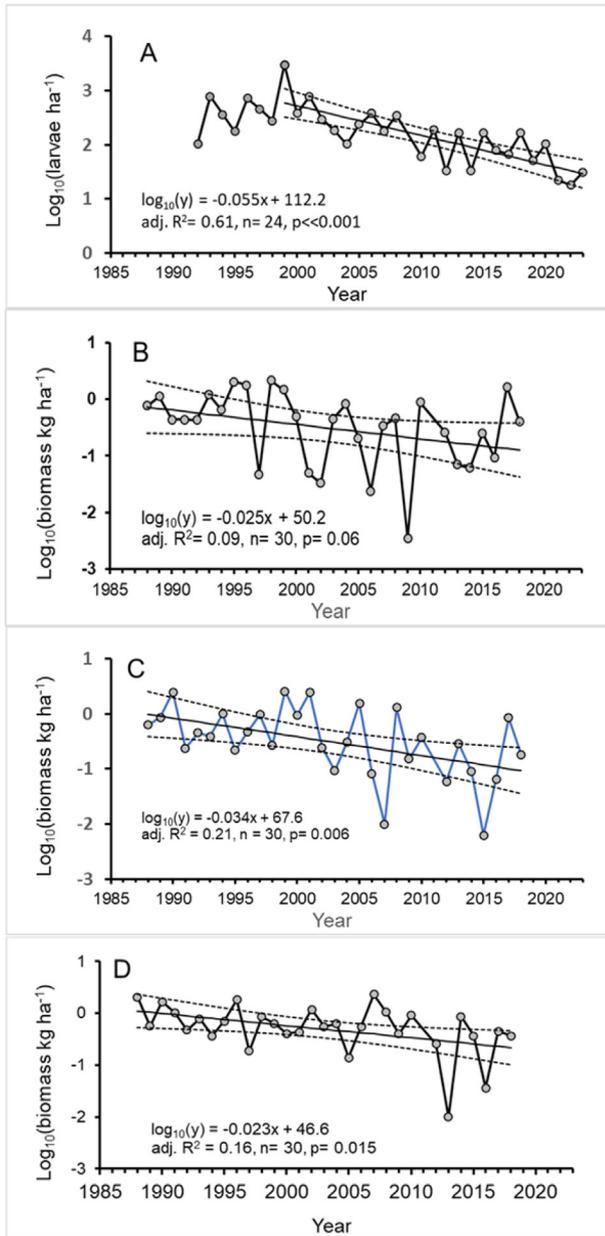
Fig. 3. (A) Density of whitefish larvae in Pyhäjärvi in spring 1992–2020, and biomass of the (B) age 0+, (C) age 1+, and (D) age 2+ whitefish in 1988–2018. Broken lines denote the 95% confidence limits.

Environmental factors and food competition had a significant role, too. Food competition during the preceding summer, described by the food availability index FAI (Appendix B), appeared as a significant factor associated with the relative fecundity, higher food availability leading to higher relative fecundity:

ln(relative fecundity)$_y$ = 0.29 ln(FAI$_y$) + 2.95 (adj. R^2 = 0.48, n = 9, p = 0.02) and consequently also to higher population fecundity.

3.4 Larval abundance in spring

In the 1990s, when the vendace population was sparse, whitefish larval density was increasing, but in the 2000s, when vendace had recovered from overfishing, and signal crayfish were abundant, the trend changed to decreasing (Fig. 3). Although the increasing slope was not quite significant, the segmented regression identified the year 1999 as the break-point, and the segmented regression explained a significantly higher proportion of the total variance than a simple linear regression (adj. R^2 0.58 *vs* 0.51, respectively). Warmer spring temperatures that are favourable for the vendace larvae, did not enhance the whitefish larval densities.

The FAI development suggested relaxed competition in the 1990s and increasing competition since 1998. The density of whitefish larvae showed similar development with a two-year delay (Appendix B). The larval density in spring was only partly explained by the population fecundity in the previous autumn, indicating that several factors were involved (Fig. 6). The H$_0$-model of constant non-density dependent survival could not be rejected, *i.e.* no significant increase in goodness of fit was gained when adding an additional density dependence parameter (H$_0$ vs H$_1$ Cushing F = 0.61, p = 0.44; H$_0$ *vs.* H$_1$ Ricker F = 0.54, p = 0.47). The H$_0$-model-based estimate of the average survival α from spawning to hatching was 3.7% (95% confidence interval 2.4–5.0%). Of the potential egg predators, the effects of ruffe and the signal crayfish on larval density were analysed. The negative correlation of signal crayfish density index (ScfD$_y$, Appendix C) with the residuals from the H$_0$-model was marginally significant (r = –0.32, p = 0.054, 1-tailed hypothesis $r < 0$) suggesting that when signal crayfish abundance increased the survival of whitefish eggs decreased. There was no correlation between the residuals and ruffe biomass (p = 0.17, 1-tailed hypothesis $r < 0$), nor between the residuals and average FAI for year y and y+1 (p = 0.13, 1-tailed hypothesis $r > 0$). The final model for larval density (LD$_{y+1}$) was

ln LD$_{y+1}$ = ln (0.049) + ln PF$_y$ + –0.014 ScfD$_y$ (Appendix F) (r^2 = 0.33, standard error of estimate = 0.87) (95% CI 0.012–0.072; –0.027–+0.00023).

3.5 One-summer old juveniles

In exploratory regression analyses the age 0+ whitefish population biomass in autumn was significantly correlated with the FAI of the preceding summer, and when population fecundity of the previous autumn was added to the multiple regression, both explanatory variables were marginally significant (R^2 = 0.12, n = 28, p = 0.09 (population fecundity), p = 0.056 (FAI) (ln-transformed)) suggesting that food competition affected the success of a cohort during its first summer (Appendix B). These FAI and population fecundity values were not correlated. In single-factor linear regressions the summer temperature showed a significant negative effect on the one-summer old whitefish (adj. R^2 = 0.11, n = 30, p = 0.04). Total phosphorus and chlorophyll were not significantly related to 0+ whitefish, neither in single-factor nor in multiple regressions with FAI as an additional explanatory variable. FAI remained significant in all

Table 1. Summary of whitefish population regulation in Pyhäjärvi, SW Finland. Successive life stages, factors affecting each, and possible effects observed (FAI = Food availability index).

Variables	Explanatory factors
Population fecundity in autumn	
Population biomass of mature females	Year-class size, fishery, FAI explains 91% of population fecundity
Adult mass at age	FAI (variable)
Egg size	FAI? (No changes)
Relative fecundity (eggs g^{-1})	FAI (decreased)
Water content of eggs	FAI (increased)
Density of larvae in spring	
Population fecundity previous autumn	Major factor
Roe quality ?	
Fertilization success ?	no data
Winter mortality due to O$_2$ deficit	Lack of O$_2$ not in Pyhäjärvi
Egg mortality, due to predators	Signal crayfish ?, ruffe ?, other fish ?
One-summer-old juveniles	
Density of larvae previous spring	Major factor
Spring mortality by starvation ?	Possible mismatch with zooplankton food production due to climate change
Spring and summer predation mortality	Predation by perch, smelt, other fishes
Spring temperature	Strengthens predation effects when low
1st winter fishing mortality	Bycatch in winter seining for vendace
1st winter predation mortality ?	Predation by perch, smelt
Adult whitefish	
2nd summer predatory mortality ?	Predation by perch, pike
2nd summer high temperature mortality ?	High temperature periods
Fishing mortality of adults	Fyke net fishery
	Gillnet fishery
	Winter seine fishery
Predatory mortality of adults	Predation by big pike

combinations suggesting that it was a useful indicator of the food competition.

The first year mortality was high. When estimating the one-summer-old whitefish numbers in the autumn from the population fecundity in the previous autumn, the H$_0$-model of constant non-density dependent effect could not be rejected (H$_0$ *vs.* H$_1$ Cushing $F = 0.0003$, $p = 0.99$; H$_0$ *vs.* H$_1$ Ricker $F = 0.015$, $p = 0.90$) (Fig. 7). The H$_0$-model-based estimate of the average survival α from spawning to the following autumn was 0.19% (95% confidence interval 0.076–0.30%), $r^2 = 0.054$. Based on the difference between the whole first-year survival and the survival from spawning to hatching, the survival estimate for larvae in spring to one-summer-olds in autumn was 5.0%.

Survival from spawning to larvae next spring showed a significant decline from the 1990s to the 2010s (Fig. 8A) ($y = -0.30x + 608$, $n = 19$, adj. $R^2 = 0.24$, $p = 0.02$), while the survival from spawning to the next autumn did not show any consistent trend (Fig. 8B). The causes of the first-year losses could not be identified. Neither the signal crayfish density index ($p = 0.364$) nor the biomass of perch ($p = 0.171$), roach ($p = 0.337$), ruffe ($p = 0.275$) and smelt ($p = 0.974$) (Appendix D) correlated significantly (1-tailed hypothesis $r < 0$) with the residuals from the H$_0$-model. The food availability index for the hatching year ($y + 1$) did not correlate

significantly with the residuals, either ($p = 0.98$, 1-tailed hypothesis $r > 0$).

3.6 Adult whitefish

The average mass-at-age of adult whitefish was higher in the 1990s compared to the 1980s, and declined again in the 2000s. The difference was visible but not significant at the age 1+, but was significant at age 2+, and marginally significant at age 3+ (Fig. 9: age 2+ 1990–2000 *vs.* 2001–2018, single factor ANOVA, $F_{1,22} = 5.41$, $p = 0.03$). At age 0+ no such temporary size change was observed, but instead, there was a slight increase in average individual 0+ mass in autumn throughout the study period (linear regression $y = 0.32x - 613$, adj. $R^2 = 0.12$, $n = 31$, $p = 0.03$). This increase did not show any correlation with FAI or with whitefish population biomass.

Whitefish competes for food with vendace and other planktivorous fish species, but in Pyhäjärvi this competition was partly alleviated by resource division. The first food items of larval whitefish in spring were copepodid and adult cyclopoids (Appendix G). When the cyclopoid *Cyclops kolensis* started hibernation and disappeared from water in June, the diet of 0+ whitefish consisted mainly of the cladocerans *Bosmina*, *Daphnia* and *Holopedium*, and when
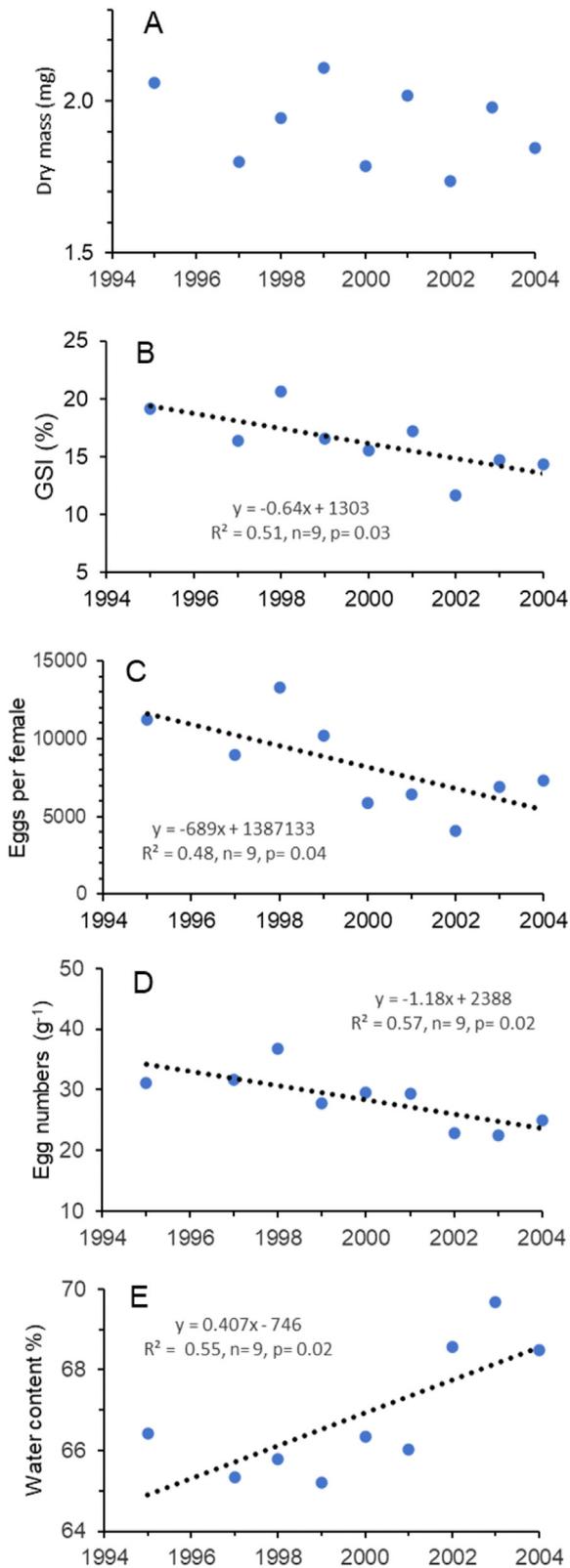
Fig. 4. Reproductive indices of whitefish in Pyhäjärvi in 1995–2004: (A) egg dry mass, (B) gonadosomatic index GSI%, (C) numerical fecundity, (D) eggs per gram female mass (relative fecundity), (E) water content (%). Significant regressions against year shown with dotted lines, and the 95% confidence intervals with broken lines.

these became scarce in July, of littoral cladocerans and macroscopic zoobenthos. In 1989, 1+ whitefish fed upon planktonic cladocerans when these were abundant in early summer and in autumn, but when zooplankton biomass decreased in summer, macrozoobenthos became the major food (Appendix G), and this combination of planktonic and benthic food sources applied to older whitefish, too. Yet data on whitefish diet in 1997 showed that during the period of reduced vendace population, even the larger whitefish were zooplanktivores, and their growth improved relative to the period of benthivory.

Besides vendace, potential competitors of whitefish are roach, young perch and smelt, while larger perch and smelt are predators of larvae and small juveniles of coregonids, complicating the relationships between these species. Perch and roach biomass increased significantly during the study period (Appendix D), consistent with the CPUE increase observed by Helminen and Sarvala (2021). In the 1990s and early 2000s, there were several warm summers favourable for the reproduction of perch and roach (Appendix E). Strong year-classes of perch emerged in 1988, 1992, 1994, 1997, 1999 and 2002 (Sarvala and Helminen, 1996; Sarvala *et al., 1999*, and unpublished). The latest warmer-than-average summers were 2006, 2010, 2011, 2016 and 2018. The highest temperatures and the strongest year-classes, CPUEs and biomasses of perch did not always coincide, but the substantial increase in perch biomass likely indicated increasing predation pressure. Roach increase was more moderate. Smelt biomass did not increase but showed recurrent 3–4-year periods of high biomass caused by strong year-classes appearing at 7–10-year intervals. In the 1990s, despite the increasing populations of perch and roach, the whitefish grew fast because the overall competitive situation was determined by the low abundance of vendace, which on an average comprised 93% of the total planktivore biomass in Pyhäjärvi. The vendace population recovered in the 2000s (Appendixs A, D), reinstating a high competitive pressure on whitefish. But then the vendace maintained only average population density while other planktivores continued to increase, being then responsible for exacerbating competition

4 Discussion

The share of vendace of the total planktivore biomass gradually decreased from 76% in the 1980s to 54% in the 1990s, to 65% in the 2000s finally to 46% in the 2010s. Whitefish always comprised a much lower proportion of the total planktivore biomass. During the vendace overfishing episode there was a slight increase of the role of whitefish from 14% in the 1980s to 20% in the 1990s, but later the whitefish proportion declined to 8% in the 2000s and <4% in the 2010s. Pyhäjärvi is thus changing from coregonid dominance to a perch and roach dominated lake, as has been happening for numerous high-latitude lakes (Smålas *et al.*, 2023).

The principal finding of the present study was the major overall decline of the whitefish population during the recent decades in Pyhäjärvi. The decline was associated with the gradual deterioration of most of the reproductive indices. The pattern was supported by published and unpublished catch records (Järvi, 1940, 1953; Sarvala *et al., 1999*; local
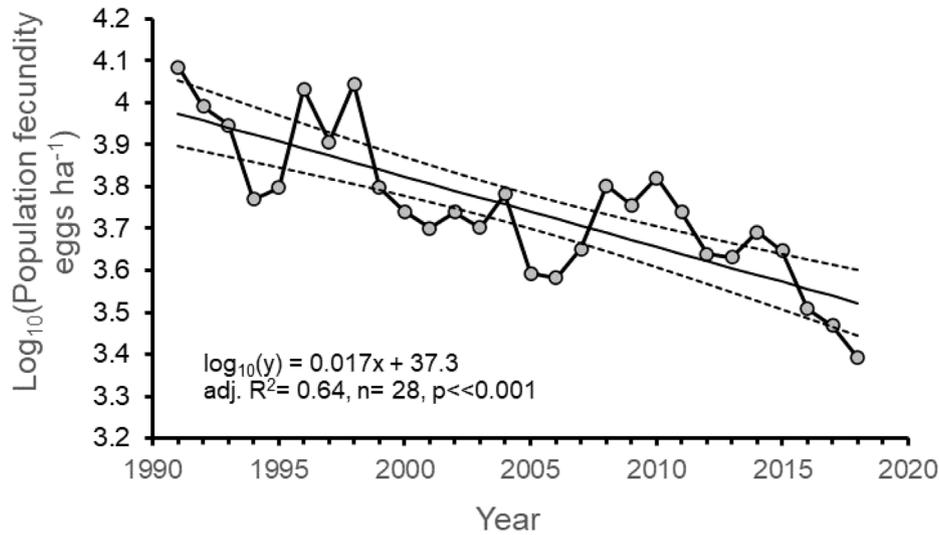
Fig. 5. Log_{10} population fecundity of whitefish in Pyhäjärvi in 1991–2018. Broken lines denote the 95% confidence limits.
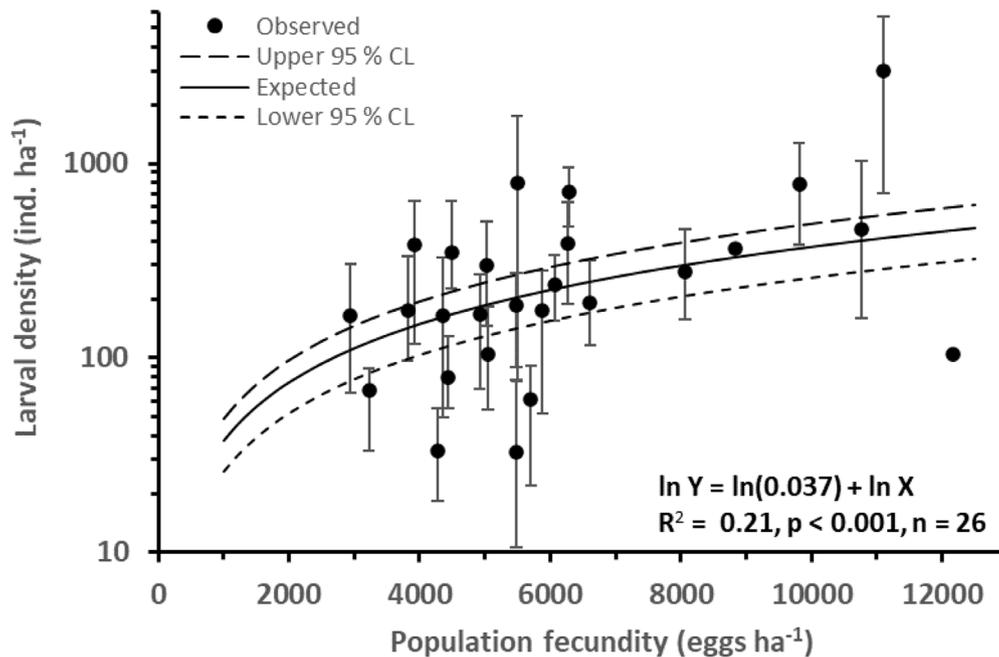

Fig. 6. Observed density of whitefish larvae in spring as a function of population fecundity in the previous autumn in Pyhäjärvi; 95% confidence intervals given.

unpublished catch statistics) indicating that the total whitefish catches from Pyhäjärvi remained roughly similar from 1921 to 2000. Ignoring the years 1921, 1957, and 1967 with exceptionally high catch estimates, the means for 1921–1976 and 1995–2000 were 7.6 and 7.0 kg ha^{-1} a^{-1}, respectively), followed by a clear decline after 2000 (mean values 3.0 and 1.3 kg ha^{-1} a^{-1} in 2001–2010 and 2011–2020, respectively; data from the local lake management association). A similar decline of whitefish was observed from 1988 to 2018 in the total winter seine catches which are more reliable. Despite similar catches, however, fishing mortalities and exploitation rates may have differed.

The population dynamics of whitefish is determined by numerous abiotic and biotic factors affecting the numbers and biomass at different phases of the life cycle (Tab. 1; Eckmann, 2013). The maximum numbers of a year-class are set by the population fecundity of the spawning stock. This is influenced by the number of ripe females, and their individual biomass and relative fecundity. The numbers of spawners depend on fishing and predation mortality, and the biomass and fecundity on food availability, here illustrated by the index FAI. At the spawning act, a variable proportion of eggs is fertilized, and the embryos are subject to predation and diseases, as well as the mortality due to other environmental factors (Eckmann, 2013).

$$\ln(Y) = \ln(0.0019) + \ln X$$
$$R^2 = 0.06, p < 0.001, n = 27$$
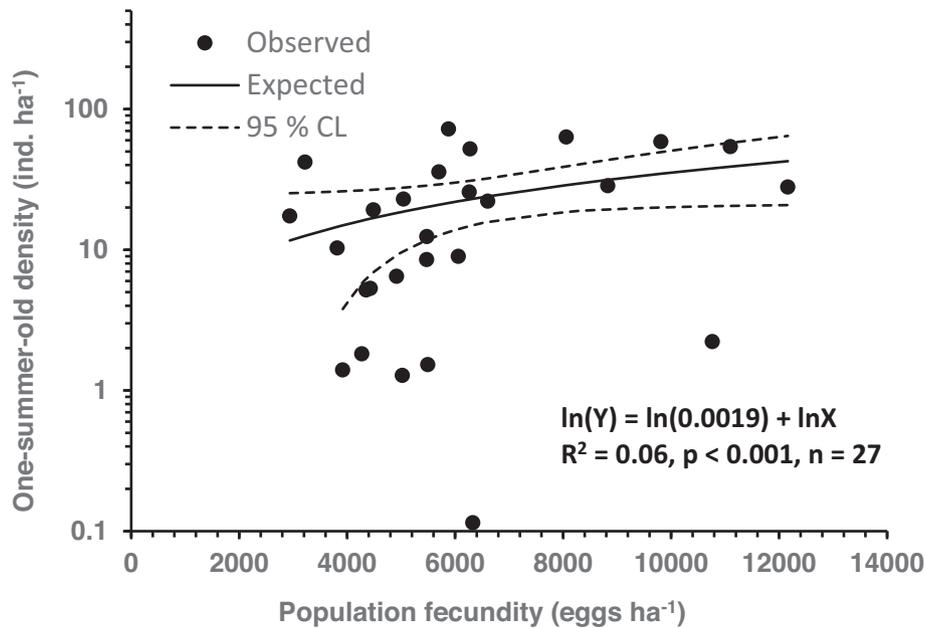
Fig. 7. Density of one-summer-old whitefish in autumn relative to population fecundity in the previous autumn in Pyhäjärvi (95% confidence interval shown).

In eutrophic lakes, whitefish embryos may suffer high mortality because of poor oxygen conditions at the sediment surface, but in Pyhäjärvi the spawning grounds of whitefish are mostly erosion bottoms with good conditions for whitefish eggs. In Pyhäjärvi, the relative fecundity, and consequently also population fecundity, was significantly dependent on the food availability during the preceding summer. High population fecundity (*i.e.*, a high number of spawners and produced eggs) makes possible a high initial larval density, which is a prerequisite for successful recruitment in coregonid fish which have high mortality especially during the first weeks of their life but also through the rest of the larval and juvenile phase (Karjalainen *et al.*, 2000). In Pyhäjärvi, the whitefish decline was associated with a general deterioration of the fecundity indicators.

The substantially lower number of larvae compared to the population fecundity observed in Pyhäjärvi might be due to low success of fertilization, but is more likely due to considerable egg predation during spawning and egg incubation. Ruffe is the most likely candidate for a fish predator of eggs (Selgeby, 1998), but predation by perch, burbot and some other bottom-feeding species as well as cannibalism by whitefish can also be important (Skurdal *et al.,* 1985). In Pyhäjärvi, however, no consistent relationship was observed between ruffe abundance and survival of whitefish eggs over winter. Years with high ruffe biomass were 1995, 2003, 2010 and 2020, while the biomass was low in 1999, 2006 and 2016 (Appendix D; the 2003 peak was due to intensified fishery). On the other hand, the survival of whitefish eggs and larvae was always low when the perch, roach, smelt or ruffe biomass was high, but survival could be high or low when the potential predator biomass was low. Potential predators of the larvae and juveniles of whitefish are perch and smelt (Huusko *et al.,* 1996; Vuorimies, 1999; Haakana *et al.,* 2007; Haakana and Huuskonen, 2009) but no links to the first summer survival

of whitefish were observed, neither when summer temperature with a lag of two years was used as a proxy of perch predation.

Benthic invertebrates, such as amphipods, and large dragonfly and caddis larvae are known to prey upon coregonid eggs (Mikkola *et al.,* 1979, Karjalainen *et al.,* 2021), but data on the abundance of potential invertebrate predators or their feeding activity do not exist from Pyhäjärvi. Judging from the catch records (Appendix C), the signal crayfish became abundant in the early 2000s, and continued to increase to the end of the study period. Feeding experiments and bioenergetic modelling showed that a dense population of signal crayfish had the capacity to eat practically every single whitefish egg spawned in Pyhäjärvi, but it remained open to what extent this potential was realised in the lake where several types of prey for signal crayfish were available (Karjalainen *et al.,* 2015b). The available data suggest that the survival of whitefish eggs, larvae and small juveniles in Pyhäjärvi is affected simultaneously by several factors causing the population decline, but none of them is decisive alone.

Additional noteworthy changes observed were a larger average size-at-age of the adult age groups during the period in the 1990s when the vendace population was sparse, and a slight but continuous increase in the average autumn mass of the 0+ age group individuals. The larger size of adults in the 1990s most likely was due to the relaxation of food competition. Besides vendace, whitefish competes for food with several other fish species such as smelt, bleak, young perch and young roach. Whitefish growth has improved in years with low vendace stocks in several Finnish lakes (Huhmarniemi *et al.,* 1985; Heikinheimo-Schmid, 1992; Raitaniemi *et al.,* 1999; Valkeajärvi *et al.,* 2012). Intraspecific competition may also be important. In Lake Constance, the growth of whitefish showed a strong negative correlation with the standing stock (Thomas and Eckmann, 2007). In the present data from Pyhäjärvi, the
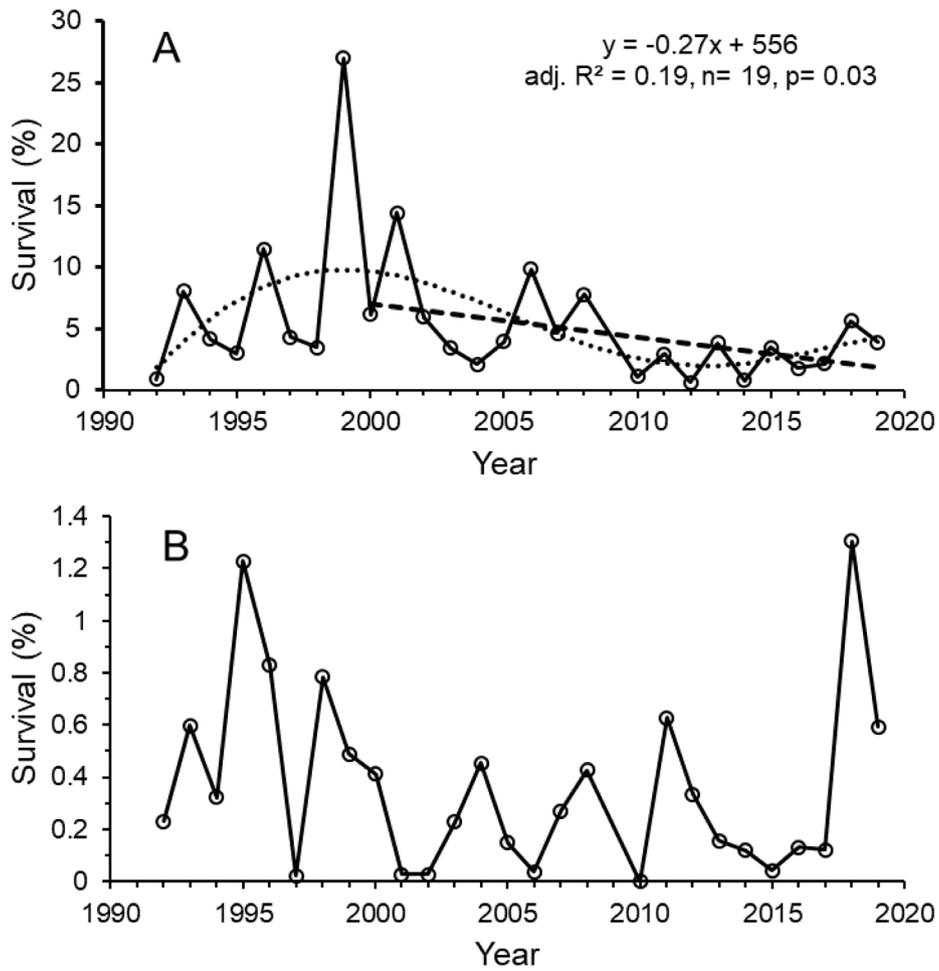
Fig. 8. Survival (%) from whitefish eggs to larvae (A) and survival (%) from spawning to 0+ next autumn (B). The dotted curve represents smoothing with 5th order polynomial. Dashed line shows the linear regression of the decline of survival from eggs to larvae during 2000–2019.
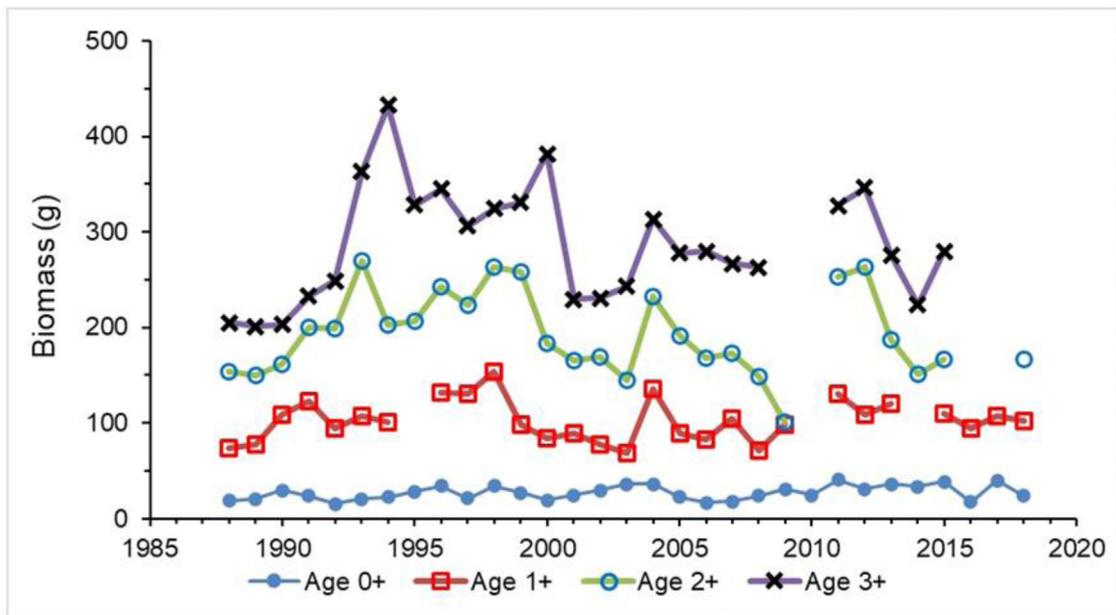
Fig. 9. Average mass in autumn of age 0+ to 3+whitefish in 1988–2018.

growth of whitefish was independent of the abundance of whitefish and of the overall level of planktivory, but in the 1920s and 1930s whitefish growth and abundance were clearly inversely related (Järvi, 1940). Therefore, the increase in the average autumn mass of the age 0+ whitefish was probably simply the result of the lengthening of the growing season (Ventelä *et al.*, 2011), although elevated summer temperatures or improved food availability due to eutrophication may also be involved.

Even in Pyhäjärvi the vendace–whitefish interactions involved diet changes. After hatching, the first food for the larvae of both species was zooplankton, but larval vendace fed upon smaller items, such as cyclopoid nauplii or even rotifers, while the whitefish larvae selected slightly larger prey (Sarvala *et al.*, 1988, 1999; Sarvala and Helminen, 2021). Later in summer when young vendace still fed on zooplankton, the whitefish consumed littoral and benthic crustaceans. Because of this resource division, the diet of the 0+ whitefish likely did not change with the fluctuating vendace abundance. In several Finnish lakes with an abundant vendace population, whitefish grow larger in their first summer than vendace (*e.g.* Lake Puula, T.J. Marjomäki, unpubl. data; Lake Konnevesi, P. Valkeajärvi, Konneveden kalatutkimus ry, unpubl.), indicating that intraspecific competition is more important regulator of growth than the interspecific competition. Resource segregation through differing habitat selection is also possible (Bøhn and Amundsen, 2004). In Pyhäjärvi, there is little difference in the first-summer growth between vendace and whitefish, which tells about relaxed intraspecific competition in vendace due to the intensive fishery. This is also evident as the exceptionally large size at age of vendace in Pyhäjärvi. Competitive situations vary seasonally, between years and between lakes. In the 1980s when the vendace population was strong, adults and juveniles of both coregonid species as well as smelt, perch and roach consumed in early summer zooplankton which was then still increasing despite the intensive consumption (Sarvala and Helminen, 2021, and unpublished). When zooplankton became scarce in July, whitefish switched to feeding on zoobenthos, while vendace continued to feed on zooplankton. But in the 1990s when the vendace population was small, zooplankton turned out to be the most common food of even the adult whitefish, which also grew faster on the plankton diet. Also elsewhere the medium-rakered lake whitefish have been found to grow faster when feeding on zooplankton food than when feeding on macrozoobenthos (Turunen and Viljanen, 1988; Miinalainen and Heikinheimo, 1998). Recent studies suggest that the nutritional quality of zoobenthos may be generally inferior to zooplankton (Taipale *et al.*, 2022).

Moderate eutrophication might be expected to improve whitefish growth and recruitment by increasing zooplankton production (*e.g.*, Straile *et al.*, 2007). This positive influence may be cancelled out, however, because at the same time, eutrophication favours competing fish species and decreases the quality of food. Eutrophication-linked phytoplankton groups, especially cyanobacteria and green algae, that are known to have poor nutritional quality for zooplankton (Taipale *et al.*, 2019), have become more common in Pyhäjärvi (Deng *et al.*, 2016). Toxicity of cyanobacterial blooms may also cause problems. The capacity to compensate for the decreasing food quality varies between species (Taipale *et al.*, 2022). Further study is needed to find out whether the

deterioration of the available food could also contribute to the whitefish population decline in Pyhäjärvi.

Climate change is one factor affecting whitefish recruitment, but the specific mechanisms may differ depending on the geographical location (Jeppesen *et al.*, 2012; Bourinet *et al.*, 2023). In general, higher temperatures enhance the growth and survival of coregonid larvae (Eckmann and Pusch, 1989; Helminen and Sarvala, 1994), partly through physiological mechanisms, and partly through the positive influence of temperature on zooplankton production. In Pyhäjärvi, however, climate warming may be unfavourable for the recruitment of whitefish, as found also in a Norwegian lake by Linløkken and Sandlund (2015). The hatching of coregonid larvae follows the ice-out which is getting earlier (Ventelä *et al.*, 2011), and because of the slow warming of water, this might result in a mismatch between the hatching of larvae and spring increase of zooplankton, or simply lengthen the slow-growth period during which the small larvae are most vulnerable to predation, and their feeding capability is limited. In the more southern Lake Geneva, the hatching date of larvae has not changed, but the phytoplankton production starts earlier, improving food availability for whitefish larvae (Gerdeaux, 2004; Anneville *et al.*, 2009; Jeppesen *et al.*, 2012). Further, the variation in the spawning time of different parental fish and the hatching time of their eggs allows at the population level even a 3 month long hatching-to-feeding window of opportunity for coregonid larvae to start their external feeding in favourable conditions (Karjalainen *et al.*, 2015a; Karjalainen 2016).

On the other hand, in a non-stratified lake such as Pyhäjärvi, without a cool hypolimnion refuge, the maximum summer temperatures (in 2018–2021 exceeding 24°C) are approaching the lethal limits for young-of-the-year of North American coregonids (Edsall and Rottiers (1976). Moreover, more frequent warm summers associated with climate change result in strong year-classes of perch and roach, thus maintaining high predation and competitive pressure on whitefish (Böhling *et al.*, 1991).

The vendace and whitefish populations of Pyhäjärvi showed different long-term development (Appendix A), implying that they were regulated by different factors, as was found in a Norwegian lake (Linløkken and Sandlund, 2015). The recruitment success of both whitefish and vendace seems to be determined during the early life stages, but the number of spawning adults is also important. In Pyhäjärvi, one difference may arise from the wintertime egg predation by the signal crayfish because whitefish is spawning in shallower areas than vendace, and the larger whitefish eggs provide more attractive food items for the crayfish.

In Pyhäjärvi vendace, strong year-classes tend to produce numerous offspring, resulting in cyclic fluctuations of abundance. In the same vein, strong whitefish year-classes tend to produce strong offspring year-classes, but because the spawning stock comprises several year-classes, the overlapping cycles are difficult to recognise. The clearly higher reproductive potential of vendace (Sarvala and Helminen, 1995) makes this species resilient to high losses as shown by its recovery from overfishing (Sarvala *et al.*, 2020).

The whitefish population in Pyhäjärvi has been subject to a strong fishing pressure, as indicated by high ratios of winter seine catches to the estimated biomass (average 0.91 for

1988–2000). In the 1970s, 1980s and 1990s the intensive exploitation of whitefish reduced the number of age-groups in the spawning stock to practically three, in some years only two, the ages 2+ and 3+. Of eight years between 1979 and 1997, the modal age group was 2+ in five and 3+ in three years. Decreasing fishing effort in the 2000s (Sarvala *et al.,* 2020) resulted in reduced catch/biomass ratios (0.55 in 2001–2010 and 0.41 in 2011–2018), and increased the number of age-groups in the spawning stock. In 2013 the modal group was 4+, and ages from 1+ to 9+ were represented, showing that there is recovery potential (Forsman, 2015). The intense exploitation during the previous decades has contributed to the decrease in population productivity by diminishing the population fecundity. The present closed season during the spawning time and control of the number and kind of fishing gear have not been sufficient measures. Although difficult, adjusting the future exploitation rate at the level required by the altered conditions of the lake ecosystem would be the simplest and most predictable way to restore the whitefish population. However, the adjustment of the fishing rules in Pyhäjärvi to protect whitefish seems not possible without harming the fishery of the other species (Forsman, 2015). But intensified fishing of competitors and predators as well as an efficient harvesting of the crayfish might help to strengthen the whitefish population.

5 Concluding remarks

The long-term declining trend of the whitefish population could not be directly linked to the abundance of any single competitor or predator, or with any single environmental factor. Neither was it caused by excessive fishing alone, although the exploitation rate was high, and together with environmental and fish community changes, has gradually led to the decline of the whitefish population. The predation by the signal crayfish on the overwintering embryos, combined with the predation on larvae and small juveniles by perch and smelt, together likely reduced the whitefish recruitment further. But the decline of the relative fecundity and most other reproductive indices suggests that the increased total competitive pressure might be also involved. The future challenge is to rephrase the rules for the whitefish fisheries management, monitoring and governance to correspond to the carrying capacity of the ecosystem altered by climate warming and eutrophication. Maintaining the vendace harvest and increasing the fishing of perch and signal crayfish might favour whitefish, and would be in the interests of fishermen.

Acknowledgements

Supplementary material

Appendix A. Population biomass of the age 0+ vendace and age 0+–2+ whitefish in autumn in 1979–2018 in Lake Pyhäjärvi. Vendace data from Sarvala and Helminen (2021). The period of vendace overfishing indicated with a horizontal blue bar. The horizontal red bar shows the average whitefish biomass during that period.

Appendix B. Biomass ratio between zooplankton and planktivorous fish (food availability index, FAI), and the density of whitefish larvae in 1987–2019 in Pyhäjärvi. Broken and dotted curves represent smoothing by 4th order polynomial.

Appendix C. Annual catches of signal crayfish from Pyhäjärvi in 2000–2022 (Source: Säkylän Pyhäjärven hoitoyhdistys).

Appendix D. Population biomass in autumn of (A) whitefish, (B) vendace, (C) perch, (D) roach, (E) smelt and (F) ruffe in Pyhäjärvi in 1988-2018. Trend lines and 95% confidence limits are shown for significant regressions of biomass vs time (NS = not significant).

Appendix E. Average June–September temperature (A), total phosphorus (B) and chlorophyll *a* (C) at 0–2 m depth in 1982–2020 in Pyhäjärvi. Broken lines show the trendlines.

Appendix F. Whitefish larval density with bootstrapped 95% confidence intervals plotted against the hatching year. Also shown are the expected values predicted from population fecundity (PF) of the previous autumn alone or in combination with the signal crayfish egg predation during spawning time and winter (PF & Scf).

Appendix G. Proportions of various food items in the diet of age 1+ (A) and age 0+(B) whitefish in 1989 in Pyhäjärvi.

Appendix H. Development of the annual ratio between catch and population biomass of whitefish in Pyhäjärvi in 1988-2018. In the 1990s, the ratios were very high, declining clearly with increasing scatter towards the end of the time series. Although the catch/biomass ratios in the early part of this time series were unrealistically high, they suggest that the high fishing pressure on whitefish has relaxed during the latest years.

The Supplementary Material is available at https://www.limnology-journal.org/10.1051/limn/2024009/olm.

References

Amundsen P-A, Sánchez-Hernández J. 2019. Feeding studies take guts − critical review and recommendations of methods for stomach contents analysis in fish. *J Fish Biol* 95: 1364–1373.

Anneville O, Souissi S, Molinero JC, Gerdeaux D. 2009. Influences of human activity and climate on the stock-recruitment dynamics of whitefish, *Coregonus lavaretus*, Lake Geneva. *Fish Manag Ecol* 16: 492–500.

Böhling P, Hudd R, Lehtonen H, Karås P, Neuman E, Thoresson G. 1991. Variations in year-class strength of different perch (*Perca fluviatilis*) populations in the Baltic Sea with special reference to temperature and pollution. *Can J Fish Aquat Sci* 48: 1181–1187.

Bøhn T, Amundsen P-A. 2004. Invasion-mediated changes in the population biology of a dimorphic whitefish *Coregonus lavaretus* population. *Ann Zool Fennici* 41: 125–136.

Bourinet F, Anneville O, Drouineau H, Goulon C, Guillard J, Richard A. 2023. Synchrony in whitefish stock dynamics: disentangling the effects of local drivers and climate. *J Limnol* 82: 2134.

Claramunt RM, Muir AM, Sutton TM, Peeters PJ, Ebener MP, Fitzsimons JD, Koops MA. 2010. Measures of larval lake whitefish length and abundance as early predictors of year-class strength in Lake Michigan, *J Great Lakes Res* 36: 84–91.

Cushing DH. 1971. The dependence of recruitment on parent stock in different groups of fishes. *ICES J Mar Sci* 33: 340–362.

Deng J, Qin B, Sarvala J, Salmaso N, Zhu G, Ventelä A-M, Zhang Y, Gao G, Nurminen L, Kirkkala T, Tarvainen M, Vuorio K. 2016. Phytoplankton assemblages respond differently to climate warming and eutrophication: a case study from Pyhäjärvi and Taihu. *J Great Lakes Res* 42: 386–396.

Eckmann R. 2013. A review of the population dynamics of coregonids in European alpine lakes. *Adv Limnol* 64: 3–24.

Eckmann R, Pusch M. 1989. The influence of temperature on growth of young coregonids (*Coregonus lavaretus* L.) in a large prealpine lake. *Rapp P-v Réun Cons Int Explor Mer* 191: 201–208.

Edsall TA, Rottiers DV. 1976. Temperature tolerance of young-of-the-year lake whitefish, *Coregonus clupeaformis*. *J Fish Res Board Canada* 33: 177–180.

Forsman T. 2015. Pyhäjärven siian (*Coregonus lavaretus*) kasvu ja ikäjakauma rysäpyynnissä kalastuksen säätelyn perustana (Growth and age structure of whitefish (*Coregonus lavaretus*) in fyke net fishing as a basis for fisheries management in Lake Pyhäjärvi (SW Finland). *M. Sc. Thesis*, 42 p. Dept Biol. Env. Sci., University of Jyväskylä. (In Finnish)

Gerdeaux D. 2004. The recent restoration of the whitefish fisheries in Lake Geneva: the roles of stocking, reoligotrophication, and climate change. *Ann Zool Fennici* 41: 181–189.

Haakana H, Huuskonen H, Karjalainen J. 2007. Predation of perch on vendace larvae: diet composition in an oligotrophic lake and digestion time of the larvae. *J Fish Biol* 70: 1171–1184.

Haakana H, Huuskonen H. 2009. Predation of smelt on vendace larvae: experimental and field studies. *Ecol Freshw Fish* 18: 226–233.

Heikinheimo-Schmid O. 1992. Management of European whitefish (*Coregonus lavaretus* L. s.l.) stocks in Lake Paasivesi, eastern Finland. *Pol Arch Hydrobiol* 39: 827–835.

Helminen H, Sarvala J. 1994. Population regulation of vendace (*Coregonus albula*) in Lake Pyhäjärvi, southwest Finland. *J Fish Biol* 45: 387–400.

Helminen H, Sarvala J. 2021. Trends in vendace (*Coregonus albula)* biomass in Pyhäjärvi (SW Finland) relative to trophic state, climate change, and abundance of other fish species. *Ann Zool Fennici* 58: 255–269.

Helminen H, Auvinen H, Hirvonen A, Sarvala J, Toivonen J. 1993. Year-class fluctuations of vendace (*Coregonus albula*) in Lake Pyhäjärvi, southwest Finland, in 1971-1990. *Can J Fish Aquat Sci* 50: 925–931.

Helminen H, Sarvala J, Karjalainen J. 1997. Patterns in vendace recruitment in Lake Pyhäjärvi, south-west Finland. *J Fish Biol* 51: 303–316.

Huhmarniemi A, Niemi A, Palomäki R. 1985. Whitefish and vendace stocks in the regulated Lake Pyhäjärvi, central Finland. In Alabaster J.S. (ed.), Habitat modification and freshwater fisheries. FAO and Butterworths, London, 165–172.

Huusko A, Vuorimies O, Sutela T. 1996. Temperature- and light-mediated predation by perch on vendace larvae. *J Fish Biol* 49: 441–457.

Järvi TH. 1940. Über den Maränenbestand im Pyhäjärvi (SW Finnland). *Acta Zool Fennica* 28: 1–86.

Järvi TH. 1953. Über den Maränenbestand im Pyhäjärvi (SW Finnland). Zweiter Beitrag: Die Jahre 1940–1945. *Acta Zool. Fennica* 74: 1–47.

Jeppesen E, Mehner T, Winfield IJ, Kangur K, Sarvala J, Gerdeaux D, Rask M, Malmquist HJ, Holmgren K, Volta P, Romo S, Eckmann R, Sandström A, Blanco S, Kangur A, Ragnarsson SH, Tarvainen M, Ventelä A-M, Søndergaard M, Lauridsen TL, Meerhoff M. 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia* 694: 1–39.

Karjalainen J, Auvinen H, Helminen H, Marjomäki TJ, Niva T, Sarvala J, Viljanen M. 2000. Unpredictability of fish recruitment: interannual variation in young-of-the-year abundance. *J. Fish Biol* 56: 837– 857.

Karjalainen J, Keskinen T, Pulkkanen M, Marjomäki TJ. 2015a. Climate change alters the egg development dynamics in cold-water adapted coregonids. *Environ Biol Fishes* 98: 979–991.

Karjalainen J, Ruokonen TJ, Marjomäki TJ, Martikainen A, Pursiainen M, Sarvala J, Tarvainen M, Ventelä A-M. 2015b. Predation by *Pacifastacus leniusculus* signal crayfish on fish eggs and its consequences for coregonid recruitment. *J Fish Biol* 86: 651–667.

Karjalainen J, Jokinen L, Keskinen T, Marjomäki TJ. 2016. Environmental and genetic effects on larval hatching time in two coregonids. *Hydrobiologia* 780: 135– 143.

Karjalainen J, Tuloisela M, Nyholm K, Marjomäki TJ. 2021. Vendace disperse their eggs widely during spawning. *Ann. Zool Fennici* 58: 141– 153.

Lahti E, Muje P. 1991. Egg quality and female condition in vendace (*Coregonus albula* L.) before and during spawning. *Hydrobiologia* 209: 175–182.

Linløkken AN, Sandlund OT. 2015. Recruitment of sympatric vendace (*Coregonus albula*) and whitefish (*C. lavaretus*) is affected by different environmental factors. *Ecol Freshw Fish* 25: 652–663.

Miinalainen M, Heikinheimo O. 1998. Siikamuotojen ravintokilpailu Vuokalanjärvessä (Food segregation between five whitefish (*Coregonus lavaretus* (L.) stocks in lake Vuokalanjärvi. *Kalatutkimuksia − Fiskundersökningar* 139: 1–39 (in Finnish).

Mikkola H, Oksman H, Shemeikka P. 1979. Experimental study of mortality in vendace and whitefish eggs through predation by bottom fauna and fish. *Aqua Fennica* 9: 68–72.

Muggeo VMR. 2008. Segmented: an R package to fit regression models with broken-line relationships. *R News* 8/1: 20–25. URL https://cran.r-project.org/doc/Rnews/.

Raitaniemi J, Malinen T, Nyberg K, Rask M. 1999. The growth of whitefish in relation to water quality and fish species composition. *J Fish Biol* 54: 741–756.

R Core Team. 2023. R: a language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. https://www.R-project.org.

Ricker WE. 1954. Stock and recruitment. *J Fish Res Board Can* 11: 559–623.

Sandlund OT, Stang YG, Kjellberg G, Naesje TF, Hambo MU. 2005. European smelt (*Osmerus eperlanus*) eats all; eaten by all: is it a key species in lakes? *Verh Internat Verein für theor und angew Limnol* 29: 432–436.

Sarvala J, Helminen H. 1995. Significance of egg size variation in the year-class fluctuations of vendace (*Coregonus albula*). *Arch Hydrobiol Spec Issues Adv Limnol* 46: 187–194.

Sarvala J, Helminen H. 1996. Year-class fluctuations of perch (*Perca fluviatilis*) in Lake Pyhäjärvi, southwest Finland. *Ann Zool Fennici* 33: 389–396.

Sarvala J, Helminen H. 2021. Two-year cycle of vendace (*Coregonus albula*) in Pyhäjärvi, SW Finland: evidence for asymmetric competition between adults and juveniles. *Ann Zool Fennici* 58: 191–213.

Sarvala J, Rajasilta M, Hangelin C, Hirvonen A, Kiiskilä M, Saarikari V. 1988. Spring abundance, growth and food of 0+ vendace (*Coregonus albula* L.) and whitefish (*C. lavaretus* L. s.l.) in Lake Pyhäjärvi, SW Finland. *Finnish Fish Res* 9: 221–233.

Sarvala J, Helminen H, Hirvonen A. 1993. Fecundity of vendace (*Coregonus albula*) in relation to year-class variations in Lake Pyhäjärvi, SW Finland, in Biology and Management of Coregonid Fishes, edited by Todd TN and Luczynski M. *Pol Arch Hydrobiol* 39: 341–349.

Sarvala J, Helminen H, Saarikari V, Salonen S, Vuorio K. 1998. Relations between planktivorous fish abundance, zooplankton and phytoplankton in three lakes of differing productivity. *Hydrobiologia* 363: 81–95.

Sarvala J, Helminen H, Auvinen H. 1999. Portrait of a flourishing freshwater fishery: Pyhäjärvi, a lake in SW-Finland. *Boreal Environ Res* 3: 329–345.

Sarvala J, Helminen H, Ventelä A-M. 2020. Overfishing of a small planktivorous freshwater fish, vendace (*Coregonus albula*), in the boreal lake Pyhäjärvi (SW Finland), and the recovery of the population. *Fish Res* 230.

Selgeby J. 1998. Predation by ruffe (*Gymnocephalus cernuus*) on fish eggs in Lake Superior. *J Great Lakes Res* 24: 304–308.

Skurdal J, Bleken E, Stenseth NC. 1985. Cannibalism in whitefish (*Coregonus lavaretus*). *Oecologia* 67: 566–571.

Smålas A, Primicerio R, Kahilainen KK, Terentyev PM, Kashulin NA, Zubova E, Amundsen P-A. 2023. Increased importance of cool-water fish at high latitudes emerges from individual-level responses to warming. *Ecol Evol* 13. https://doi.org/101002/ece310185.

Straile D, Eckmann R, Jungling T, Thomas G, Löffler H. 2007. Influence of climate variability on whitefish (*Coregonus lavaretus*) year-class strength in a deep, warm monomictic lake. *Oecologia* 151: 521–529.

Svärdson G. 1979. Speciation of Scandinavian *Coregonus*. *Freshwat Res Drottningholm Rep* 57: 3–95.

Taipale SJ, Vuorio K, Aalto SL, Peltomaa E, Tiirola M. 2019. Eutrophication reduces the nutritional value of phytoplankton in boreal lakes. *Environ Res* 179: 108836.

Taipale SJ, Ventelä A-M, Litmanen J, Anttila L. 2022. Poor nutritional quality of primary producers and zooplankton driven by eutrophication is mitigated at upper trophic levels. *Ecol Evol* 12: e8687.

Thomas G, Eckmann R. 2007. The influence of eutrophication and population biomass on common whitefish (*Coregonus lavaretus*) growth − the Lake Constance example revisited. *Can J Fish Aquat Sci* 64: 402–410.

Turunen T, Viljanen M. 1988. Biology of whitefish (*Coregonus lavaretus* L) in Lake Suomunjärvi, Eastern Finland. *Finnish Fish Res* 9: 191–195.

Urpanen O, Marjomäki TJ, Viljanen M, Huuskonen H, Karjalainen J. 2009. Population size estimation of larval coregonids in large lakes: Stratified sampling design with a simple prediction model for vertical distribution. *Fish Res* 96: 109–117.

Väänänen T, Marjomäki TJ, Ranta T, Karjalainen J. 2024. The effect of water level changes on the density of newly hatched European whitefish (Coregonus lavaretus (L)) larvae in unregulated and regulated lakes. *Int J Limnol*.

Valkeajärvi P. 1992. Effects of increased fishing efforts on the European whitefish (Coregonus lavaretus L sl) in Lake Päijänne. *Pol Arch Hydrobiol* 39: 817–825.

Valkeajärvi P, Marjomäki TJ, Raatikainen M. 2012. Päijänteen Tehinselän muikku- ja siikakannat 1985–2010 Riista- ja kalatalous. *Tutkimuksia ja selvityksiä* 2012: 1–35 (In Finnish English abstract: Vendace and whitefish stocks in Lake Päijänne in 1985–2010)

Ventelä A-M., Kirkkala T, Lendasse A, Tarvainen M, Helminen H, Sarvala J. 2011. Climate related challenges in long-term management of Säkylän Pyhäjärvi (SW Finland). *Hydrobiologia* 660: 49–58.

Ventelä A-M, Amsinck SL, Kauppila T, Johansson LS, Jeppesen E, Kirkkala T, Søndergaard M, Weckström J, Sarvala J. 2016. Ecosystem change in the large and shallow Lake Säkylän Pyhäjärvi, Finland, during the past 400 years − implications for management. *Hydrobiologia* 778: 273–294.

Vuorimies O (ed). 1999. Ahvenen ravinto Puruvedessä (The food of perch in Lake Puruvesi) *Kalatutkimuksia-Fiskundersökningar* 162: 1–44 (In Finnish)

Walters CJ, Hilborn R. 1976. Adaptive control of fishing systems. *J Fish Res Board Can* 33: 145–159.

Walters CJ, Ludwig D. 1981 Effects of measurement errors on the assessment of stock-recruitment relationships. *Can J Fish Aquat Sci* 38: 704–710.

Winkler KA, Pamminger-Lahnsteiner B, Wanzenböck J, Weiss S. 2011. Hybridization and restricted gene flow between native and introduced stocks of Alpine whitefish (Coregonus sp.) across multiple environments *Mol Ecol* 20: 456–472.