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Lifting the vendace, *Coregonus albula*, on the life table: survival, growth and reproduction in different life-stages during very high and low abundance regimes

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We analyzed the variability in vendace population parameters in the context of a life table. Parameters related to growth, fecundity and survival were estimated for post-recruitment (age > 1 growing season) life stages of Lake Southern Konnevesi vendace in both very high and low population abundance regimes. Pre-recruitment survival producing population stability was then determined. We found a very strong compensatory density dependence in growth, fecundity and survival: during low abundance, a lifetime reproductive output of a female was almost 20 times that of the abundant regime. To maintain the low abundance regime, pre-recruitment survival must counterbalance it by decreasing to a very low level. Potential drivers of high variability in pre-recruit survival and potential for depensation, Allee effect, are discussed, as well as the implications of the results on fisheries management and risk of extinction due to anthropogenic stressors such as global warming or extensive predator stocking.

Introduction

Vendace populations are characterised by strong inter-annual fluctuations (Järvi 1920). In addition to short-term variability, this also manifests itself in longer, even more than a decade-long, very low and very high abundance regimes (Järvi 1942), with abundance difference of more than two orders of magnitude (e.g. Valkeajärvi & Marjomäki 2013). The high variability in abundance is reflected in the vendace population parameters.

Exceptionally high compensatory density-dependent variability in size-at-age, thus also in growth rate of an individual fish, has been doc-

umented in many Finnish lakes (e.g. Järvi 1920, Viljanen 1986, Marjomäki & Kirjasniemi 1995, Valkeajärvi & Bagge 1995, Karjalainen *et al.* 2016). Consequently, the age-specific fecundity is strongly compensatory density-dependent, too. However, the age at maturation (two growing seasons), average size-specific fecundity and egg quality remain virtually constant despite high variability in abundance (Karjalainen *et al.* 2016, comparison of four Finnish lakes with very different population abundance and growth), and these do not appear to contribute significantly to population regulation. Nevertheless, the rate of reproduction is strongly compensatorily density-dependent in vendace populations. Both the

high biomass of spawners (thus high population fecundity) and the high density of the previous year-class suppress the per capita reproduction rate of the spawners by suppressing pre-recruitment survival of their offspring (Helminen *et al.* 1993, Marjomäki *et al.* 2014). However, not much is known about the density dependence of pre-recruitment survival at a very low population level as the precision of population indices at that stage is very poor.

The density dependence of fishing mortality can take diverse forms depending on the gear, the state of professionalism of fishing, the economic aspects, etc. (*see e.g.* “Sustainable operation window” in Marjomäki 2003), and compensatory density-dependent catchability due to compensatory density-dependent growth (Järvi 1914–1915, Marjomäki 2005, Wanke *et al.* 2021). However, in Finnish vendace fisheries at a very low population level, fishing has virtually ceased, so the density dependence has been eventually compensatory then (*e.g.* Marjomäki *et al.* 1995). To date, the natural mortality of vendace after recruitment has rarely even been estimated, let alone its density dependence analyzed.

The combination of strong compensatory changes in individual growth and consequently age-specific fecundity, in per capita reproduction rate and most likely also in post-recruit mortality should facilitate the strong resilience of vendace population, more specifically rapid recovery from occasional low abundance situations. This has been documented to have happened, *e.g.* in Lake Puulavesi, central Finland (Marjomäki *et al.* 2014). In this respect, the occasionally seen prolonged stagnation of population density at a low abundance regime (Järvi 1942, Haakana *et al.* 2007, Valkeajärvi & Marjomäki 2013) even in several lakes simultaneously is unexpected and suggests a more complex system of population regulation. Predator–prey-relationship between vendace and perch (*Perca fluviatilis*) has been proposed to be one possible explanation for a long low abundance regime (Valkeajärvi & Marjomäki 2004) and even a compensatory functional response of predation to prey density has been proposed (Heikinheimo 2001). Contrary to the above, Haakana *et al.* (2007) suggested that the effect of perch on natural mortality of young

of the year vendace in Lake Höytiäinen was marginal during a low abundance period.

In this study, we quantified the combinations of vendace population parameters during very high and very low abundance regimes in Lake Southern Konnevesi, Finland, to reveal the maximum potential for density-dependent compensation and thus resilience. In particular, our goal was to quantify the pre-recruitment survival required to maintain the low abundance regime despite the above-described substantial compensatory mechanisms in the post-recruitment stage. We applied static life table analysis (*e.g.* Krebs 1985), assuming an equilibrium and two life stages: pre-recruitment (age less than 1 growing season) and post-recruitment consisting of older immature and mature (age at least two growing seasons). Finally, we put certain anthropogenic stressors of vendace populations, fishing, predator stocking and climate warming, into the context of life table analysis to demonstrate their effects on resilience and persistence in northern European lakes.

Material and methods

Lake Southern Konnevesi (for short S Konnevesi) is located in central Finland (62°40'N, 26°30'E). Its area is 120 km², and mean and maximum depths are 12.5 m and 56 m, respectively. The lake is oligotrophic and its color low (15–25 mg Pt l⁻¹). The mean total phosphorus content during 1980–2010 was 6 µg l⁻¹ (SD = 1) with no significant trend (data from observation station Konnevesi 64, March, depth 25 m, open data, www.syke.fi/avoointieto).

In S Konnevesi, vendace has traditionally been caught with seines, especially during autumn and winter, and with gill nets. During the low abundance period, there was practically no fishing targeting vendace (Valkeajärvi 1993a). After the stock recovery, commercial trawling was started. Recreational vendace fishing by gill nets is common, especially during the spawning season.

The relative abundance of vendace population at different life stages, *e.g.* the index of spawning biomass of at least two-growing-seasons-old mature individuals and the index of density of one-growing-season-old recruits in

autumn, based on seine catch per unit effort, the age structure in catch samples and size at age were monitored from the 1970s onwards (for methods *see* Valkeajärvi & Bagge 1995), Valkeajärvi & Marjomäki 2013, Marjomäki *et al.* 2021). For this study, we selected two dynamic equilibrium sections of the time series: a low population abundance regime in years 1984–1996 and a very abundant regime of years 2000–2010 (Fig. 1).

We estimated the average age-specific total length (L_i , mm, where i is the growing season) for one-, two-, three- and four-growing-season-old individuals in the autumn by arithmetic mean of average length in different years during a regime. We selected the average lengths of year-classes 1984–1995 in seine catch samples to represent growth at low abundance regime and year-classes 2000–2009 the very abundant regime. All the year-classes from 1984 to 2009 were considered to represent the “average” growth in S Konnevesi. We then fitted the von Bertalanffy (1938) growth model to these three data sets for age groups from one to four growing seasons using iterative least squares. Then we estimated the L_i for ages 1–10 growing seasons using the estimated parameter values. We assumed that these estimates apply to female fish.

We estimated the age-specific average fecundity at different ages based on L_i in both regimes assuming that all individuals reach maturity at the age of two growing seasons (Karjalainen *et al.* 2016). First, we estimated the general relationship between age-specific L_i and the average fecundity of female eggs f_i , assuming that 50% eggs are female, based on data from Karjalainen *et al.* (2016) for four Finnish lakes, including S Konnevesi, and a very large range of densities using the following formula:

$$f_i = 0.000292L_i^{3.063}, R^2 = 0.95 \quad (1)$$

For simplicity, we assumed that survival after recruitment (from the age of one growing season) was constant at different ages. We estimated the regime-specific average proportion (ap_i , %) of each age group in the population as an arithmetic mean of annual proportion estimates for each age group in the autumn seine catch samples within a regime. One- and two-growing-season-

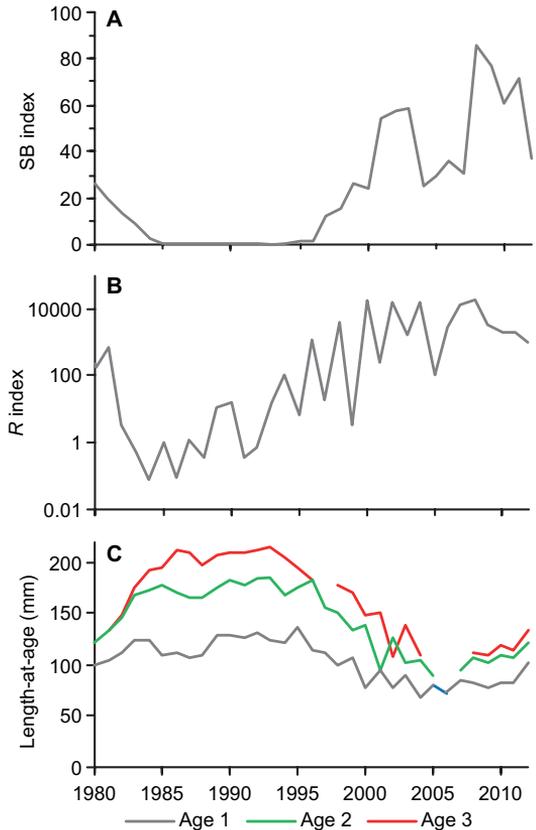


Fig. 1. (A) Vendace spawning stock biomass (SB) index (seine catch per unit effort, kg haul⁻¹), (B) recruitment (R) index (CPUE of age 1+ individuals in seine two summers after hatching, index placed to the years of hatching), and (C) average age-specific total length in autumn samples at the age of one, two and three growing seasons in Lake Southern Konnevesi.

old fish were not included in the calculation of the proportions because they may be only partially recruited to the gear, especially during the high abundance regime. Second, we created a regime-specific Heincke (1913) catch curve and fitted the unweighted least squares regression of age i on $\ln(ap_i)$ (e.g. Jensen 1985, but *see* Smith *et al.* 2012 for bias) excluding the old age groups with only a few specimens in the samples and therefore very low precision of proportion. The slope of the linear regression was used as an estimate of the instantaneous total mortality $Z_{\text{post-rec.}}$ and was converted to the proportional average post-recruitment survival as follows:

$$S_{\text{post-rec.}} = \exp(-Z_{\text{post-rec.}}) \quad (2)$$

Age groups 0+ and 1+, first and second growing seasons, were not included because these fish were not considered fully recruited to seine fishing, especially during high abundance period with very small size at age.

All the years 1984–2009 were used to estimate the growth and survival to represent the “average” parameters for S Konnevesi.

We constructed a life table (e.g. Krebs 1985, description in Table 1) for both regimes and the whole data average using regime-specific f_i estimates and a given value of $S_{\text{post-rec.}}$ and solved the pre-recruit survival $S_{\text{pre-rec.}}$ required to achieve stability, i.e., the net reproduction rate $R_0 = 1$. We assumed that the observed post-recruitment population parameters during low abundance regime represent the maximum potential growth and survival of Lake S Konnevesi vendace. Based on this, we estimated the minimum average $S_{\text{pre-rec.}}$ value for different levels of $S_{\text{post-rec.}}$, which guarantees stability, i.e., the long-term persistence of S Konnevesi vendace population.

Results

The vendace population fluctuated greatly in S Konnevesi (Fig. 1). Based on the spawning biomass index, recruitment and length-at-age, there was roughly a decade long low abundance period starting in 1984, and a very abundant period starting from 2000.

The levels of population parameters in the post-recruitment age-groups differed considerably between these sparse and abundant population regimes. Length-at-age during the

low abundance regime was about twice that of the very high abundance regime in mature age groups (Fig. 2A) ($p < 0.001$ for differences in age-specific average length between regimes for ages 1–4 growing seasons). Consequently, the fecundity-at-age estimate for the low abundance regime was about 6–8 times that of the high abundance regime (Fig. 2B). Finally, the annual survival during the low abundance regime was much higher ($S = 62\%$, $Z = 0.48$) as compared with that during the high abundance regime ($S = 40\%$, $Z = 0.91$) (Fig. 2C) ($p < 0.01$ for difference in regime-specific instantaneous total mortality Z). For the whole period, the “average” S and Z were 52% and 0.66, respectively.

Combined, compensation in population parameters in the post-recruit life-stages produced the potential for about 17-fold relative increase in the expected lifetime egg production per recruit from very abundant (340 female eggs per recruit) to the low abundance regime (5900 female eggs per recruit). To decompensate this potential for population increase and thus maintain a low abundance regime, the pre-recruitment survival must decrease proportionally to this increase. The stability yielding ($R_0 = 1$) estimate of pre-recruitment survival for the high abundance period was about 0.3% and for low abundance period as low as about 0.017%, which corresponds to the above-mentioned relative increase in the product of post-recruit survival and fecundity (Fig. 3). The pre-recruitment survival matching with long-term “average” post-recruitment parameters was about 0.06%. Thus, on the “average”, offspring from roughly one of the 2000 eggs laid survives to one-grow-

Table 1. A static age/stage-specific life table for vendace. Pre-recruitment survival (set in boldface) can be solved to gain $R_0 = 1$ when every other variable is given a constant value.

Age (growing season, i)	Female fecundity (eggs, f_i)	Survival (S , %) from i to $i + 1$	Standardized number alive (n_i)	$f_i \times n_i$
0 (spawned egg)	0	$S_{\text{pre-rec.}}$	1.0	0
1 (recruit)	0	$S_{\text{post-rec.}}$	$n_0 \times S_{\text{pre-rec.}}$	0
2 (100% maturation)	f_2	$S_{\text{post-rec.}}$	$n_1 \times S_{\text{post-rec.}}$	$f_2 \times n_2$
3	f_3	$S_{\text{post-rec.}}$	$n_2 \times S_{\text{post-rec.}}$	$f_3 \times n_3$
...				
10	f_{10}	$S_{\text{post-rec.}}$	$n_9 \times S_{\text{post-rec.}}$	$f_{10} \times n_{10}$

Static: Net reproduction rate $R_0 = 1 = \sum f_i \times n_i$

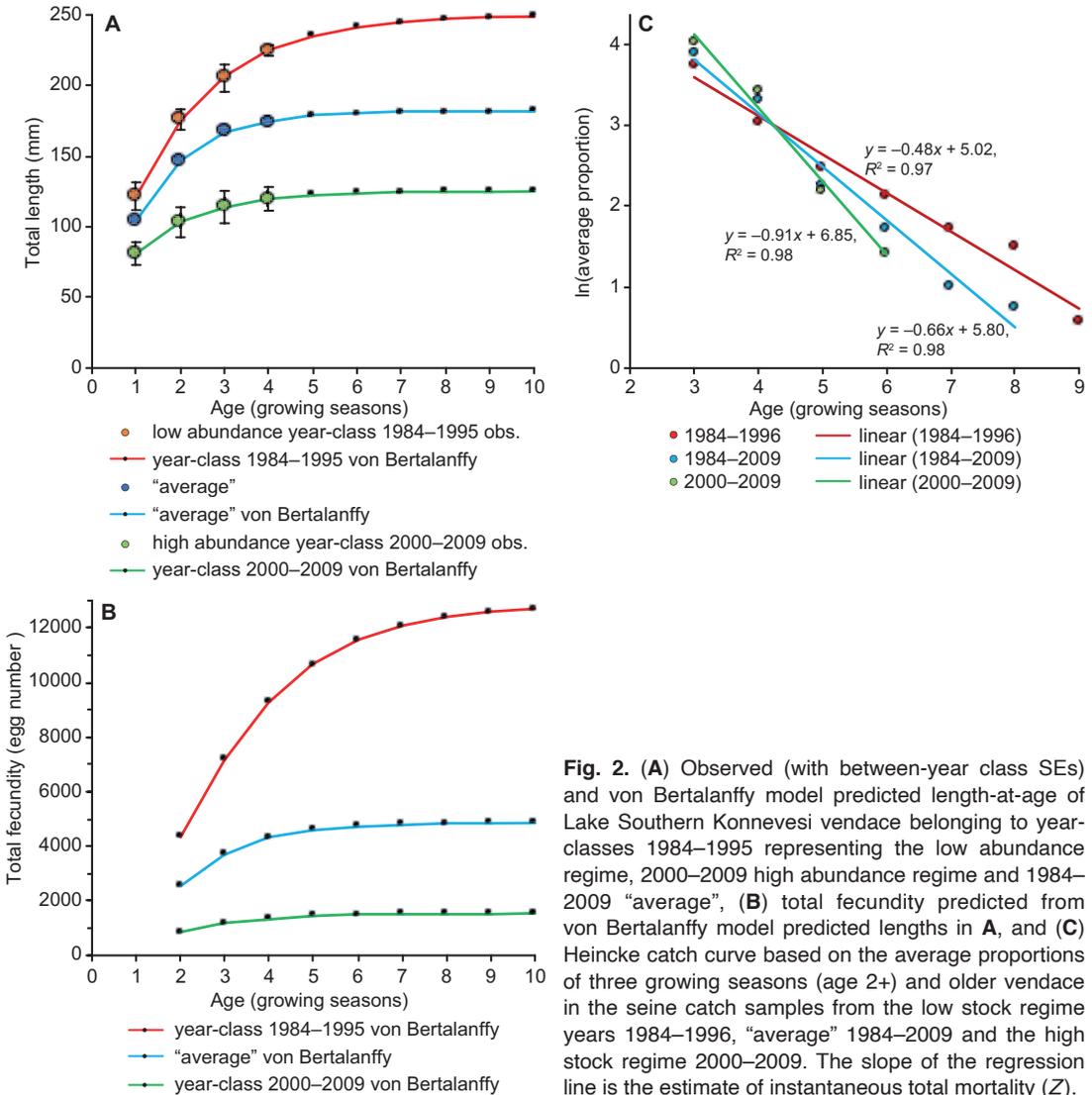


Fig. 2. (A) Observed (with between-year class SEs) and von Bertalanffy model predicted length-at-age of Lake Southern Konnevesi vendace belonging to year-classes 1984–1995 representing the low abundance regime, 2000–2009 high abundance regime and 1984–2009 “average”, (B) total fecundity predicted from von Bertalanffy model predicted lengths in A, and (C) Heincke catch curve based on the average proportions of three growing seasons (age 2+) and older vendace in the seine catch samples from the low stock regime years 1984–1996, “average” 1984–2009 and the high stock regime 2000–2009. The slope of the regression line is the estimate of instantaneous total mortality (Z).

ing-season-old recruit the following autumn, and offspring from one of the 4000 eggs reaches maturity. To maintain a high abundance regime, these odds for the pre-recruitment survival must be as high as about 1:300 and 1:800, respectively, and to maintain a low abundance regime, as low as 1:6000 and 1:9000, respectively.

Obviously, there is a negative relationship between the minimum average pre-recruitment and post-recruitment survival required to ensure long-term persistence ($R_0 = 1$) (red curve in Fig. 3): if the average post-recruitment survival is e.g. 30% ($Z \approx 1.2$), about five-fold minimum pre-recruitment mortality (0.09%) is required

for persistence in comparison with that (0.02%) required for post-recruitment survival of 60% ($Z \approx 0.5$).

Discussion

We applied a static life table approach to a fish species with very high population variability to assess the level of pre-recruit survival. We considered this permissible because especially in S Konnevesi, but also in several other lakes, e.g. in Keitele (Järvi 1942), Höytiäinen (Haakana *et al.* 2007) and Puruvesi (<http://www.paijanne>).

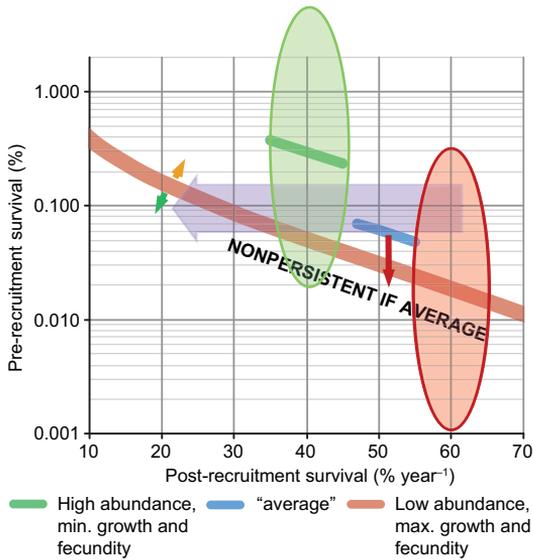


Fig. 3. Pre- and post-recruitment survival producing a stable state population equilibrium life table (the net reproduction rate $R_0 = 1$) for Lake Southern Konnevesi vendace. The equilibria for both the high and low abundance regimes and the “average” are shown. Ovals indicate that there is always high between-year variability within a dynamic equilibrium. The oval size reflects the authors’ expert view on the typical range of variability, and should not be considered quantitative estimate. The purple arrow indicates the decrease in post-recruitment survival and the red arrow the decrease in pre-recruit survival. The green arrow indicates the effect of the increase in maximum growth and fecundity on the scope of persistence and the orange arrow the effect of the decrease in maximum capacity of growth, e.g. due to size-selective fishing.

org/pages/fi/projektit/cornet/tuloksia.php), vendace variability implies shifts between alternative equilibria, i.e. dynamic regimes, rather than just one long-term dynamic equilibrium. We quantified the population parameters required for stability during the very high and very low abundance regimes, and thus the scope of compensation from increased age-specific fecundity and post-recruitment survival and the required decrease in pre-recruitment survival to counterbalance those to maintain the low abundance regime.

To fully evaluate the range of variability in density dependent population parameters, the data must contain prolonged periods of abundance extremes. S Konnevesi is optimal for this kind of analysis, as the available data do

not only include a decade-long low abundance regime with all the population density proxies at extremely low level and very fast growth (Fig. 1; see also Valkeajärvi & Bagge 1995, more data in Marjomäki et al. 2021), but also a long, high abundance period with the highest densities of newly hatched larvae ever recorded for vendace in any lake (<http://www.paijanne.org/pages/fi/projektit/cornet/tuloksia.php>) and extremely slow growth of older fish. In addition, fishing effort and consequently fishing mortality were low during the very abundant regime due to the low or non-existent market value of stunted fish.

The scope of density-dependent growth in S Konnevesi vendace was exceptional compared with that of other fish species (Lorenzen & Enberg 2001): the “average” asymptotic length of vendace being < 70% of the maximum during the low abundance regime, and the minimum asymptotic length during the high abundance regime being < 50% of the maximum. Consequently, the potential of density-dependence in growth of vendace to regulate population biomass and fecundity is considerable. Then again, the range of variability in vendace population density in S Konnevesi was also exceptional as compared with other reported results (see Lorenzen & Enberg 2001).

The maximum growth of vendace in S Konnevesi was only marginally slower than the maximum in the fastest growing vendace populations in Finland (Pyhäjärvi, southwest Finland, Sarvala et al. 1998; Lake Päijänne, Tehinselkä basin, Valkeajärvi et al. 2012), which in turn are comparable to fast growing vendace populations in central and southern European lakes (Fischer et al. 2012, Japoshvili 2012, Wanke et al. 2021). Päijänne and Pyhäjärvi are located in southern Finland, having longer growing season and higher nutrient levels and primary production than S Konnevesi. Therefore, we consider that the range of growth in S Konnevesi represents the scope of vendace growth in oligotrophic lakes in Finnish lake district and more generally at comparable latitudes, and thus, the maximum potential of vendace to compensate for the decrease in density with increase in growth and fecundity.

Regarding the maximum lifetime egg production of vendace, it must be emphasized that

practically all S Konnevesi female vendace reach maturity already after two growing seasons, which is typical of the species (e.g. Järvi 1919, Hamrin & Persson 1986, Karjalainen *et al.* 2016). Only seldom, in very fast growing populations, some individuals reach maturity already after the first growing season producing eggs of about half the size of the eggs of older fish (Sarvala *et al.* 1992). Karjalainen *et al.* (2016) found in a laboratory experiment that the fertilization rate of the eggs of one-summer-old females was zero. Thus, it is very unlikely that one-summer-old fish could contribute significantly to the reproduction potential of a vendace population, and that vendace could significantly increase its scope of compensation by maturing at the earlier age than two growing seasons. It should also be noted that our results are not directly applicable to the vendace populations of certain Scandinavian lakes, e.g. Mjøsa and Osensjøen, where most individuals reach maturity at the age of three growing seasons and do not spawn in lakes but in running water (e.g. Aass 1972, Sandlund *et al.* 1991), and possibly even belong to another sub-species.

Our estimates of post-recruitment survival in S Konnevesi correspond to those in previous studies (Viljanen 1986, Valkeajärvi 1983). The level of survival during the low abundance regime was clearly higher than during the high abundance regime. During the low abundance regime, there was virtually no vendace fishing (Valkeajärvi 1993a). The instantaneous total mortality (Z) estimate for that period can be thus used as an estimate of instantaneous natural mortality (M) of vendace in S Konnevesi. This corresponds well to the estimate by the general equation by Then *et al.* (2015) assuming that the maximum lifespan of vendace is about 14–15 years (the maximum age determined from scales by authors in gill net catch samples from S Konnevesi during the low abundance period was 14+). Rapid growth had to facilitate the escape of vendace from gape-limited predators, e.g. brown trout and perch. During the high abundance regime, post-recruitment survival was considerably lower and the increase in mortality was due to a moderate increase in fishing effort, but also to higher predation pressure on very small-sized post-recruit vendace. Valkeajärvi (1983) estimated that the instantaneous natural mortality of S Konnevesi vendace was about 0.6–0.9 during the earlier high-abundance period in the early 1980s. The natural mortality of a highly variable key prey fish population in a simple fish community in an oligotrophic lake cannot therefore in any case be assumed to be a temporally constant parameter, nor can it be casually lent from or to other lakes.

Interestingly, the catch curve from the third growing seasons onwards — when fish should be fully recruited to fishing even during very high abundance and slow growth — appeared linear, implying a fairly constant mortality at different ages. Unfortunately, the level of mortality in the earlier part of post-recruitment life-stage could not be estimated from the age distribution data. This is because the catchability of especially one summer old (0+) but occasionally also two summers old individuals in seine fishing is lower than that of older individuals and, importantly, varies from year to year according to their abundance and growth. Especially during periods of high abundance and slow growth, a considerable proportion of especially 0+ fish can escape through the cod end of the gear. Moreover, immature individuals do not aggregate in the spawning areas as much as mature fish. For simplicity, the survival was assumed constant throughout the post-recruitment life-stage. In reality, the predation mortality of young and small individuals is likely to be considerably higher than that of older fish, but on the other hand, their fishing mortality is lower. In addition, mature fish may suffer from mortality related to spawning stress (Karjalainen & Marjomäki 2018). Admittedly, the constant post-recruitment mortality is thus a rough approximation. Further, it must be noted that the survival was estimated from the data containing both sexes, but typically the oldest fish are predominantly females, implying their higher survival in comparison with males. Therefore, our analysis may slightly underestimate the level of female survival. All the above factors may give rise to certain error and/or bias in pre-recruitment survival estimates, but the observed differences in pre-recruitment survival required for stability of different regimes are so prominent that these issues do not compromise the overall validity of the results.

The estimated average level of pre-recruitment survival for the whole studied period (about 0.06%) corresponds well to the order of magnitude of the survival estimate for comparable Lake Puulavesi (Marjomäki *et al.* 2014). There, the long-term average, estimated directly from quantitative estimates of spawning population biomass (8.5 kg ha⁻¹) and recruitment (734 indiv. ha⁻¹), was about 0.1%. It is somewhat higher than the average in S Konnevesi, but the average growth and survival in Puulavesi were slower due to only a very short low-abundance period and higher average fishing mortality. Karjalainen *et al.* (2021) estimated in S Konnevesi the survival from spawning to one-week-old larva during one winter to be about 3%. Further, the average survival from larva to recruitment in autumn is roughly 2% (e.g. Karjalainen *et al.* 2000, Marjomäki 2003). Combining these, the estimate for the whole period from spawning to recruitment is about 0.06%, which corresponds to the order of magnitude of our population parameter-based indirect estimate for S Konnevesi. The average survival in both periods, from spawning to hatching and from hatching to recruitment, thus appears to be of the same order of magnitude. However, the inter-annual variability is very high for both (see fig. 3 in Marjomäki *et al.* 2021).

Wanke *et al.* (2021) estimated the average pre-recruitment survival in three central European lakes to be about 0.1%, 0.07% and 0.01%; the two first correspond to the levels in Finnish lakes. Interestingly, the lowest one, from a more eutrophic lake, is at the level or even below the survival in S Konnevesi during the low abundance regime. In that lake, vendace — growing faster than S Konnevesi maximum — egg survival is low, and it is exposed to considerable fishing mortality and consequently suffers from recruitment overfishing (Wanke *et al.* 2021).

We propose that the estimated average pre-recruitment survival during the low abundance regime in S Konnevesi (about 0.02%) represents the minimum level required for the persistence of vendace population in oligotrophic lakes in central Finland when the maximum capacity for density-dependent compensation is in operation and fishing has ceased.

Average survival in the static life table approach of this work was interpreted as long-

term average determining certain (dynamic) equilibrium. Yet, it must be emphasized that the short-term inter-annual variability of pre-recruitment survival is very high (e.g. Marjomäki 2003, 2004) while the variability in post-recruitment mortality is obviously proportionally much lower. The variability of pre-recruitment mortality was high even within a regime: e.g., in S Konnevesi during the high abundance regime, the recruitment varied by an order of magnitude between consecutive years despite the fact that the spawning stock biomass was rather constant (Marjomäki *et al.* 2021). Thus, the pre-recruitment survival does not have to be high every year to maintain this regime but high survival from an ample spawning stock every second to third year is enough. On the other hand, only a few more consecutive years of low pre-recruitment survival can end the high abundance regime. Vendace fisheries management must thus always be adapted to this high uncertainty about future with precaution, up to date monitoring and high flexibility in operation and management.

A huge decrease in long-term average pre-recruitment survival is required to bring about the stage shift in the fish community from vendace-dominated to a prolonged period of very low vendace abundance and *vice versa*. Based on population monitoring and modeling, Valkeajärvi and Marjomäki (2004) suggested that the decrease in pre-recruitment survival in S Konnevesi was due to a significant increase in the abundance of small perch. One or a few very abundant perch year classes emerged in the early 1980s and induced high pre-recruitment mortality in vendace and maintained it for several years. Intensive brown trout stocking during the same period (Valkeajärvi 1993b) may also have contributed to this. Similarly, Helminen *et al.* (1997) proposed that predation by perch would regulate the recruitment of Pyhäjärvi (southwestern Finland) vendace. However, the onset of population decline in S Konnevesi was not necessarily caused by perch. The first few poor year classes may have been the result of, e.g. unfavorable weather conditions, which are important stochastic external factors in the population dynamics of vendace (Marjomäki *et al.* 2004, 2014).

An interesting question is, whether the density-dependent dependence, analogous to the

Allee effect (Allee 1931, 1932, Odum 1953, detailed description in e.g. Rowe & Hutchings 2003), was responsible for prolonging the low abundance period. On the one hand, the increase in perch abundance and its effect could have been just an environmentally induced temporary stressor that suppressed vendace recruitment. In terms of SB–*R* relationships, this means that the maximum per capita reproduction rate (e.g. $a \times f(\text{perch density})$ in Ricker or Cushing models) would decrease considerably with increasing perch abundance, as modeled by Valkeajärvi and Marjomäki (2004). Note that the decrease in this rate parameter must be even higher than the actual relative decrease in pre-recruitment survival estimated in this study, as it represents the reproduction rate at very low density without density dependent compensation, whereas the pre-recruitment survival was estimated for abundant population with strong compensation.

On the other hand, reproduction, growth or/and abundance of perch may very well be negatively dependent on vendace abundance. This would mean depensatory density-dependence for vendace. During high vendace abundance, due to its strong planktivory-induced (e.g. Hamrin & Persson 1986, Helminen & Sarvala 1994) resilience (*sensu* Holling 1973), vendace may be able to self-stabilize (*sensu* Scheffer *et al.* 2001) its own population, but also the very simple boreal oligotrophic lake fish community and ecosystem more widely into a vendace population-dominated regime. If vendace recruitment fails for external reasons for a few consecutive years, e.g. perch as a food competitor in larval and juvenile stages will benefit from the scarcity of vendace and increase in abundance and, as a predator, increase pre-recruitment mortality of vendace. The effect is, of course, stronger if, e.g. warm years facilitating good perch recruitment co-occur with this. This highly plausible scenario would clearly induce depensatory density dependence in vendace population dynamics and would slow at least if not prevent the stage shift to abundant population, which would be otherwise expected based on the vast compensation in post-recruitment survival and growth. Another potential depensatory force in the case of vendace may be highly nonlinear functional form of the predator–prey relationship (e.g. Myers *et al.*

1995, for vendace Heikinheimo 2001). During the very high vendace abundance period, both pre- and post-recruitment predators can be saturated and their effect on vendace mortality can be proportionally low. This effect again acts as a self-stabilizing force during the high-abundance regime. During low abundance, in a simple community with limited opportunities for prey shift, the proportional predation mortality may be much higher, thus again depensatory. This must act especially in early pre-recruitment life soon after hatching, as the growth of vendace is fast during low abundance and predators are gape-limited.

Then again, the actual shift in Konnevesi from the low to very abundant regime was eventually ultimately rapid after the perch population decline — about five years of build-up of SB from a very low level to a very high one. This implies that the depensation, Allee effect, if present, was not strong enough (*sensu* Wang & Kot 2001) to prevent the recovery. Hutchings (2000) found that rapid recovery from low abundance state is typical of early-maturing species exploited with highly selective gear, such as herring and related species. The vendace surely matches with this category of fish species. From the community/ecosystem regime view point the fast recovery implies that the self-stabilising forces of this regime were not strong at this level of lake trophy, its resilience was low and stability weak.

Despite the fact that the opposite changes in the density of vendace and perch in Konnevesi provide indirect evidence of the ability of perch to regulate the dynamics vendace population, very little is known about the actual spatio-temporal distribution and level of predation pressure and contribution of perch on the natural mortality of vendace. Tolonen (2000) studied the perch diet in Konnevesi after the recovery of the vendace population in the late 1990s. He found a high proportion of slow-growing young of the year vendace in pelagic perch catch samples in the summer and autumn. No larval predation was observed. On the other hand, Haakana *et al.* (2007) studied the diet of perch in Lake Höytiäinen during a low vendace abundance period by littoral gill netting in May and June, and came to the conclusion that the perch contributed only marginally to natural mortality of

larval and young juvenile vendace. More field data are needed on perch diet in different habitats and seasons and at different vendace abundances to fully assess the effect the predator and competitor relationship between vendace and perch.

Anthropogenic stressors

The increase in fishing as well as stocking of salmonid predators (Valkeajärvi *et al.* 1997) both increase the post-recruitment mortality of vendace (purple arrow in Fig. 3). This causes a decrease in average density with some compensation in individual growth and fecundity. However, in order for the population to persist, let alone to have a high abundance, a considerable compensatory increase in *per capita* pre-recruitment survival is required. In any case, the population is driven closer to the maximum capacity of compensation (red curve in Fig. 3) and the lower potential of self-stabilisation. Consequently, the stability and resilience will deteriorate. Especially salmonid stocking (Valkeajärvi *et al.* 1997), but also fishing, if the gear catches or induced mortality to individuals escaping from the trawl (Suuronen *et al.* 1995) or seine cod-end, reduce also the pre-recruitment survival (red arrow in Fig. 3). This will again bring the abundance closer to the full compensation capacity with the above-mentioned combination. The sum of both vectors naturally makes the population even less resilient by reducing the scope of compensation. An important difference between fishing- and stocking-induced mortality is that fishing effort usually decreases when the vendace abundance falls below the profitability threshold (Marjomäki 2003) but stocking intensity may not be linked to vendace abundance and furthermore, predation may induce a functional response which causes depensation. On the other hand, size-selective fishing may reduce the maximum capacity of growth by excluding the individuals with potential for fastest growth (e.g. Kuparinen & Hutchings 2012). If this trait is genetically regulated, fishing may decrease the potential for post-recruitment compensatory effects. Consequently, the minimum level of pre-recruitment survival required to guarantee persistence will increase (orange arrow in Fig. 3).

Climate change is predicted to affect lake ecosystems in various ways (e.g. Havens & Jeppesen 2018). From the perspective of this study, the main effects are an increase in average temperature and length of growing season, an increase in nutrient loading from the catchment area and thus increased sedimentation and lower oxygen concentrations in winter. From the perspective of the regime stability domain, Schaffer (2001) argues that “gradually changing conditions may have little effect on the state of the ecosystem, but nevertheless reduce the size of the attraction basin. This loss of resilience makes the system more fragile in the sense that can easily be tipped into a contrasting state by stochastic events. Such stochastic fluctuations may often be driven externally; however, they can also result from internal system dynamics.” In presently oligotrophic boreal lakes, the enhancing effects of climate change on water temperature and trophy promote reproduction and growth, and consequently abundance of perch (e.g. Le Cren 1958, Lehtonen & Lappalainen 1995, Sarvala & Helminen 1996, Linlökken 2003, Hayden *et al.* 2017, Kokkonen *et al.* 2019). The average level of perch-induced predation mortality of vendace, especially at pre-recruitment stage, may increase (red arrow in Fig. 3). Warming and eutrophication may to some extent also increase the growth of vendace and therefore the maximum age-specific fecundity and consequently the scope of compensation and persistence (green arrow in Fig. 3). On the other hand, the decrease in oxygen level at the egg incubation sites and potential mismatches in phenology will cause the decrease in pre-recruitment survival (red arrow in Fig. 3). As a consequence of all effects, the attraction basin for high abundance vendace planktivory regime will thus shrink and the attraction basin of a regime with low abundance for vendace and high abundance for perch widen. As a result, the shift from high abundance vendace regime will be favored but the opposite will be made more difficult. It is likely that the vendace-dominated lakes will turn into percid-dominated where vendace is a marginal species if not extinct as, e.g. in northern part of Lake Päijänne where the vendace abundance has remained at a very low level despite re-oligotrophication after pollution (Urpanen *et*

al. 2008) or in Pyhjärvi, southwest Finland, where the vendace population has not recovered after the decline in the 1990s to as high abundance state as before the decline (Sarvala *et al.* 2020).

Conclusions

The results highlight the huge potential for density dependent compensation in vendace through growth and individual fecundity as well as post-recruitment survival due to decrease in natural mortality. An enormous shift in pre-recruitment survival is required to maintain the low and high vendace abundance regimes. The shift between the regimes can be rapid.

The life table is a useful tool for assessing the typical parameter combinations required during different long-term density regimes typical of vendace and for illustrating at the population parameter level the effects of various anthropogenic stressors.

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