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Occurrence of two-year cyclicality, “saw-blade fluctuation”, in vendace populations in Finland

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The tendency towards two-year cyclicality is considered typical of many Fennoscandian vendace populations, especially in fluctuation of recruitment, based on time series of individual lakes. We used two robust indicators to identify and quantify two-year cycles in vendace population proxy time series at different life-stages — spawning stock biomass (SB), density of newly hatched larvae (LD) and recruitment (REC) — from 22 Finnish lakes. Then we applied Fisher’s meta-analytical test to assess the adequacy of the evidence to support the hypothesis that vendace population dynamics include two-year cyclicality. The results supported this hypothesis for REC but not for SB or LD. Yet, the indicators and test are conservative and time-series of SB and LD are shorter than those for REC. The appearance of cycles in REC is associated with high post-recruitment mortality, consequently practically only one spawning per cohort. Cycles may be typical for the recovery period from low abundance period also. Still, some populations with moderate post-REC mortality and non-cyclic SB abundance exhibited cycles in REC. Such dynamics presuppose the existence of more complex regulation based on the interaction of different life stages.

Introduction

The tendency towards two-year cyclicality, or as illustratively expressed by local vendace fishers “saw-blade fluctuation”, is considered typical of many Fennoscandian vendace populations,

especially in fluctuation of recruitment (REC, referring most often to one-summer-old juveniles in autumn or winter) (Table 1). The models predict that this tendency can be driven by three mechanisms: (1) High post-recruitment mortality causes the population to approach semelpar-

ity (reproduction only once in a lifetime) and generation length to approach two years, the age of first maturation in vendace. Thus, next year's spawning stock biomass (SB) will be more closely proportional to the previous year REC (e.g., for roach (*Rutilus rutilus*) Townsend 1989, Townsend *et al.* 1990, for sockeye salmon (*Oncorhynchus nerka*) Myers *et al.* 1997, 1998, for vendace (*Coregonus albula*) Helminen 1994, Marjomäki 2005, Marjomäki *et al.* 2014). This process alone is capable of producing damped oscillations in REC. (2) Low level of density-dependent compensation in the SB–REC-model renders REC more closely directly proportional to the SB producing it (e.g., Marjomäki *et al.* 2014). (3) Delayed density-dependent suppressive effect (*see* more detailed definitions and mechanisms in Marjomäki *et al.* 2014) of a previous year strong year class on the next can lead to a strong and persistent cycle (e.g., Helminen *et al.* 2002, Marjomäki *et al.* 2014). The last was suggested to be the main reason for the two-year cycles in vendace recruitment (Hamrin 1979,

Hamrin & Persson 1986), and the mechanism of suppression is asymmetric competition between the very abundant young-of-the-year pre-recruits and the previous year-class simultaneously at their second growing season before maturing. Older fish should suffer from this competition with dramatic consequences for their egg quality, leading to poor recruitment. However, this actual mechanism was not supported in a study comparing reproductive success of vendace which had been exposed to different levels of competition (Karjalainen *et al.* 2016), and if the suppressive effect is real, it is likely that many factors will have to act in concert (*see* discussion in Marjomäki *et al.* 2014 and Sarvala & Helminen 2021). All in all, when a very abundant year-class emerges, e.g. due to favorable environmental conditions at the pre-recruit life stage, all the above processes should promote and prolong the duration of two-year damped oscillations, and in an extreme case lead to two-year limit cycle.

Thus, the models predict that SB may also perform two-year cycles when post-recruitment

Table 1. Sources in which two-year cyclicity in vendace population proxies is suggested. SB = spawning stock, REC = recruitment, year class strength, NFA = no formal analysis, suggestion based on appearance of data, A = analysis, suggestion based on formal statistical analysis; for lake locations *see* Fig. 1.

| Reference | Lake | SB | REC |
|---|------------------------------------|-----|-----|
| Airaksinen (1967) | Varmavirta, Saimaa | – | NFA |
| Nissinen 1972 | Puruvesi, Oulujärvi | NFA | NFA |
| Lind 1976 | Puruvesi ¹⁾ , Irnijärvi | – | NFA |
| Hamrin 1979, Hamrin & Persson 1986 | Bolmen, Sweden | NFA | NFA |
| Auvinen 1987, 1988, 1994 | Pyhäjärvi SE Finland | – | NFA |
| Valkeajärvi 1983 | northern Konnevesi | – | NFA |
| Viljanen 1988 | Suomunjärvi, Onkamo | – | NFA |
| Helminen <i>et al.</i> 1993a, 1997 | Pyhäjärvi, SW Finland | – | A |
| Salmi & Huusko 1995 | several, <i>see</i> Table 2 | NFA | NFA |
| Auvinen <i>et al.</i> 2000 | Onkamo | NFA | NFA |
| Karjalainen <i>et al.</i> 2000 | Several | – | NFA |
| Viljanen <i>et al.</i> 2004 | Suomunjärvi | – | NFA |
| Marjomäki 2004, Marjomäki <i>et al.</i> 2014 | Puulavesi | – | A |
| Huusko & Hyvärinen 2005 | Oulujärvi | NFA | A |
| Valkeajärvi & Marjomäki 2004 | Southern Konnevesi | – | NFA |
| Marjomäki <i>et al.</i> 2021a | Southern Konnevesi | – | NFA |
| Sarvala <i>et al.</i> 2020, Sarvala & Helminen 2021 | Pyhäjärvi SW Finland | NFA | NFA |
| H. Auvinen & J. Jurvelius unpubl. data | Paasivesi | – | NFA |

¹⁾ More specifically, according to Lind's classification, based on age structure of annual catch samples, the lakes belong to the class "2–3 year long age-group cycle", catch consisting every second year of one-summer-old and every second year of two-summer-old individuals and sometimes a cohort may appear in catches for three years. An abundant year-class appears thus every second or third year. Valkeajärvi (1983) and Viljanen (1986) considered the data to imply periodicity of two years.

mortality is high enough for the population to approach semelparity, and consequently at least amplifying the tendency for cycles in REC. Two-year cycle in SB has been suggested to occur in some lakes (Table 1) as well as by modelling (Marjomäki 2005). Recently, quantitative monitoring of the density of newly hatched larvae (LD) has also become possible with sufficient precision (e.g. Urpanen *et al.* 2009). This life-stage is close to mid-point between spawning and recruitment. So far, no study has suggested occurrence of two-year cycle in LD. Examining the tendency to two-year cyclicity at this stage could reveal new details about the timing of cycle formation.

Detecting true two-year cycles in population dynamics is methodologically challenging. First, time series are often short, typically only a few decades. Second, the observed abundance proxies are less than ideal, with only modest precision at best, and are likely to contain uncontrolled trends in their components, causing temporal bias. Often the population proxies are based on catch per unit effort (CPUE) but catchability (q) may change gradually (e.g. Salmi & Huusko 1995). In virtual population analysis, natural mortality is often assumed to be constant but in reality it can change significantly due to changes in predator abundance, e.g. pikeperch (*Sander lucioperca*; Vainikka & Hyvärinen 2012). In echo-sounding, variation in the smelt (*Osmerus eperlanus*) stock may interfere with estimates of vendace density, changes in fish growth may affect age-specific catchability, etc. Third, considerable uncertainty about correct model and error variance distribution render time-series data cleaning difficult, e.g. when using SB–REC models to identify the effect of SB on REC (Marjomäki 2004). For the reasons outlined above, parametric time-series analysis methods, e.g., the autocorrelation function, are often not ideal or powerful, if not even suitable. Finally, the studies analyzing cyclicity have typically focused on one lake at a time. Thus, spurious correlations are likely to occur in a data set of many independent lake-specific studies and publication bias (Sterling 1959) may have promoted their conspicuousness.

Our aim was to test two simple and robust indicators to identify two-year cycles in less than ideal population proxy time-series at differ-

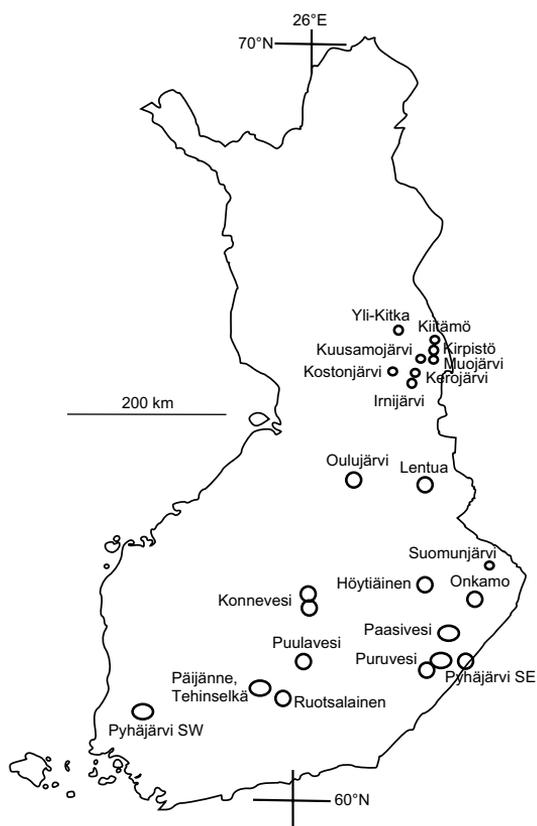


Fig. 2. Lake locations.

ent life-stages of vendace. The indicators were based on the identification of whether the next year's proxy value is higher or lower than the previous one, regardless of the magnitude of the difference. Based on the indicators, we used a meta-analytical approach to assess whether the evidence supports the tendency of vendace populations to perform two-year cycles; H_1 hypothesis: vendace population dynamics include two-year cyclicity. Finally, we tried to deduce from the actual time-series certain conditions that promote such cycles.

Material and methods

We used proxies of spawning stock biomass (SB), density of newly hatched larvae (LD), typically about one week after ice-off (for details see e.g. Urpanen 2009, Urpanen *et al.* 2009), and recruitment (REC) from 22 lakes (Table 2 and Appendix 1). Some of the previously published

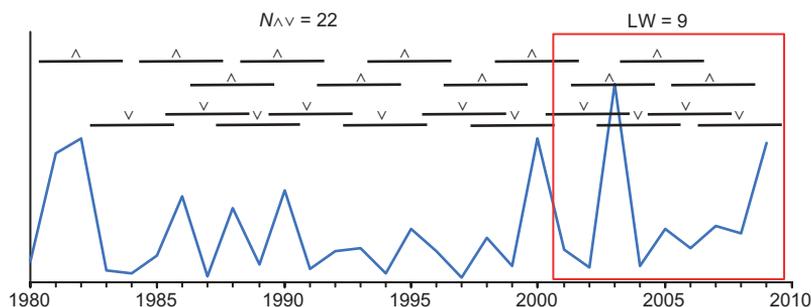


Fig. 2. A simulated time-series illustrating the two indicators of two-year cyclicality: LW = length of longest incessant saw-blade sequence in the time-series, including the first and last years of the sequence (red box). $N_{v^}$ = number of basic three-year higher–lower–higher (v) or lower–higher–lower (^) blocks in the data.

values were updated based on new information and some time series were supplemented with more recent observations. Most of the

proxy data for SB and REC were based on CPUE from seine or trawl split into SB and REC using random catch samples. Recently,

Table 2. Methods of estimating spawning stock biomass (SB, biomass units), larval density (LD, indivi. ha⁻¹) and recruitment (REC, number) in different study lakes with references to a more detailed description of the methods. CPUE = catch per unit effort from semicommercial seining or commercial trawling, VPA = virtual population analysis, BS = beach seine, SB&T = stratified bongo and tube sampler (see Urpanen *et al.* 2009), C = catch, F = instantaneous fishing mortality rate, M = instantaneous natural mortality rate, Echo = echo-sounding; for lake locations see Fig. 1.

| Lake | Method | | | Source |
|-----------------------|-----------------|----------|--------------------------------------|---|
| | SB | LD | REC | |
| Yli-Kitka | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Kiitämä | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Kirpistö | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Muojärvi | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Kuusamojärvi | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Kostonjärvi | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Kerojärvi | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Irnijärvi | CPUE | – | CPUE | Salmi & Huusko 1995 |
| Oulujärvi | VPA | – | VPA, M = 0.3 | Huusko & Hyvärinen 2005 |
| Lentua | – | – | VPA, M = 0.5 | Huusko & Sutela 1998 |
| Suomunjärvi | CPUE, VPA | – | CPUE, VPA | Viljanen <i>et al.</i> 2004 |
| Höytiäinen | – | SB&T | – | Haakana <i>et al.</i> 2007 |
| North Konnevesi | CPUE | – | CPUE | Valkeajärvi & Marjomäki 2013 |
| South Konnevesi | CPUE | BS, SB&T | CPUE | Urpanen <i>et al.</i> 2009 Marjomäki <i>et al.</i> 2021a Valkeajärvi & Marjomäki 2013 |
| Onkamo | CPUE | SB&T | CPUE | Auvinen <i>et al.</i> 2000 |
| Paasivesi | CPUE, Echo | – | CPUE, Echo | H. Auvinen & J. Jurvelius unpubl. data |
| Puruvesi, Hummonselkä | – | SB&T | CPUE | Karjalainen <i>et al.</i> 2000 |
| Puruvesi, Harvanselkä | – | SB&T | CPUE | Karjalainen <i>et al.</i> 2000 |
| Pyhäjärvi, SE Finland | CPUE | – | CPUE | Auvinen 1987, 1988, 1994 |
| Puulavesi | CPUE | SB&T | CPUE | Marjomäki <i>et al.</i> 2014 |
| Päijänne, Tehinselkä | CPUE | SB&T | CPUE | Valkeajärvi & Marjomäki 2013 |
| Ruotsalainen | – | SB&T | – | Urpanen <i>et al.</i> 2009 |
| Pyhäjärvi, SW Finland | C, adjust. by F | SB&T | CPUE ¹⁾ , w ²⁾ | Helminen <i>et al.</i> 1993a, 1993b, Sarvala <i>et al.</i> 2020 |

¹⁾ Depletion in CPUE during a fishing season, ²⁾ w = mean weight after first growing season.

the density of larval vendace was quantified based on depth-zone-stratified bongo-net and tube sampling. In some lakes, the beginning of the time-series consists of proxies based on the CPUE of larval beach seine.

We used raw proxy data as such, i.e., without transformations, or removal of trend or of the effects of other variables (e.g. with the SB-REC model). The main principle of the data analysis was robustness: we focused only on finding out if the next year's proxy value is higher or lower than the previous one, regardless of the magnitude of the difference. The two-year cyclicity was defined as consecutive proxy values oscillating in higher-lower-higher (or *vice versa*) manner.

The following two-year cyclicity indicators were developed (Fig. 2):

LW: cycle sequence in the time-series, including the first and last year of that sequence (red box in Fig. 2).

$N_{\vee\wedge}$: the number of basic three-year \vee (higher-lower-higher) or \wedge (lower-higher-lower) shaped blocks (which can overlap) (Fig. 2).

The observed LW and $N_{\vee\wedge}$ values in the time-series were evaluated against the probability (p) of gaining as high or even higher indicator value in equally long time series of independent, normally distributed random proxy values, i.e. the risk of accepting a sequence of random numbers as an indication of tendency of two-year cyclicity. The p values for each LW and $N_{\vee\wedge}$ in a time series of a given length were approximated from their probabilities in the data from at least 50 000 time-series of random numbers obeying normal distribution (Appendices 2 and 3). However, in this assessment of p , the random numbers do not have to obey normal distribution, but a distribution with limits, e.g. uniform [0, 1], or with generally decreasing probabilities for high and low extremes.

The following Fisher's (1932) combined probability test was used as a method of a simple meta-analysis:

$$X = -2\sum_{i=1}^k \ln(p_i) \quad (1)$$

where k is the number of independent (here lake-

or basin-specific) studies. X follows the χ^2 distribution with $2k$ degrees of freedom. X combines the p values of lake-specific time series studies into a more general assessment of evidence to support the H_1 hypothesis. When using Fisher's test, it must be assumed that different studies are independent regarding the phenomenon under study.

Results

For the spawning stock biomass proxy (SB), neither of the saw-blade indicators LW or $N_{\vee\wedge}$ revealed any exceptional two-year cyclicity in any lake (Table 3), i.e. typically the probability (p) of equal or higher LW and $N_{\vee\wedge}$ value in random number time-series was very high in comparison with vendace SB proxy time-series. Only in Lake Onkamo, $p < 0.1$ was found for LW. Further, Fisher's combined p value was very high for both saw-blade indicators. Thus, the combined data do not suggest a general tendency for two-year cyclicity in the vendace SB.

In the density of newly hatched larvae in spring (LD), the LW and $N_{\vee\wedge}$ values were not significantly ($p > 0.05$) higher than what can be expected to appear in a random number time-series in any other lake than Puruvesi, Harvanselkä basin, where the probability of as high or higher LW in a random number time-series was only 0.03 (Table 3). However, the value of $N_{\vee\wedge}$ was not significant there either. Fisher's combined p was > 0.4 in both saw-blade indices, thus not supporting the appearance of two-year cycles in the vendace LD.

In the recruitment proxy (REC), a significant ($p < 0.05$) two-year cyclicity, measured with either or both LW and $N_{\vee\wedge}$, occurred in several lakes (Table 3 and Fig. 3). Fisher's test also implied a significant tendency for two-year cyclicity.

Discussion

This analysis, based on robust non-parametric indicators and their general meta-analytical assessment, suggests that two-year cyclicity in the vendace recruitment time-series is a real

Table 3. Values of the two-year cycle indicators LW and $N_{V\wedge}$, time series length (L , from year X to year Y , including years in between with missing value) and probabilities (p) of the observed or higher indicator values in random number time-series for the population proxies spawning stock biomass, density of newly hatched larvae and recruitment in time series of vendace populations in Finnish lakes; for lake locations see Fig. 1.

| Lake | Spawning stock biomass (SB) | | | | Density of newly hatched larvae (LD) | | | | Recruitment (REC) | | | | | | |
|----------------------|-----------------------------|-----------------|-----|---------|--------------------------------------|----------------|-----------------|-----|-------------------|------------------|----------------|-----------------|-----------------|---------|------------------|
| | LW | $N_{V\wedge}$ | L | $p(LW)$ | $p(N_{V\wedge})$ | LW | $N_{V\wedge}$ | L | $p(LW)$ | $p(N_{V\wedge})$ | LW | $N_{V\wedge}$ | L | $p(LW)$ | $p(N_{V\wedge})$ |
| Yli-Kitka | 4 | 9 | 20 | 0.998 | 0.975 | — | — | — | — | — | 5 | 12 | 21 | 0.956 | 0.736 |
| Kitämö | 4 | 8 | 18 | 0.997 | 0.970 | — | — | — | — | — | 4 | 9 | 19 | 0.998 | 0.946 |
| Kirpistö | 5 | 10 | 19 | 0.939 | 0.851 | — | — | — | — | — | 7 | 12 | 20 | 0.548 | 0.612 |
| Muojärvi | 7 | 13 | 19 | 0.514 | 0.257 | — | — | — | — | — | 6 | 12 | 21 | 0.788 | 0.736 |
| Kuusamojärvi | 10 | 14 | 19 | 0.118 | 0.104 | — | — | — | — | — | 7 | 13 | 21 | 0.560 | 0.537 |
| Kostonjärvi | 6 | 8 | 14 | 0.596 | 0.637 | — | — | — | — | — | 4 | 5 | 15 | 0.990 | 0.998 |
| Kerojärvi | 7 | 10 | 16 | 0.430 | 0.462 | — | — | — | — | — | 7 | 11 | 17 | 0.463 | 0.384 |
| Irnijärvi | 6 | 13 | 20 | 0.770 | 0.392 | — | — | — | — | — | 7 | 14 | 21 | 0.560 | 0.327 |
| Oulujärvi | 12 | 19 | 45 | 0.141 | 1.000 | — | — | — | — | — | 10 | 29 | 45 | 0.340 | 0.526 |
| Lentua | — | — | — | — | — | — | — | — | — | — | 9 | 8 | 11 | 0.077 | 0.116 |
| Suomunjärvi | 8 ^a | 18 ^b | 29 | 0.506 | 0.596 | — | — | — | — | — | 8 ^c | 15 ^d | 28 | 0.486 | 0.906 |
| Höytäinen | — | — | — | — | — | 6 | 7 | 12 | 0.512 | 0.552 | — | — | — | — | — |
| North Konnevesi | 6 ^e | — | 21 | 0.788 | 0.537 | — | — | — | — | — | 6 | 8 | 15 | 0.630 | 0.777 |
| South Konnevesi | 5 | 15 | 35 | 0.994 | 0.999 | 12 | 21 | 36 | 0.108 | 0.813 | 14 | 25 | 36 | 0.042 | 0.233 |
| Onkamo | 12 | 16 | 25 | 0.064 | 0.475 | 7 | 9 | 13 | 0.341 | 0.206 | 18 | 22 | 26 | 0.003 | 0.003 |
| Paasivesi | 5 | 6 | 13 | 0.820 | 0.904 | 6 | 10 | 17 | 0.695 | 0.623 | 7 ^f | 7 ^f | 12 ^f | 0.304 | 0.552 |
| Puruvesi Hummonselkä | — | — | — | — | — | 6 | 8 | 17 | 0.695 | 0.935 | 4 ^f | 3 ^f | 8 ^f | 0.866 | 0.925 |
| Harvanselkä | — | — | — | — | — | 12 | 11 | 17 | 0.031 | 0.384 | 6 | 12 | 21 | 0.788 | 0.736 |
| Pyhäjärvi SE Finland | 6 | 6 | 13 | 0.557 | 0.904 | — | — | — | — | — | 7 | 9 | 14 | 0.374 | 0.371 |
| Puulavesi | 5 | 13 | 25 | 0.980 | 0.920 | 8 | 14 | 21 | 0.366 | 0.327 | 20 | 22 | 25 | 0.001 | 0.001 |
| Päijänne Tehinselkä | 5 | 8 | 26 | 0.982 | 1.000 | 5 | 10 | 20 | 0.948 | 0.917 | 18 | 19 | 26 | 0.003 | 0.112 |
| Ruotsalainen | — | — | — | — | — | 6 | 8 | 12 | 0.512 | 0.270 | — | — | — | — | — |
| Pyhäjärvi SW Finland | 11 ^e | 24 ^g | 34 | 0.163 | 0.137 | 7 ^a | 17 ^h | 27 | 0.679 | 0.538 | 16 | 38 | 49 | 0.024 | 0.015 |
| Fisher's test X | | | | 25.5 | 20.3 | | | | 20.6 | 14.0 | | | | 72.4 | 60.1 |
| df | | | | 36 | 36 | | | | 20 | 20 | | | | 42 | 42 |
| p | | | | 0.903 | 0.984 | | | | 0.423 | 0.829 | | | | 0.002 | 0.035 |

^a two missing cases, no effect on the number; ^b one of the missing cases, value 17 or 19, mean 18; ^c two missing cases, value most probably 8; ^d two missing cases, value from 14 to 16, mean 15; ^e one missing case, no effect on the value; ^f several missing cases, value taken from the longest continuous sequence; ^g one missing case, value most probably 24; ^h two missing cases, value from 16 to 19, mean 17.

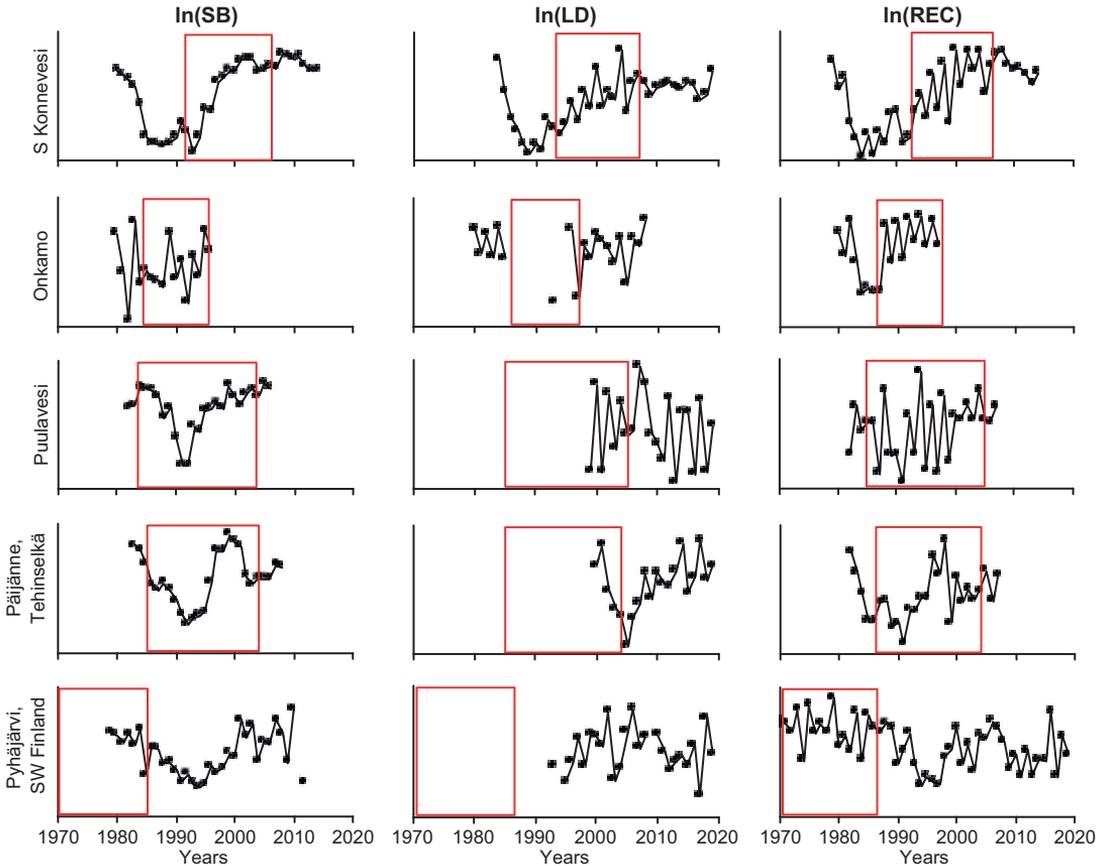


Fig. 3. The time-series of $\ln(\text{spawning stock biomass})$ [$\ln(\text{SB})$], $\ln(\text{larval density})$ [$\ln(\text{LD})$] and $\ln(\text{recruitment})$ [$\ln(\text{REC})$] proxies in five lakes with significant level of two-year cyclicality in recruitment (Table 3). The red boxes indicate the time-sequence of two-year cycle in REC; for lake locations see Fig. 1.

phenomenon (saw blades longer/more frequent than expected from completely random population variability). On the other hand, we found no support for the general tendency for cyclicality in spawning stock biomass or larval density.

Cyclic variation in year-class strength with various cycle lengths has been observed in many taxa (e.g. Myers 2018), including several fish species. Generation cyclicality in semelparous *Oncorhynchus* species with extremely high post-recruitment mortality has been extensively studied (see e.g. Levy & Wood 1992, Myers 1997, 1998). Two-year cycles have been found to occur in, e.g., roach (Townsend 1989, 1990 and references therein), cod (*Gadus morhua*, Bjørnstad *et al.* 1999 and references therein), and rainbow smelt (*Osmerus mordax*, Lantry & Stewart 2000 and references therein). Density-dependent inter-life stage interactions, either

competitive or cannibalistic, are suggested to cause these cycles. In this context, it should be noted that no external biological, physical or chemical environmental variable relevant to vendace is known to perform two-year cycles. Nor is the abundance of any important vendace predator, except perhaps vendace itself (cannibalism suggested by Nordqvist 1944 and observed in laboratory conditions by Urpanen *et al.* 2012), known to cycle biannually. Aquatic predators are also generalists, capable of diet shift. Inter-specific predator–prey interaction (Volterra 1931, May 1973) as a driver of the two-year cycle is thus unlikely and the damped cycles in vendace recruitment must occur due to the intra-specific population regulation.

Typically, the temporal variation in the SB does not at all appear to perform a two-year cycle, on the contrary, it is “sluggish” in compar-

ison to random variation. This is understandable because in real time-series with at least moderate post-recruitment survival, SB should resemble the weighted moving average of the previous few years REC because, after all, SB consists typically of certain previous year classes that survive in the spawning stock for more than a year. Thus, increasing or decreasing local trends of several consecutive years should emerge due to strong variability in REC. Our results support this: typically, a very high probability of as high or higher value of LW and NVA in random time-series compared to observed implies “stiffness” in the time series. However, when post-REC survival is low, SB should consist for the most part of previous year REC only. Consequently, SB should generally be low and fluctuate more (Ricker 1958) — asymptotically as the previous REC. Even a two-year cycle should be present in SB if one exists in REC. We did not study correlations between proxies at different life stages but evidence to support this notion has previously been found in several lakes, most of them exposed to intensive fishing (Table 1) or having naturally high post-recruitment survival (Lake Bolmen, Hamrin & Persson 1986).

Support for two-year cyclicity in LD was negligible. This is as expected because the LD is closely related to the spawning stock (and thus to the population fecundity), which in turn did not show cyclicity either. A positive association between SB and LD was found in lakes Onkamo (Auvinen *et al.* 2000), for certain periods in Pyhäjärvi, SW Finland (Helminen *et al.* 1997, Sarvala *et al.* 2020), and S Konnevesi (Marjomäki *et al.* 2021a). Nissinen (1972) suggested, without formal analysis, that the relationship between SB and egg density in spring was directly proportional.

Unfortunately, the available LD time-series were short and did not match temporally with REC data in many lakes. Of those lakes with significant two-year cycle in REC (Fig. 3), a long sequence of larval data matching temporally with the cycle in REC was available only from S Konnevesi, Paasivesi and Pyhäjärvi, SW Finland. A positive association was found between LD and REC in these lakes (Sarvala *et al.* 2020, Marjomäki *et al.* 2021a; H. Auvinen & J. Järvelius unpubl. data), as well as between three-

week-old larvae and REC in Suomunjärvi (Viljanen 1988) and Onkamo (Auvinen *et al.* 2000). Therefore, based on the available data we do not know exactly at what life-stage the two-year cycle in REC emerges, and we cannot rule out the possibility that it typically appears already in larval stage. Thus, it may be more common for LD than what our data reveal. The considerable measurement error in LD estimates may also mask the cyclicity. High spatial variation in the larval abundance, timing of sampling in relation to the hatching peak of larvae and high mortality of larvae during first weeks after hatching cause the uncertainty in LD estimates. This problem of precision apparently also applies to proxies of SB and REC, but the LD estimate is the only one of those for which the precision was actually estimated. Especially when SB is low, it is difficult, if not impossible, to discern the between-year variation (Sarvala & Helminen 2021).

The fact that our meta-analysis confirmed two-year cyclicity in REC is also not surprising, as it is consistent with previous evidence from several single-lake studies using different methods from mere judging by eye to formal time series-analysis with, e.g. an auto-correlation function (Table 1). The mechanisms causing the cyclicity in REC are outside the scope of this analysis, but we can draw some general conclusions about the states of affairs that facilitate its emergence.

The cycle in REC typically arises in situations in which SB consists of only a few year classes e.g., due to high post-recruitment (fishing) mortality or during recovery from a collapse. Then SB is on average at a low level, so the actual level of density-dependent compensation can be expected to be low in the SB–REC-relationship. Afterwards, the cycle in SB can induce or boost and prolong the cycle in REC directly. The cycle in SB must apparently have been based on a single, possibly accidental successive occurrence of a very abundant and very low recruitment, which induces the onset of damped generation cycle oscillation (*see e.g.* Myers *et al.* 1998).

The existence of a SB-boosted cycle in REC is supported by the current data from the high post-recruitment mortality population in Lake Onkamo, for which the most extreme prob-

ability value for the cycle in SB was found (Auvinen *et al.* 2000), as well as by previous studies from lakes Puruvesi (Nissinen 1972) and Bolmen, Sweden (Hamrin & Persson 1986). In addition, a two-year cycle in REC emerged in Oulujärvi, when fishing mortality increased (Huusko & Hyvärinen 2005). Salojärvi (1987) reported the change in the fluctuation cycle and turnover in Kiantajärvi, when fishing effort was increased. Also, the differences in fluctuation of REC between intensively and practically non-exploited parts of Pyhäjärvi, SE Finland, support the conclusion that fishing affects vendace fluctuations (Auvinen 1994). The SB data matching temporally with REC from the most intensively exploited population in Pyhäjärvi, SW Finland, are short but had a two-year cycle during periods of strong stock in both SB and REC (Sarvala *et al.* 2020, Sarvala & Helminen 2021). Interestingly, three-year generation cyclicality was found during a period of intensive fishing in Lake Mjøsa (Sandlund *et al.* 1991), where the age of maturation of vendace is three growing seasons. The pattern of fluctuation changed, when fishing ceased. Thus, the data support the conclusion that fishing, especially when targeting effectively already pre-mature individuals promotes the shift of cyclical variability to short wave-length cycles. These may induce cascading cycles in the ecosystem more widely.

However, in northern Finnish lakes with very high fishing mortality (Salmi & Huusko 1995) there was typically no significant two-year cyclicality in REC. Partly, this may be because of the short time series (low test power), but it may also be due to the fact that closer to the latitudinal edges of distribution, population dynamics is often proportionally more driven by external climatic factors than the population regulation (e.g. Sæther *et al.* 2003). For vendace, the association between summer temperature and REC in Lake Inari (latitude 69°N) (Salonen 1998), the association between ice-off time and REC in lakes in southern Sweden (Nyberg *et al.* 2001) and the heatwave-associated vendace mortality in shallow Lake Peipsi, Estonia/Russia (Tammiksaar & Kangur 2020) support this conclusion. Therefore, deeper understanding of the effects of climate change on the factors affecting dynamics of ectothermic aquatic populations is essential

in forecasting its consequences, not only trends in the average state of populations, but changes in their variability (e.g. Sæther *et al.* 2003, García-Carreras & Reuman 2013) as well.

The lakes where the cycle in REC was temporally associated with recovery from the collapse were S Konnevesi, Tehinselkä in Päijänne and perhaps Onkamo (Fig. 3).

Finally, there were a few interesting cases where a two-year cycle in REC prevailed for a long time in a population with abundant and non-cyclical SB and only moderate mortality. These include at least S Konnevesi (Marjomäki *et al.* 2021b) and Puulavesi. As lake-specific risk levels (p values) are very low, $\ll 0.01$, these proxy data are unlikely to show spurious significance either (likelihood e.g. for at least one spurious significant series among a set of 23 series with risk level $p = 0.001$ is about 2%). Importantly, since the cycle in REC in these data is very likely not considerably induced or boosted by a cycle in SB, these data are the strongest evidence of the existence of a delayed suppressive effect of the previous year-class on the next. Previously, Helminen *et al.* (2002) showed that delayed density dependence is essential in order to mimic the intensity of the two-year fluctuation observed in SW Pyhäjärvi.

Meta-analysis increases the reliability and generality of the results because conclusions based on published single-lake studies are prone to spurious correlations, even possibly amplified with publication bias (Sterling 1959). On the other hand, in case of a single lake, the test power may be low due to short time-series. In addition, the low precision of population proxies can mask cycles, especially during a low-density period when the relative precision of the proxies is lowest. However, random measurement errors can also produce false cycles in observed proxy time-series, which apparently also applies to the new indicators LW and NVA . Combining the lake-specific evidence should allow these challenges to be overcome to some extent.

An important prerequisite in Fisher's combined probability test is that the combined p values must stem from independent hypothesis tests. In principle, different lakes can be thought of as test benches for independent experiments. However, Marjomäki *et al.* (2004)

showed that the population proxies of nearby lakes are temporally synchronised. Thus, some large-scale environmental variables act as Zeitgebers, occasionally inducing e.g. a very strong year class in several lakes simultaneously. It should be emphasised that none of the environmental variables studied in the context of vendace population dynamics has shown significant two-year cyclicality. Therefore, despite occasional phase-synchronisation, populations of different lakes were considered independent for their short-term fluctuation.

Robust indicators LW and $N_{\vee\wedge}$ proved useful in identifying two-year cycles in time series that hardly obey the assumptions of parametric methods. Yet, the results of previous, methodologically more advanced assessments [e.g. SW Pyhäjärvi (Helminen & Sarvala 1994), Puulavesi (Marjomäki *et al.* 2014)], were in line with the present robust assessment.

LW and $N_{\vee\wedge}$ obviously correlate with each other. LW is in principle a more sensitive saw-blade indicator with a wider range of p values. Yet it is sensitive to low-precision induced false *observed* cuts anywhere in the true cycle or to real random phase shifts due to e.g. extreme state of environmental variable affecting pre-recruitment survival. In addition, LW does not take into account any other, shorter sequence, but only to the longest. For example, the REC time-series from SW Pyhäjärvi, contained separate 9-year and 12-year two-year cycle sequences in addition to the longest 16-year sequence. Thus, LW is a conservative index with a tendency to type-II errors, i.e. a bias in the direction of maintaining the H_0 -hypothesis of no significant two-year cyclicality as opposed to random series. $N_{\vee\wedge}$ was developed to more fully grasp the information about cyclicality by identifying the rudimentary cycle blocks anywhere in the data. This incurs cost in the case of short time series: the test power is low, which in turn makes the indicator prone to type-II errors. In a long series, e.g. in the example above, it was able to detect the saw-blade information more efficiently. Finally, the length of a true population-regulated dampening cycle needs not necessarily be longer than a “random”, accidental environmental-variability-induced cycle. Again, this makes the test conservative towards the hypothesis of random variability (H_0). In view

of all the above, our assessment with these indicators is a conservative one and therefore the main result indicating significant two-year cyclicality in REC (H_1) is very likely to be reliable.

Surprisingly heuristically, in the random time series, the LW and $N_{\vee\wedge}$ indices did not correlate with the Pearson autocorrelation function (ACF) with lag 1 at all (in this test, the random variables were normally distributed as must be assumed). Thus, high LW and $N_{\vee\wedge}$ values do not necessarily mean that a negative serial correlation could be expected. This is obviously due to the fact that the new indices do not take into account the magnitude of the difference between successive observations. Within a time series, the vendace density may vary for a long time around different stable states in completely different order of magnitude (Marjomäki *et al.* 2021b) or around a trended sliding mean (as in S Konnevesi data) potentially still following saw-blade dynamics around that local mean. Our new indicators were quite robust towards these issues, but in order to apply e.g. ACF, one must de-trend the data, possibly remove the effect of SB, and normalize the residuals before the analysis. As mentioned in the introduction, this can be difficult with “dirty” proxies. In contrast, the new indicators, because they only look at two consecutive observations at a time, are quite insensitive to, for example, catchability trends and the statistical distribution of the proxies.

Conclusions

Our results support the interpretation that there is a tendency for two-year cyclicality in vendace recruitment. The results are consistent with the previous model-based prediction that high post-recruitment mortality facilitates the direct loop REC \rightarrow SB \rightarrow REC, enhancing generation cyclicality, prolonging damped oscillation, but that the more direct suppressive effect of the previous REC on the next must be present to adequately explain all the observations.

LW and $N_{\vee\wedge}$ serve as independent robust indices of two-year cyclicality. However, we must emphasize that analytical methods would be recommended for long time-series of high-precision data. ACF (e.g. Helminen *et al.* 1993a, Sarvala *et*

al. 2020) and model-based quantification of the effect of SB and the previous year's REC (e.g. Marjomäki *et al.* 2014) may be more efficient in terms of test power and importantly they reveal the association between different stock indices. Finally, be careful with your eyes: the saw blade easily hits the observer's eye: "random" unpredictable variation just "looks" like a saw blade, when you are tuned into finding regularity.

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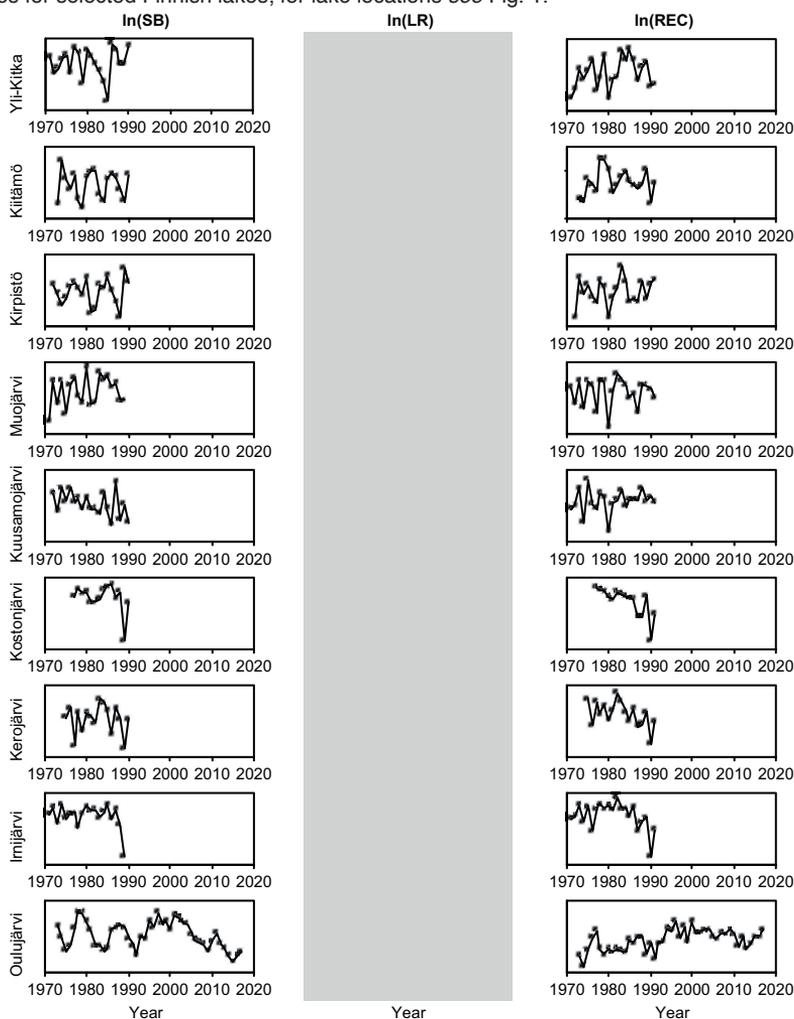
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Appendix 1. The time-series of $\ln(\text{spawning stock biomass})$ [$\ln(\text{SB})$], $\ln(\text{larval density})$ [$\ln(\text{LD})$] and $\ln(\text{recruitment})$ [$\ln(\text{REC})$] proxies for selected Finnish lakes; for lake locations see Fig. 1.



Appendix 1. Continued.

