

# Trends in vendace (*Coregonus albula*) biomass in Pyhäjärvi (SW Finland) relative to trophic state, climate change, and abundance of other fish species

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Catches of vendace (*Coregonus albula*) from Pyhäjärvi, a boreal lake in SW Finland, were exceptionally high for decades. Gradually, however, eutrophication and climate warming significantly changed the lake environment. From the 1970s to the 2010s, total phosphorus and chlorophyll *a* levels increased two- and threefold, respectively, while the average June–September surface temperature increased by 0.34 °C decade<sup>-1</sup>. The highest population biomass of the young-of-the-year vendace in autumn, 6–18 (mean = 14) kg ha<sup>-1</sup>, was recorded in 1973–1989, a period of sustainable fishery. Overfishing in 1990–1999 reduced autumn biomass of young-of-the-year vendace biomass to 3–11 (mean = 6) kg ha<sup>-1</sup>, allowing the competing planktivores perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and smelt (*Osmerus eperlanus*) to increase and consume a larger part of the plankton resources. Eutrophication and climate warming appear to have favoured these species, and the new resource division persisted even after the vendace population recovered.

## Introduction

Fish production and yield are both predictable from primary production (Downing *et al.* 1990, Sarvala *et al.* 2003). Predictions of fish yield are more variable, however, because the proportion of fish production that is taken as catch depends on the fishing effort and fishery conditions (Sarvala *et al.* 1999, 2003). An extreme example of such variability was observed in Pyhäjärvi, a lake in southwestern Finland, where fish yields were an order of magnitude higher than expected from known relationships between fish yield and nutri-

ent concentrations or primary production (Sarvala *et al.* 1999). In Pyhäjärvi, sustainable fish catches were 0.7%–0.8% of primary production, i.e. quite comparable to, or greater than, those in coastal seas (Sarvala *et al.* 1999, 2003). The reason for these exceptionally high yields appears to have been efficient fishing of the small planktivorous coregonid vendace (*Coregonus albula*) (Sarvala *et al.* 1999). The annual harvest rate of vendace approached its total production (Helminen *et al.* 1992, Sarvala *et al.* 2020).

The catches and population dynamics of vendace in Pyhäjärvi have been monitored since

1971, and the patterns of year-class fluctuations were analysed in several papers (Helminen *et al.* 1993a, 1993b, Helminen & Sarvala 1994, Helminen *et al.* 1997, Sarvala *et al.* 2020). In most cases vendace matured and spawned for the first time in their second autumn, and some survived to spawn again in the following years. The larvae hatched around ice-out in spring, and despite variation in first-year growth across years, young-of-the-year (YOY) recruited to the fishery in autumn (Helminen *et al.* 1993b). The major proportion of the total vendace catch was taken with seine nets in winter when the lake was covered with ice (Helminen *et al.* 1993a).

In the 1980s, vendace year-classes in Pyhäjärvi were strong (Helminen *et al.* 1993a), but in the early 1990s, the population collapsed, remaining at low densities for ten years. Unfavourable spring weather and unusually high abundance of predators were identified as the major causes of this collapse (Helminen & Sarvala 1994, Helminen *et al.* 1997), but the low population status was maintained in 1990–1999 by overfishing during which the spawning stock was limiting recruitment (Sarvala *et al.* 2020). Because of the ensuing poor earnings, fishing effort soon decreased which allowed the recovery of the stock in a few years.

While the period of overfishing was temporary, there are other, long-term problems that the vendace population in Pyhäjärvi is now facing. Pyhäjärvi is suffering from eutrophication caused by external nutrient loading (Ventelä *et al.* 2011, 2016). The effects of eutrophication are further reinforced by warming-induced shifts in fish assemblages and size structure (Teixeira-de Mello *et al.* 2009). Jeppesen *et al.* (2012) thought that the observed overall declining trend in year-class strength of vendace in Pyhäjärvi, might be linked to an increase in the maximum summer water temperature.

The recent changes threaten the existence of fisheries which has been vital in the Pyhäjärvi region for centuries (Sarvala *et al.* 1999), and consequently there is an urgent need for a better understanding of the ongoing development. We used the exceptionally long-term ecosystem monitoring data from Pyhäjärvi, as well as published and unpublished information from the early 1970s until 2020 (Table 1) to explore the

responses of vendace and other planktivorous fish to eutrophication and climate change.

## Study area, material and methods

### Study lake

Pyhäjärvi is a shallow (mean depth 5.4 m, maximum depth 26 m; 94% of the lake is < 7 m deep), but large (area 155 km<sup>2</sup>) boreal lake in southwestern Finland (61°00'N, 22°18'E). There is no long-term stratification during the open-water season. Up to the 1990s, the lake used to be covered by ice from November to April–May, but the length of the ice-covered season is shortening with the warming climate (Ventelä *et al.* 2011). The lake is mesotrophic (mean total phosphorus concentration in summer up to 25 µg l<sup>-1</sup>, primary production 26–56 g C m<sup>-2</sup> a<sup>-1</sup>, Secchi depth 2.4–3.9 m) (Sarvala *et al.* 1984, Sarvala & Jumppanen 1988, Ventelä *et al.* 2011). Phytoplankton, zoobenthos, zooplankton, and fish production were predicted from the physical and chemical environment similarly as for other lakes (Sarvala *et al.* 1999). The fish assemblage in Pyhäjärvi consists of 18 species, dominated by perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*), roach (*Rutilus rutilus*), smelt (*Osmerus eperlanus*), bleak (*Alburnus alburnus*), whitefish (*Coregonus lavaretus*), and vendace (Sarvala *et al.* 1999).

### Indicators of ecological state

Pyhäjärvi water quality has been monitored since 1962 by environmental authorities, university researchers, and the Pyhäjärvi Institute. Among the numerous physical and chemical variables, the most relevant for our analyses were total phosphorus (P<sub>tot</sub>), chlorophyll *a* (CHL) concentrations (µg l<sup>-1</sup>), and temperature (TEMP, °C), each measured 6–24 times per year in the surface water (0–2 m) at the *Pyhäjärvi Deep* study site. The data for June to September 1973–2020 were retrieved from the Hertta database of the Finnish Environment Institute (SYKE). Following the European Union Water Framework Directive (WFD) practices, we calculated averages for

June–September not published earlier. Volume-based total wet mass estimates of phytoplankton (ten 0–5 m column samples combined into one composite sample per date 6–24 times per year) were retrieved for 1980 to 2018 from the Hertta database. Although May–October averages were published by Ventelä *et al.* (2016), we used the previously unpublished June–September data.

Crustacean zooplankton was sampled weekly or at 2–3 week intervals during the open-water season (May–October) since 1987, with additional samples from 1977, 1980, 1982, 1984 and 1986. Samples were taken in the daytime from 0 to 5 m depth with a 0.5- or 1-m-high tube

sampler (volume 3.4 or 6.8 l) at ten locations selected using a stratified random design. The samples were concentrated with a 50- $\mu$ m mesh net and combined in the lab to form one composite sample per date. Subsamples were then enumerated until 50–200 individuals of the dominant crustacean species had been counted and measured. Counts and measurements were converted into zooplankton biomass using carbon-length regressions (Sarvala *et al.* 1998). Previously unpublished June–September averages of total crustacean zooplankton were used.

Temporal changes in TEMP,  $P_{\text{tot}}$ , and CHL, as well as in phytoplankton biomass (PHB) and

**Table 1.** Sources of the data.

Variable	Origin of data, method	Years	Source
Vendace year-class size	DeLury method when the CPUE decline was significant	1971–1978, 1981–1982, 2007, 2010–2011, 2013–2019	Helminen <i>et al.</i> 1993a, Sarvala <i>et al.</i> 2020
	When the CPUE data were lacking or the decline was not significant, estimated from an exponential regression between the average autumn mass of age 0+ vendace and year-class size obtained for the 28 years when the DeLury method was applicable	1971–1978, 1981–1982, 2007, 2010–2011, 2013–2019	Helminen <i>et al.</i> 1993a, Sarvala <i>et al.</i> 2020
Vendace YOY mass in autumn	Catch samples, own data, Pyhäjärvi Institute	1973–2019	Yearly values new data
BPUE of perch, roach, and smelt	Standard monitoring with the Nordic multi-mesh gillnets, Pyhäjärvi Institute, LUKE	2000, 2004, 2006, 2009, 2012, 2015, 2019	New data
Annual CPUE of vendace, whitefish, perch, roach, bleak, smelt	Catch samples from winter seining, fishermen's records of vendace catches, own data, Pyhäjärvi Institute	1985–2011	New data
Water quality data (temperature, total phosphorus, chlorophyll <i>a</i> )	Pyhäjärvi Institute, Finnish Environment Institute's Hertta database	1973–2020	Averages for June–September new
Phytoplankton biomass	University of Turku, Pyhäjärvi Institute, Finnish Environment Institute's Hertta database	1977–2018	Averages for June–September new
Crustacean zooplankton biomass	Own data, Pyhäjärvi Institute	1982–2019	Averages for June–September new

zooplankton biomass (ZPB), were examined by regressing the annual June–September averages against the calendar year. The status of these variables was also assessed relative to the WFD criteria used to evaluate the ecological state of lakes. The assessments were made according to the protocols of Aroviita *et al.* (2019).

### Vendace biomass

Vendace year-class sizes at the start of the winter seining season were estimated and published in our earlier studies (Helminen *et al.* 1993a, 1993b, 1997, Sarvala *et al.* 2020, Sarvala & Helminen 2021). Year-class sizes were primarily computed from the declining CPUE in the seine net fishery during each winter (Table 1). When the CPUE data were lacking or the decline was not significant, year-class numbers were calculated from the exponential regression between the average autumn mass of YOY vendace and year-class strength, obtained for the 28 years when the DeLury method was applicable (Sarvala *et al.* 2020). Biomasses of different cohorts (VenB) were then calculated by multiplying year class numbers by the average individual mass of YOY vendace at the end of the growing season. For the analysis of temporal change in vendace biomass the years before, during, and after the overfishing period 1990–1998 (Sarvala *et al.* 2020) were distinguished. The overfishing period was delimited on the basis of a spawning stock  $< 0.6 \text{ kg ha}^{-1}$  (average  $0.34 \text{ kg ha}^{-1}$ ); the average spawning stock before and after the overfishing period was  $2.5$  and  $3.7 \text{ kg ha}^{-1}$ , respectively (when based on the YOY numbers as in Sarvala *et al.* (2020) and Sarvala & Helminen (2021), the overfishing period was 1990–1999), Average cohort biomass for three periods was published by Sarvala *et al.* (2020), but the annual values are published here for the first time. Vendace biomass was compared to the winter fishing effort from Sarvala *et al.* (2020: the number of seine hauls during winter corrected for an increase in seine net size during the study period, based on the YOY vendace catch per haul in the first 50 seine hauls each winter relative to year-class strength).

### Catches of planktivorous fish

Data on the species, size and age composition of the catches from the commercial winter seine fishery originated from 12–80 catch samples each winter (1988–2010), taken on 5–16 dates (in 2008 only six samples on a single date because of a short seining season; Helminen *et al.* 1993a, Sarvala *et al.* 1999, Ventelä *et al.* 2011, Sarvala & Helminen 2021). Total catch for YOY vendace was obtained from the fishermen's daily records. Catch estimates for adult vendace and other species were calculated from the proportions in catch samples relative to those of YOY vendace. To accommodate for changes in catch composition during the winter, the total catch estimates were summed from the results of shorter, usually monthly periods. For 1985–1987, in the absence of catch samples, catches for the other species except vendace, were based on the annual reports of the Pyhäjärvi Fisheries Management Association. The catch estimates were recalculated as catch per unit effort (CPUE) by dividing the total winter catch by the winter fishing effort obtained from Sarvala *et al.* (2020). Each CPUE was assigned to the year when that winter started (i.e., CPUE for the winter 1990–1991 was assigned to 1990). Although the catch estimates were published earlier (e.g. Ventelä *et al.* 2007, 2011), the CPUE values are presented here for the first time. The perch CPUE includes even the piscivorous big perch, but due to the intense fishery, the largely planktivorous small size groups (length  $< 15 \text{ cm}$ ) dominated the perch biomass in most years. Similar situations prevailed for smelt.

### Standard gillnet monitoring of the fish assemblage

Previously unpublished results of standard monitoring with Nordic multi-mesh gillnets (CEN 2005) for the years 2000, 2004 and 2006 were obtained from the Pyhäjärvi Institute, and those for 2009, 2012, 2015 and 2019 from the database of Natural Resources Institute Finland (LUKE). Biomass per unit of effort (BPUE, kg per gillnet night, arithmetic mean) was used as an index of fish abundance. Gillnet catches tend to overestimate the abundance of percids and under-

estimate that of cyprinids and smelt (Olin & Malinen 2003), and the bias is most pronounced concerning the smallest and largest fish (Olin *et al.* 2009). In Pyhäjärvi, where big fish are sparse due to the high fishing pressure, the European standard multimesh gillnets should give a rather reliable view of the fish assemblage (Deceliere-Vergès *et al.* 2009, Šmejkal *et al.* 2015), at least for following temporal changes by species.

In 2000, 2004 and 2006 the lake was divided in three zones: the littoral area < 3 m deep, an intermediate zone 3–7 m deep, and the deepest area 7–25 m deep. The fishing effort was allocated among the zones in proportion to their area, with 7, 41, and 6 gillnet nights in each zone, respectively. In the littoral, only bottom nets were used, in the 3–7-m area nets were set both at the bottom and surface, and in the deepest area the bottom and surface nets were complemented with gillnets set at intermediate depths. The gillnets were set in the evening and left overnight for 12–14 hours. Three fishing rounds with 54 gillnet nights each were performed in June, August and September–October.

Since 2009, the fishing effort was restricted to 16 km<sup>2</sup> around the deepest point of the lake. One fishing round was performed in late July–early August, with 56 gillnet nights allocated to 0–3, 3–10 and 10–20 m depth zones, and with the gillnets set to surface, intermediate and bottom positions as described earlier. The standard fishing period in Finland is between 15 July and 31 August. In 2000, 2004 and 2006, unit catches varied markedly between seasons, being lowest in autumn and highest in August. Therefore, only the July–August catches were used in the comparisons of biomass per net night (BPUE) between years; both bottom and pelagic nets were included.

## Statistical methods

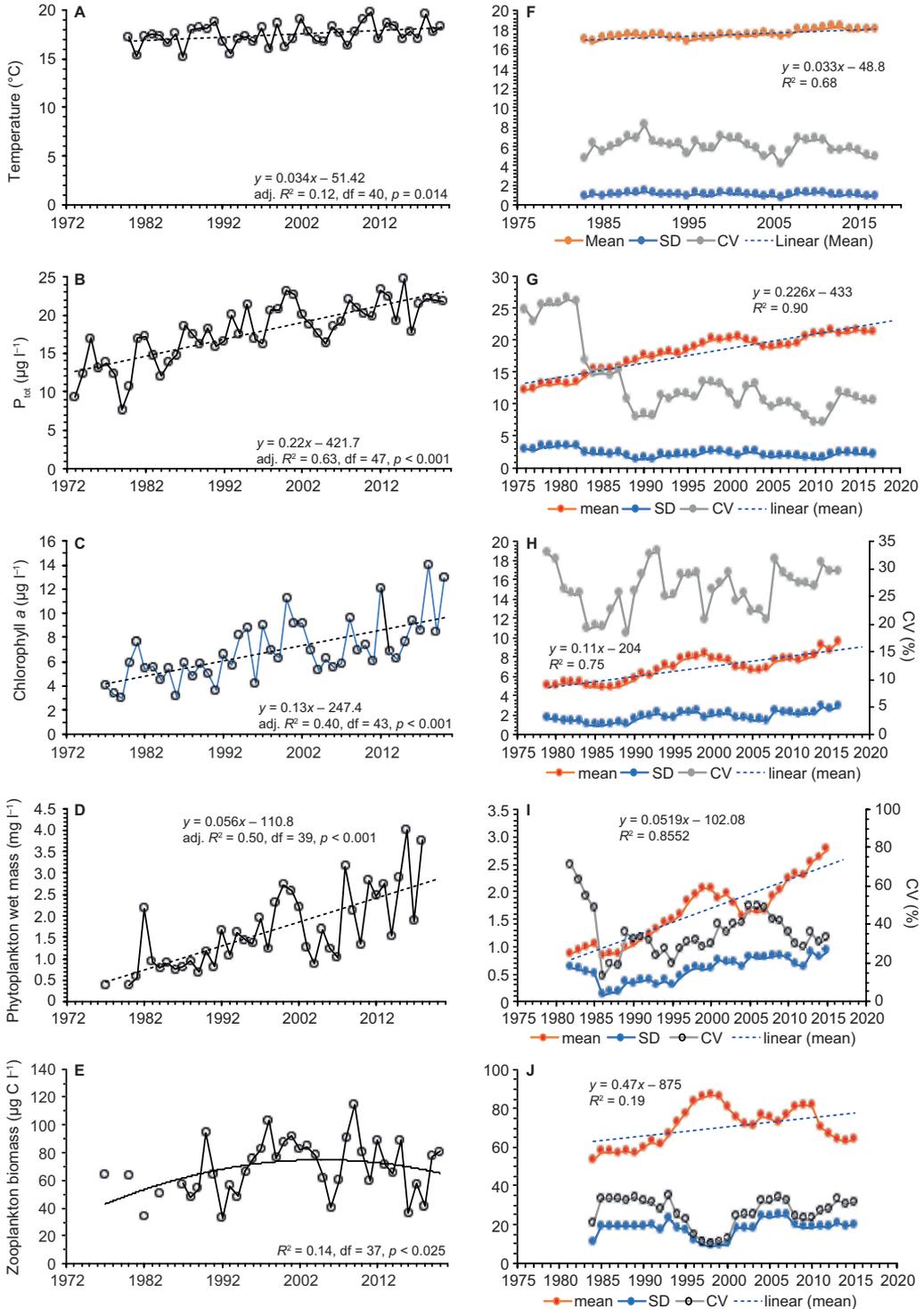
Various combinations of multiple and single-factor linear regressions were used to examine the temporal trends of the environmental and fish variables as well as their mutual relationships. The normality, linearity and homoscedasticity of error variation of each variable were checked visually from the distribution of residuals and

normal probability plots, as well as using the Shapiro-Wilk test. Deviations from normality and homoscedasticity were addressed with log<sub>10</sub>-transformations. In few cases when the linearity assumption was not fulfilled, a curvilinear regression was applied. Seven-year moving averages with standard deviations and coefficients of variation were also calculated for the environmental variables. Most of the CPUE distributions of individual fish species were non-normal, and therefore the analyses of the temporal CPUE changes were mainly based on a visual examination of the figures. Only the combined CPUE of all planktivorous fishes including vendace (untransformed) or excluding vendace (log-transformed) were used in regression analyses. Statistics were calculated with Microsoft Office Excel 2016 and Statistix. Proportions were arcsin-transformed before analyses.

## Results

### Ecological state of Pyhäjärvi

Pyhäjärvi slowly eutrophicated during the study period. P<sub>tot</sub> and CHL concentrations as well as the PHB increased significantly from the 1970s to 2020 (Fig. 1 and Table 2). In the 1970s and early 1980s, the P<sub>tot</sub> was 8–17 µg l<sup>-1</sup>, while in the 2010s it fluctuated from 18 to 25 µg l<sup>-1</sup> (Fig. 1B and G). The P<sub>tot</sub> increase slowed down slightly towards the end of the time series, resulting in a slightly but significantly higher coefficient of determination in the quadratic regression of P<sub>tot</sub> against time as compared with that for the linear one ( $F = 4.545$ ,  $df = 1, 45$ ,  $p < 0.05$ ). Yet the error variation of the untransformed variable did not deviate significantly from normal. Like P<sub>tot</sub>, the CHL levels gradually increased over the years from low values of 3–8 µg l<sup>-1</sup> in the 1970s to 6–14 µg l<sup>-1</sup> in the 2010s (Fig. 1C and H, Table 2). The highest values were associated with algal blooms. There were some irregularities in the overall linear increase, particularly a period of five years in 2003–2007 with values lower than predicted from the linear regression. The untransformed CHL distribution was non-normal and showed weak heteroscedasticity, but both could be corrected by log<sub>10</sub>-transformation.



**Fig. 1.** (A, F) Temperature at 0–2 m depth, (B, G) total phosphorus concentration (0–2 m), (C, H) chlorophyll *a* (0–2 m), (D, I) Phytoplankton wet mass (0–5 m), and (E, J) crustacean zooplankton biomass (0–5 m) in Pyhäjärvi (SW Finland) in June–September 1973–2020. Linear (curvilinear for zooplankton) regressions and their equations are shown where significant. In F–J the corresponding seven-year moving averages, standard deviations and coefficients of variation, together with linear regressions are shown.

The development of PHB (Fig. 1D and I) was similar to that of CHL, but the amplitude of fluctuations was wider and heteroscedasticity stronger; both were corrected with  $\log_{10}$ -transformation. Moving averages revealed a period of higher values in the late 1990s and lower values in 2003–2007. Crustacean ZPB did not show any

overall linear trend (Fig. 1E and J). A quadratic model gave a satisfactory fit, but even it did not remove the heteroscedasticity of the residuals. There was a period of high values in 1996–2004, with a declining trend in the 2000s and 2010s (Fig. 1E and J). ZPB was particularly low in 1992, 2006, 2016 and 2018.

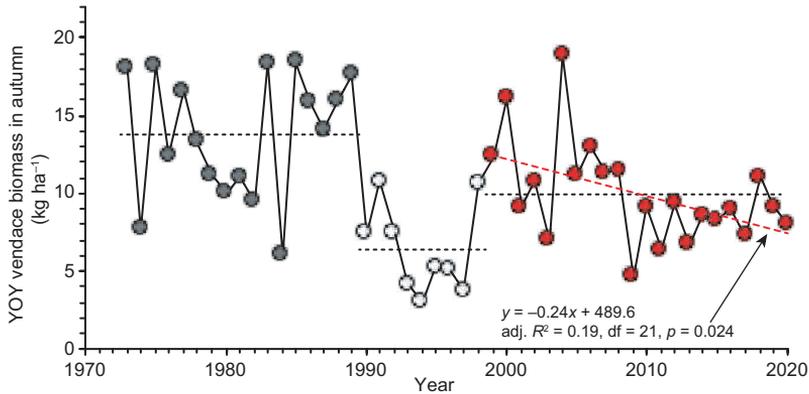
**Table 2.** Summary of significant ( $p < 0.05$ ) linear regressions between fish and ecological state variables in Pyhäjärvi. June–September averages were used for all environmental variables, and annual values for the fish variables. CPUE = unit catches in the winter seine fishery, BPUE = unit catches in the standard gillnetting, TEMP = surface temperature,  $P_{\text{tot}}$  = total phosphorus concentration, CHL = chlorophyll *a* concentration, PHB = phytoplankton biomass, ZPB = crustacean zooplankton biomass, VenB = vendace 0+ population biomass, VenCPU = vendace CPUE, PlaCPU = summed CPUE of all planktivorous fish, PlaCPU<sub>UnV</sub> = summed CPUE of all planktivorous fish except vendace, PerchCPU = perch CPUE, RoachCPU = roach CPUE, PlaBPU<sub>UnV</sub> = summed BPUE of all planktivorous fish except vendace, VenBPU = vendace BPUE, SmeltBPU = smelt BPUE, VenPro = the proportion of vendace of the total CPUE of planktivorous fish.

Dependent variable	Independent variable	Period	adj. $R^2$	df	$p$	slope	SE
TEMP	Year	1980–2020	0.12	40	0.013	0.034	0.013
$P_{\text{tot}}$ *	Year	1973–2020	0.63	47	< 0.001	0.22	0.02
$\log_{10}$ CHL	Year	1977–2020	0.43	43	< 0.001	0.008	0.001
$\log_{10}$ PHB	Year	1980–2018	0.52	38	< 0.001	0.015	0.002
$\log_{10}$ CHL	$P_{\text{tot}}$	1977–2020	0.53	43	< 0.001	0.032	0.005
VenB	Year	1973–2020	0.13	47	0.006	−0.12	0.04
VenB	Year	1999–2020	0.19	21	0.024	−0.24	0.10
VenB	$\log_{10}$ PHB	1980–2018	0.08	38	0.042	−5.82	2.76
VenCPU	VenB	1985–2010	0.53	25	< 0.001	20.14	3.70
VenCPU	VenB	1999–2010	0.71	11	< 0.001	31.7	5.99
PlaCPU	Year	1985–2010	0.46	25	< 0.001	17.3	3.67
PlaCPU <sub>UnV</sub>	Year	1985–2010	0.43	25	< 0.001	13.8	3.08
$\log_{10}$ PerchCPU	Year	1985–2010	0.67	25	< 0.001	0.06	0.008
$\log_{10}$ RoachCPU	Year	1985–2010	0.47	25	< 0.001	0.04	0.008
PlaBPU <sub>UnV</sub>	Year	2000–2019	0.67	6	0.015	46.2	12.7
$\log_{10}$ VenBPU	Year	2000–2019	0.75	6	0.007	−0.070	0.016
SmeltBPU	Year	2000–2019	0.50	6	0.045	21.6	8.14
PlaCPU	$P_{\text{tot}}$	1985–2010	0.17	25	0.019	35.7	14.2
PlaCPU	PHB	1985–2010	0.12	25	0.047	111.4	53.3
PlaCPU	$\log_{10}$ ZPB	1987–2010	0.14	23	0.039	621.5	284.4
$\log_{10}$ VenBPU	$\log_{10}$ PlaBPU <sub>UnV</sub>	2000–2019	0.65	6	0.017	−3.37	0.96
arcsinVenPro	Year	1985–2010	0.13	25	0.041	−0.015	0.0068

#### Multiple regressions

Dependent variable	Independent variable	Period	overall $R^2$	df	$p$	slope	SE
$\log_{10}$ CHL	$P_{\text{tot}}$ & TEMP	1980–2020	0.51	40			
	$P_{\text{tot}}$ TEMP				< 0.001	0.065	0.010
$\log_{10}$ PHB	$P_{\text{tot}}$ & TEMP	1980–2018	0.56	38			
	$P_{\text{tot}}$ TEMP				0.037	0.067	0.031
$\log_{10}$ PHB	$P_{\text{tot}}$ & TEMP	1980–2018	0.56	38			
	$P_{\text{tot}}$ TEMP				< 0.001	0.055	0.008
					0.028	0.054	0.024

\* The increase in  $P_{\text{tot}}$  with time slowed down towards the end of the study period, indicating curvilinearity of the relationship. A 2nd degree polynomial fitted well, with  $R^2 = 0.67$ ,  $df = 47$ ,  $p < 0.001$ .  $\log_{10}$ -transformation over-corrected exaggerating the curvilinearity, therefore, the untransformed  $P_{\text{tot}}$  was used in the regression analyses.



**Fig. 2.** Vendace young-of-the-year subpopulation biomass in the first autumn of the cohort in Pyhäjärvi (SW Finland) in 1973–2020. Black dashed lines indicate mean values for the three successive periods 1973–1989 (grey dots), 1990–1998 (overfishing period, white dots), and 1999–2020 (red dots). The regression line indicating decreasing vendace biomass in 1999–2020 is shown with red dashed line.

The mean surface (0–2 m) water temperature in June–September increased significantly during 1982–2020. Its variability was low, and linearity, normality and homoscedasticity requirements were fulfilled. The average warming rate was  $0.34\text{ }^{\circ}\text{C decade}^{-1}$  (Fig. 1A and F, Table 2).

Some of the environmental variables were closely associated, showing high collinearity in regression analysis. TEMP and  $P_{\text{tot}}$  represent two independent ultimate factors determining the productivity of the lake ecosystem; in our data set they did not correlate significantly with each other. At the next trophic level, both phytoplankton variables, CHL and PHB, were predictable mainly from  $P_{\text{tot}}$  with a minor contribution from TEMP (Table 2). Both variables could be used as indicators of changes in primary productivity in Pyhäjärvi, while ZPB was a direct indicator of food resources available for the planktivorous fish.

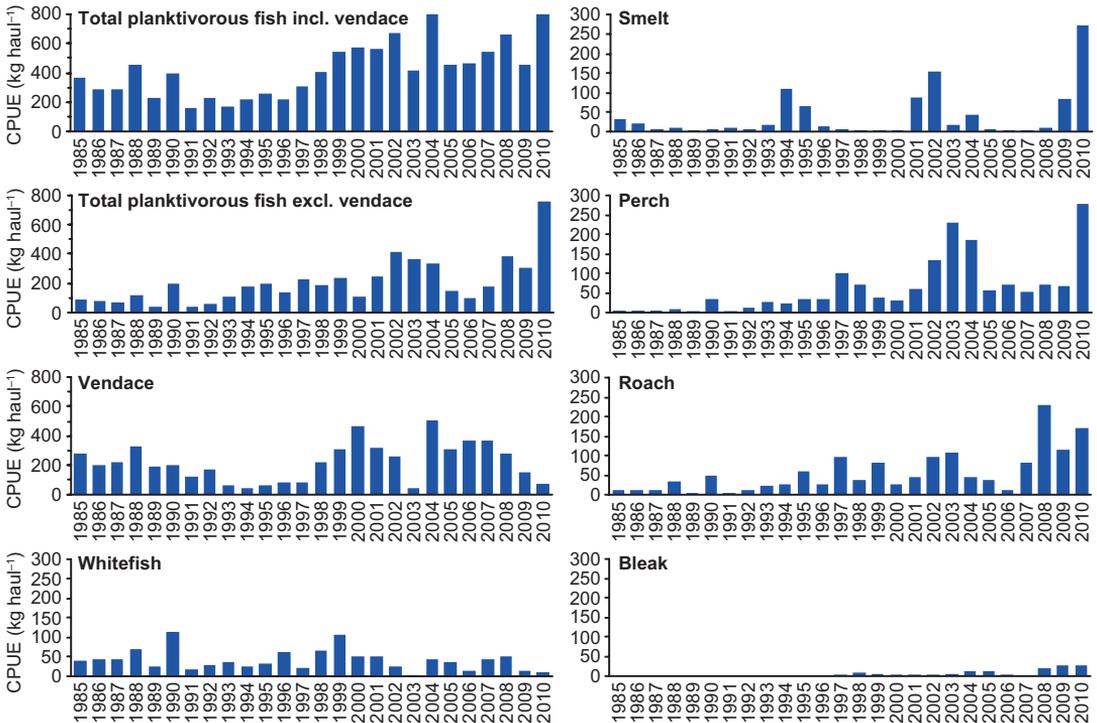
### Vendace biomass

The autumn biomass of YOY vendace in Pyhäjärvi showed a weak but statistically significant decreasing trend during the whole study period 1973–2020 (Table 2). The normality and linearity requirements were satisfactorily fulfilled, but the residuals showed strong heteroscedasticity, because the three periods defined on the basis of spawning stock size

showed different development (Fig. 2). Vendace biomass was lowest during the overfishing period 1990–1998 (mean YOY biomass  $99.3\text{ t}$  or  $6.4 \pm 2.0\text{ kg ha}^{-1}$ ; range  $3.0\text{--}10.8\text{ kg ha}^{-1}$ ). Before overfishing, in 1973–1989, biomass was high with no significant temporal trend but oscillating between higher and lower values (Fig. 2; mean biomass  $214.0\text{ t}$  or  $13.8 \pm 1.9\text{ kg ha}^{-1}$ ; range  $6.0\text{--}18.5\text{ kg ha}^{-1}$ ). After the overfishing period, biomasses returned close to the values before overfishing, but this was followed by a significant decline in 1999–2020 (Fig. 2; mean YOY biomass  $153.6\text{ t}$  or  $9.9 \pm 1.4\text{ kg ha}^{-1}$ ; range  $4.7\text{--}18.9\text{ kg ha}^{-1}$ ). Although the weak vendace stock in the 1990s was due to overfishing, in the whole time series vendace biomass was not significantly associated with the fishing effort.

### Changes of planktivorous fish populations

The total CPUE of planktivorous fish increased significantly during the study period (Fig. 3 and Table 2), and its variability was lower than that of the individual non-coregonid species (coefficients of variation  $0.45\text{ vs. }0.97\text{--}1.68$ ). The increase was similar when the vendace was excluded from the combined planktivore CPUE (Fig. 3 and Table 2). The vendace CPUE showed major fluctuations closely related to the development of the YOY biomass, with high values in the



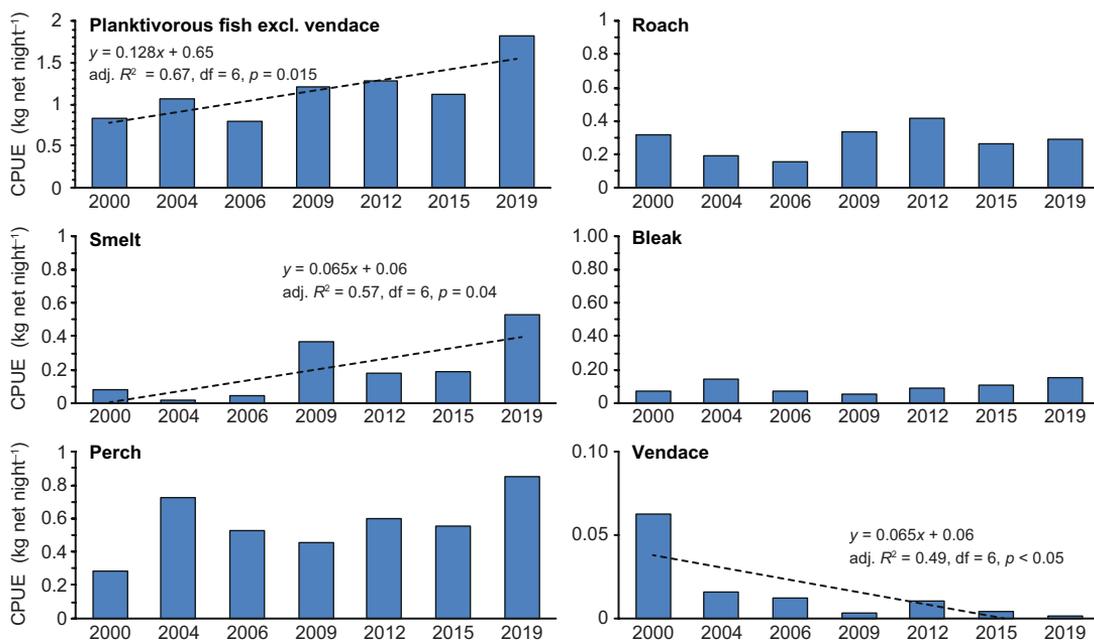
**Fig. 3.** Catch per unit effort (CPUE) of planktivorous fish by species in the winter seine fishery in Pyhäjärvi (SW Finland) in 1985–2010 (winters 1985–1986 to 2010–2011).

1980s (mean = 245 kg haul<sup>-1</sup>), low values during the overfishing period (mean = 135 kg haul<sup>-1</sup>), and increased values (mean = 285 kg haul<sup>-1</sup> in 2000–2010) followed by a declining trend after it. There was no consistent trend over the whole study period. The linear regression of vendace CPUE on vendace biomass was highly significant in the whole study period and during the last two decades (Table 2). Before the overfishing period (1985–1989), the proportion of vendace of the total catch of the planktivorous fish (vendace, small perch, roach, bleak, smelt and whitefish) was high (mean = 0.78). During the overfishing period 1990–1999, when the vendace CPUE declined to 135 kg haul<sup>-1</sup>, its proportion in the total planktivore CPUE declined to 0.46. The total planktivore catches also remained somewhat low for a few years during that period, but, with some delay, they increased during the late 1990s. After the recovery from overfishing, even if vendace CPUE rose at first to higher values than before overfishing, nevertheless the proportion of vendace of the planktivore catch did not return to the levels preceding overfishing

but remained similar to the values in the 1990s (0.52).

The CPUE of perch and roach increased significantly, but there were substantial fluctuations, caused by the occurrence of strong year-classes (Fig. 3 and Table 2). Variations in the smelt CPUE reflected the appearance of strong year-classes at 8–10-year intervals (Fig. 3), and there was no overall trend (Fig. 3).

The results of standard gillnetting provided complementary information on fish stock development in the 2000s and 2010s (Fig. 4). For perch and roach, the 95% confidence interval varied in different years between  $\pm 29\%$  and  $\pm 43\%$  of the mean BPUE, for smelt and vendace a little wider,  $\pm 28\%$  to  $\pm 57\%$  of the mean. As expected, the sum of planktivorous fish (excluding vendace) was less variable, with the 95% confidence interval of  $\pm 21\%$  of the mean. For most species, the linear trends in BPUE were not significant, but the combined planktivorous fish BPUE (excluding vendace) showed significant increase, approximately doubling from 2000 to 2019, to a BPUE of 1.825 kg net-night<sup>-1</sup>



**Fig. 4.** Catches of planktivorous fish in standard gillnet fishing in Pyhäjärvi (SW Finland) in July–August. Mean biomass catches (BPUE kg net-night<sup>-1</sup>) are shown for total biomass without vendace, and for smelt, perch, roach, bleak, and vendace (whitefish catches of 0–0.005 kg net night<sup>-1</sup> not shown) in 2000, 2004, 2006, 2009, 2012, 2015 and 2019. Linear regressions and their equations are shown when significant. Note the different scale in the first and last panels.

(Fig. 4 and Table 2). Same was observed in the trend in the winter seine CPUE. The catch biomass of perch per net night increased threefold (BPUE 0.850 kg net-night<sup>-1</sup> in 2019; Fig. 4), while that of roach was quite stable. In 2019, the total BPUE of cyprinids (roach and bleak) was 0.440 kg net-night<sup>-1</sup>, and their proportion in total fish catch biomass (BPUE) was 0.22. Although the standard gillnetting is not well suited for estimating the abundance of coregonids, the vendace BPUE showed a significantly declining trend in 2000–2019 (Table 2), consistent with the development of the winter seine CPUE and population biomass.

### Links between fish and explanatory variables

None of the multiple regressions between fish abundance variables and explanatory variables, and only few of the single-factor regressions were statistically significant. Nevertheless, the results gave a consistent view of the develop-

ments in the lake. The regressions of total planktivores on the summer TEMP or  $P_{tot}$  were not significant, but the total planktivore CPUE was positively associated with PHB and ZPB (Table 2). According to the regression, a 1-mg increase in phytoplankton wet mass per litre would increase planktivore CPUE by about 110 kg haul<sup>-1</sup>. The relationship of planktivore CPUE with CHL was similarly positive but not significant. The regression of the vendace YOY biomass on PHB over the whole study period was also significant, although the explained variance was very low (Table 2). This is typical for field conditions where the outcome is determined by numerous interacting factors. Vendace BPUE in standard gillnetting was inversely associated with total planktivore BPUE (Table 2).

### Discussion

Vendace cohort biomass, catches per effort in the winter seine fisheries and in the standard gillnet monitoring consistently indicated similar changes

in the fish assemblage of Pyhäjärvi during the last 50 years. Vendace showed the most pronounced fluctuations, the early high-stock period being followed by a collapse of the population in 1990–1991 perhaps as a consequence of slow warming of water after the ice-out, combined with high abundance of natural and stocked predators (Helminen *et al.* 1997). Overfishing then kept the stock at low densities for 10 years (Sarvala *et al.* 2020), and the recovery to almost the levels preceding the overfishing was followed by a decline during the last 20 study years. A major change, partly linked to the vendace decline, happened around the mid-1990s when the other planktivores, particularly small perch, roach, bleak and smelt, started to increase in abundance. At least three factors likely contributed to this change: interspecific competition, eutrophication, and climate warming. The overall increase of the planktivores was likely related to eutrophication. However, during the vendace low-stock period in 1993–1997, small perch and roach appear to have taken advantage of the plankton resources that became available when the food consumption of the diminished vendace population decreased. Their continued increase even after the recovery of vendace was possible because of eutrophication, and was consistent with changes reported for increasing trophic status in other lakes (Olin *et al.* 2003).

Although we could not here identify any significant links between fish abundance and the increasing temperature using the summer-season data, the climate change is certainly affecting the fish populations in Pyhäjärvi in several ways. The elevated temperatures favour northern populations of warm-water species, while particularly the southern populations of cold-water species tend to suffer (Jeppesen *et al.* 2012). The  $0.34\text{ °C decade}^{-1}$  increase in surface water temperature observed in June–September 1980–2020 was not far from the July–August warming rate of  $0.40\text{ °C decade}^{-1}$  obtained by Lathrop *et al.* (2019) for Pyhäjärvi in 1982–2017. In spring, warming was faster ( $1.1\text{--}2.1\text{ °C decade}^{-1}$ ), but autumn temperature increased less, while the ice-free summer season became substantially longer (Lathrop *et al.* 2019). The moderate summer warming was likely to have little effect on the recruitment success of vendace or other

fish; for vendace, the spring temperature development seems to be more important (Helminen & Sarvala 1994). But behind the averages is hiding the occasional appearance of very warm summers that favour reproductive success of the spring-spawning percids and cyprinids (Böhling *et al.* 1991, Sarvala & Helminen 1996). Warmer and longer summers lead to improved first-summer growth, contributing to better survival of YOY percids and cyprinids over their first winter (Post & Prankevicius 1987, Kirjasniemi & Valtonen 1997). Increasing summer temperatures thus likely increase both the competitors and predators of vendace, and indirectly affect the vendace population. From the 1980s to the 2010s, at least 12 warm summers with strong perch recruitment could be identified (Sarvala & Helminen 1996, and unpubl.). For vendace, a steady warming of water in the three–four first weeks after the ice-out improve the survival of larvae, but early ice-out combined with slow warming is detrimental (Helminen & Sarvala 1994, Kangur *et al.* 2020). On the other hand, the maximum summer temperatures may be approaching lethal levels for vendace (Kangur *et al.* 2020, Sarvala *et al.* 2020). Although climate warming can thus have some positive effects on vendace, the overall effect seems to be negative.

Extensive surveys of northern lakes have shown that with eutrophication, percids increase first, replacing coregonids, and cyprinids become dominant at higher eutrophy levels (Persson *et al.* 1991, Olin *et al.* 2002). In Finnish lakes, roach start to become dominant when  $P_{\text{tot}}$  exceeds  $30\text{ }\mu\text{g l}^{-1}$  (Helminen *et al.* 2000, Olin *et al.* 2002), a level not yet reached in Pyhäjärvi. Roach affect vendace primarily through food competition, but the relationships of vendace with perch and smelt are more complicated and include both competition and predation. Young perch and smelt are food competitors of vendace, but at larger size they become important predators of larvae and juveniles of vendace (Sterligova 1979, Sarvala *et al.* 2003).

The ultimate driver of eutrophication in Pyhäjärvi appears to be increasing  $P_{\text{tot}}$ : in the 1980s, 70% of the between-year variation in phytoplankton primary production was explained by  $P_{\text{tot}}$  (Sarvala & Jumppanen 1988). In 1985–2010, CHL and PHB were predictable from  $P_{\text{tot}}$  con-

centration, and the CPUE of the planktivorous fish showed significant positive correlation with  $P_{\text{tot}}$ , PHB and ZPB. These relationships were consistent with bottom-up regulation of the food web. In contrast, ZPB was not significantly correlated with PHB or CHL. Moreover, the lowest values of ZPB were observed when the planktivory index indicated highest predation pressure by the planktivores (Ventelä *et al.* 2011 and authors' unpubl. data). Such changes in ZPB can be interpreted as signs of top-down regulation of zooplankton through predation by the planktivorous fish. In top-down regulated systems, increasing primary production leads to increased zooplankton production, but this is not reflected to the ZPB but is instead visible as higher fish production and biomass (Carpenter *et al.* 2001). In our earlier studies (Helminen & Sarvala 1997) in Pyhäjärvi we found that in 1979–1992 the late summer CHL showed positive correlation with the  $P_{\text{tot}}$  concentration in lake water, and negative correlation with the biomass of crustacean zooplankton, particularly that of big cladocerans. The latter in turn was negatively correlated with planktivorous fish abundance. A multiple regression of CHL on  $P_{\text{tot}}$  and big cladocerans indicated approximately equal roles of the bottom-up and top-down regulations (Helminen & Sarvala, 1997, Sarvala *et al.* 1998). According to the present analyses, however, the bottom-up regulatory chain seems to have been dominating in recent decades in Pyhäjärvi. Therefore, external loading of nutrients continues to be the most significant threat for water quality in this lake, particularly due to increased delivery of soluble reactive phosphorus from nonpoint sources via tributaries (i.e., labile P fractions at the soil surface and transmission of soluble P via subsurface drainage) (Jarvie *et al.* 2017).

Another possible explanation for the failure of zooplankton to benefit from the increasing phytoplankton might be the worsening nutritional quality of phytoplankton when cyanobacteria increased with eutrophication (Ventelä *et al.* 2011, 2016, Taipale *et al.* 2019). The trophic relationships and regulation of water quality in lakes are more complicated than suggested by the simple bottom-up/top-down dichotomy.

One way to further analyse long term changes in Pyhäjärvi is to compare its ecological status

over time using the criteria of EU Water Frame Directive (WFD). According to WFD, ecological status is an assessment of the quality of the structure and functioning of surface water ecosystems. It shows the influence of pressures (e.g. pollution and habitat degradation) on the identified quality elements. In the latest WFD Classification Status Cycle 3 (unpublished preliminary version; data set 2012–2017), the overall ecological classification status for Pyhäjärvi was *moderate*. Then also the  $P_{\text{tot}}$  and CHL indicated a moderate status (limit values for good status:  $18 \mu\text{g l}^{-1}$  for  $P_{\text{tot}}$  and  $7 \mu\text{g l}^{-1}$  for CHL). The fish parameters showed conflicting indications. According to WFD criteria the fish biomass suggested a *bad* status (limit value BPUE  $1659 \text{ g net-night}^{-1}$ ), while the parameter *biomass share of cyprinids* indicated an *excellent* status (limit value 37.8 %).

An exception to the generally *moderate* condition prevailing since the mid-1990s was the period 2003–2007, when  $P_{\text{tot}}$  and CHL decreased below the *good* limit. At that time, nutrient loads were minimal because of low river flows, and CHL also decreased because of the removal of more than 1 500 000 kg ( $20\text{--}50 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) of smelt, perch, and roach from Pyhäjärvi in 2002–2004 (Ventelä *et al.* 2007).

When the WFD criteria were applied to the past  $P_{\text{tot}}$  and CHL data of Pyhäjärvi beyond the 2000s, it appeared that these variables indicated good ecological status for the last time in the early 1990s. The trophic state goal for the management of Pyhäjärvi has been thought to be the oligotrophic period in the early 1900s (Ventelä *et al.* 2016). In terms of the WFD criteria, this means that the water quality of Pyhäjärvi should attain an *excellent* ecological status (limit values  $10 \mu\text{g l}^{-1}$  for  $P_{\text{tot}}$  and  $4 \mu\text{g l}^{-1}$  for CHL). Then, the production of vendace would obviously decrease because zooplankton production would diminish due to lower primary production. Such oligotrophication happened in Lake Constance, which recovered from eutrophication thanks to successful lake drainage-area management (Güde *et al.* 1998). Total phosphorus ( $P_{\text{tot}}$ ) concentrations dropped by an order of magnitude to levels ( $6\text{--}8 \mu\text{g l}^{-1}$ ) that were typical for the early 1950s prior to massive eutrophication (Jochimsen *et al.* 2013). Phytoplankton and zooplankton populations declined as predicted, and the overall pro-

ductivity decreased, contributing to the reduction of the commercially important whitefish catches (Thomas & Eckmann 2007).

The case of Lake Constance shows that oligotrophication of once eutrophicated waterbodies is possible, but it requires truly significant reductions in external nutrient loading. In Pyhäjärvi, in spite of continued attempts, the nutrient load from the catchment has remained too high (Ventelä *et al.* 2007, 2011). Moreover, the internal loading of phosphorus from the sediment seems to be increasing (Nürnberg *et al.* 2012), considerably complicating the struggle for a permanently improved ecological state. For about half a century, vendace was the trademark of Pyhäjärvi fisheries. Now, both eutrophication and climate warming have reduced vendace recruitment. Historical data suggest that the optimum water quality for vendace populations prevailed when the ecological status of the lake was good. Strong interventions are required if we want to restore a flourishing vendace population in Pyhäjärvi.

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