

Two-year cycle of vendace (*Coregonus albula*) in Pyhäjärvi, SW Finland: evidence for asymmetric competition between adults and juveniles

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Long-term monitoring of the planktivorous vendace (*Coregonus albula*) in Pyhäjärvi, a lake in SW Finland, revealed periods characterised by different types of population regulation. In 1971–1989, the vendace stock was strong and exhibited a two-year cycle. In 1990–1999, extreme weather conditions and predation resulted in recruitment failures, after which overfishing kept year-classes small. From 2000 onwards, the two-year oscillations were re-established at a lower level. Here, we show that the two-year cyclicity prevalent in the 1980s was consistent with the hypothesis of asymmetric competition between adults and juveniles. Food consumption by juveniles of strong year-classes retarded growth and weakened condition of the co-occurring adults, resulting in less abundant year-classes. In 2000–2018, the role of intraspecific competition diminished due to interspecific competition from increased populations of other planktivorous fish, preventing vendace from attaining higher abundance. Elevated temperature probably confounded the effects of competition, but its direct role was masked by simultaneous gradual eutrophication and fish assemblage changes.

Introduction

Populations of the small coregonid planktivore vendace (*Coregonus albula*) are known for wide fluctuations of year-class strength (Aass 1972, Viljanen 1986). Several of density-independent and density-dependent factors causing this variation have been identified, including spring weather conditions, abundance of predators, fishing intensity, as well as intrapopulation mechanisms (Auvinen 1988, 1994, Marjomäki 2003). In many populations, the year-class strength

variation seems to be cyclic with a period of two years.

As reviewed by Marjomäki *et al.* (2014), cyclic year-class fluctuations may arise through several mechanisms. External factors affect vendace year-class strength, but we do not know of any such environmental variation that would follow a two-year cycle. When mortality is high, however, major perturbations caused by external factors might result in gradually decaying oscillations with a period of one generation, in the case of vendace mostly two years (gen-

eration cycling; Jansen *et al.* 1990, Townsend *et al.* 1990, Myers *et al.* 1998). More persistent year-class cycles could, however, be caused by negative inter-cohort effects. One possible inter-cohort mechanism driving two-year cycles is asymmetric food competition between the adults and juveniles, proposed by Hamrin and Persson (1986). According to this hypothesis, also called “juvenile dominance hypothesis” (Sandlund *et al.* 1991), juveniles would have an advantage in the competition so that the young-of-the-year of a strong cohort would suppress the reproduction of the adult cohorts.

The universal negative relationship between growth and abundance, documented for many vendace populations (Viljanen 1986, Marjomäki & Kirjasniemi 1995, Sarvala *et al.* 2020), proves the commonness of strong intraspecific competition in this species. Although the two-year cycle has been confirmed in several empirical and model studies (Helminen & Sarvala 1994a, Helminen *et al.* 2002, Huusko & Hyvärinen 2005, Marjomäki *et al.* 2014), the detailed mechanism of how the adult–juvenile competition would actually regulate the cycle has remained elusive. Moreover, in some vendace populations, it is adults that seem to be dominant in the intraspecific competition (Sandlund *et al.* 1991). Currently, no single mechanism responsible for cycles in vendace population dynamics can thus be designated, and several mechanisms may be operating simultaneously (Marjomäki *et al.* 2014, Karjalainen *et al.* 2016).

The vendace population in Pyhäjärvi, a lake in SW Finland, had been monitored for 50 years (1971–2020), and a wealth of data have been published over the years on its abundance, growth and feeding (Helminen *et al.* 1990, 1993a, 1997a, 1997b, 2002, Helminen & Sarvala 1994a, 1994b, Sarvala *et al.* 1999, 2020). These long-term data are suitable for evaluating the importance of different factors in year-class regulation.

In the beginning and towards the end of the time series, the main feature of the vendace year-class variation was an oscillation between alternating strong and weak year-classes (Sarvala *et al.* 2020). Three periods with different characteristics could be distinguished. The first was in 1971–1989, when the vendace stock was on an average strong with no trend, and a two-

year cycle of abundance with a wide amplitude was prevalent. We suggested earlier that this variation was due to the asymmetric adult–juvenile competition (Helminen *et al.* 1993a). The two-year cycle was disrupted in the late 1980s and early 1990s by unusually early ice-out followed by slow warming of water, combined with exceptional abundance of predators. The population collapsed, and subsequently overfishing kept it small for ten years (1990–1999), during which the two-year cycle was absent (Sarvala *et al.* 2020). In the third period (2000–2019), after recovery from overfishing, the two-year cycle returned, even though weather anomalies again caused disturbances by impeding winter seine fisheries due to poor ice conditions in mild winters. It seems thus that the vendace population in Pyhäjärvi has a strong tendency towards a two-year cycle of year-class strength. Therefore, we had good reasons to expect that, if anywhere, in Pyhäjärvi we should be able to find evidence for the existence of the asymmetric adult–juvenile competition.

Asymmetry here means that the consequences of competition are not the same for both competitors (Begon *et al.* 2006: 233). Asymmetric competition arises from different abilities of competitors to use resources. The effects of asymmetric competition in vendace manifest themselves at the sub-population level as differences in the recruitment of successive cohorts. Such inter-cohort competition is common among fishes. Size differences often play a role in the competitive asymmetries, and in many cases the larger individuals have the competitive edge, for example due to their better ability of searching and catching prey. In contrast, the juvenile dominance hypothesis assumes that the smaller young-of-the-year (YOY) vendace are better than the adult fish in competing for the zooplankton resource because of their smaller individual metabolic demands, and ability to utilise smaller food items (Hamrin & Persson 1986, Sandlund *et al.* 1991).

We analysed published and unpublished data from our earlier studies from a new perspective, evaluating the hypothesis that asymmetric intraspecific competition between adults and juveniles was driving the two-year cycle of the vendace population in Pyhäjärvi. A prerequisite

for competition is that the potential competitors share the same resources. Another condition for competition is that the shared resources are in short supply, limiting growth and eventually reproduction. To evaluate whether such conditions apply to the age group relationships in the Pyhäjärvi vendace population, overlaps in the resource use of the adult and juvenile vendace were examined from detailed seasonal information on the taxonomic composition and size-frequency distributions of diet in three years in the 1980s when the two-year cycle was most prominent. Seasonal and annual food consumption estimates were calculated to illustrate the intensity of competition. Effects of competition on adult growth and condition, and finally on the strength of the new year-class were examined. Data on year-class strength existed from all the years from 1971 to 2020, but shorter time series had to be used for other variables depending on the availability of data. The long time-series enabled us to assess possible changes in the year-class regulation over the decades. Although the focus of this paper was in exploring the importance of intraspecific competition in the determination of vendace year-class size, we included in the analyses one environmental factor, temperature, as an indicator of climate change.

Study area and methods

Study lake

Pyhäjärvi is a shallow (mean depth 5.4 m, maximum depth 26 m), but large (area 155 km²) boreal lake in southwestern Finland (60°54'–61°06'N, 22°09'–22°25'E). There is no prolonged stratification during the open-water season; 94% of the lake area is < 7 m deep. 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 in summer 11–25 µg P l⁻¹, Secchi depth 2.4–3.9 m) (Sarvala *et al.* 1984, Sarvala & Jumppanen 1988, Ventelä *et al.* 2011, Helminen & Sarvala 2021).

Pyhäjärvi has been famous for its high fish yields for centuries. Yet phytoplankton, zoo-

plankton, zoobenthos, and fish production were similarly related to the physical and chemical environment as in other lakes, and the main reason for the high yields was the unusually efficient fishery (Sarvala *et al.* 1999). The fish assemblage 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). Vendace was introduced in Pyhäjärvi in 1948–1952, establishing a self-sustaining population. The first vendace appeared as by-catch in the whitefish (*Coregonus lavaretus*) fyke net fishery in the mid-1950s, and starting from the early 1960s, a winter seine fishery principally targeting vendace developed in Pyhäjärvi.

Methods

We used the data from our earlier studies in 1983–2020. The original data were checked and re-analysed from a point of view of the intraspecific competition hypothesis. Here we give only a brief overview of the methods used while more complete descriptions are found in the publications cited.

Temperature data were downloaded from the Hertta database of the Finnish Environment Institute, and June–September averages at 0–2 m depth were calculated. According to literature information, adult vendace avoid temperatures higher than 18–19 °C, preferring temperatures around 15–16 °C (Kangur *et al.* 2020). Therefore, to evaluate the possible effect of the warming climate on vendace recruitment, the number of days when temperature exceeded 17 °C in each year was also included.

Vendace year-class sizes were obtained from our earlier studies (Table 1). Numbers of one-summer-old vendace in autumn (year-class size, YCS) were estimated with the DeLury method from the decline of catches per seine haul during the winter (28 years) (Helminen *et al.* 1993a, 1993b). If the unit catch decline was not significant, the negative relationship between the average mass at the end of the first growing season and year-class strength was used to estimate YCS (21 years) (Sarvala *et al.* 2020). Ages

Table 1. Year-class sizes of vendace in Pyhäjärvi (SW Finland) in 1971–2019, with an overview of estimation methods (DeLury = year-class size estimated with the DeLury method from CPUE decline in the winter seining, Growth = year-class size estimated from the first-summer growth); some –2 SE and +2 SE for the DeLury estimates are also shown. When the decline of the catch per winter seine haul (CPUE) was significant, the adjusted (adj.) R^2 is given (ns = not significant, na = data not available). The next column gives the source for each year-class estimate. The four rightmost columns show the average individual mass and length of 0+ vendace in autumn in the beginning of the winter seining period, and the mean mass and length of age 1+ fish in the winter catch.

Year	Winter	Year-class size ($\text{indiv.} \times 10^6$)	–2 SE	+2 SE	Method	Adj. R^2	Source for the year-class size	Age 0+		Age 1+	
								mass (g)	length (mm)	mass (g)	length (mm)
1971	1971/72	14.8			Growth	na	Sarvala <i>et al.</i> 2020, recalculated from	16.8			
1972	1972/73	11.8			Growth	na	Helminen <i>et al.</i> 1993a Sarvala <i>et al.</i> 2020, recalculated from	17.6			
1973	1973/74	22.6			Growth	na	Helminen <i>et al.</i> 1993a	12.0			
1974	1974/75	4.8			Growth	na	Helminen <i>et al.</i> 1993a	25.0			
1975	1975/76	26.5			Growth	na	Helminen <i>et al.</i> 1993a	11.0			
1976	1976/77	11.4			Growth	na	Helminen <i>et al.</i> 1993a	17.0			
1977	1977/78	14.8			Growth	na	Helminen <i>et al.</i> 1993a	16.9	140	63	210
1978	1978/79	11.8			Growth	na	Helminen <i>et al.</i> 1993a	18.0			
1979	1979/80	33.5			DeLury	0.70	Helminen <i>et al.</i> 1993a	5.2	102	31.3	182
1980	1980/81	7.3			DeLury	0.67	Helminen <i>et al.</i> 1993a	21.3	152	32.9	176
1981	1981/82	10.3			Growth	ns	Helminen <i>et al.</i> 1993a	16.7	143	49.0	216
1982	1982/83	6.3			Growth	ns	Helminen <i>et al.</i> 1993a	23.3	157	46.2	177
1983	1983/84	21.6	18.2	25.0	DeLury	0.58	Helminen <i>et al.</i> 1993a	13.2	134	54.4	204
1984	1984/85	4.8			DeLury	0.67	Helminen <i>et al.</i> 1993a	19.5	149	42.8	190
1985	1985/86	19.9			DeLury	0.83	Helminen <i>et al.</i> 1993a	14.4	136	53.6	209
1986	1986/87	13.5			DeLury	0.73	Helminen <i>et al.</i> 1993a	18.2	142	42.9	198
1987	1987/88	11.8			DeLury	0.79	Helminen <i>et al.</i> 1993a	18.5	147	66.6	208
1988	1988/89	15.6			DeLury	0.71	Helminen <i>et al.</i> 1993a	15.9	141	45.4	200
1989	1989/90	13.6	12.4	15.7	DeLury	0.83	Helminen <i>et al.</i> 1993a, Sarvala <i>et al.</i> 2020	20.1	157	54.3	204
1990	1990/91	4.4	4.4	4.4	DeLury	0.82	Helminen <i>et al.</i> 1993a, Sarvala <i>et al.</i> 2020	26.2	162	74.2	220
1991	1991/92	6.6	6.4	7.0	DeLury	0.65	Sarvala <i>et al.</i> 2020	25.3	155	70.4	226
1992	1992/93	11.2	10.9	11.7	DeLury	0.63	Sarvala <i>et al.</i> 2020	10.3	121	56.6	206
1993	1993/94	4.4	4.4	4.4	DeLury	0.88	Sarvala <i>et al.</i> 2020	14.6	138	56.9	205
1994	1994/95	2.2	2.2	2.2	DeLury	0.86	Sarvala <i>et al.</i> 2020	21.3	149	67.2	211

continued

Table 1. Continued.

Year	Winter	Year-class size ($\text{indiv.} \times 10^6$)	-2 SE	+2 SE	Method	Adj. R^2	Source for the year-class size	Age 0+		Age 1+	
								mass (g)	length (mm)	mass (g)	length (mm)
1995	1995/96	2.9	2.6	4.1	DeLury	0.41	Sarvala <i>et al.</i> 2020	28.2	163	66.7	209
1996	1996/97	2.5	2.3	3.0	DeLury	0.35	Sarvala <i>et al.</i> 2020	31.3	162	74.5	221
1997	1997/98	2.3	2.2	2.5	DeLury	0.75	Sarvala <i>et al.</i> 2020	25.5	159	75.0	219
1998	1998/99	5.3	4.9	6.0	DeLury	0.64	Sarvala <i>et al.</i> 2020	31.2	170	77.9	230
1999	1999/00	7.0	6.6	7.6	DeLury	0.78	Sarvala <i>et al.</i> 2020	27.6	163	61.9	219
2000	2000/01	13.4	12.3	15.1	DeLury	0.83	Sarvala <i>et al.</i> 2020	18.7	149	57.1	213
2001	2001/02	4.3	3.8	5.4	DeLury	0.62	Sarvala <i>et al.</i> 2020	32.6	173	57.6	212
2002	2002/03	7.8	7.2	9.0	DeLury	0.62	Sarvala <i>et al.</i> 2020	21.4	149	75.7	229
2003	2003/04	3.5			DeLury	0.45	Sarvala <i>et al.</i> 2020	31.4	162	74.2	215
2004	2004/05	10.4	8.4	18.7	DeLury	0.33	Sarvala <i>et al.</i> 2020	28.3	157	79.5	224
2005	2005/06	9.3	8.1	12.4	DeLury	0.46	Sarvala <i>et al.</i> 2020	18.8	140	51.3	200
2006	2006/07	16.1	12.1	27.1	DeLury	0.86	Sarvala <i>et al.</i> 2020	12.5	124	43.1	188
2007	2007/08	13.5			Growth	ns	Sarvala <i>et al.</i> 2020	13.0	126	34.1	180
2008	2008/09	8.4	6.0	32.6	DeLury	0.19	Sarvala <i>et al.</i> 2020	21.3	144	42.2	183
2009	2009/10	3.8	3.4	4.8	DeLury	0.49	Sarvala <i>et al.</i> 2020	19.1	138	55.6	201
2010	2010/11	5.8			Growth	0.66	Sarvala <i>et al.</i> 2020	24.4	151	58.4	203
2011	2011/12	2.9			Growth	ns	Sarvala <i>et al.</i> 2020	33.6	168	67.9	214
2012	2012/13	6.6	4.4	28.2	DeLury	0.13	Sarvala <i>et al.</i> 2020	21.9	150	73.1	226
2013	2013/14	3.1			Growth	na	Sarvala <i>et al.</i> 2020	33.0	166	57.5	203
2014	2014/15	5.0			Growth	na	Sarvala <i>et al.</i> 2020	26.3	154	81.1	228
2015	2015/16	4.8			Growth	na	Sarvala <i>et al.</i> 2020	27.0	157	61.8	210
2016	2016/17	22.2			Growth	na	Sarvala <i>et al.</i> 2020	6.3	102	45.5	197
2017	2017/18	3.0			Growth	na	Sarvala <i>et al.</i> 2020	33.5	166	43.9	186
2018	2018/19	10.0			Growth	na	Sarvala <i>et al.</i> 2020	17.0	136	54.3	199
2019	2019/20	5.8			Growth	na	Sarvala <i>et al.</i> 2020	24.4			

were determined from scales; in vendace, ageing from scales is reliable up to three years (Viljanen 1988). In most years, the 0+ age group could be identified solely based on fish size. Numbers of age 1+ and older vendace in the autumn, based on the total winter catch of each age group corrected with the intensity of fishery, were obtained from the data of Sarvala *et al.* (2020).

Later in this paper, larval and juvenile vendace in their first summer are called young-of-the-year (YOY), while vendace in their second summer are called adults; these fish will spawn in their second autumn at the age 1+, which means that their gonads mature in late summer and autumn. Due to intense fishery in Pyhäjärvi, in most years the spawning stock consisted practically only of the age 1+ vendace (Sarvala *et al.* 2020).

We re-analysed the detailed growth and diet data of the YOY and adult vendace collected in May–December 1987 (partly published by Helminen *et al.* 1990, who focused on the estimation of food consumption with a bioenergetic model) and March–December 1989 (partly published by Karjalainen *et al.* 1997b, in a comparison with smelt). Similar but less complete data available from 1984 were used for comparison.

Growth and diet data for the early life of YOY were obtained from larval sampling which started in 1984 for monitoring larval abundance in Pyhäjärvi and continued to the 2000s (Sarvala *et al.* 1988, 1994, Helminen *et al.* 1997a, Karjalainen *et al.* 1997b); here we used data for 1987 and 1989. YOY vendace over 20 mm in length were caught in June–July 1987 and 1989 with a special small trawl, and from July to September with gillnets. Older vendace (almost exclusively age 1+) were caught with gillnets at an interval of one or two weeks in May–November but also with the small trawl in late July. Gillnets (4.8 × 30 m, mesh sizes 10–25 mm knot-to-knot) were set on the average for 1.5 hours.

For diet analyses, the gut contents of preserved vendace larvae were spread in glycerol on a slide (Sarvala *et al.* 1988). Prey animals were identified and measured under a 100× magnification. To study the diets of YOY and adult vendace, the stomachs of 5–20 freshly caught fish per age group and date were preserved for microscopy, either individually, or in groups of

4–10 fish of the same size and age (Helminen *et al.* 1990).

Stomach fullness was estimated visually on the scale 0–10. Food items were identified to species level when possible and measured. For plankton prey, subsampling was often necessary. Carbon-to-length regressions or tables of carbon mass per size group were used to convert the measurements to carbon biomass (Sarvala *et al.* 1998). By adding all diet items we thus obtained the reconstructed biomass of prey at the moment of feeding. The ratio between reconstructed prey biomass and fish mass constituted a second measure of gut fullness, the relative stomach contents. Whole fish body mass was used here, and sexes were not separated. In the 1980s in Pyhäjärvi, the growth trajectories of the age 1+ male and female vendace started to diverge in August (own unpubl. data), while the critical period for feeding began earlier, in July. Possible variation in the sex ratio in samples increases the variability of the relative stomach contents of adults in late summer and autumn, but this should not affect our conclusions, because the stomachs of adult vendace were then almost empty.

Data on zooplankton prey available were obtained from monitoring samples of crustacean zooplankton collected in 1984 and annually since 1987 at weekly or fortnightly intervals from the ice-out to late October or November (e.g. Ventelä *et al.* 2011). The water column at ten study sites selected using a stratified random design was sampled with a tube sampler from surface to bottom (0–5 m), then samples were concentrated with a 50-µm mesh, and preserved in 70% ethanol. In the laboratory, column samples were combined into a single composite sample for each date. Using an inverted microscope, crustacean zooplankton was identified to species and stage and counted from subsamples until 50–200 individuals of each dominant species were measured. Length measurements were converted to carbon mass with carbon-to-length regressions as in Sarvala *et al.* (1998). Zooplankton later in this article denotes crustacean zooplankton.

Body condition of vendace was calculated by dividing the mean body mass by mass predicted from total length with the following power function of the mass–length relationship in Pyhäjärvi vendace in winter during the years 1983–2019:

$$\text{Condition} = M \times (0.0036\text{TL}^{3.216})^{-1}$$

where M is the body mass (g) and TL is the total length (cm).

For both YOY and adults, the body mass and length used in calculating the body condition were obtained from the winter seine catch samples. In several years, the YOY showed some growth during winter, and therefore for this group the average body mass during the first month of winter seining was used. The much smaller sample size for the adults did not allow for temporal splitting of the data, and therefore for adults the average mass for the whole winter was used.

Sex was not recorded in all years, but in the five years when it was, the median ratio of males to females was 0.99. These adults had spawned in the autumn, and so the variation in the sex ratio was not likely to confound the estimation of condition. The ranges of the average body size were 102–173 mm and 5.2–33.6 g for YOY, and 176–229 mm and 31.3–79.5 g for the adults (age 1+). Instantaneous growth rate (IGR) of adults during their second summer was calculated for each year from the initial and final average age-specific body masses (BM) obtained from the seine catches of successive winters:

$$\text{IGR} (\text{season}^{-1}) = \ln(\text{BM}_1 \times \text{BM}_0^{-1})$$

Differences in the taxonomic composition between the diets of YOY and adult vendace were examined by calculating proportional similarity indices (Renkonen 1938, Wolda 1981). Differences between the size-frequency distributions of the diets and zooplankton prey were tested with the Kolmogorov–Smirnov (KS) test in Microsoft Excel 2016. A Mann-Whitney (MW) U -test was used to evaluate the significance of the differences in relative stomach contents between the adults and YOY.

The relationships between the adult body condition or growth rate and the YOY abundance, or temperature variables, were examined by calculating ordinary linear and curvilinear regressions with one or two independent variables in Microsoft Excel 2016. Changes in growth rates of the YOY and adult vendace during summer were examined by fitting piecewise linear regres-

sions of individual mass against time with the “segmented” package 1.3.0 in the R environment (Muggeo 2008, RStudio ver. 1.3.1093; and R ver. 4.0.3, R Core Team 2020).

As an indicator of the competitive pressure caused by the YOY vendace, their total food consumption was calculated for the open-water period May–October each year. Calculations were done with the Fish Bioenergetics 4.0 programme in the R environment (Deslauriers *et al.* 2017), using an improved set of parameters (*see* Appendix) and data. A proxy for the population consumption by the YOY was obtained by multiplying the cumulative individual consumption estimates with the numbers of YOY in the autumn. The dependence of vendace year-class size on the previous summer’s food consumption by YOY and temperature variables was then examined with linear and curvilinear regressions in Microsoft Excel 2016.

To study the seasonal patterns and the relative roles of the age groups in resource use, the daily food consumption by the YOY and adult vendace was calculated for May–October in 1984, 1987 and 1989. For YOY, a total mortality rate of 50% was assumed between 1 May and 31 October. For the age 1+ adults the mortality was estimated comparing the numbers of a cohort surviving through their first winter (year-class numbers minus the numbers caught in the winter fishery) to the numbers alive next autumn (the spawning stock).

The overfishing period 1990–1999 when the spawning stock was limiting recruitment (Sarvala *et al.* 2020) was excluded from bioenergetic calculations and part of the regression analyses. Linear regressions were calculated for periods with different year-class patterns mentioned in the introduction: (1) years 1982–1989 when the vendace stock was strong and showed significant two-year cycling, (2) years 2000–2018, when the vendace population was moderately strong after recovery from overfishing, and showed two-year cyclicity (the autocorrelation was not statistically significant (Sarvala *et al.* 2020), but the two-year cyclicity was obvious in the sense of Marjomäki *et al.* (2021), and (3) the cyclic periods combined, i.e., the years 1982–1989, and 2000–2018. In some cases, all the years from 1982 to 2018 were included to clarify the long-term changes

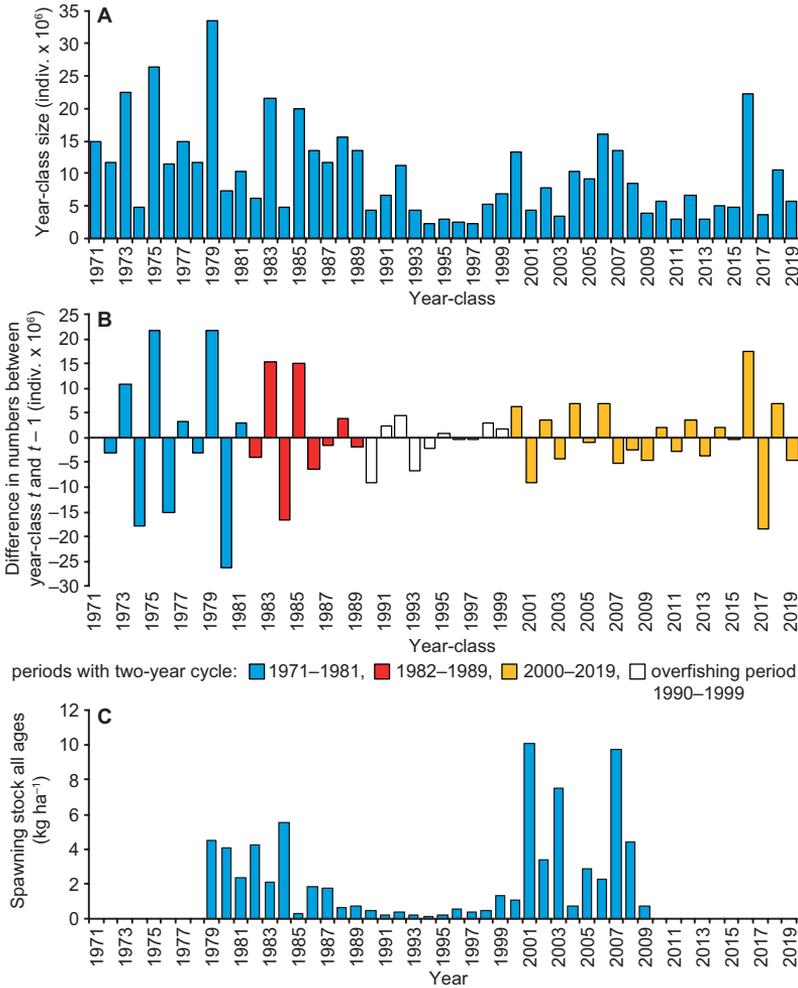


Fig. 1. (A) Vendace year-class size in 1971–2019 in Pyhäjärvi (redrawn from Sarvala *et al.* 2020). (B) Differences in vendace year-class size between successive years in 1971–2019 (redrawn from data of Sarvala *et al.* (2020)). (C) Vendace spawning stock in 1979–2009. Redrawn from data of Sarvala *et al.* (2020); no spawning stock data before 1979, those after 2006 unreliable because of small catches.

and for comparison with the shorter periods, and for regressions with temperature.

In all regression analyses, 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 Shapiro-Wilk's test.

Results

The overall pattern in vendace abundance variation with a two-year cycle between high and low values in the beginning and the end of the time series, and almost constant low values during the overfishing period in the middle, was clearly visible in the YCS and adult stock estimates (Fig. 1).

The number of days when the water temperature exceeded +17 °C increased significantly from 1982 to 2020 (Table 2 first row), six days per decade. This variable showed substantial between-year variation, ranging from 22 to 100 days. The increase in average summer temperature was also significant (Table 2).

In 1987 and 1989, the diets of YOY and adult vendace were quite similar both taxonomically (Fig. 2) and in length frequency distributions (Fig. 3), except in the first month after the ice-out. In May 1987, the lengths of the diet items eaten by the YOY, such as rotifers and cyclopoid nauplii and copepodids, were smaller than those of the prey of adults or the average zooplankton, while the length distributions of adult diet items and zooplankton did not differ (KS test: $K_D =$

69.08, $n_1 = 11$, $n_2 = 10$, $p = 0.05$; $K_D = 61.16$, $n_1 = 11$, $n_2 = 10$, $p < 0.05$; $K_D = 20.3$, $n_1 = 10$, $n_2 = 10$, $p > 0.1$, respectively).

Adult vendace fed on cyclopoid copepodids and adults and *Bosmina* and *Daphnia* cladocerans. Also in May 1989, the YOY preyed upon smaller food items than adult vendace (KS test: $K_D = 103.18$, $n_1 = 11$, $n_2 = 10$, $p < 0.001$). In August 1987, none of the differences in length frequency distributions were statistically significant, and both YOY and adults fed on prey of all lengths. Likewise in August 1989, the length-frequency distributions of the diets of both vendace age groups and of zooplankton were practically identical (KS test: $K_D = 13.7$, $n_1 = 10$, $n_2 = 10$, $p > 0.1$; $K_D = 4.6$, $n_1 = 4$, $n_2 = 10$, $p > 0.1$; $K_D = 8.16$, $n_1 = 10$, $n_2 = 4$, $p > 0.1$). For both age groups, the length of the smallest food items was < 0.3 mm. In agreement with these results,

proportional similarity of the taxonomic compositions in the diets of YOY and adult vendace were lower in spring, particularly in 1987, but from July onwards similarity was high in both years (Fig. 4).

During spring and early summer, there was no shortage of food resources. Zooplankton biomass was increasing up to late May in 1989 when spring was early, to early June in 1984, and to mid-June in 1987 (Fig. 5). A decline followed, with the lowest biomass in late June (1989) or mid-July (1984, 1987), and a second peak appeared in early August (1989), mid-August (1987), or September (1984). The cladoceran *Bosmina*, a favourite prey of vendace, showed only the early summer peak in 1987 and 1989, while there was an additional September peak in 1984. The total July–August zooplankton biomass was clearly lowest in 1984.

Table 2. Parameters of linear regressions between successive year-class sizes, and between growth and condition of adults and abundance, condition or food consumption of the YOY vendace. Regressions were originally calculated separately for each period, and for combinations of periods, but only significant results are shown here (Years = the range of data included, SE = standard error of the slope estimate); relationships with summer temperature variables are also included. Mean temp. = June–September average temperature at 0–2 m, YOY abund. = numbers of the young-of-the-year of a year-class in autumn, $YCS(t)$ = year-class numbers in year t , $YCS(t + 1)$ = year-class numbers in year $t + 1$, PF = power function, DeL = exponential function between YOY growth and abundance for the years when DeLury method was used, YOY growth = average mass of the YOY in the beginning of the winter seining period, YOY cond. = YOY body condition. Adult growth = instantaneous growth rate of age 1+ vendace in their second summer, Adult cond. = average adult body condition in winter, YOY cons. = Food consumption of the YOY subpopulation in May–October, na = not applicable.

Independent variable	Dependent variable	Years	Adj. R^2	df	p	slope	SE
Year	Days $> +17$ °C	1982–2020	0.16	38	0.007	+0.65	0.23
Year	Mean temp.	1980–2020	0.12	40	0.013	+0.034	0.013
$YCS(t)$	$YCS(t + 1)$	1982–1989	0.47	7	0.036	–0.78	0.29
YOY abund.	YOY growth	1979–2012 DeL	0.64	27	< 0.0001	na	na
Year	YOY cond.	1983, 1984, 1987–2018	0.46	33	< 0.0001	+0.006	+0.001
YOY abund.	YOY cond.	1983, 1984, 1987–2018	0.12	33	0.028	–0.006	–0.003
Mean temp.	Adult growth	1982–2018	0.09	36	0.041	–0.093	0.044
Days $> +17$ °C	Adult growth	1982–2018	0.11	36	0.025	–0.0062	0.0027
YOY abund.	Adult growth	2000–2018	0.24	17	0.022	–0.034	0.013
YOY abund. PF	Adult growth	1979–1989, 2000–2018	0.19	29	0.009	na	na
YOY abund.	Adult growth	1979–2018	0.17	39	0.005	–0.021	0.007
YOY abund. PF	Adult growth	1979–2018	0.21	39	0.002	na	na
YOY cond.	Adult cond.	1983, 1984, 1987–2018	0.21	33	0.004	+0.36	0.11
YOY abund.	Adult cond.	2000–2018	0.28	18	0.012	–0.007	0.002
YOY abund.	Adult cond.	1983–1989, 2000–2018	0.18	22	0.027	–0.005	0.002
YOY abund.	Adult cond.	1983, 1984, 1987–2018	0.17	33	0.010	–0.005	0.002
YOY cons.	$YCS(t + 1)$	1982–1989	0.64	7	0.010	–0.018	0.005

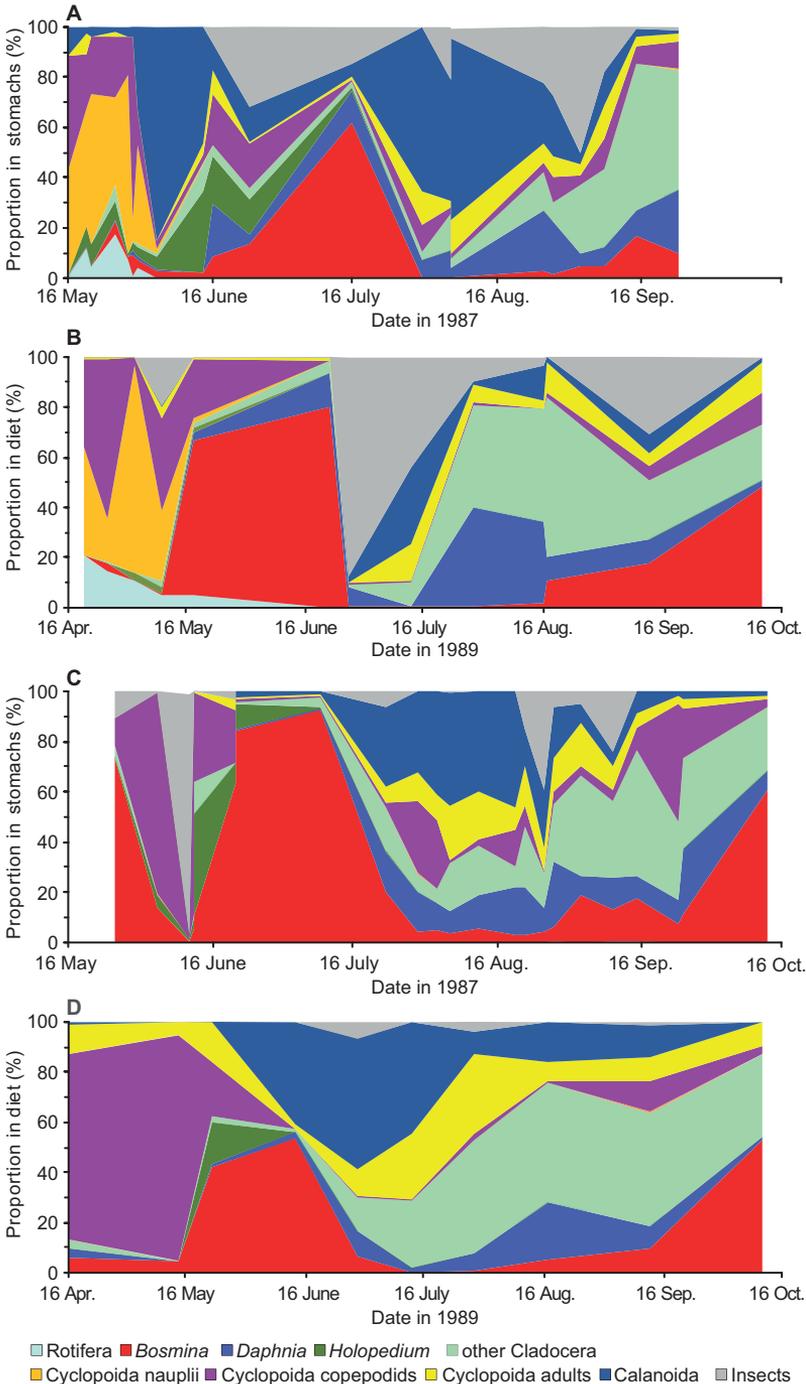


Fig. 2. Taxonomic composition of the stomach contents of the YOY and adult vendace in the summers 1987 and 1989 (proportion of the reconstructed carbon mass of all prey). (A) YOY in 1987, (B) YOY in 1989, (C) adults in 1987, (D) adults in 1989.

Despite considerable scatter and differences in details, both stomach fullness measures gave similar picture of the overall seasonal development. The stomach fullness in all age groups was highest in early summer and declined in

late summer; particularly in 1987 the decline was earlier in the adult vendace (Fig. 6). In late summer in both years, the adult vendace had eaten significantly less food than the YOY (MW *U*-test for the difference in stomach fullness in

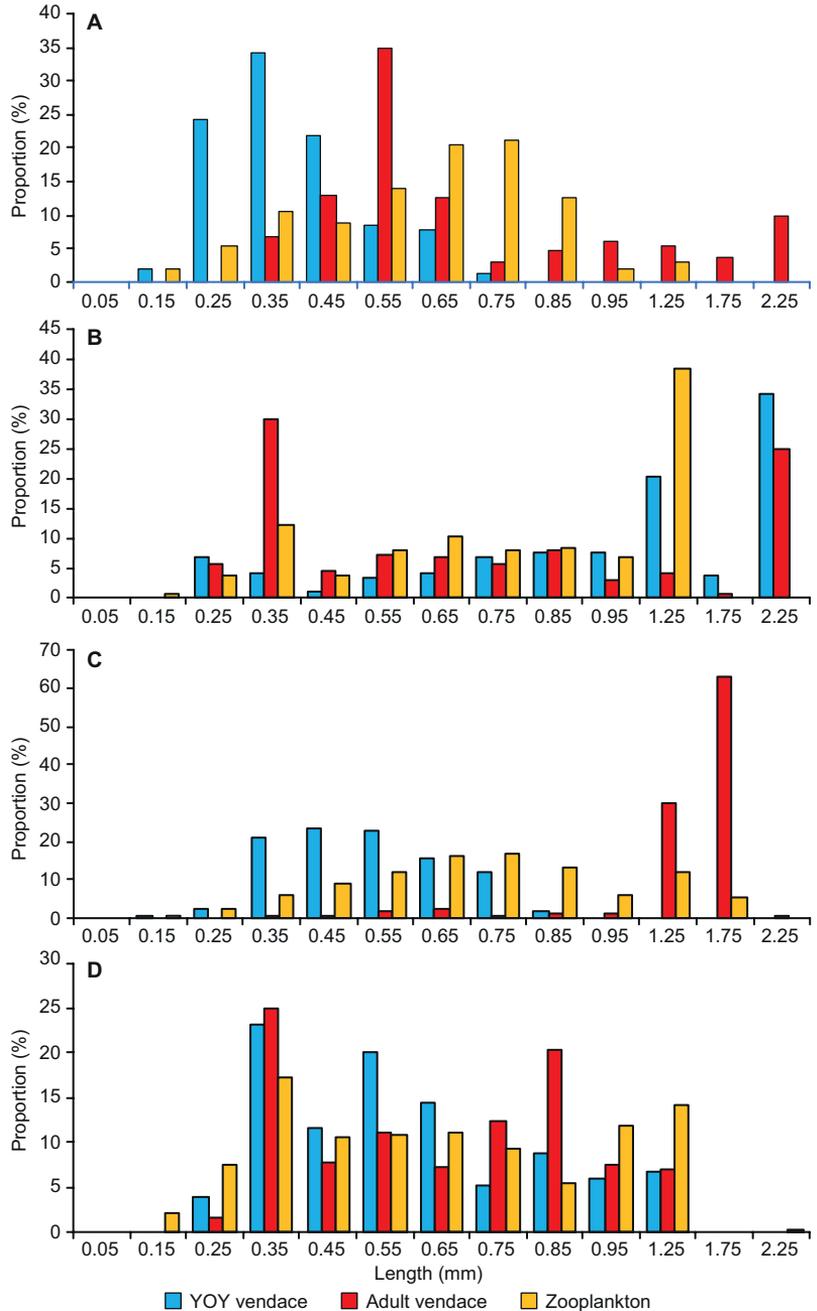


Fig. 3. Proportions of prey of different lengths in the guts of the YOY and adult vendace as well as the length distributions of zooplankton on the same dates in (A) May 1987, (B) August 1987, (C) May 1989, and (D) August 1989.

mid-July–mid-September 1987: $U = 21.5$, $n_0 = 8$, $n_1 = 12$, $p < 0.05$; for difference in relative gut contents: $U = 21$, $n_0 = 8$, $n_1 = 11$, $p < 0.10$; MW U -test in late June–mid-September 1989 for the difference in relative gut contents: $U = 3$, $n_0 = 6$, $n_1 = 5$, $p = 0.015$; for difference in stomach fullness: $U = 3$, $n_0 = 5$, $n_1 = 4$, $p = 0.056$), and

particularly the stomachs of adults were almost empty towards the autumn. This pattern was consistent with the abundance of zooplankton prey in early summer and the developing shortage of food in late summer and suggests that the YOY were more successful than adults in feeding on the mid- and late summer zooplankton.

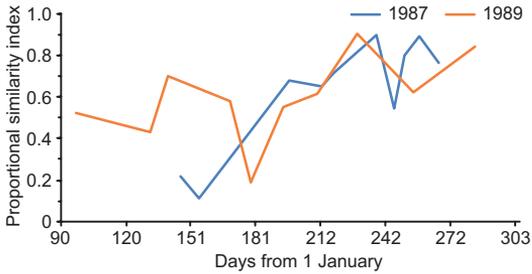


Fig. 4. Course of changes in the proportional similarity index (Renkonen 1938) between the taxonomic composition of the YOY and adult vendace stomach contents from spring to autumn in 1987 and 1989.

Consistent with this seasonality, growth of body mass of age 1+ fish significantly slowed down in late summer, while the fast linear body mass growth of the YOY continued from May–June to late October (Fig. 7). According to the segmented linear regression, in 1984 the adults started their early summer fast growth around 14 May and slowed down after 10 July, while in 1987 there was only one significant breakpoint in the adult growth curve: 16 June marked the start of slower growth which remained higher than in 1984 or 1989. In 1989, two significant breakpoints were recognised. Accelerated growth after the winter began on 29 April, while 6 July was the start of slower growth. For YOY, short-interval growth data were not available for 1984. In 1987 the first breakpoint on 9 July marked the start of fast growth which slowed down slightly after the second breakpoint on 26 August. In

1989 there were two breakpoints: 10 June and 21 October, defining a long period of fast growth.

Higher abundance of YOY was associated with slower first-summer growth (Fig. 8A) and weaker condition of the same cohort (Fig. 8B and Table 2), confirming that food resources were the limiting factor. YOY and adult condition were positively associated, suggesting that body condition indeed reflected the general food situation. The abundance of adult vendace did not affect significantly YOY or adult condition or growth (non-significant regressions not shown), not even in multiple regressions with both YOY and adults as independent factors. YOY condition increased significantly during the studied period. The YOY abundance affected negatively the adults: the second summer growth (Fig. 9A) and condition in the second winter (Fig. 9B) decreased with increasing abundance of co-occurring YOY vendace (Table 2). In the first cyclic period 1982–1989, the negative effect of YOY abundance on adult growth or condition was not significant, but it became significant in the later cyclic period 2000–2018, for which we had more data points. The negative relationship held also in the whole data set including the overfishing period (Fig. 9).

The low proportion of explained variation in adult growth was more than doubled when either of the temperature variables — the June–September average temperature, or the number of days when temperature exceeded 17 °C — was included with the YOY abundance as another independent variable (in both cases, both slopes

Table 3. Multiple linear regressions of adult vendace growth on the YOY abundance (year-class size) and water temperature for 1982–2018. Adult growth = instantaneous growth rate of adult vendace during second summer, YCS = concurrent year-class size (numbers of young-of-the-year of a year-class in autumn), T = June–September mean water temperature at 0–2 m depth, Days > 17 = the yearly number of days when the surface water temperature exceeded +17 °C.

Model 1: Adult growth = $a + b(\text{YCS}) + c(T)$							
Adjusted multiple R^2	df	Overall p		Coefficient	SE	p	
0.26	36	0.002	YCS	−0.023	0.008	0.0046	
			T	−0.103	0.039	0.014	
Model 2: Adult growth = $a + b(\text{YCS}) + c(\text{Days} > 17)$							
Adjusted multiple R^2	df	Overall p		Coefficient	SE	p	
0.27	36	0.002	YCS	−0.022	0.007	0.006	
			Days > 17	−0.006	0.002	0.012	

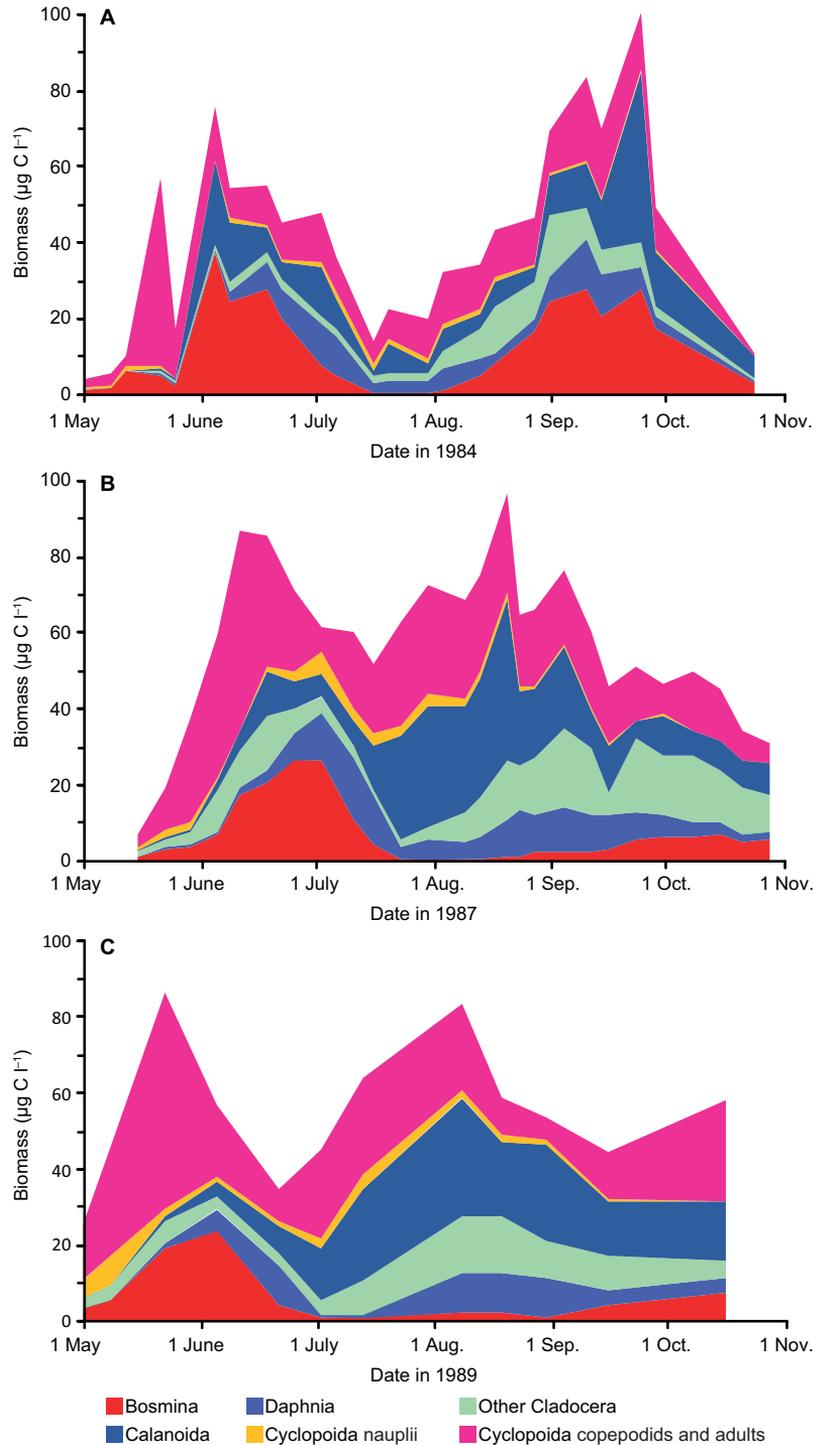


Fig. 5. Course of changes in the biomass of the main groups of crustacean zooplankton in Pyhäjärvi in (A) 1984, (B) 1987, and (C) 1989.

were negative) (Table 3). Even alone, both temperature variables affected negatively the 2nd summer growth of adults (Table 2).

Proportions of the age groups in the total population food consumption varied during summer (Fig. 10). In spring and early summer, the adults

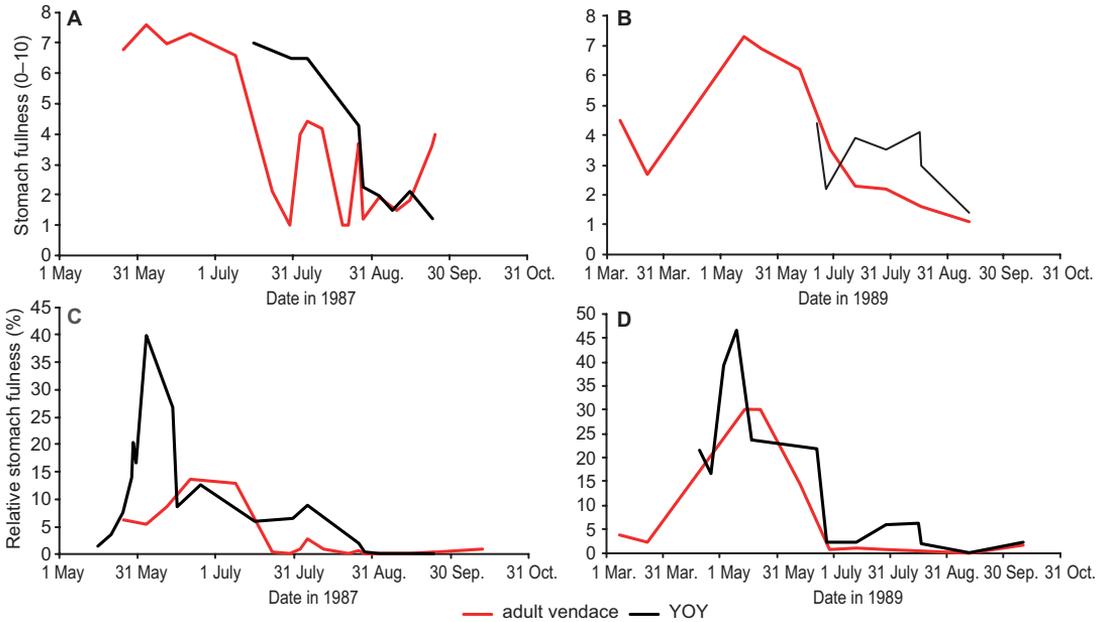


Fig. 6. Stomach fullness in YOY and older vendace estimated visually by dissection in (A) 1987 and (B) 1989. Relative stomach fullness as the ratio between the reconstructed stomach contents and fish mass (mg g^{-1} fresh mass) in (C) 1987 and (D) 1989.

were responsible for most of the total food consumption. Then the prey populations were increasing (Fig. 5) which means that there was no

shortage of food, even though other fish species were fed on the same prey (own unpubl. data). In late summer, YOY dominated the food consumption,

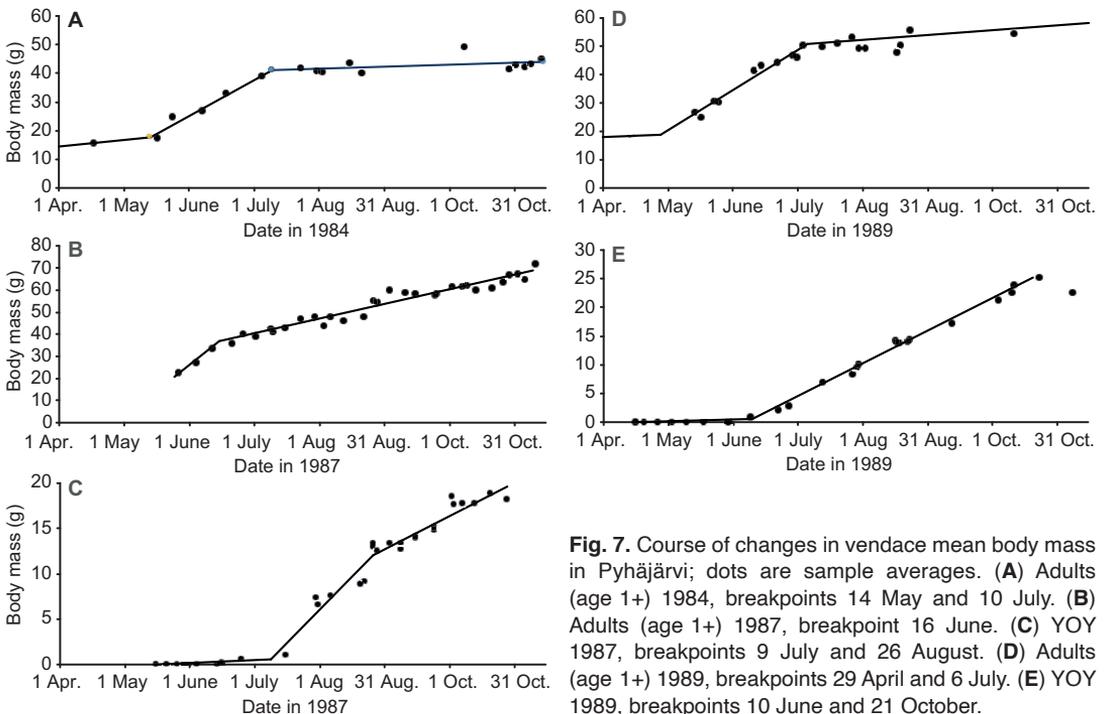


Fig. 7. Course of changes in vendace mean body mass in Pyhäjärvi; dots are sample averages. (A) Adults (age 1+) 1984, breakpoints 14 May and 10 July. (B) Adults (age 1+) 1987, breakpoint 16 June. (C) YOY 1987, breakpoints 9 July and 26 August. (D) Adults (age 1+) 1989, breakpoints 29 April and 6 July. (E) YOY 1989, breakpoints 10 June and 21 October.

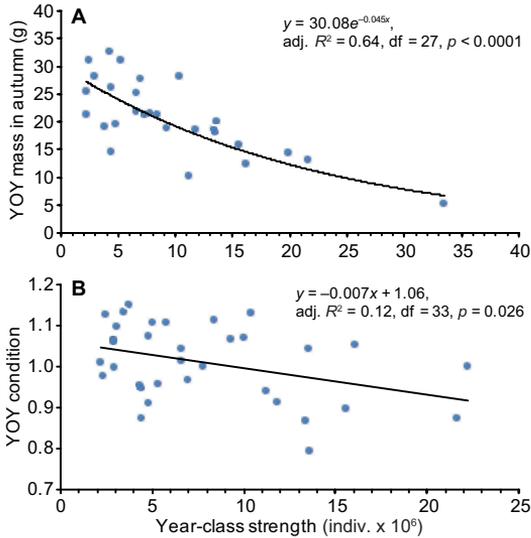


Fig. 8. (A) First-summer growth of vendace relative to the year-class size in 1979–2012 in Pyhäjärvi (only years when the decline of unit catches was significant and the DeLury method was used), and (B) YOY condition relative to their abundance in Pyhäjärvi.

and the lack of the second peak of *Bosmina* suggested that competition for food resources was likely at least in 1987 and 1989. The timing of the dominance shift from adults to YOY varied among years depending on the abundance of each age group (Fig. 10). In 1984, the new year-class was small, and an unusually high number of the 1983 year-class vendace had survived until the summer 1984. Consequently, the share of adults in the total food consumption remained high until early September, and the next year-class (1985) was strong. In 1987, the YOY dominance started earlier, and the next year-class (1988) was close to average. In 1989, the adult subpopulation was small due to heavy fishing mortality, and the YOY accounted for the majority of the total food consumption already since early June, and the next year-class (1990) was weak.

In the abundant-population period of 1982–1989, the YCS was inversely related to the previous year-class size (Table 2), but by far the best predictor of year-class size was the food consumption by the YOY in the previous year (Table 2), which is the most straightforward measure of competition. Yet, neither the previous YCS nor the food consumption by the YOY were significant predictors of YCS in 2000–2018 after

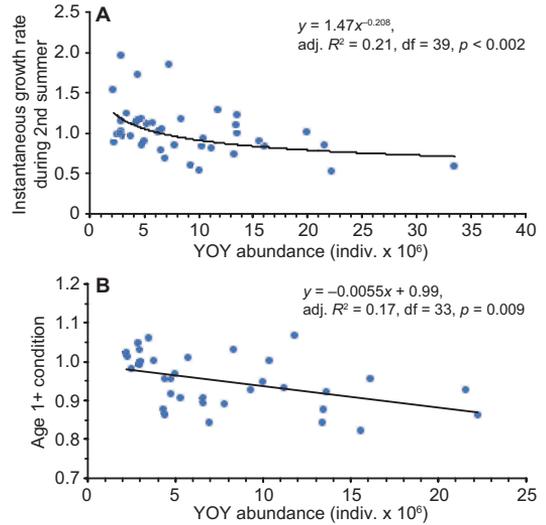


Fig. 9. (A) Adult growth in second summer vs. concurrent YOY abundance, and (B) adult condition in their second winter vs. YOY abundance previous summer.

the overfishing period (non-significant regressions not shown).

The fact that in the longer time series the YOY food consumption was no more a significant predictor of YCS, while the temperature attained significance, indicates that there was a change in the vendace year-class regulation between the early and late parts of the time series. Indeed, when the year-class sizes were plotted against the previous summer's YOY food consumption, the years 1982–1989 were all located on a linear slope decreasing with increasing consumption (Fig. 11). This is consistent with the hypothesis that asymmetric adult–juvenile competition was driving the two-year population cycle during the strong-stock period. In contrast, the year-class sizes in the 2000s remained smaller than expected from the 1982–1989 relationship, aggregating to the lower left part of the figure without showing any trend (Fig. 11). Four of the years, 2004, 2005, 2006 and 2015, however, stood apart from the general pattern of the 2000s and fitted the 1982–1989 relationship.

Discussion

Our analyses suggested that during the two-year cycle period in the 1980s, the YCS dynamics

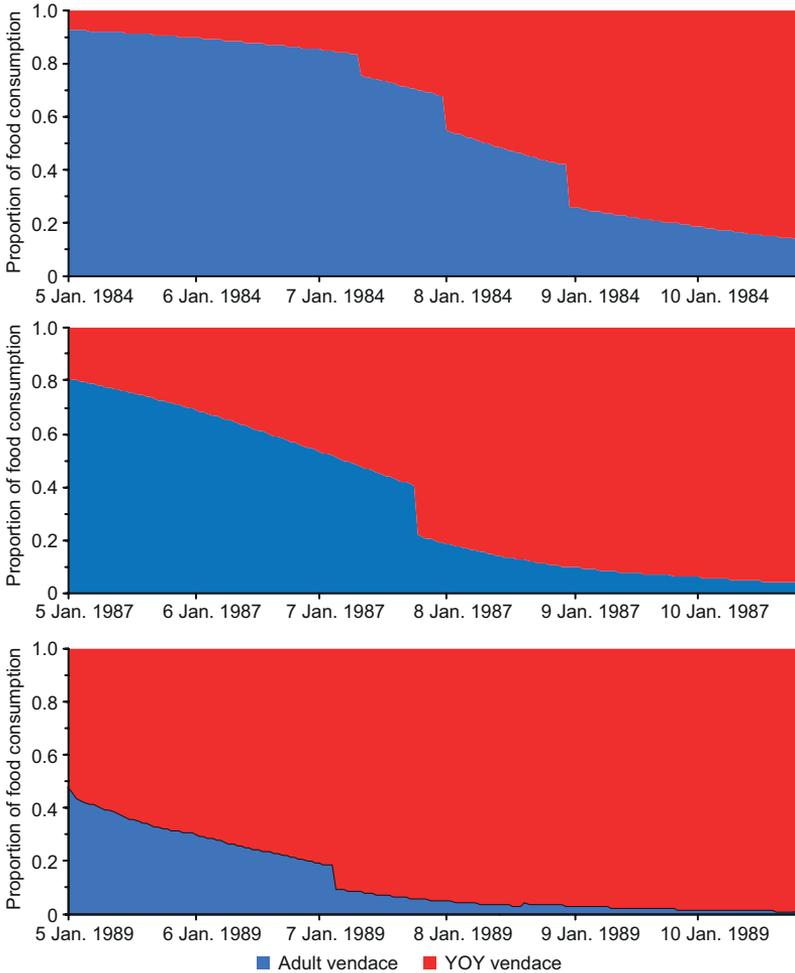


Fig. 10. Proportions of food consumed per day by the YOY and adult vendace in 1984, 1987 and 1989, as calculated with the FB4 bioenergetic model.

of the Pyhäjärvi vendace population was similar to that predicted by the asymmetric adult–juvenile competition hypothesis. According to

this hypothesis (Hamrin & Persson 1986), due to their lower metabolic requirements, and the ability to feed on smaller food items not available to larger fish, the small-sized YOY would have a competitive advantage over the larger adults under the prevailing conditions of low abundance and small average size of available zooplankton prey. The severe food competition between the YOY of a strong year-class and concurrent adult fish would then lead to slow growth and weakened condition of mature fish with deterioration in some essential quality components of the eggs or sperm. Reproductive products of poor quality would then further lead to a low survival of embryos or larvae, and thus less successful recruitment of the next year class.

According to this hypothesis, abundant YOY can indeed significantly decrease the abundance

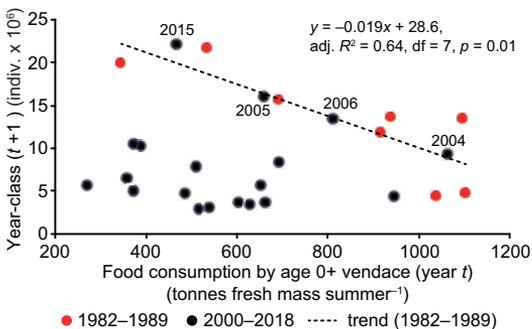


Fig. 11. Year-class strength in year $t + 1$ as a function of the food consumption by age 0+ vendace in year t . Years before (1982–1989) and after (2000–2018) the overfishing period are shown separately.

of their prey. In Pyhäjärvi, this was evident from the negative correlation between crustacean zooplankton biomass and vendace year-class strength (Sarvala *et al.* 1998). A comparison of different sub-areas of Pyhäjärvi in 1990 also showed that the spring development of zooplankton was depressed in areas with a high abundance of vendace larvae (Sarvala *et al.* 1994). In summer 1992 when YOY vendace were very abundant until late summer, the crustacean zooplankton was almost eliminated for two months from mid-June to mid-August (biomass $9 \mu\text{g C l}^{-1}$, compared with $50\text{--}200 \mu\text{g C l}^{-1}$ in 1987–1991; Helminen & Sarvala 1997). The next lowest average zooplankton biomass, $36 \mu\text{g C l}^{-1}$, was recorded in 2016 when the vendace year-class was very strong. Similar inverse relationships between pelagic crustaceans and vendace abundance were reported from the Swedish Lake Bolmen (Hamrin & Persson 1986).

In both Pyhäjärvi and Bolmen (Hamrin & Persson 1986), the diets of YOY and adult vendace were very similar, although the seasonal pattern differed between the lakes. In spring, gut contents analyses showed that the diets of the age groups differed in Pyhäjärvi, while in Bolmen the diets of both age groups were similar. In Pyhäjärvi, rotifers, cyclopoid nauplii and copepodids were important food items particularly for the vendace larvae, while in Bolmen, vendace were not found to feed on so small prey. This may be due to the lack of early spring samples from Bolmen, but the main reason was likely that in Pyhäjärvi cyclopoid *Cyclops kolensis* had its peak breeding season in spring, providing an abundant food source for vendace during the first weeks after the ice-out. In Bolmen a comparable small-sized but abundant early spring food resource was lacking. Although the differences in spring diet of YOY and adult vendace in Pyhäjärvi indicated that the YOY vendace were more successful than the adults in feeding on small food items, these early summer differences did not matter for the competition. According to the zooplankton data the prey populations were then increasing in spite of intense feeding by vendace and other planktivores, and thus there was no shortage of plankton food. Accordingly, the fastest growth of adults was always in early summer both in Pyhäjärvi and in Bolmen (Hamrin & Persson 1986). In contrast,

in late summer food was likely limiting, as the minimum crustacean zooplankton biomass usually prevailed from early July to mid-August (Helminen & Sarvala 1994b, Helminen *et al.* 1990), and both age groups were then feeding on the same taxa and size groups.

In deeper lakes, thermal stratification allows vertical segregation of the YOY and adult vendace, possibly resulting in different diets and alleviating competition between the age groups; this happened in July in Lake Bolmen (Hamrin & Persson 1986). Even in Pyhäjärvi, a partial vertical segregation of the YOY and adult vendace was documented by Sydänoja *et al.* (1995). In early summer, when the larvae were small and still concentrated along the shores, the adult vendace moved in the whole water column, although slightly closer to the bottom. In late summer, when the juveniles entered the open lake, the adults stayed deeper away from the surface. The YOY occupied the surface layers at night but migrated near the bottom in the daytime. In Pyhäjärvi, this partial habitat segregation does not, however, prevent food competition between the age groups, because the lake is mixing to the bottom and therefore the same zooplankton assemblage is available for fish near the surface and close to the bottom.

The diet information thus showed that food competition was likely to occur in late summer, and the higher stomach fullness of the YOY in late summer in Pyhäjärvi indicated that the YOY were having an advantage over the adults in this competition. This was confirmed by asymmetric relationships between age groups, with negative effects of YOY abundance on growth and body condition of adults but not *vice versa*. We also found that the effects of competition extended to the next year-class so that high YOY food consumption in the previous summer was associated with reduced year-class strength next year.

Similar results were obtained in three large Swedish lakes: while young vendace were not affected, strong year-classes of vendace negatively affected the body condition of the older fish and prevented the appearance of strong year-classes (Axenrot & Degerman 2016). As in Pyhäjärvi, the growth of the YOY vendace in Lake Bolmen was retarded by its own abundance, and the second-summer growth of the

next older cohort was even negative in late summer and autumn (Hamrin & Persson 1986).

The original asymmetric adult–juvenile competition hypothesis focused on the size-based asymmetries in the competitive abilities (Hamrin & Persson 1986). Similar outcomes may, however, arise simply from different abundances of the age groups. In Pyhäjärvi, because of an intense fishery, the population structure was simplified so that the sub-population biomass of YOY was an order of magnitude higher than that of the adult sub-population, which comprised practically only one year-class. Accordingly, in mid- and late summer and autumn, the youngest age group usually accounted for most of the total food consumption of the vendace population. Changes in the food consumption of adults were usually small compared with the total consumption. In other lakes with lower mortality rates, the adult age groups may comprise the majority of the total population biomass. Then they are responsible for most of the total food consumption and are expected to be dominant in food competition. Such cases were indeed documented by Sandlund *et al.* (1991), and as indicated by the situation in 1984, in exceptional years the dominance relationships may be reversed even in Pyhäjärvi.

The key factor determining the character of the population dynamics is the mortality rate (Townsend *et al.* 1990, Sandlund *et al.* 1991, Huusko & Hyvärinen 2005, Marjomäki *et al.* 2014). General models of population dynamics show that high mortality making the population practically semelparous is a prerequisite for population cycles, which disappear when mortality is low and several reproducing adult year-classes are present at the same time. In the Norwegian Lake Mjøsa, though, the adult-dominated vendace population with more than ten adult year-classes showed cycles with a period equalling the generation length (Sandlund *et al.* 1991). In the Norwegian cases described by Sandlund *et al.* (1991), in which there were numerous co-occurring adult age groups and where adults always dominated in the population biomass, the adults stopped somatic growth altogether after the first spawning. In Lake Inari in the northernmost Finland, the vendace population also comprises numerous co-occurring adult

year classes but these continue to grow (Salonen 2021). Unfortunately, the seasonality of growth has seldom been studied in vendace so that we do not know how the adult growth would change under less competitive conditions.

In practice, it seems impossible to decide from field data alone whether the abundance differences of the age groups are sufficient to produce cyclic population dynamics, or whether size-based differences in competitive ability are required. There have been some modelling attempts to elucidate the mechanisms involved. Simulations of the Pyhäjärvi vendace population with an individual-based model showed that to mimic the observed cyclicity, a negative effect of the abundance of the previous year-class on the next year recruitment was necessary (Helminen *et al.* 2002). Similar conclusions followed from an analysis of the population dynamics of the vendace in Lake Puulavesi with an age-structured population model (Marjomäki *et al.* 2014). Earlier modelling in Puulavesi suggested that both YOY and older vendace can suffer from inter- and intra-sub-population competition (Marjomäki & Kirjasniemi 1995). None of these modelling exercises, however, tackled the actual mechanism mediating the negative effects of the previous year-class to recruitment. Moreover, as noted by Marjomäki *et al.* (2014), even simple age-structured models can display the whole spectrum of dynamics from equilibrium to chaos, so that modelling is not a panacea.

Besides competition, other factors may contribute to the different seasonal growth patterns of the age groups in vendace. Adult vendace have a lower optimum temperature than the YOY (17 °C or less, and 19 °C, respectively; Tapaninen *et al.* 1998, Kangur *et al.* 2020). In stratified lakes, adult vendace may move to deeper areas with preferred temperature, but in the shallow and unstratified Pyhäjärvi, they cannot escape the higher temperatures and may become stressed during hot spells in summer. High temperature also accentuates food shortage. Such temperature effects may contribute to the cessation of growth in late summer. In 1987, water temperature exceeded the optimum for adult vendace for 22 days, but always by less than 1 °C, and the adult growth showed only minor slowing down in late summer. In

1984 and 1989, in contrast, water temperature exceeded the optimum for adult vendace on 47 and 68 days (with more than one degree on 30 and 46 days), and the adult growth showed almost total stop after early July. In whole period 1 (1982–1989), however, adult growth was not significantly related to temperature either alone or in combination with YOY food consumption. Physiological changes associated with the maturation of gonads might also affect the growth of adults in late summer and autumn, but the slowing of growth started before that period.

In the 1980s, the cessation of adult vendace growth in their second summer in Pyhäjärvi was confirmed from the characteristic structure of scales which usually showed in the middle of the second year's growth field a belt of densely spaced growth rings indicating a period of slow or wholly ceased growth. Without knowledge of this specific growth pattern, this zone could be interpreted as an annual winter ring, resulting in erroneous age determination. Such scale structure is not common in other Finnish vendace populations, suggesting that the competition between adults and juveniles might be less important in other lakes, and even in Pyhäjärvi it seems to be absent in recent years when productivity of the lake has considerably increased (Helminen & Sarvala 2021). Because temperatures have also increased, this observation contradicts the possible importance of temperature alone in the cessation of adult growth. But high-temperature tolerance might improve with increasing food availability.

Our analyses revealed that during our study period a major change occurred in the recruitment system of vendace. In the 1980s, all evidence consistently supported the hypothesis of asymmetric adult–juvenile competition as the main driver of year-class variation. The food consumption of YOY during summer, a measure quantifying the degree of competition, explained 64% of the variation in the abundance of the next year-class (Table 2).

In most years in the 2000s, however, the year-class sizes were smaller than expected from the 1982–1989 relationship (Fig. 11). Two differences between the 1980s and the 2000s may explain these observations. In the 1980s, intraspecific between-cohort competition largely

determined the year-class sizes. During the over-fishing period in the 1990s, intraspecific competition was relaxed because of the reduced population density of vendace. At the same time, however, the populations of other planktivorous fishes increased (Helminen & Sarvala 2021). Fish monitoring data suggest that the biomass of the whole planktivorous fish assemblage more than doubled from the 1980s to the 2010s, thus increasing competition and preventing the vendace population from returning to its earlier abundance. The year-classes of 2005, 2006 and 2007, which were predictable from the YOY food consumption in the summers 2004, 2005 and 2006 according to the 1982–1989 relationship, appeared in a period when the commercially unwanted fish populations in Pyhäjärvi were reduced by intensified fishery (Ventelä *et al.* 2007, 2011). The removal fishery in 2002–2006 was efficient enough to result in water quality improvement, and therefore it was also likely to relax the interspecific competition, allowing better vendace recruitment in those years.

The fourth deviation from the general pattern of the 2000s was the appearance of a very strong year-class 2016. This may be related to specific temperature conditions. The summer 2015 was cold which was favourable for adult vendace developing their gonads, likely resulting in good-quality eggs (Sarvala & Helminen 1995). This was followed in spring 2016 by fast warming of water after the hatching of larvae, which is known to promote larval growth and survival resulting in strong year-classes (Helminen & Sarvala 1994a).

The overall climate warming may be the second reason for the differences in vendace recruitment between the 1980s and the 2000s. Water temperature had significantly increased in the last decades (Table 2; Helminen & Sarvala 2021), increasing the number of days when temperature exceeded the optimum for adult vendace. In the unstratified Pyhäjärvi, the high temperatures may result in temperature stress which reduces adult growth and may lower the quality of eggs, thus contributing to smaller than expected year-classes. Although our data are consistent with this reasoning, uncertainty is caused by the fact that the temperature increased at the same time as eutrophication and other

planktivorous fishes. Moreover, the coefficients of determination for the temperature effects in the regressions were low, indicating that temperature was only one of numerous factors simultaneously affecting vendace recruitment.

Here, using data from Pyhäjärvi from the 1980s, we could show that intraspecific competition by young-of-the-year vendace reduced the feeding and growth of the adults preparing for reproduction. For the same period, we also showed that the extent of food consumption by the YOY was associated with the size of the next year-class, supporting the hypothesis that asymmetric adult–juvenile competition indeed can affect vendace recruitment and contribute to the maintenance of the two-year abundance cycle. But we also showed that in the 2000s, the intraspecific competition was no more the major factor determining vendace year-class dynamics, increased interspecific competition and temperature conditions likely being more important regulators.

Although the effects of intraspecific competition on the adults could be tracked up to the autumn before spawning, the actual mechanisms how the competitive effects are translated into the final numbers of the next generation remained unknown. Differences in egg numbers associated with the effects of competition were far too small to explain the two-year cyclicity (Sarvala *et al.* 1992). Similar situation was shown to prevail in northern Germany lakes (Wanke *et al.* 2017). Then, if the quantity of eggs is not the factor mediating effects of competition to recruitment, there have to be differences in egg quality. Unfortunately, detailed studies of egg quality are lacking. In our studies, we used the dry mass of eggs as one potential aggregate quality measure (Sarvala & Helminen 1995). A general expectation is that larger eggs produce larger larvae (Kamler 2005) which are likely to survive better through the critical three first weeks of the larval life of vendace (Viljanen 1988). In a short time series from Pyhäjärvi, we indeed found a positive correlation between the dry mass of eggs and the resulting numbers of recruits (Sarvala & Helminen 1995), but there was no clear link between competition and egg size; instead, egg size was inversely related to egg numbers and temperature. Further detailed studies are needed to reveal

the actual mechanisms of year-class regulation in vendace which may be more complicated than hitherto understood.

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Appendix. Revised bioenergetics model for juvenile vendace (*Coregonus albula*) courtesy of J. Karjalainen, University of Jyväskylä. An earlier bioenergetic model for vendace (Karjalainen *et al.* 1997a), using the exponential functions of the maximum consumption (C_{\max}) and routine metabolic rates (RMR), has been updated to include the optimum (CTO, RTO) and maximum (CTM, RTM) temperature parameters. The functions were fitted to the data from Karjalainen *et al.* (1995, 1997a) using a non-linear regression function (IBM SPSS statistics 26) applying the model structure of Kitchell *et al.* (1979) which is model 2 for both the maximum consumption and metabolic rate in the Fish Bioenergetics 4.0 (Deslauriers *et al.* 2017). The maximum temperature (lethal RTM) for metabolic rate was taken from Tapaninen *et al.* (1998) and the maximum temperature (CTM) for the maximum food consumption was adjusted according to information from Kangur *et al.* (2020). The coefficients for specific dynamic action, egestion and excretion were according to Karjalainen *et al.* (1997a).

Parameters of the revised bioenergetics model for vendace (*Coregonus albula*): non-linear metabolic functions of the maximum food consumption ($C_{\max} \pm \text{SE}$, $\text{g g}^{-1} 24 \text{ h}^{-1}$) and routine metabolic rate (RMR $\pm \text{SE}$, $\text{g(O}_2\text{)} \text{ g}^{-1} 24 \text{ h}^{-1}$) for juvenile (young-of-the-year) fish. Data from Karjalainen *et al.* (1995, 1997a).

Parameters	C_{\max}	RMR
Maximum temperature (CTM or RTM)	24	27 ¹
Optimum temperature (CTO or RTO)	19 ^{1,2}	23
Q_{10} rate (CQ or RQ)	1.584 \pm 0.259	1.743 \pm 0.167
Intercept of the mass function (CA or RA)	0.425 \pm 0.046	0.006 \pm 0.001
Slope of the mass function RB	-0.167 \pm 0.166	-0.151 \pm 0.025
R^2 of nonlinear regression	0.647	0.753
Number of cases	6	20
Specific dynamic action	0.17 ³	0.17 ³
Egestion	0.19 ³	0.19 ³
Excretion	0.07 ³	0.07 ³

¹⁾ Tapaninen *et al.* 1998, ²⁾ Kangur *et al.* 2020, ³⁾ Karjalainen *et al.* 1997a.