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Title: Vendace populations on the life table : between-lake variation and the association between early life and mature survival and growth

Year: 2024

Version: Published version

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Please cite the original version:

Marjomäki, T. J., Auvinen, H., Helminen, H., Huusko, A., Huuskonen, H., Hyvärinen, P., Jurvelius, J., Karels, A., Sarvala, J., Valkeajärvi, P., & Karjalainen, J. (2024). Vendace populations on the life table : between-lake variation and the association between early life and mature survival and growth. *International Journal of Limnology*, 60, Article 11.
<https://doi.org/10.1051/limn/2024011>

Vendace populations on the life table: between-lake variation and the association between early life and mature survival and growth

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Received: 18 January 2024; Accepted: 18 June 2024

Abstract – The vital rates related to reproduction and survival dictate the resistance and persistence of a population under perturbations. Freshwater fishes perform high levels of phenotypic plasticity thus these rates may differ widely between populations and temporally within a population. Knowledge of their ranges enables understanding the scope of population persistence and predicting the effects of environmental stressors. Time series of vendace (*Coregonus albula*) catch samples from 22 lakes were applied to estimate the lake-specific average length-at-age and survival in mature age groups (mS). Assuming an age-at-maturity of 2 yr and a constant length–fecundity relationship, survival from spawning to age 1 (firstS) and 2 (premS, prematurity survival) were estimated using a life table assuming a stable state. The average length at age 2 yr (L2) varied two-fold between populations, <100 – > 200 mm, and the estimated fecundity approximately eight-fold. Also, mS varied considerably, <10–70%a⁻¹. L2 and mS were positively associated. The premS estimate varied ~30-fold among lakes, <0.01 – > 0.2% per 2 yr, being highest in populations with low L2 and fecundity combined with low mS. The range of firstS estimate was even higher, 0.01–2%. This high between-lake variability seems to occur especially after hatching during the first summer. Its level is set by the factors external to the population, *e.g.*, the abundance of key predators. Persistence with low early life survival is possible because of the wide scope of compensation in the size- and fecundity-at-age and mS. Early life survival is expected to decrease due to climate change while the compensation has its limits, increasing the risk of local extinctions.

Keywords: Early life stages / global warming / life history / mortality / persistence / population regulation

1 Introduction

A sufficient level of net reproduction rate (*e.g.*, Krebs, 1985) is essential to the persistence of populations. In the long run, this rate depends on the combination of several vital rates: survival in prematurity and mature life stage as well as fecundity-at-age and quality of the sexual products. In fish populations, since the age of recruitment to fishing, average survival can be strongly reduced from its natural level by fishing mortality. To maintain population persistence, corresponding compensatory change is required in other vital rates.

On the other hand, the average level of early life survival is determined by various environmental factors of the ecosystem, *e.g.*, oxygen concentration at egg incubation sites and abundance of predators during egg, larval and juvenile stages. These factors may vary considerably between ecosystems. They are not temporally constant either, but may, in addition to their unpredictable short-term, interannual variation, change more permanently directionally due to ecosystem changes, *e.g.*, due to eutrophication or climate change, and/or perform autocorrelated variability dominated by long-period cycles, “coloured” spectrum variability (Steele and Henderson, 1984; Vasseur and Yodzis, 2004), *e.g.*, the density fluctuations of a long-lived key predator. To maintain persistence, the effects of these differences and changes on average early life survival

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must be successfully compensated at later life stages by phenotypic plasticity (Nussey *et al.*, 2007) and/or genotypic changes in some characteristics affecting the vital rates.

Vendace (*Coregonus albula*) is renowned for strong compensatory density-dependent variability of its vital rates in different life stages, *e.g.*, prerecruitment survival (Valtonen and Marjomäki, 1988; Auvinen, 1988, 1994; Helminen and Sarvala, 1994; Salmi and Huusko, 1995; Marjomäki, 2003), growth rate (Järvi, 1919, 1920; Lind, 1976; Hamrin and Persson, 1986; Viljanen, 1986; Auvinen, 1994; Marjomäki and Kirjasniemi, 1995; Salmi and Huusko 1995) and consequently age-specific fecundity (Karjalainen *et al.*, 2016) as well as post-recruit natural mortality (Marjomäki *et al.*, 2021a). Consequently, vendace populations are harnessed with a high level of resistance, the capacity to withstand disturbances, and resilience, the capacity to recover to its original state after perturbation (Westman 1978; Webster *et al.*, 1983), creating the scope of compensation against high levels of fishing mortality (but see Sarvala *et al.*, 2020) or changes in early life survival. The vital rates are thus strongly regulated by the actual population density at different life stages (*e.g.*, review by Marjomäki, 2003; Marjomäki *et al.*, 2014) within the preconditions set by the typical levels of the factors external to the vendace population within the ecosystem. These external factors are far from being constant temporally. In addition to strong inter-annual variability, they may induce permanent changes in the level of vendace population abundance or shifts between alternating low and high abundance regimes (*e.g.*, Valkeajärvi and Marjomäki, 2004). Some of these factors may even be partly regulated by vendace density, *e.g.*, perch population dynamics (*e.g.*, Marjomäki *et al.*, 2021a) or predation by brown trout (Hyvärinen and Huusko, 2006).

Data on the vital rates of vendace at the life stages that are potentially targeted by fishing, typically from the late juvenile stage at the age of 1 yr (from spawning to the autumn after the first growing season), are available from annual catch samples in many lakes. However, early life survival has been quantified to a lesser extent because its quantification requires data on population density indices, which are less often available. When the density data has been available, quantitative studies have often concentrated on analysing the form of spawner–recruit relationship, the level of density-dependent compensation and the level and causes of short-term, inter-annual variability in early life stage survival, *i.e.*, recruitment variability, typically under the assumption of temporally stable average spawner–recruit-relationship (*e.g.*, Valtonen and Marjomäki, 1988; Viljanen, 1988a, b; Auvinen, 1988, 1994; Marjomäki, 2003; Marjomäki *et al.*, 2014). Much less attention has been paid to the average level of early life survival itself and its periodical variability within a lake (Marjomäki *et al.*, 2021a) or differences in average early age survival between different lakes (Karjalainen *et al.*, 2000, Marjomäki 2003). Relevant questions in this context are to what extent the differences in average early-life survival are or could be compensated by the later-life vital rates and what is their scope of compensation that determines the scope of persistence of the population. Marjomäki *et al.* (2021a) applied retrospective life table analysis to quantify and compare the vital rates in one vendace population between periods of very high and low abundance regimes, finding a large difference in

average prematuration survival and consequently large compensatory changes in length- and fecundity-at-age as well as survival at the mature life stage. The present study aims to expand that analysis to several vendace populations, quantifying the average level of their vital rates and in some populations even separately for periods of very sparse and abundant vendace population as well as the association between the rates. The geographical range of the lake ecosystems reaches from 60° 30' N, in the southern edge of the boreal zone, to over 66° N, close to the Polar Circle, their trophy from ultra oligotrophic to meso-eutrophic and their vendace population abundance from sparse to abundant, providing a possibility to estimate the full scope of the variability of vendace vital rates, especially its seldom studied early life survival.

2 Material and methods

The vendace data were collected from 22 lakes or basins of large lakes (Fig. 1, Tab. 1) in Finland (one lake located presently in Russia but part of Finland during the data collection). The lakes were selected based on the sufficient length of the time series, the minimum being 9 yr. The oldest data were collected in the first part of the 20th century, 1908 at the earliest, but most of the data stem from the period from the 1970s to the 2000s (Tab. 2), the newest from 2022.

Random samples have been collected from vendace catches either close to spawning in autumn, typically October, and/or during winter fishing season (under ice seining, typically from January to April). In most lakes, samples were collected from seine catches but, in some lakes consistently and in some lakes occasionally from trawl and gill nets (Tab. 2). All samples were accepted for the analysis. In different years they may stem from different fishers and basins within the lake which may affect the lake-specific variance of the variables (*e.g.*, Lind, 1976), but this is considered negligible compared to the actual between-year variability. The mesh size of the gear was usually set so that the size and age structure of the catch represented well those in the population, except for the youngest fish (age 1) which may have been underrepresented because of being very small in some years (especially trawl catches), and in autumn because of not gathering in the spawning and fishing sites in the same proportion as the mature individuals. In Lake Vesijärvi, the samples were partly selected in 3 yr, thus not thoroughly random (Järvi, 1947). Still, they were accepted for the analysis because the average survival estimate was not very sensitive to data from those years.

Fish were measured for their total length (L, mm), except for the samples by Järvi (1942a, b, 1947) where fork length (FL) was measured. FL was converted to total length by multiplying it by 1.1 (*e.g.*, Keränen and Lind, 1973; Czerwiejewski and Filipiak, 2002; Fiszler *et al.*, 2012). The age was determined from scales and the sex of mature individuals was visually determined.

For each lake, the grand average over the annual estimates of average length was calculated for each age group. For Lake Pyhäselkä, back-calculated length was used instead of the observed because several samples were not collected at the end of the growing season. The oldest age groups, typically 4–6 yr



Fig. 1. Study lakes.

onwards, with a low number of annual estimates (typically < 5) were omitted, because these were mostly available only for slow-growing abundant year classes. The [von Bertalanffy \(1938\)](#) growth function was fitted to the age-specific grand averages of length starting from age 1 by the iterative nonlinear least squares method assuming normally distributed residuals. The lake-specific parameter estimates are given in [Table 2](#).

The prominent fluctuations in the population abundance ([Tab. 2](#)) were interpreted roughly based on the annual average length of 2 yr old individuals (L2). The growth of vendace is strongly density-dependent (*e.g.*, [Järvi 1919, 1920; Viljanen, 1986](#)) and the growth of both the young-of-the-year and older subpopulations is affected by the density of both ([Marjomäki and Kirjasniemi, 1995](#)). Thus, the temporal variability of L2

bears information on the density, relative to lake-specific resources, of the whole population during a preceding 2 yr period. The rough growth-based interpretation of density fluctuations is in good agreement with vendace density indices in the lakes where these are available (*e.g.*, [Helminen *et al.*, 1993; Marjomäki and Kirjasniemi, 1995; Salmi and Huusko 1995; Valkeajärvi *et al.*, 2012; Marjomäki *et al.*, 2021a, b](#)).

The age of maturity for every female vendace was assumed to be 2 yr (*e.g.*, [Järvi, 1919, 1920; Lind, 1976, Viljanen, 1986; Karjalainen *et al.*, 2016](#)). It was assumed that a general average length-at-age (L_i)–fecundity-at-age (f_i , eggs per individual) equation,

$$f_i = 0.000583L_i^{3.0626},$$

Table 1. The morphometrics of the study lakes, range of their total phosphorus concentration (Tot. P) and colour content for the water sampling period. For the period, the first and the last year of water samples are given, but sampling did not occur necessarily every year. The selected water samples were taken during winter and from the middle of the water column, if available. N.A. = not available, * Values from a much more recent period than the vendace study period.

Lake	Area km ²	Ave. depth m	Max. depth m	Tot. P µl ⁻¹	Color content mg Ptl ⁻¹	Period, depth
Yli-Kitka	237	6.6	41	2–10	5–20	1974–1992, 15 m
Kiitämö	19	6.7	22	4	5	1973, 10 m
Kirpistö	21	N.A.	17	6	14	1973, 1 m, 10 m
Kuusamo	47	3.4	18	6–17	15–30	1979–1991, 10 m
Muojärvi	55	5.4	36	5–10	10–20	1976–1992, 10 m
Kostonjärvi	44	5.1	17	8–28	35–59	1979–1987, 5 m
Kerojärvi	21	N.A.	17	8–11	29–40	1973–1985, 1 m
Imijärvi	32	5.6	24	4–18	15–60	1973–1992, 10 m
Oulu	887	7.6	35	5–28	30–80	1974–2006, 15 m
Ylä-Keitele	79	8.8	66	3–10	30–50	1991–2004*, 10 m
Keski-Keitele	327	6.6	33	5	25–38	1965–1970*, 10 m
Southern Konnevesi	122	12.5	57	4–7	15–30	1984–2009, 25 m
Onkamo	32	3.6	12	6–21	10–25	1980–2012, 1 m
Pyhäselkä	361	8.8	67	5–11	50–110	1990–2009, 30–34 m
Puruvesi	416	8.8	61	3–8	5–10	1973–2017, 15 m
Pyhäjärvi SE Finland	248	7.8	27	3–7	5–20	1984–2017, 13–15 m
Puula	331	9.2	62	2–5	10–32	1984–2022, 25 m
Päijänne, Tehinselkä	250	>16.0	61	7–11	24–40	1981–1991, 25 m
Southern Saimaa	621	8.4	70	4–10	25–45	2001–2021, 20 m
Vesijärvi	108	6.1	40	20–25	10–20	1967–1970*, 15 m
Pyhäjärvi SW Finland	155	5.5	26	10–34	10–40	1978–2021, 15 m
Pyhäjärvi Kar. Isthm.	68	N.A.	30	N.A.	N.A.	

applies to all populations (data from [Karjalainen *et al.*, 2016](#); [Marjomäki *et al.*, 2021a](#)). It was further assumed that 50% of the eggs were females. The average fecundity-at-age of female eggs was estimated for each population using the von Bertalanffy model -predicted average length-at-age.

For each lake, the age distributions of all seasonal (autumn and/or winter) vendace samples were standardised to percentages and the age-specific percentages were averaged. Then, these seasonal percentages were averaged over the study period. These grand average percentages were logarithmised and the constant total mortality was estimated using linear regression,

$$\ln(p_i) = a + -Zi,$$

$$mS = \exp(-Z),$$

where p_i = age-specific grand average percentage, Z = instantaneous total mortality (a^{-1}), i = age, minimum 2 yr, and mS = annual proportional survival for mature age groups, age 2 and older). In Southern Konnevesi, age group 2 was not used in the estimation due to low catchability ([Marjomäki *et al.*, 2021a](#)). The oldest age groups with only a few observations and $p_i < 1\%$ (typically from age 4–6 onwards, as for length above) were omitted to minimise bias (see [Marjomäki *et al.*, 2023](#)) in the mortality estimate.

Assuming a population steady state, the prematurity survival (premS) from fertilisation to first spawning in the second autumn at age 2 yr was estimated for each population

based on the fecundity-at-age estimates of female eggs, and constant annual survival in mature age groups (mS) using a static life table (e.g., [Krebs, 1985](#)) as described in detail by [Marjomäki *et al.* \(2021a\)](#). Further, assuming that the survival for the second year of life equals mS , the first-year survival (firstS) was estimated by,

$$\text{firstS} = \text{premS}/mS.$$

A comparison between the life-table-based steady-state estimates of first-year mortality (Z) and direct estimates from certain lakes is presented in [Appendix 1](#).

Lakes Southern Konnevesi and Puruvesi experienced long both very abundant and extremely sparse population periods. For those lakes, all parameters were estimated separately for these extreme states, in addition to the whole study period, to illustrate the within-lake differences in population parameters during different abundance regimes. Details for Southern Konnevesi are given in [Marjomäki *et al.* \(2021a\)](#).

3 Results

The whole study period average length at age 2 yr (L_2) for different populations had a very wide range, from less than 100 mm in Yli-Kitka to over 200 mm in Pyhäjärvi southwest Finland ([Fig. 2a](#)), the average being 141 mm. L_2 was lower in the northernmost populations than in the southernmost ones. However, the lake-specific range of annual average length at age 2 yr was quite wide as well in many lakes, e.g., Kerojärvi,

Table 2. The vendace sampling period (L = length, mS = mature survival) and reference to more detailed material and methods, gear (S = seine, G = gill net, T = trawl), the von Bertalanffy growth equation parameter estimates and trends in population abundance as interpreted from size at age (+ = increasing, − = decreasing, ! = strongly). *varia* = Keränen and Lind, 1973, 1975; Ellonen and Lind, 1974; Hyrynkangas and Lind, 1976; Hanski and Lind, 1977, 1978, 1980, 1984, 1985, 1987 a, b, c, 1988, 1989, 1990, 1991, 1992; Myllylä and Lind, 1982, 1983; Piekkola and Lind, 1980.

Lake	Period (samples)	Data	Gear	Von bertalanffy equation Lmax	K	t0	Trend
Yli-Kitka	1973–1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	234	0.13	−2.22	no
Kiitämä	1974–1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	160	0.47	−0.71	+ −
Kirpistö	1973–1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	157	0.55	−0.48	no
Kuusamo	1973–1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	178	0.75	−0.21	−
Muonijärvi	1973–1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	140	0.56	−0.54	−
Kostonjärvi	1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	179	0.30	−1.07	−!
Kerojärvi	1976–1978, 1980–1992	<i>varia</i> ; Salmi and Huusko, 1995	S	229	0.25	−1.11	−!
Imijärvi	1973–1978, 1980–1990, 1992	<i>varia</i> ; Salmi and Huusko, 1995	S	198	0.26	−1.12	+ −!
Oulu	1973–1984, 1986–2017	<i>varia</i> ; Salmi and Huusko, 1995	S, T	166	0.57	−0.53	+!
Ylä-Keitele	1908, 1911–1941	Järvi, 1942a	S	169	0.57	−0.55	− + −
Keski-Keitele	1908, 1917, 1919–1931, 1941	Järvi, 1942a	S	165	0.45	−0.71	no
Southern Konnevesi	1984–2009	Marjomäki <i>et al.</i> , 2021a	S, G	182	0.80	−0.07	−! +!
Onkamo	1980–1993, 1995–2012	Auvinen <i>et al.</i> , 2000, unpubl.	S	205	0.50	−0.82	no
Pyhäselkä	1989–1990, 1992–2009	A. Huuskonen, unpubl.	T	197	0.67	−0.39	+!
Puuvеси	1973–1990, 1992–2017	<i>varia</i> ; Auvinen, unpubl.	S	480	0.08	−2.78	−! +!
Pyhäjärvi SE Finland	1978–1992, 1994–2000, 2004, 2008, 2010, 2014	Auvinen <i>et al.</i> , 1987, unpubl.	S	229	0.54	−0.55	−!
Puula	1984–2022	Marjomäki <i>et al.</i> , 2014, unpubl.	S	152	0.72	−0.30	no
Päijänne, Tehinselkä	L 1981–2009, mS 1984–2010	Valkeajärvi <i>et al.</i> , 2012	T	233	0.84	0.06	no
Southern Saimaa	2001–2021	A. Karels, unpubl.	T	206	0.52	−0.29	+!
Vesijärvi	1914–1916, 1919, 1920, 1929, 1940, 1943, 1945	Järvi, 1947	S, G?	237	0.97	0.15	−
Pyhäjärvi SW Finland	1978, 1980–2020	Sarvala <i>et al.</i> , 2020	S	288	0.46	−0.57	− + − +
Pyhäjärvi Karelian Isthmus	1913–1917, 1919, 1920, 1922–1938	Järvi, 1942b	S, G	231	0.61	−0.10	− +

Irnijärvi, S. Konnevesi, Puruvesi and Pyhäjärvi southeast Finland, that have presumably (Tab. 2) experienced wide density variation during the study period. In S. Konnevesi and Puruvesi, abundant and sparse population regime-specific averages of L2 differed as much as over 70 mm (Fig. 2a).

Assuming a general length–fecundity relationship for all populations, the whole time-series average fecundity at age 2 varied almost by an order of magnitude between lakes from 370 female eggs in Yli-Kitka with the lowest L2 to 3300 female eggs in Pyhäjärvi SW Finland with the highest L2 (Fig. 2a). The difference in average fecundity at age 2 was 4–5-fold between the abundant and sparse population regimes in Puruvesi and S. Konnevesi.

Also, the average proportional annual survival of mature fish (mS) varied considerably between lakes (Fig. 2b) being lowest in intensively fished populations of Pyhäjärvi SW Finland and certain Northern Finnish lakes and highest in the fast-growing population of Vesijärvi with very sparse population and hence low fishing mortality. The geometric mean of lake-specific mS estimates was 27%. There was also a considerable difference in mS between the abundant population regime with commercial vendace fishing and the sparse regime with very low fishing mortality in Puruvesi and S. Konnevesi. The general association between lake-specific mS and growth-related variables L2 (Fig. 3) and K was not a decreasing one, but rather increasing (Spearman; mS vs. L2, $r = 0.41$, $p = 0.056$; mS vs. K, $r = 0.56$, $p = 0.007$).

The life-table-based estimate of average premature S (two first years, premS) required for population steady state varied between lakes enormously from as high as over 0.2% in Yli-Kitka to less than 0.01% in Vesijärvi, a 30-fold difference (Fig. 4a), the geometric mean being 0.05% (mean $Z = 7.5$). The within-lake differences between the sparse and abundant regimes in S. Konnevesi and Puruvesi were high as well, about an order of magnitude. The range of the survival estimate for the first year (firstS, from spawning to the first autumn before the onset of any considerable fishing mortality) was even higher, more than two orders of magnitude, from about 2% in Yli-Kitka to as low as about 0.01% in Vesijärvi, (Fig. 4b). The geometric mean first-year survival was 0.2% (mean $Z = 6.2$).

The large between-population variability in premS required for population steady state for certain fixed mS (Fig. 4) results from large differences in size and thus fecundity between populations. While the mS estimates *e.g.*, in Päijänne (Tehinselkä), S. Konnevesi and Puula were at a similar level, much lower premS is required for steady state in Päijänne than in the latter two because of the large size-at-age (Fig. 5). The difference in size-at-age also is the reason for the premS required in Pyhäjärvi SW Finland being much less than in Yli-Kitka even though the mS in Pyhäjärvi is lower than that in Yli-Kitka (Figs. 4a and 5). The proportional variability in prematuration S due to differences in mature survival at certain fixed L2 was considerable, too (Fig. 5).

4 Discussion

The quite exceptional density-dependent variability in growth that is not limited to early life stages only, and thus fecundity (*e.g.*, Lind, 1976; Viljanen, 1986; Helminen *et al.*, 1993; Marjomäki and Kirjasniemi, 1995; Marjomäki, 2003;

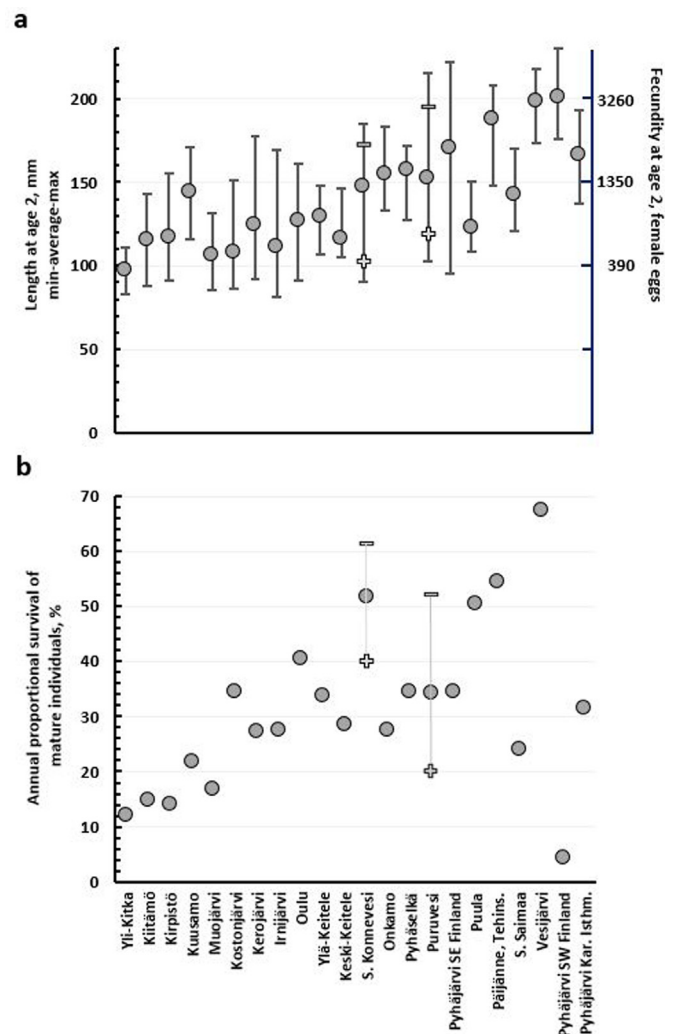


Fig. 2. a) The von Bertalanffy model -calculated average length at maturity (age 2, L2) and fecundity (female eggs) estimates for different vendace populations put in the order of their location from north to south. The bars show the minimum and maximum annual values. b) The constant survival estimates for mature (2 yr and older, mS) vendace. The symbols + and - show the averages for abundant and sparse population regimes, respectively, in Lake S. Konnevesi and Puruvesi.

Karjalainen *et al.*, 2016; Marjomäki *et al.*, 2021a) facilitates a wide scope of compensation within a typical vendace population. Compensatory reserve is defined as the “sum of all density-dependent phenomena that affect the size and growth of individuals in a population” (Goodyear, 1980), referring mostly to the level of intra-specific food competition, and it reflects the degree of population resilience to perturbations (Youn, 2017). Because of considerably smaller size-at-age at higher densities and therefore likely higher predation mortality (Marjomäki *et al.*, 2021a), some scope of compensation seems also to take place in the natural mortality, adding to the capacity for resilience. The scope of

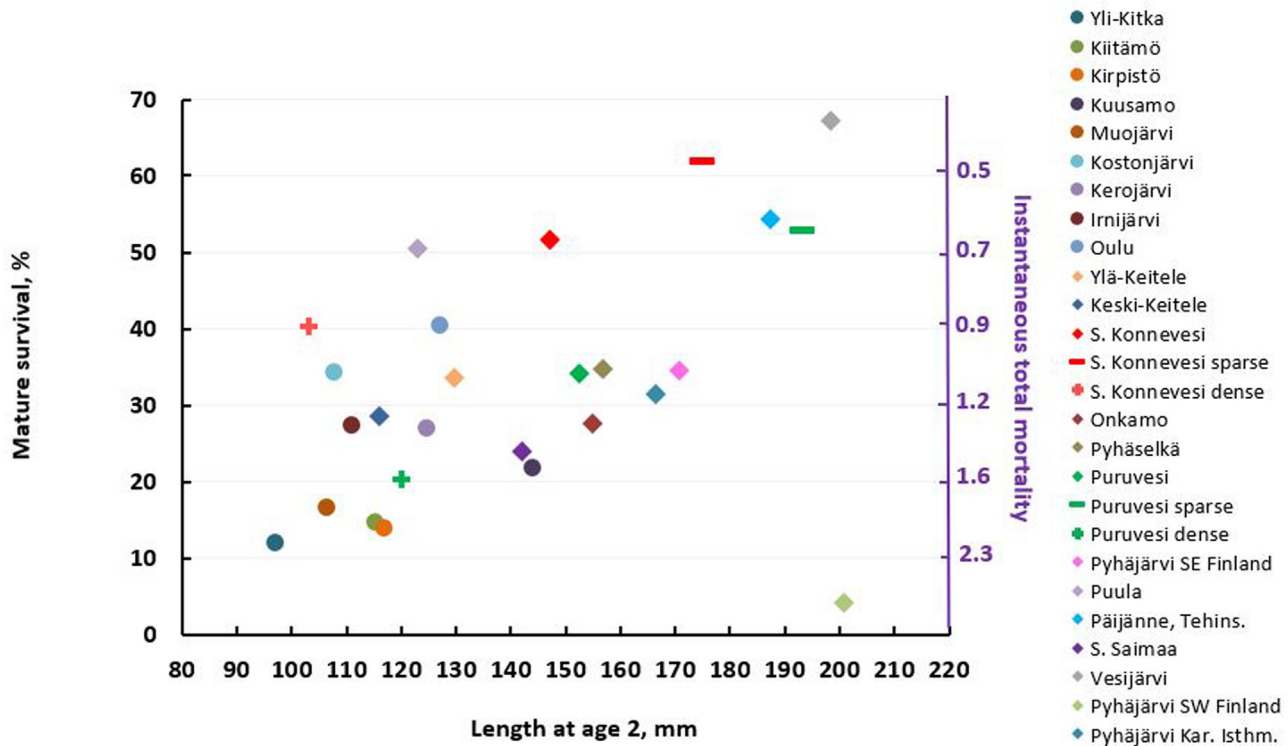


Fig. 3. The lake-specific von Bertalanffy model -predicted average length at age 2 (L2) vs. the annual constant mature survival (mS) and instantaneous mortality (Z, purple axis) estimate for different vendace populations.

compensation in a population is further facilitated by the considerable compensatory density dependence of first-year survival in vendace (*e.g.*, Auvinen 1988; Valtonen and Marjomäki, 1988; Viljanen, 1988a; Helminen and Sarvala, 1994; Salmi and Huusko, 1995; Helminen *et al.*, 1997; Marjomäki, 2003, 2004; Marjomäki *et al.*, 2014). All these phenomena make the vendace populations very resilient, resistant, and consequently persistent towards high and variable mortality at different life stages, as well as fishing mortality, the typical cause of human-induced perturbation.

The average size-at-age is an important variable for determining the average fecundity-at-age and consequently, the estimate of prematurity survival (premS) from a lifetable. In our data, the average size at age 2 yr (L2) decreased with the increase in the latitude. This can be partly because of the latitudinal trend in the temperature and the length of the growing season. Lind (1976) and Viljanen (1986 review and references therein) noted the same but suggested that differences in lake productivity and vendace population density are also responsible for the observed latitudinal differences. The same conclusion holds for our data. The phosphorus concentration in the southern lakes was typically higher than that in the northern lakes. Further, the vendace density in the northern Finnish lakes has very likely been higher in proportion to resources than that in the southern Finnish lakes. The severe prolonged vendace population decline at the turn of the 1980s and 1990s, thus within our study period in many lakes, occurred in central and southern Finland while the populations in northern Finland remained abundant (Valkeajärvi *et al.*, 2002). Growth of vendace equally fast as the fastest in southern Finland has also been recorded in

northern Finland: in the oligotrophic–mesotrophic Lake Iso-Venejärvi, 80 km north of our northernmost study lake, Yli-Kitka, the average length at age 2 was about 200 mm (Alanne, 2004). A long day length with a higher level of illumination at night, facilitating feeding and a lower, and thus more suitable epilimnion temperature during the summer, may compensate for the lower temperature sum during the growing season and food production in higher latitudes to a certain extent.

One might expect based on the general theory of exploitation that the relationship between mature survival (mS) and length-at-age is a decreasing one: the lower the average survival, the lower the average population density and the faster the growth, at least within a population. This was not the case in our data of average lake-specific mature S and L2 estimates from several lakes but rather the opposite. The relationship and causality appear more complicated: First, the combination of high mature S and large L2 is typical for the population experiencing a sparse population regime, the reason for which is a period of very low prematurity S induced by environmental factors, *e.g.*, sparse periods in S. Konnevesi (Marjomäki *et al.*, 2021a), Puruvesi and Vesijärvi. During the sparse population regime, the fishing mortality is very low because vendace fishing is not profitable, while the natural adult mortality may also be low due to the large size of fish (Marjomäki *et al.*, 2021a), consequently high mature S. Simultaneously, the strongly density-dependent size-at-age and fecundity are maximal due to minimal intra-population competition for food. Together high mature S and length-at-age, the compensatory capacity being in full use, can compensate for the low prematurity S and facilitate the persistence of the population. But there is a maximum for the

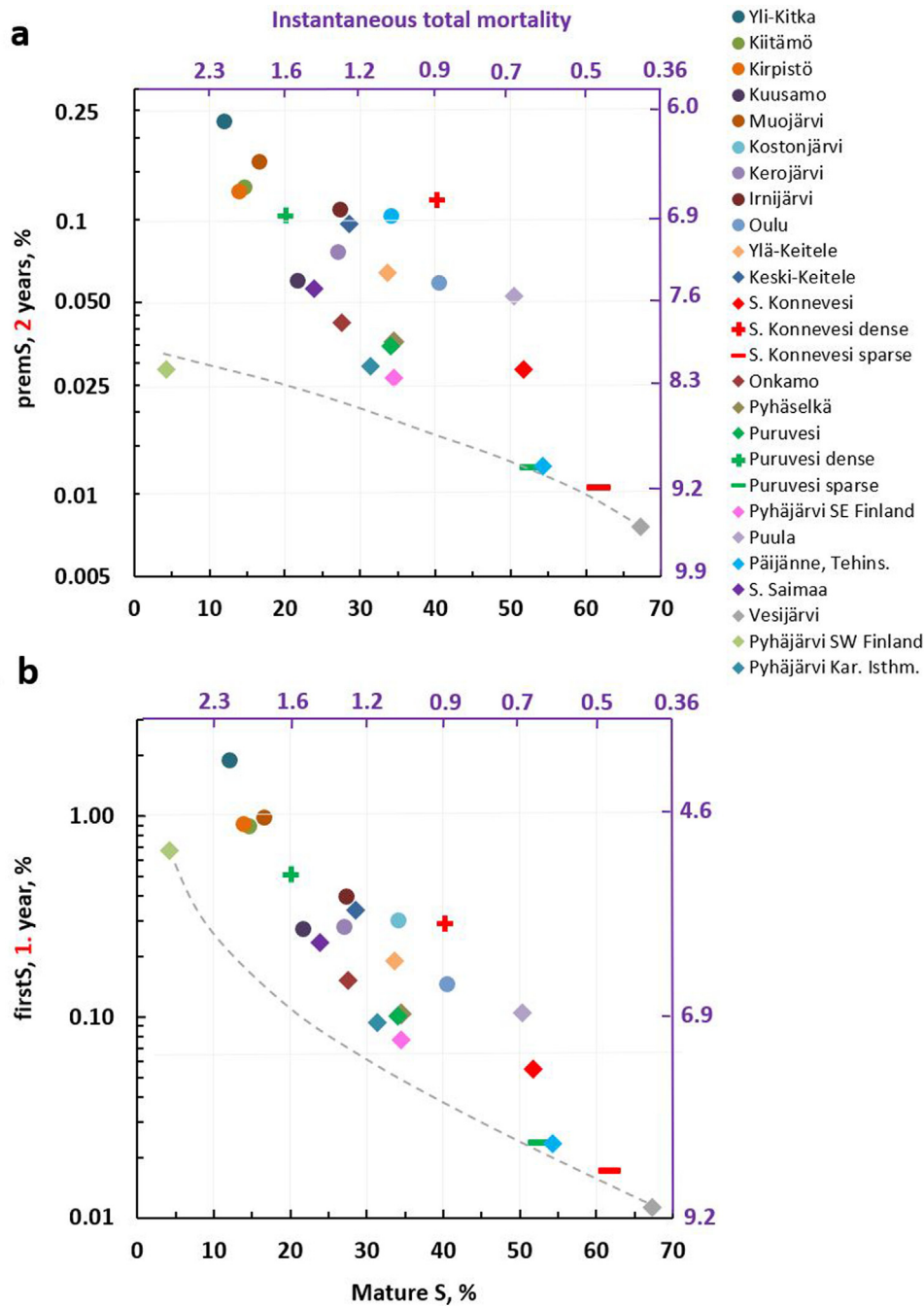


Fig. 4. a) The average prematurity survival estimates (premS, the first 2 yr) b) the average first-year survival estimates (firstS) vs. constant mature survival estimates for different vendace populations and those during the abundant (+) and sparse (−) population regimes in lakes Southern Konnevesi and Puruvesi. The grey dashed lines are the premS and firstS that would be required for a stable state in different levels of mature survival (mS) for Lake Vesijärvi vendace with the observed fast growth.

compensatory capacity of growth, fecundity and mature survival, and the lake ecosystems with even lower prematuration S, dictated by environmental variables, cannot appear in the data because their vendace populations must have gone extinct if ever established in the first place.

At the other extreme, very low mature S, mostly due to the very intensive fishing starting already in the first winter has kept the density of Pyhäjärvi SW Finland vendace at so low

level that very fast growth was possible (Sarvala *et al.*, 2020). Meso-eutrophy of this lake and its location in southern Finland may also have facilitated fast growth there. However, during a period of very intensive fishing (extremely low mature S, << 10%) with simultaneous poor environmental conditions for newly hatched larvae (lower than average prematuration S), the population collapsed as there was no compensatory reserve available in the growth and fecundity of fish.

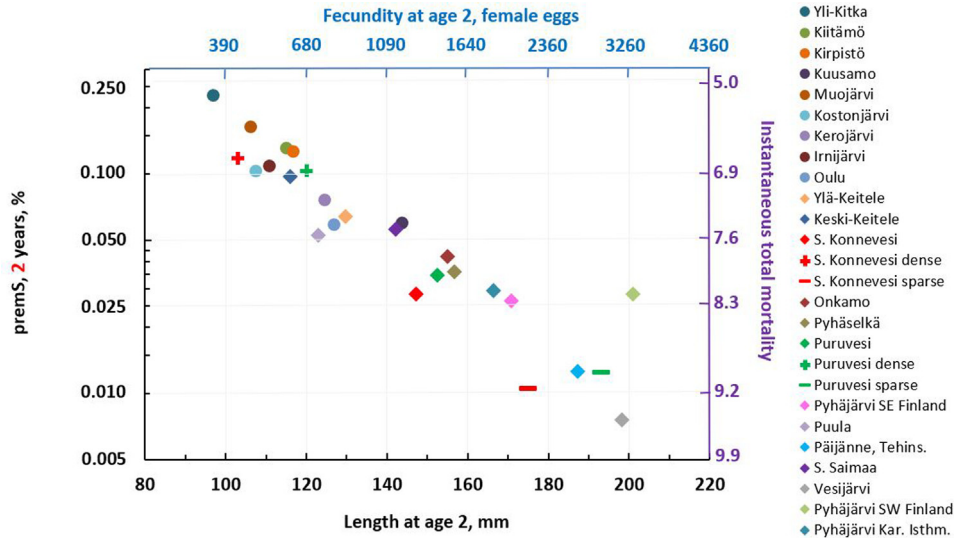


Fig. 5. The average prematurity survival (prems, the first 2 yr) estimate vs. the average length (L2) and fecundity at age 2 for different vendace populations.

On the contrary, in some northern Finnish populations, the density stayed at a high level throughout the study period and the size-at-age was extremely small despite the low average mature S caused by mortality due to intensive winter seining. According to the life-table analysis, the first-year survival must have been very high in those lakes to ensure population stability in the situation of small size-at-age, and consequently low fecundity, due to the high density of young fish. The very high first-year S estimates in these ecosystems thus imply exceptionally favourable environmental conditions for early life survival. Again, if a vendace population had failed to compensate for low mature S with high prematurity S, the abundance would have declined, size-at-age increased and mature S increased due to a decrease in fishing mortality and the population would have appeared in a different position in our figures.

The very high prematurity S and first-year S with very slow growth is even more surprising when put into the context of intra-population competition. It has been hypothesised for vendace populations that high density, thus low per capita food resources, induces severe competition which leads to low quality of sexual products and consequently low per capita reproductive rate (Hamrin and Persson, 1986), thus low first-year S and prematurity S. This hypothesis was developed originally to explain the 2 yr cyclicity in a vendace population by food competition between young-of-the-year and maturing fish at their second year of life; the maturing fish would suffer from food competition by younger fish. If the hypothesis was extrapolated to limited food resources on a wider scale than one population, one would predict that in the northern lakes with the poorest growth, the average prematurity S and first-year S is more likely low than among the highest, and in that case, the observed very low mature S would not be possible. The hypothesis was supported by the findings from a comparative study by Karjalainen *et al.* (2016): the Lake Pyhäjärvi SW Finland vendace with fast growth produced larger eggs with higher survival than those from very abundant

S. Konnevesi. It can be thus deduced that the external factors in the ecosystem must have set the general level of early life survival, and this level varies very much between ecosystems.

An important piece of knowledge in assessing the importance of different external factors in setting the general level of early-life survival of vendace is how the high first-year mortality is distributed temporally to the periods before and after the hatching of larvae. So far there is not much information to assess this because quantitative lake-specific data on the variables required – population fecundity, number of hatching larvae and number of recruits at age 1 – are scarce. However, in recent years a new method to estimate population fecundity based on quantitative egg sampling has been developed (Karjalainen *et al.*, 2021). The first results from Lake S. Konnevesi imply about 3–4% survival of the eggs from spawning to hatching (including the non-fertilised eggs) and the level was very similar in two consecutive years (Karjalainen *et al.*, 2021). Earlier, Viljanen (1988) estimated that the winter survival in Lake Suomunjärvi was about 2–4%. The average winter survival estimated from population fecundity and larval density in spring in Puula has been about 1% (data from Marjomäki *et al.*, 2014; <https://www.jyu.fi/en/research-groups/coregonid-fish-research>). On the other hand, in Pyhäjärvi SW Finland, the average post-hatching survival for the first growing season was about 15–30% (Helminen *et al.*, 1997; Karjalainen *et al.*, 2000). Based on that and the life-table-estimated average first-year S 0.6% there, the average pre-hatching winter survival estimate is at the level 2–5%, corresponding with the level that Helminen *et al.* (1997) estimated directly from population fecundity and larval density in spring. In lakes Puruvesi and Onkamo, the average post-hatching survival estimates were about 5 and 3% (Karjalainen *et al.*, 2000), and the life-table-estimated average of first-year S about 0.1 and 0.15% (this study), leading to pre-hatching survival estimates of about 2% and 5%, respectively. A similar level was found in *in situ* cage experiments (Zawisza and Backiel, 1970; Zuromska, 1982). Thus, all estimates imply that

the average level of winter survival (from spawning to hatching) is at a level of a few percent. Still, our estimates, based on the data that is temporally not fully matching, are broad order magnitude estimates as both the pre- and post-hatching survival may have high inter-annual variability (e.g., Viljanen, 1988b; Karjalainen *et al.*, 2000; Marjomäki *et al.*, 2021b).

The mortality of vendace eggs in winter has been linked to predation (Zawisza and Backiel, 1970; Shemeikka *et al.*, 1978; Zuońska, 1982; Karjalainen *et al.*, 2021) by macro-invertebrates and certain fish species such as ruffe (*Gymnocephalus cernua* L.), perch (*Perca fluviatilis* L.) and whitefish (*C. lavaretus* L.), pathological microbes (Zawisza and Backiel, 1970) and poor oxygen conditions (Zawisza and Backiel, 1970; Koho, 2002). In Yli-Kitka, where the first-year S was the highest, both the winter seine yield per unit effort (Salmi and Huusko, 1995) and the larval densities (Karjalainen *et al.*, 2000) were at the same level as in other lakes (Karjalainen *et al.*, 2000; <https://www.jyu.fi/en/research-groups/coregonid-fish-research>), not implying to extraordinarily high winter survival there. The high first-year S in Yli-Kitka and some other northernmost lakes thus implies high post-hatching survival during the first summer, despite the slowest growth of fish. The level of the first summer survival of vendace has been suggested to be regulated by the characteristics of the fish community, especially the abundance of the predators of young-of-the-year vendace (Lind, 1976; Koho, 2002), such as young perch (Auvinen, 1994; Helminen *et al.*, 1997; Valkeajärvi and Marjomäki, 2004) which may be linked to abundant and sparse regime shifts typical of vendace (Valkeajärvi and Marjomäki, 2004; Marjomäki *et al.*, 2021a). Salmi and Huusko (1995) suggested that the general level of abundance of the vendace population is lake-specific and likely connected to the composition of the fish community. They suggested that the reason for the low abundance of vendace in Lake Kuusamo in comparison to other lakes nearby was the differences in their fish communities. Also, our estimates of first-year S and prematuration S were low in Lake Kuusamo. Unfortunately, standardised monitoring of fish community structure and species abundances has been lacking during the study period. So, no comparable lake-specific predator abundance indices are available. Generally, it is known that the abundance of percids correlates positively with temperature as well as with an increase in productivity from oligotrophy to mesotrophy (e.g., Leach *et al.*, 1977; Ranta and Lindström, 1993; Voutilainen and Huuskonen, 2010; Linløkken, 2023). The fish communities in subarctic lakes are predicted to shift from salmonid to percid dominance with climate change and benthic macroinvertebrate density is predicted to increase during the shift from oligotrophy to mesotrophy (Hayden *et al.*, 2017). These trends predict lower early life survival of vendace, which must be compensated by an increase in size- and fecundity-at-age and/or decrease in later life natural and/or fishing mortality. Despite the high flexibility of the vendace growth and fecundity, the scope of compensation is ultimately limited and diminishing capacity for fishing mortality and even local extinctions of vendace populations are expected to occur.

Our study concerns mostly lakes that had active vendace fisheries during the study period because only the populations with regular fishing can provide catches that can be sampled

for population monitoring. Also, the long-term monitoring of these populations may have been motivated by their value as a resource. Thus, the vital rates estimated in this study may not represent a typical/average vendace population. The studied populations are likely generally more productive than an average vendace population and their prematuration S therefore perhaps an overestimate of the average. In addition, the prematuration S and first-year S were estimated under the assumption of population steady state, while the density of some populations had a trend during the study period ("Trend" in Tab. 2). In those cases, the estimated prematuration S and first-year S do not represent the actual steady state level in those populations (see Appendix 1). These facts must be considered when lending parameter values from this study to any assessment of the sustainable yield potential for the vendace populations with limited prior knowledge about the vital rates.

The data covers vendace populations with a life history that is typical in Finnish lakes: the age of first spawning is categorically 2 yr, and the spawning occurs in late autumn–early winter. However, there is considerable flexibility within the species in these characteristics. Later maturation occurs regularly in certain lakes, e.g., Lake Mjøsa and Osensjøen (Sandlund, 1992) and Inari (Amundsen *et al.*, 2012). Later maturation must be compensated for by higher annual prematurity survival to meet population stability. Interestingly, no plasticity at the age-at-maturity between two and 3 yr has been reported in the lakes in the present study despite the very high variability in density and growth both within and between lakes. Quite conversely, in the fast-growing population of Pyhäjärvi SW Finland, a small proportion of 1 yr old females have been reported to produce eggs (Sarvala *et al.*, 1992a; Sarvala and Helminen, 1995). However, the egg size was only about half of that of older individuals, and in a laboratory experiment (Karjalainen *et al.*, 2016) no fertilisation was observed for the eggs of 1 yr old females. Their contribution to reproduction is probably negligible.

Typically, spawning of vendace occurs in late autumn, October–November, but in some lakes spawning in winter even as late as late April has been detected (e.g., Svärdsön, 1957; Airaksinen, 1968; Vuorinen, 1980 and references therein; Mehner *et al.*, 2021), mostly allopatrically but in some lakes sympatrically with autumn spawning. The late-spawning populations have been reported to have differences in morphology, spawning depth and genome in comparison to the autumn spawning population (Airaksinen, 1968; Svärdsön, 1979; Vuorinen, 1980). Vuorinen (1980) has suggested that delayed spawning is an adaptation to higher-than-normal winter temperatures in these lakes. In Lake Kajojärvi, eggs are much larger than those of typical autumn spawners (Eronen and Lahti, 1988; Lahti 1991). Low-latitude coregonine populations spawn frequently in early winter or in spring and adjusting the time of spawning has been suggested to be an efficient tactic in warming climate in high-latitude populations also (Stewart *et al.*, 2021). Adjusted spawning time with associated changes in egg size is a good example of providing a solution to the environmental constraint that can set the survival of eggs laid in autumn at a level that is insufficient for persistence, if there is genetic variability in the population to facilitate that trait.

Contrary to our simplifying assumption of a constant length–fecundity relationship for all populations, some variability in egg weight, gonad weight and fecundity-at-size has been observed within populations between years and between populations in general (e.g., Zawisza and Backiel, 1970; Auvinen, 1988; Sarvala *et al.*, 1992a, 1992b; Sarvala and Helminen, 1995; Marjomäki, 2003; Böhn *et al.*, 2004). However, these differences are proportionally small: typical deviation of the lake- and year-specific average fecundity-at-length from the mean is only some tens of percent at maximum, transferring into the same order magnitude of proportional difference in first-year S and premature S estimates. This is negligible in comparison to the about an order of magnitude (1000%) difference in the age-specific fecundity and estimated premS between sparse and abundant regimes within a population, let alone between sparse and abundant populations in different lakes.

5 Conclusions

The present data suggest that the average level of early life survival in different vendace populations is highly variable and set by the factors external to the vendace population, such as the abundance of key predators. The long-term variability of these external factors may also induce changes in the general level of survival and consequently decade-long regime shifts in the vendace population abundance. The wide variability of early life survival without extinction is possible because of the exceptional scope of density-dependent compensation in size- and fecundity-at-age and survival at all life stages of vendace. The early life survival is expected to decrease in the future due to the consequences of climate warming. Further understanding of the pre- and post-hatching survival, their between-population and between-year variability and causes of mortality can be gained by simultaneous quantitative long-term monitoring of vendace population fecundity, population density at the larval stage and later life stages, accompanied by the monitoring of the fish and benthic macroinvertebrate communities as well as physical and chemical characteristics of several selected reference lakes representing different latitudes and lake types.

Appendix 1

Comparison between life table estimates and direct estimates of first-year mortality

The availability of yield per unit effort (YPUE) data from fishing records and catch samples enables direct estimation of annual and time-series average of the first year (from spawning to one summer old next autumn or winter) survival and mortality for lakes Yli-Kitka, Kiitämö, Kirpistö, Kuusamo, Muojärvi, Kostonjärvi, Kerojärvi, Irnijärvi, Oulu and Puula. For Puula, data for direct estimation was available for years 1984–2007 but it was assumed comparable with the longer period for the life table estimate. These fishery-provided data and methods are described in the references given in Table 2 and Marjomäki (2004) and Marjomäki *et al.* (2014).

The index of population fecundity in year y was very roughly estimated by,

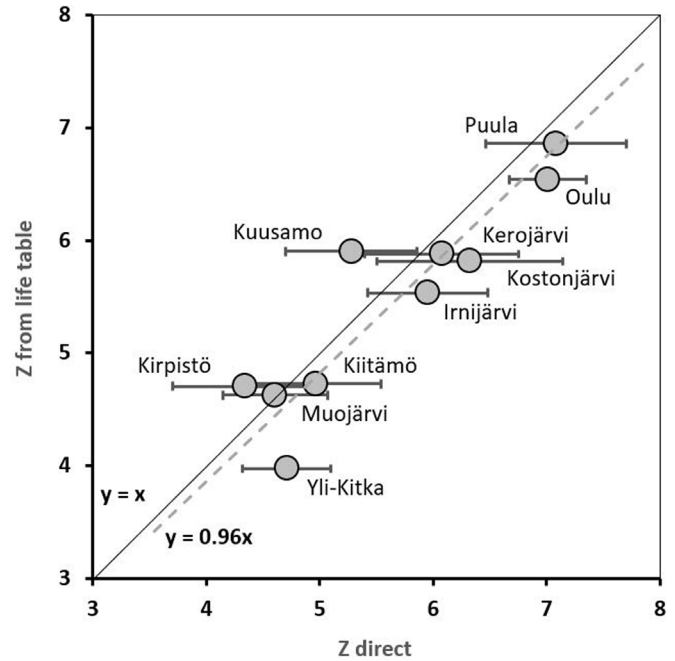


Fig. A1. Direct and life-table-based estimates of the average instantaneous total mortality (Z) during the first year of life for vendace in certain Finnish lakes. The error bars indicate the 95% confidence interval.

$$PF_y = YPUE_y * pAdult_y * pFemale * Fg,$$

where,

YPUE = yield (g) per unit of effort in autumn or winter following the spawning

pAdult = proportion of ≥ 2 yr old individuals of the weight of catch samples

pFemale = assumed proportion of females in yield of ≥ 2 yr old individuals, 60%.

This rough assumption is based on the typical increasing female dominance in adult individuals (Marjomäki *et al.*, 2023) and on the higher length-specific average weight of females than that of males during spawning.

Fg = number of eggs per 1 g fresh weight of adult female vendace; 114 eggs g^{-1} assumed (Karjalainen *et al.*, 2021)

The index of 1 yr old vendace recruitment in the following autumn or winter was estimated by,

$$R_{y+1} = YPUE_{y+1} / w_{y+1} * p_{y+1},$$

where,

w = average weight (g) of individuals in catch samples

p1 = proportion of 1 yr old individuals in catch samples.

The instantaneous total mortality was estimated for the first year of life by

$$Z_{y-y+1} = -\ln(R_{y+1} / PF_y),$$

The average Z and its 95% confidence interval (CI) were estimated for the whole time series available. The CI was

estimated based on the assumption that the density function for average Z obeys Normal distribution (Central Limit Theorem).

The life-table-based estimates of average Z were generally of the same order of magnitude as the average estimated directly from the density indices (Fig. A1). The linear regression between them did not differ significantly ($p > 0.05$) from the line $y=x$. The interannual variability of Z within the lake was very wide and therefore the uncertainty of the direct estimate of average Z was considerable as indicated by a wide 95% confidence interval. The uncertainty is further increased by the unquantifiable uncertainties and possible bias in the variables p_{Female} and F_g which are not incorporated in CI.

Auvinen (1988) estimated directly the first year S in Pyhäjärvi SE Finland. Those estimates had strong between-year variability but were of the same order of magnitude as our estimate for a considerably longer period.

The difference between the direct and life-table average estimates may stem *e.g.*, from the following:

- The recruitment index may be underestimated, especially in the lakes and years with very small 1 yr old fish that may escape through the cod end of the gear. This bias leads to an overestimation of first-year mortality in direct estimation. This is especially likely in the lakes with the poorest growth: Yli-Kitka, Muojärvi and Kostonjärvi.
- In such lakes the life-table-based first year mortality estimate ($Z_{0-1}=Z_{0-2}-Z_{1-2}$) may be an under-estimate. It was assumed that the second-year mortality (Z_{1-2}) is equal to later-life mortality but if the catchability during the second year of life is lower, at least the fishing mortality may be lower than that for later life. Consequently, Z_{1-2} may be overestimated and Z_{0-1} underestimated.
- Life table estimate is based on the assumption of population steady state, but in reality, the population density may have had *e.g.*, a decreasing trend, thus there must have been a higher Z_{0-1} (lower survival) than the steady-state-based estimate, especially Irnijärvi, Kostonjärvi and Kerojärvi (see the trend in Tab. 2).
- Biases in average mature mortality and fecundity (assumed constant at length) will bias the life-table-based mortality estimates. The mature mortality estimate was based on the age distribution of both sexes combined, while the mortality of females is generally lower than that of males (Marjomäki *et al.*, 2023). However, because of considerable mature mortality, the proportion of old fish is typically low. Thus, there should not be a serious bias due to that.

Acknowledgements

We owe our gratitude to the fishers who collected and the persons who processed the samples, especially the various University of Oulu students guided by Mikko Keränen, Tuomo Ellonen, Sisko Hyrynkanas, Kari Hanski, Sisko Piekkola and Markku Myllylä over the years. Special thanks to Suomen Kalakirjasto (The Fishlibrary of Finland, <https://www.suomenkalakirjasto.fi>) for rescuing and delivering the published data. This study is dedicated to Toivo H. Järvi and Esko A. Lind who set the example of viewing vendace populations from a comparative perspective.

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Cite this article as: Marjomäki TJ, Auvinen H, Helminen H, Huusko A, Huuskonen H, Hyvärinen P, Jurvelius J, Karels A, Sarvala J, Valkeajärvi P, Karjalainen J. 2024. Vendace populations on the life table: between-lake variation and the association between early life and mature survival and growth. *Int. J. Lim.* 60: 11: