Author(s): Väänänen, Tuula; Marjomäki, Timo J.; Ranta, Tomi; Karjalainen, Juha

Title: The effect of water level changes on the density of newly hatched European whitefish (Coregonus lavaretus (L.)) larvae in unregulated and regulated lakes

Year: 2024

Version: Published version

Please cite the original version:

Väänänen, T., Marjomäki, T. J., Ranta, T., & Karjalainen, J. (2024). The effect of water level changes on the density of newly hatched European whitefish (Coregonus lavaretus (L.)) larvae in unregulated and regulated lakes. International Journal of Limnology, 60, Article 23. https://doi.org/10.1051/limn/2024019

Int. J. Lim. 2024, 60, 23
© EDP Sciences, 2024
https://doi.org/10.1051/limn/2024019

Available online at:
www.limnology-journal.org

Special issue - Biology and Management of Coregonid Fishes - 2023
Guest editors: Orlane Anneville, Chloé Goulon, Juha Karjalainen, Jean Guillard, Jared T. Myers and Jason Stockwell

RESEARCH ARTICLE OPEN ACCESS

The effect of water level changes on the density of newly hatched European whitefish (*Coregonus lavaretus* (L.)) larvae in unregulated and regulated lakes

Tuula Väänänen[1,*], Timo J. Marjomäki[1], Tomi Ranta[2] and Juha Karjalainen[1]

[1] University of Jyväskylä, Department of Biological and Environmental Science, PO BOX 35 40014 University of Jyväskylä, Finland
[2] Fisheries Centre of Häme, Kustaankuja 2 17200 Vääksy, Finland

Received: 17 January 2024; Accepted: 26 August 2024

Abstract – The effect of the water levels during the period from spawning to hatching of whitefish (*Coregonus lavaretus* (L.)) on the density of newly hatched larvae was examined from a 23-year time series. The density of larvae was estimated in four lakes with contrasting water level regulation regimes in Central Finland using depth zone stratified bongo and tube net sampling in 2000–2022 and 2008–2022. In the regulated Tehinselkä, larval density was also modeled as a function of the whitefish spawning stock, vendace stock indices, and water levels. Larger water level maximum drops during winter were observed in three regulated lakes (41–68 cm) than in the unregulated lake (35 cm). The average larval densities were highest in the unregulated Lake Southern Konnevesi and regulated Tehinselkä, with densities >20 individuals ha^{-1}. The regulated lakes Ruotsalainen and Puula had lower average densities, <10 individuals ha^{-1}. Significant synchrony in the inter-annual variation in the density time series was observed between Tehinselkä and S. Konnevesi as well as Tehinselkä and Ruotsalainen. None of studied water level variables were associated with larval density in any lake. Thus, the small-scale regulation in these Finnish lakes did not show any direct effects on the production of whitefish larvae. Our analysis did not provide information on the potential effects of water level regulation on later life. For example, it did not cover the impact on whitefish food resources or the abundance of competitors and predators regulating whitefish growth and mortality in the juvenile stage.

Keywords: Coregoninae / egg incubation / fish larvae / spawning stock indices / water level regulation

1 Introduction

Several natural factors, such as changes in food quantity and quality, predation, and competition within and between species affect the variation in the abundance and structure of fish populations. In addition, the impact of human activity on fish populations is undeniable, and these effects can be either direct or indirect (Eckmann, 2013; Senlu *et al.*, 2022). An anthropogenic impact on the hydro-morphological and biological factors of lakes and rivers is the regulation of water level for energy production in hydroelectric power plants (Vuorio *et al.,* 2015; Kuriqi *et al.*, 2021). The effects of water level regulation are case-specific and complex, influenced by factors such as amplitude, timing, frequency, and rate of change in water level, as well as morphometry, geology, and biotic community of the lake (Hirsch *et al.,* 2017).

European whitefish (*Coregonus lavaretus* (L.)) is a polymorphic fish species, with its various ecomorphs differing from each other morphologically and ecologically, for example for their morphological measurements, diet, trophic and thermal niches, and spawning habitat (Svärdson, 1979; Kahilainen and Østbye, 2006; Kahilainen *et al.,* 2014; Bitz-Thorsen *et al.,* 2020). European whitefish can be littoral or profundal spawners and their spawning depth is known to vary from a depth of about half a meter up to 200 m (Eckmann and Rösch, 1998; Valkeajärvi *et al.,* 2001). European whitefish spawn in autumn, and their eggs incubate over the winter at the bottom of the lake for five to seven months in boreal regions (Karjalainen *et al.,* 2015). Particularly in lakes with long incubation periods, various factors can impact the development and survival of the whitefish eggs, including the trophic state of the lake, sediment quality, oxygen concentration, and egg predation (Müller, 1992, *C. sp.*; Mills *et al.*, 2002, *C. clupeaformis* (Mitchill); Wahl and Löffler, 2009, *C. lavaretus*; Karjalainen *et al.*, 2021, *C. lavaretus*).

The littoral habitat and biota and littoral spawning fish species and morphs in general, seem to be most vulnerable and sensitive to water level regulation (Carmignani and Roy, 2017;

*Corresponding author: tuula.m.vaananen@jyu.fi

Hirsch *et al.*, 2017). Strong water level regulation has been associated with poor reproduction in whitefish populations (Sutela and Mutenia, 2001, *C. lavaretus*; Sutela *et al.*, 2002, *C. peled* (Gmelin); Mills *et al.*, 2002, *C. clupeaformis*; Winfield *et al.*, 2004, *C. lavaretus*). Often the water level drops in regulated lakes towards spring, and the eggs of autumn-spawning salmonids can be exposed to dehydration and freezing (Brabrand *et al.,* 2002). The effect of thick ice alone reaching the bottom in the shallow littoral area of the lake, without any decrease in water level, has been estimated to cause 5% egg destruction of littoral spawning European whitefish in Lake Päijänne (Valkeajärvi *et al.,* 2001), where whitefish spawn in the shallow littoral zone near the shoreline, and the maximum egg density has been observed at a depth of 0.75 m. The magnitude of the decrease in water levels during the winter and the spawning depth are essential factors in determining the magnitude of the effect of the water level on the survival of whitefish eggs. For example, in Lake Päijänne, a 40 cm drop in water level during winter has been estimated to typically cause 30% (20–40%) mortality of eggs of the littoral zone spawning European whitefish (Valkeajärvi *et al.,* 2001). Additionally, low water levels in late April due to regulation, and wave action after early ice-off have been found to negatively impact European whitefish recruitment (Linløkken and Sandlund, 2016).

Approximately one-third of the total area of all Finnish lakes (more than 300 lakes), is water level regulated or covered by various water level regulatory projects (waterinfo.fi 4.12. 2023). Water level regulation requires a permit, and the permit holder must monitor the effects of regulation on fish stocks and biota in general (Water Act 587/2011). Our study is part of the long-term monitoring stipulated by the water level regulation permit for Lake Päijänne and Lake Konnivesi–Ruotsalainen in Central Finland (ISY, 2002; VHO, 2004; KHO, 2006; Väänänen *et al.,* 2022).

Coregonine fish are the most important target species for inland fishing in Finland. In Tehinselkä basin in Lake Päijänne, there are three different morphs of European whitefish: a large sparsely rakered morph (LSR), a small sparsely rakered morph (SSR), and a densely rakered (DR) morph (Valkeajärvi, 1987; Valkeajärvi *et al.*, 2012; Kahilainen and Østbye, 2006). A negative correlation between vendace (*Coregonus albula* (L.)) and whitefish stock indices has been observed in Lake Päijänne (Valkeajärvi *et al.,* 2012). Competition with vendace is known to negatively affect the growth rate of European whitefish (Raitaniemi *et al.,* 1999; Valkeajärvi *et al.,* 2012), potentially increasing predation mortality and decreasing population fecundity among whitefish. Vendace has the potential to eat whitefish eggs (Berezina *et al.,* 2024) and newly hatched coregonid larvae (Urpanen *et al.,* 2012). This suggests that vendace may, to some extent, affect the production of whitefish eggs and larvae. The negative effect on growth can be caused by food competition between species with similar zooplankton diets (Svärdson, 1979; Sandlund *et al.,* 2013). Dense vendace stocks may decrease the amount of zooplankton in the European whitefish diet and force plankton feeder whitefish to change their diet and eat more benthic food (Svärdson, 1979; Salojärvi, 1992; Pulkkinen *et al.*, 1999). Usually, the diet of European whitefish is associated with habitat, but they can be flexible in their choice of food (Zubova *et al.*, 2023). For example, four different European whitefish morphs in Lake Kuetsjarvi show low specialization of food and use the most abundant resources in the lake (Zubova *et al.*, 2023). One of those is even more versatile than other whitefish morphs and effectively uses both macrozoobenthos, zooplankton, and fish. However, European whitefish morphs with similar trophic position, morphology, diet, and habitat use as vendace are more sensitive to competition by vendace (Sandlund *et al.*, 2013).

This study aimed to investigate the effect of the actual water level and its change during the period from spawning in late autumn to hatching in spring on the density of newly hatched European whitefish larvae in three regulated lakes and one unregulated lake. More detailed data for the Tehinselkä basin in regulated Lake Päijänne enabled the inclusion of the effects of the abundance indices of the spawning population of the whitefish and the possible competing species, vendace, on the whitefish larval density in addition to the variables related to the water level.

We hypothesized that the European whitefish larval density is associated with 1a) the annual wintertime water level change (level drop being negative change), 1b) the water level in spawning time in autumn, or 1c) the minimum water level during the egg incubation period. If the water level is low in autumn there could be less suitable spawning habitat available. The low water level in spring and especially the large drop in water level during the egg incubation period could reduce egg survival as they get exposed to ice compression. We also hypothesized that 2) lakes experiencing a large negative wintertime water level change on average also exhibit lower larval densities on average. This could be attributed to the chronic negative impact of regulation on the average level of survival of eggs from spawning to hatching, consequently influencing average spawning population size and average annual egg production. Our third hypothesis concerns the more intensively studied Tehinselkä basin in Lake Päijänne, where we assume that 3a) European whitefish spawning stock abundance, 3b) vendace abundance, and/or 3c) water level in autumn or spring, or wintertime water level change affects whitefish egg survival and larval density. In addition to the direct positive effect, the effect of European whitefish spawning stock abundance on larval density may include compensatory density-dependent mortality. The vendace population may have a negative or positive effect on whitefish egg survival and larval density. The hypothesized negative effect is the deterioration of the quality of gametes due to food competition between vendace and the European whitefish spawning population in summer/autumn. The hypothesized positive effect is that a higher abundance of the vendace spawning population results in a higher density of coregonids (vendace + whitefish) eggs in autumn, reducing predation mortality of European whitefish eggs and newly hatched larvae and leading to higher larval density in spring.

2 Materials and method

2.1 Study lakes

We studied four oligotrophic boreal lakes in the Kymijoki drainage system in Central Finland. Lake Päijänne (study area Tehinselkä basin, a 25 350 ha central part of a 108 201 ha lake, Valkeajärvi *et al.*, 2012) and Lake Ruotsalainen (study area 4 650 ha central part of a 7 407 ha lake, Väänänen *et al.*, 2022),

are the most strongly regulated lakes. Lake Puula (study area a *ca*. 20 000 ha central part of a 32 911 ha lake, Marjomäki and Huolila, 2001), is moderately regulated, and Lake Southern Konnevesi (12 105 ha) is an unregulated lake (Fig. 1, Tab. 1). According to the Water Framework Directive (2000/60/EC) of the European Union, these lakes are classified as large low-humus lakes (HERTTA, open database of Finnish Environment Institute).

2.2 Water level variables

To determine the intensity of regulation and natural fluctuations of water level during the whitefish egg incubation period, lake-specific daily water level data (in centimeters above sea level, using the NN Geodetic height system in Finland, with the zero point of the water level scale situated at Katajanokka, Helsinki) were obtained from the open data service (HERTTA) of the Finnish Environment Institute. The annual wintertime water level change Δh was calculated using equation (1) (Valkeajärvi *et al.,* 2001):

$$\Delta h = hm_y - h_{Nov15\,y-1} \quad (1)$$

where hm_y = minimum water level before the ice-off in year y (year of hatching of whitefish larvae) and $h_{Nov15\ y-1}$ = water level on November 15 in year $y-1$ (previous autumn, spawning year). November 15 is assumed to be the typical spawning time of European whitefish (Valkeajärvi *et al.,* 2001).

Water levels (altitude system NN, cm above the sea level) in autumn and spring varied considerably between the study years. The range of water levels in autumn ($h_{Nov15\ y-1}$) was in Tehinselkä 76 cm (min. 7780 cm in 2018 and max. 7856 cm in 2012), in Ruotsalainen 26 cm (min. 7736 cm in 2013 and max. 7762 cm in 2008), in Puula 44 cm (min. 9435 cm in 2002 and max. 9479 cm in 2011) and S. Konnevesi 63 cm (min. 9481 cm in 2006 and max. 9544 cm in 2012). The range of minimum water levels in spring (hm_y) was in Tehinselkä 111 cm (min. 7750 cm in 2003 and max. 7861 cm in 2020), in Ruotsalainen 59 cm (min. 7684 cm in 2011 and max. 7743 cm in 2018), in Puula 58 cm (min. in 9421 cm in 2011 and max. 9479 cm in 2020) and S. Konnevesi 56 cm (min. 9479 cm in 2003 and max. 9535 cm in 2020). Synchrony in inter-annual variation in $h_{Nov15\ y-1}$ and hm_y was observed between all lake pairs (Pearson correlation test, all $p < 0.028$, Supplementary material Tab. S1).

Both positive and negative wintertime water level changes (Δh) were observed during the study years in both regulated study lakes Tehinselkä and Puula and the unregulated S. Konnevesi. However, in regulated Ruotsalainen, Δh values were consistently negative in all study years (Supplementary material Fig. S1). The average Δh for all study years was the smallest, indicating the largest average drop in water level during winter, in the regulated Ruotsalainen (average −27 cm, min. −55 cm in 2012–2013, max. −3 cm in 2007–2008) and Tehinselkä (average −13 cm, min. −68 cm in 2012–2013, max. +59 cm in 2019–2020), while moderately regulated Puula (average −5 cm, min. −41 cm in 2012–2013, max. +31 cm in 2019–2020) and unregulated S. Konnevesi (average +3 cm, min. −35 cm in 2012–2013, max. +39 cm in 2019–2020) had larger average of Δh indicating a smaller average drop in water level during winter (Supplementary material Fig. S1). Synchrony in inter-annual variation in Δh was observed between all lake pairs (Pearson correlation test, all $p < 0.009$, Supplementary material Tab. S2).

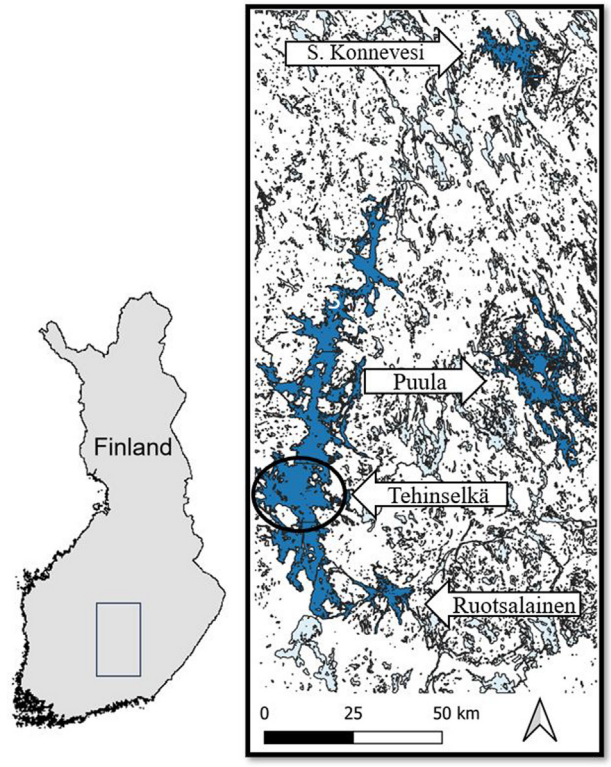

Fig. 1. Locations of study lakes in Central Finland (National land survey of Finland, open topographic data).

2.3 Fieldwork and estimation of larval densities

Newly hatched whitefish larvae were collected on one sampling occasion annually, typically 1−3 weeks after the ice-off in 2000–2022 (Ruotsalainen in 2008−2022) (Supplementary material Tab. S3) using depth-zone stratified bongo and tube net sampling. Identical sampling method, equipment, and stratified sampling design were used in all lakes (Karjalainen *et al.,* 1998; Urpanen *et al.,* 2009). Egg incubation experiments and otolith analyses in the laboratory and field observations from multiple lakes in Finland show that the hatching of the majority of coregonid larvae is triggered by the warming of the water from 1−2 °C to 4−6 °C (Urpanen *et al.,* 2005; Urpanen, 2011; Karjalainen *et al*., 2015). Hatching occurs during the short period before and after (±2 weeks) ice-off and the maximum density of larvae is observed about 2 weeks after the ice-off (Urpanen *et al.,* 2005; Urpanen, 2011). The sampling plots (30 per lake) were randomly selected yearly from the study area of each lake before the year 2010 and kept fixed since 2010 (Lake Ruotsalainen since 2008). Of these, 20 were in the littoral zone and 10 in the pelagic zone. A total of 9 samples were collected from each littoral sampling plot, allocated to different depth strata (0–0.5, 0.5–1, 1–2, and

Table 1. Basic information and water quality in (A) March 2023 and (B) minimum and maximum values for the whole study period in the study lakes (Sampling depth 1 m) The water quality values used for Tehinselkä (Lake Päijänne) were from the nearest deep (over 50 m) sampling point (Central-Päijänne Judinsalonselkä) located 10 km north of Tehinselkä. Information from the Finnish Environment Institute open data service HERTTA 15.9.2023.

	Tehinselkä	Ruotsalainen	S. Konnevesi	Puula
Location	N 61° 29'	N 61° 14'	N 62° 36'	N 61° 47'
	E 25° 26'	E 25° 57'	E 26° 34'	E 26° 41'
Lake area (ha)	108 201	7 407	12 105	32 911
Study area (ha)	25 350	4 650	12 105	20 000
Maximum depth (m)	95	56	57	69
Mean depth (m)	14.2	9.9	12.5	9.2
A) Total phosphorus ($\mu g\,L^{-1}$)	6	6	7	3
B) Total phosphorus ($\mu g\,L^{-1}$)	4−14	2−12	3−14	3−8
A) Colour ($mg\,L^{-1}$ Pt)	38	25	20	27
B) Colour ($mg\,L^{-1}$ Pt)	20−45	20−40	10−40	10−43

2–10 m depending on the lake) and vertical sampling depths (0–0.3 m and 0.3–0.6 m) in the strata with bottom depth ≥ 1 m. Two samples were collected from each pelagic plot (vertical sampling depths 0–0.3 m and 0.3–0.6 m). The annual total sample number was 200 samples per lake. In S. Konnevesi every two years, the pelagic zone sampling depths were 0–0.6 m and 0.7–1.3 m (Supplementary material Tab. S4). Samples from the shallowest littoral stratum (0–0.5 m bottom depth) were collected by wading with a pushed tube net. If the shore was so steep that wading was not possible, the samples were collected using a tube net kept on the side of the boat. In some cases of no sampling in 0–0.5 m due to a very steep depth profile, the density of the shallowest stratum was substituted by the density in the 0.5–1 m stratum of the same sampling plot. All other samples were collected using a bongo net attached in front of a motorboat (length of boats 5 and 9 m). The mesh size of the bongo and tube net was 500 μm. The volume of each sample was determined by a flowmeter attached to the mouth of the net. The typical volume of the tube net sample was approximately 1 m^3, while that of the bongo net sample was approximately 100 m^3 in the littoral zone and 500 m^3 in the pelagic zone The catches were preserved in the field in an ethanol–formalin solution (Karjalainen, 1992).

The species of Coregoninae fish larvae (vendace or European whitefish) was identified based on the number of myomeres, as described by Karjalainen *et al.* (1992), and the number of larvae in each sample was counted in the laboratory. Using the number of larvae and the sample volume, the larval densities (individuals 100 m^{-3}) were calculated for each sampling stratum of the sampling plots (Urpanen *et al.,* 2009). The density outside the sampled vertical depth zone, >0.6 m deep up to 2 m and some cases in the pelagic samples from S. Konnevesi 1.3−2 m), was estimated based on the larval density of samples taken from 0−0.3 m and 0.3−0.6 m depth (and some cases in the pelagic samples from S. Konnevesi 0–0.6 and 0.7–1.3 m), assuming that the rate of density reduction is constant concerning depth (Urpanen *et al.,* 2009). It was assumed that no larvae occupy a depth deeper than 2 m from the surface.

The total number of larvae for the study area in each lake was calculated by multiplying the average density in each depth stratum by the volume of the stratum (Supplementary material Tab. S5). Then, the average larval density (individuals ha^{-1}) in the study area was calculated by dividing the total number of larvae by the study area (Tab. 1). The 95% confidence intervals of the annual average densities in each lake were calculated by bootstrapping, involving the extraction of 5000 new random samples, with replacement, of 20 littoral and 10 pelagic plots from the annual plots. Then, plot-specific sets of observed densities were used to estimate the average larval density as described above. The 2.5% and 97.5% percentiles of these 5000 bootstrap estimates were used as the lower and upper limits of the 95% confidence interval (Karjalainen *et al.,* 2021). During the resampling process, uncertainty regarding depth zone area data was also simulated by drawing them from statistical density functions describing our uncertainty about the true areas. Therefore, the 95% confidence intervals account for the uncertainty stemming from both the spatial variability of fish density and the uncertainty in hypsographic data.

2.4 Association between water level variables and larval density and variation in larval densities between lakes

Because fish density typically does not follow a normal distribution, but more likely *e.g.*, Poisson distribution, all average larval density (D) estimates were ln(D + 1)-transformed before conducting variance, correlation, or regression analyses. In Lake Puula in 2019, the larval density estimate was zero. Therefore, the number 1 was added to the average densities for all years and lakes, enabling a logarithmic transformation and comparability of the data.

The association between annual average larval density and water level variables (Δh, $h_{Nov15\ y-1}$ or hm_y) was analyzed using Spearman's rank correlation coefficient with one-tailed significance test H1: positive association.

The differences between the average of the time series of larval densities both between lakes and between years were tested using analysis of variance (2−ANOVA and Tukey post hoc test) with two-tailed H1: there are differences in the averages of larval densities.

In addition, the temporal variation in larval densities was studied using linear trend analysis. A decreasing linear trend in

annual larval densities could potentially indicate the negative long-term effect of regulation. The synchronicity of the interannual variation in larval density between lakes was analyzed using the Pearson correlation test. In this context, the log-transformed time series were first standardized (mean = 0, standard deviation = 1). Then, to eliminate the effect of the trend, time series were made stationary by linear regression detrending, and Pearson correlation analysis was subsequently performed on the stationarized data (regression residuals).

2.5 Combined effects of spawning stock biomass, vendace abundance, and water level variables on larval density in Tehinselkä

More extensive data was available for Tehinselkä, which enabled more detailed analyses of the impact of water level variables on whitefish larval density.

In Tehinselkä, the whitefish SSR morph is known to spawn in the lake while the DR morph spawns in streams and it is mainly maintained by stockings. The trawl catch per unit effort (CPUE) and catch sample data suggest a very sparse population of LSR morph in Tehinselkä (Valkeajärvi *et al.,* 2012; Puranen and Ranta, 2017). Based on the information presented above, we assumed that the larvae in our study in Tehinselkä stem from the spawning stock of SSR morph. The majority of females (89%) of SSR morph reach sexual maturity at the age of four growing seasons (3+ years) (Valkeajärvi *et al.,* 2012). The proportion of mature SSR morph in the CPUE was estimated based on trawl catch samples (Valkeajärvi *et al.,* 2012, and personal/written communication; Puranen and Ranta, 2017, and unpublished material by Häme Fisheries Centre). The index of lake-spawning SSR whitefish spawning stock biomass (SB_{y-1} in formula 2) was the CPUE (kg h^{-1}) of mature (3+ years and older) SSR morph in a commercial trawl in August.

Additionally, the index of vendace stock abundance was determined using the CPUE (kg h^{-1}) of age 1+ years and older vendace, also obtained from the same data. The vendace population can have a negative or positive impact on the larval density of whitefish in year y. The factor with the hypothesized negative impact in the model is the vendace abundance index (ages 1+ years and older) in year y due to potential food competition during the growing season of the previous year y−1 (then ages 0+ and older) or predation on whitefish eggs (Berezina et al., 2024) in winter and newly hatched larvae (Urpanen *et al*., 2012) in spring y. The factor with the hypothesized positive impact in the model is the vendace abundance index (ages 1+ years and older) in year y−1, assuming that a high abundance of the vendace spawning population can result in a high number of eggs in year y–1, potentially reducing predation mortality of whitefish eggs and hatching larvae in spring y and leading to high survival rate from spawning to hatching.

The whitefish larval density was modeled as functions of the whitefish spawning population biomass index, three water level variables (Δh, $h_{Nov15\ y-1}$, hm_y), and two vendace population density indices (years y–1 and y) to study the association between the larval density and the above-mentioned factors. The water level variables were not included in any model together because of their correlation (multicollinearity). The same applies to vendace CPUE indices for years y and y–1. In all model fitting, least squares regression was used (see detailed description below).

If the survival and mortality of whitefish eggs are not dependent on egg density determined by spawning biomass, then the larval density (D_y) in year y is directly proportional to the whitefish spawning stock (SB_{y-1}) index:

$$D_y = \alpha * SB_{y-1} * \exp(\varepsilon), \tag{2}$$

$$\ln D_y = \ln\alpha + \ln SB_{y-1} + \varepsilon, \tag{3a}$$

where α = constant (density-independent) index of egg survival from spawning to hatching ($\alpha = D_y$ / SB_{y-1}), ε = random error, $\varepsilon \sim N(0, \sigma^2)$, y = year of hatching of larvae and SB_{y-1} = SSR whitefish spawning stock biomass index (CPUE) in year y−1. The index SB_{y-1} is directly proportional to the number of eggs produced by the population (population fecundity) assuming that the sex ratio of the spawners and the fecundity relative to fish weight (eggs g^{-1}) are constant from year to year.

The survival of eggs can also depend compensatorily on density *e.g.*, following the model of Ricker (1954)

$$D_y = \alpha * SB_{y-1} * \exp\left(-\beta * SB_{y-1}\right) * \exp(\varepsilon), \tag{4}$$

$$\ln D_y = \ln\alpha + \ln SB_{y-1} - \beta * SB_{y-1} + \varepsilon, \tag{5a}$$

where β = survival density dependence term.

Environmental factors (X) were included in the equations (3a) and (5a)

$$\ln D_y = f\left(SB_{y-1}\right) + \varphi_t * f(X_t) + \ldots, \tag{3b, 5b}$$

where $f(X_t)$ is a standardization function

$$f(X_t) = (X_t - \text{mean of } X_t)/(\text{standard deviation of } X_t) \tag{6}$$

The suitability of the nested models (3a and 5a and all combinations of 3b and 5b) was compared using the *F*-test. Models are nested when a simpler model is a special case of a more detailed model, *e.g.*, Model 3a is included in Model 5a, as a special case of Model 5 with $\beta = 0$. In addition, Akaike (1973) Information Criterion corrected for small sample sizes (AICc) and Akaike weight (w_i = the probability that the model is the best among the whole set of considered models) were calculated (equations for least squares regression models, *e.g.*, in Glatting et al., 2007).

For every model, it was visually checked whether the model residuals (observation − estimate of dependent variable) implied deviation from normal distribution, heteroskedasticity, or nonlinearity of the effect of the independent variables. No such implications were found.

Statistical tests were conducted using Excel (version 2307, Microsoft Co., Redmond, WA, USA) and SPSS software (version 22.0, IBM Co., Chicago, IL, USA). The threshold for statistical significance was set at 0.05. Based on the Precautionary principle approach of the FAO Code of Conduct of Responsible Fisheries, we tried to keep the test power as

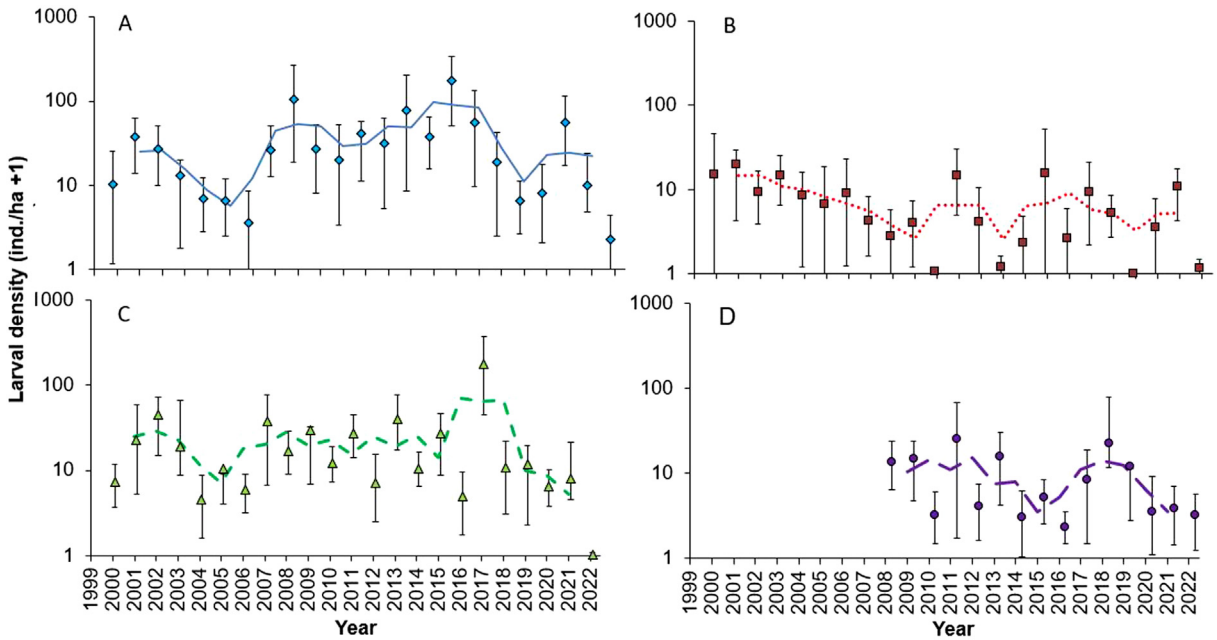

Fig. 2. Average newly hatched whitefish larvae density in spring (*y*-axis logarithmic, vertical line = 95% confidence interval) and sliding mean (3 years) in A) unregulated Southern Konnevesi, B) moderately regulated Puula, C) regulated Tehinselkä (years 2000–2022) and D) regulated Ruotsalainen (years 2008–2022).

high as possible, and for that reason 1) one-way hypotheses were used based on prior knowledge of the factors potentially reducing whitefish egg survival, and 2) Bonferroni correction was not applied for *p*-values. However, when interpreting the results, it should be noted that this increases the risk of rejection of true H_0 (false positive, type I error).

3 Results

3.1 Variation of larval density in study lakes and comparison of larval densities between lakes and years

The inter-annual variation in the larval density estimates (non-transformed data) was high in all lakes, with coefficients of variation ranging from 89% to 159% (Fig. 2 and Tab. 2). The highest annual density estimate during the study period was observed in Tehinselkä in 2017 (178 ind. ha^{-1}) and the lowest in Puula in 2019, where no whitefish larvae were caught (Fig. 2). No significant linear temporal trend was observed in the log-transformed annual larval density of Tehinselkä, S. Konnevesi, and Ruotsalainen in the study years. In Puula, there was a significantly decreasing trend in whitefish larval density over time (Tab. 2 and Supplementary material Fig. S2).

Significant synchrony in inter-annual variation in larval densities (indicated by a positive correlation between time series) was observed in the standardized and log(D+1)-transformed and stationarized larval densities between the pairs Tehinselkä–S. Konnevesi and Tehinselkä–Ruotsalainen (Tab. 3 and Fig. 2).

For the entire study period, there were statistically significant differences in averages of whitefish larval density both between lakes ($F = 11.655$, df = 3, $p < 0.001$) and between years ($F = 2.169$, df = 22, $p = 0.010$). Based on the Tukey test the average larval density for the entire study period was highest and at a similar level in unregulated S. Konnevesi (34 ind. ha^{-1}) and regulated Tehinselkä (23 ind. ha^{-1}), while in regulated Ruotsalainen and moderately regulated Puula, the average larval density was lower and at a similar level, < 10 ind. ha^{-1} (Fig. 2, Tabs. 2 and 4). Temporally, the average larval densities (all lakes) in the time series were lowest in the year 2022, differing significantly from the years 2001, 2002, 2011, 2015, and 2017 (Fig. 2, Supplementary material Tab. S6).

3.2 Association between water level variables and larval density

There was no significant association between larval density and wintertime water level change (Δh, Fig. 3), the water level in autumn ($h_{Nov15\ y-1}$, Fig. 4) or water level in spring (hm_y, Fig. 5) in any of the study lakes (all $p > 0.05$, 1-tailed H_0: positive Spearman correlation between larval density and the water level variable). Only in Lake Ruotsalainen, was the association between larval density and water level in autumn indicative significant, $p = 0.05$ (Fig. 4).

3.3 Effects of water level variables, spawning stock biomass of whitefish, and vendace abundance on larval density in Tehinselkä

Based on the models (3a and 5a), the survival of whitefish eggs in Tehinselkä was not compensatorily dependent on the density of the spawning stock *i.e.*, the larval density was directly proportional to the spawning stock density. The value of parameter β did not differ significantly from zero (Supplementary material Tab. S7) and the goodness of fit of model 5a was not significantly higher than that for model

Table 2. Average larval density (individuals ha^{-1}, non-transformed data), standard deviation = s.d., median = Md and coefficient of variation = CV (standard deviation / average * 100%) and significance of linear trend (ln(D + 1)-transformed data) (*p*-value) of the time series in the study areas.

Study area	Period	Average	s.d.	Md	CV	Trend *p*
Tehinselkä	2000–2022	23	36	11	159%	0.318
Ruotsalainen	2008–2022	8	8	4	90%	0.225
S. Konnevesi	2000–2022	34	40	25	118%	0.985
Puula	2000–2022	6	6	4	89%	0.019

Table 3. Pearson correlation coefficients (r), significance levels (p) for one-tailed H1: positive correlation and number of observations (n) for the standardized ln(D+1)-transformed larval density time-series between the study lakes shown on grey background and those for stationarized (regression residuals) time-series on white background. Statistically significant correlation coefficients are **bolded**.

		S. Konnevesi	Puula	Tehinselkä	Ruotsalainen
S. Konnevesi	r		0.027	**0.482**	0.033
	p		0.451	0.010	0.454
	n		23	23	15
Puula	r	0.029		0.281	0.201
	p	0.448		0.097	0.236
	n	23		23	15
Tehinselkä	r	**0.493**	0.205		**0.536**
	p	0.008	0.174		0.020
	n	23	23		15
Ruotsalainen	r	−0.168	0.204	**0.441**	
	p	0.725	0.233	0.050	
	n	15	15	15	

Table 4. Mean differences in the ln(D + 1)-transformed larval density time series between the study lakes. 2 − ANOVA, multiple comparison: Tukey HSD. Mean difference risk levels (p) according to the two-tailed hypothesis (H1: average larval densities are different) and 95% confidence interval (CI). Statistically significant mean differences are in **bold.**

		Mean difference	*p*	CI
S. Konnevesi	Puula	**1.40**	< .001	0.73–2.08
	Tehinselkä	0.41	0.375	−0.26–1.09
	Ruotsalainen	**1.09**	0.002	0.33–1.85
Tehinselkä	Puula	**0.99**	0.002	0.31–1.66
	Ruotsalainen	0.68	0.096	−0.08–1.44
Ruotsalainen	Puula	0.31	0.702	−0.45–1.07

3a ($F = 0.048$, df1 = 1, df2 = 21, $p = 0.829$). Based on model 3b, neither the water level variable parameters ϕ1: Δh, $h_{Nov15\ y-1}$ or hm_y (Supplementary material Tabs. S8 and S9), nor the vendace population (age 1+ and older) abundance parameters ϕ2 (year y or year y−1) (Supplementary material Tabs. S8 and S9) had a significant effect on the density of whitefish larvae (all *p*-values > 0.351, all *F*-values < 0.43 in comparison to model (3a). The AICc-statistics support the same conclusion; the simple one parameter (α = constant density-independent survival index) model (3a) was most probably ($w_i = 29.7\%$) the best of all models compared (Supplementary material Tab. S10). Thus, the most parsimonious model was

$$\ln(\text{larval density}) = \ln(\alpha) + \ln(\text{whitefish spawning stock index}),$$

where $\alpha = 2.23$, 95% conf. interval = 1.09−3.37 (assuming $\alpha > 0$) and $r^2 = 0.25$.

4 Discussion

No support was found for the hypotheses 1) that the whitefish larval density is positively associated with the annual wintertime water level change (Δh) or water level in autumn ($h_{Nov15\ y-1}$) or water level in spring (hm_y), or that 2) lakes with a large average negative Δh exhibit lower larval densities on average. The observed average larval densities were the highest and at a similar level in both the regulated Tehinselkä with considerable average negative Δh and the unregulated Konnevesi with considerable average positive Δh. The lowest

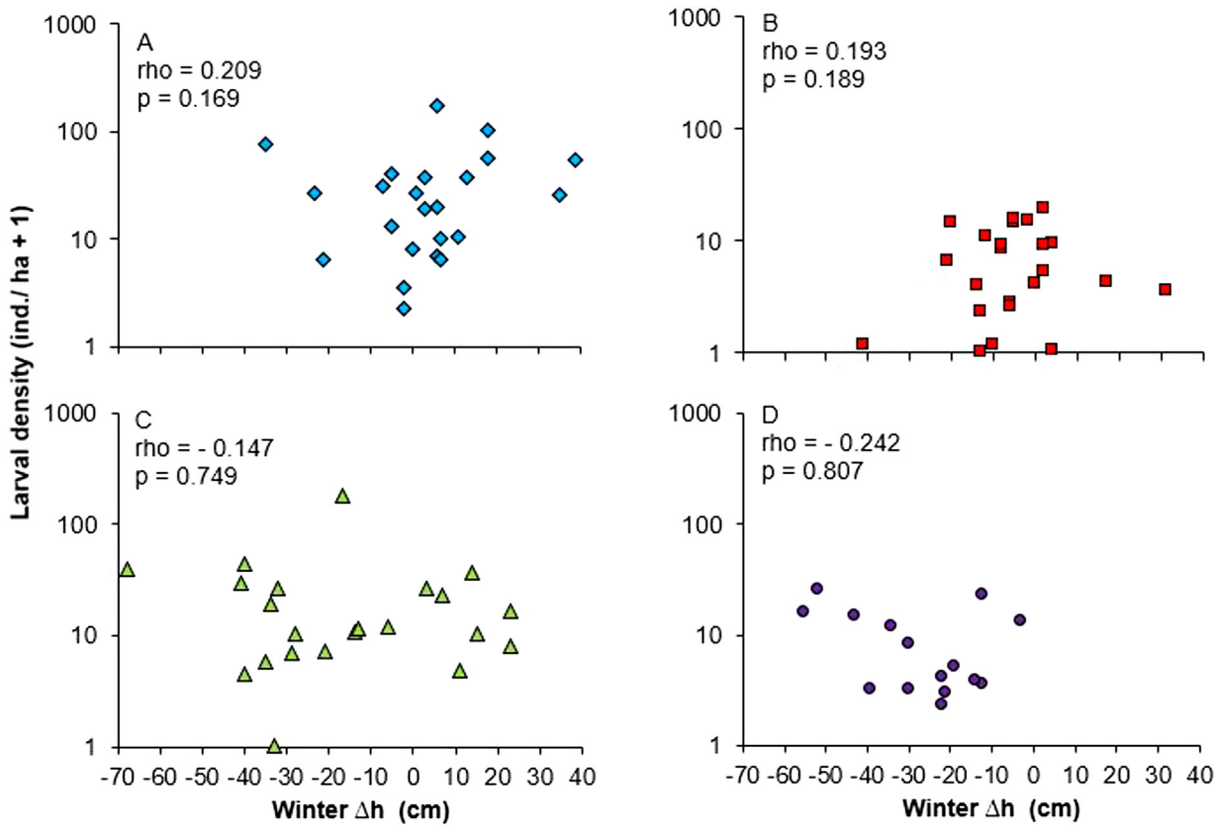

Fig. 3. Association between wintertime water level change, Δh (minimum water level in spring − water level 15.11.) and density of newly hatched whitefish larvae in spring (*y*-axis logarithmic) in A) unregulated Southern Konnevesi, B) moderately regulated Puula, C) regulated Tehinselkä (years 2000–2022) and D) regulated Ruotsalainen (years 2008–2022). Spearman correlation coefficients (rho) and significance level (p) according to the one-tailed hypothesis (H1: positive correlation). Negative Δh = a decrease in water level.

larval densities (all lakes) in the time series were in 2022. However, in the winter of 2021–2022, the Δh was not abnormally negative (large drop) but at the level of the average of the time series.

There was no significant negative trend in the annual larval density of regulated Tehinselkä and Ruotsalainen in the study years. This result also did not support our hypothesis 2) that regulation causes a negative long-term effect on the reproductive efficiency of the spawning stock and a chronic negative impact on larval production. These results align with the conclusions of a previous study (Valkeajärvi *et al.,* 2001), which suggested that egg losses due to water level changes in winter do not significantly regulate the abundance of European whitefish year classes in Tehinselkä. Also, Marttunen (1992) has estimated that the effects of regulation on the carrying capacity of the reproduction areas have a more important role on the European whitefish stocks than regulation-induced changes in egg mortality. However, in moderately regulated Puula, a decreasing trend in European whitefish larval density was observed over the time series. The reason for the decline in Puula remains unknown. No increase in trophy or potential egg predator populations has been reported in Puula. Cunningham and Dunlop (2023) observed significant declines in larval densities of lake whitefish (*Coregonus clupeaformis*) in Lake Huron between the historical (1977–1986) and contemporary time periods (2017–2019, 2021). They found that Dreissenid mussels have a negative association with larval density and water level in November was positively associated with higher larval densities, but the reduced water levels were not a primary factor in the substantial declines in larval densities (Cunningham and Dunlop 2023). Our results for Lake Ruotsalainen implied an indicatively positive association between the water level in November and larval density in the following spring, as Cunningham and Dunlop (2023). The positive association we found may very well be spurious but, according to the precautionary principle, warrants future monitoring.

The lakes in our study are close to each other and therefore exposed to very similar variations in climatic factors that affect water level which causes strong synchrony in the variability of water level variables between all lakes. There was significant synchrony in stationarized and standardized annual larval densities only between Tehinselkä (regulated) and Konnevesi (non-regulated) in 2000–2022 and between Tehinselkä and Ruotsalainen (the largest average drop in water level) in 2008–2022. However, as the water level variables were not associated with larval density, variations in larval density are more likely driven by some other factors. Synchronicity in the variability of populations on a scale of 100–200 km has been found in vendace (*C. albula*, Marjomäki *et al.*, 2004) but it is more likely related to the synchronicity in the inter-annual variability of the regionally correlated exogenous environ-

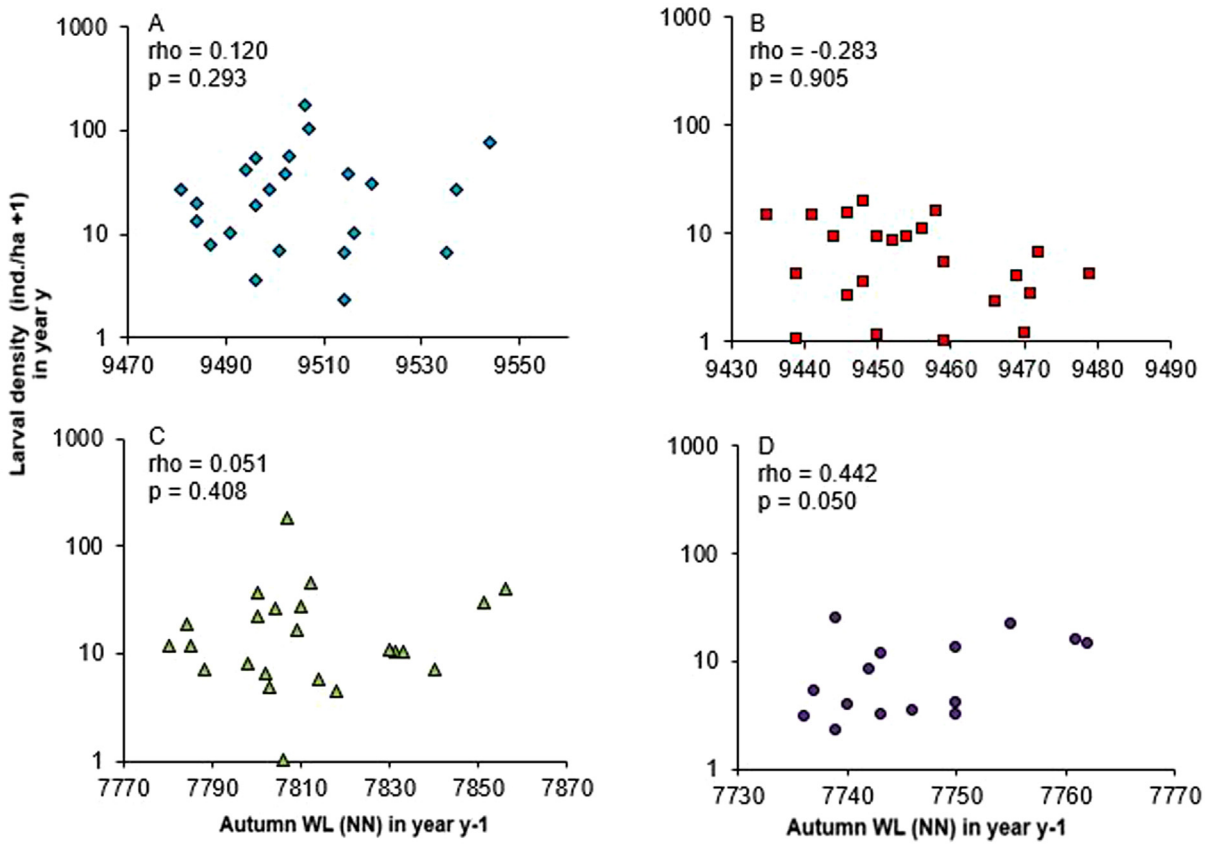

Fig. 4. Association between water level (NN = cm, above the sea level) in autumn, $h_{Nov15\ y-1}$ (water level on November 15. year y−1) and density of newly hatched whitefish larvae in spring y (*y*-axis logarithmic) in A) unregulated Southern Konnevesi, B) moderately regulated Puula, C) regulated Tehinselkä (years 2000–2022) and D) regulated Ruotsalainen (years 2008–2022). Spearman correlation coefficients (rho) and significance level (p) according to the one-tailed hypothesis (H1: positive correlation).

mental factors such as weather-driven phenology of food availability, growth and abundance of predators during the critical periods of early development (Marjomäki *et al.*, 2004).

During the study period from 1999 to 2022, the maximum water level drops (negative Δh) in Tehinselkä were −40 cm in years 2002, 2004, and 2009, and −68 cm in 2013. According to the field observations by Valkeajärvi *et al.* (2001), a drop of about 40 cm should result in 30% (20–40%) additional mortality of European whitefish eggs. This 30% includes the effect of natural water lowering and ice (10%). However, the observed year-to-year variation in larval density estimates was several times larger than the variation in the expected loss. Based on Valkeajärvi *et al.* (2001), the most extreme drop of 68 cm in 2013 should cause a 50% (40–60%) additional mortality of eggs, with about 25% attributed to natural lowering and ice. Surprisingly, despite this substantial water level decrease, the larval density in spring 2013 was not low; in fact, it was the third highest in the entire Tehinselkä time series.

Strong water level regulation has been found to be associated with reduced reproductive success in European whitefish populations (Sutela and Mutenia, 2001; Winfield *et al.,* 2004). Kemijärvi is the most heavily regulated lake in Finland. The amplitude of the water level change varies in different parts of the lake due to bottom dams and natural barriers. During the winter, the water level in the upper part of the lake decreases by 3 m, and in the lower part by 7 m, thus reducing the area of spawning grounds and causing freezing of eggs (Marttunen *et al.,* 2004). Based on interviews with local fishermen, the spawning depth of European whitefish in Kemijärvi ranges from 1 to 6 m, and lake-spawning whitefish can only reproduce in the northern parts of Kemijärvi, where bottom dams have been constructed. It is estimated that regulation has destroyed 90% of the spawning grounds of lake-spawning whitefish (Heikinheimo-Schmid and Huusko, 1987). When examining Kemijärvi as a whole, the reproductive performance of whitefish has been estimated to be poor (Marttunen *et al*., 2004). The proportion of whitefish in total fish catches has decreased since water regulation began (Kerätär *et al.,* 2003). However, even more moderate regulation can be harmful to the reproduction of Coregoninae. For example, Sutela *et al.* (2002) found that the year-class strength and egg survival of peled (*Coregonus peled*) in the two study lakes in Northern Finland were associated with the water level minimum in late winter. In man-made Lokka and Porttipahta reservoirs, peled spawn in areas where water depth ranges from 1 to 3 m. The mean amplitude of regulation of the

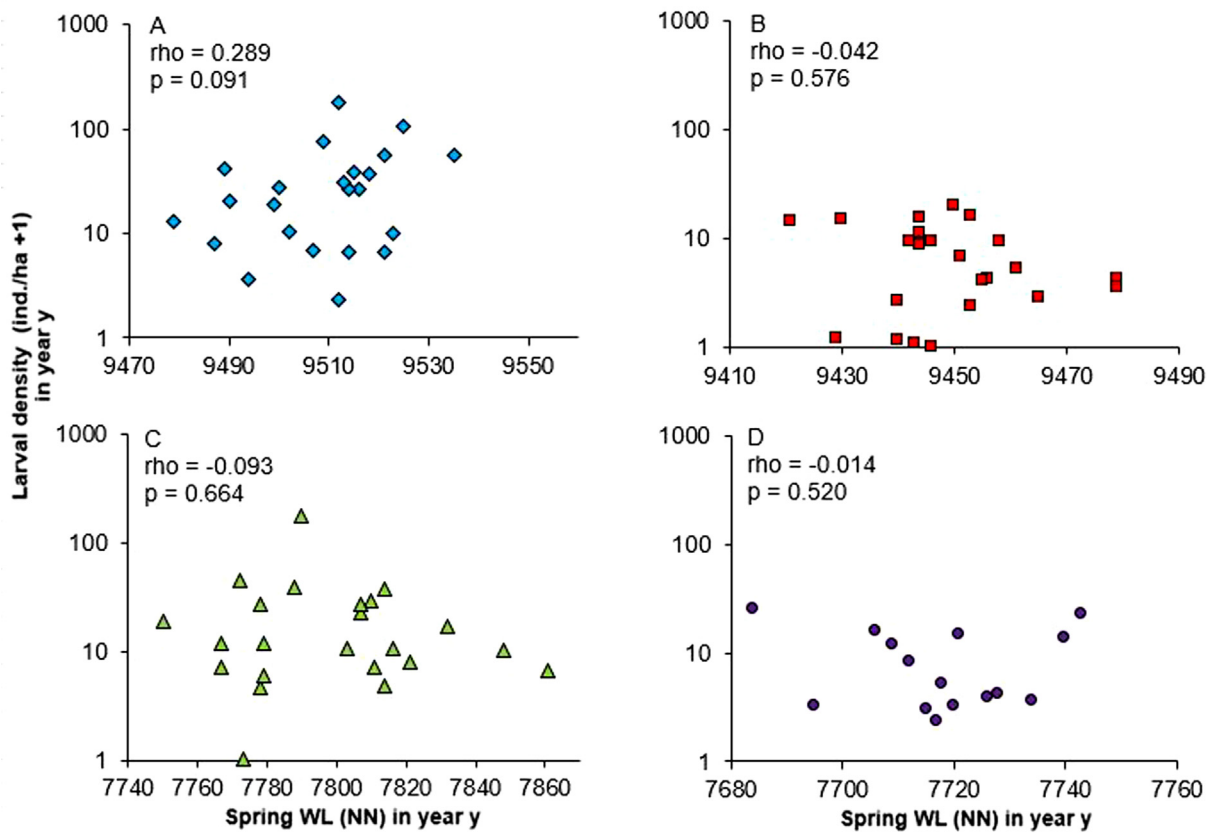

Fig. 5. Association between water level (NN = cm, above the sea level) in spring, hm_y, (minimum water level in spring y before ice off) and density of newly hatched whitefish larvae in spring *y* (*y*-axis logarithmic) in A) unregulated Southern Konnevesi, B) moderately regulated Puula, C) regulated Tehinselkä (years 2000–2022) and D) regulated Ruotsalainen (years 2008–2022). Spearman correlation coefficients (rho) and significance level (p) according to the one-tailed hypothesis (H1: positive correlation).

water level (between the annual lowest and highest levels) was 2.3 m in Lokka and 2.5 m in Porttipahta. It was observed that the strength of the peled year-class was influenced by winter drawdown, likely due to egg desiccation (Sutela *et al.,* 2002). In Lake Päijänne, the spawning areas of European whitefish are located in the shallow littoral zone (1 – 5 m) and eggs are most often found at a depth of 0.75 m (Valkeajärvi *et al.,* 2012). While the spawning depth of whitefish in our study area Tehinselkä in Lake Päijänne is shallower than in the previously mentioned Kemijärvi, Lokka, and Porttipahta, the scale of Δh was also much smaller, and therefore it did not affect whitefish larval densities. In all, the morphometry of the lake affects considerably the potential influence of the water regulation. Finnish lakes are shallow with numerous islands, and long, ragged shoreline with narrow capes and, long and shallow bays which makes the influence of water regulation spatially more complex on them. In shallow bays, even $a < 1$ m water drop may mean hundreds of meters of drying lake bottom or freezing bottom sediment. On the other hand, the ragged shoreline may provide protection for eggs and larvae against wind and turbulence in autumn and spring. The complex littoral zone dispenses spatially and temporally a highly variable habitat for the early development of coregonines, which we have not, yet being a very important aspect, included in our study.

The water level has been found to be one of the environmental factors related to the recruitment dynamics of some other freshwater species. For example, abundances of weekly cohorts of Gizzard shad (*Dorosoma cepedianum* (Lesueur)) larvae were influenced by water temperature and water level in Pomme de Terre and Stockton reservoir lakes (used for both, flood control and hydropower generation) (Michaletz, 1997). The density of newly hatched yellow perch (*Perca flavescens* (Mitchill)) larvae in Lake Saint-Pierre (fluvial lake of the regulated St. Lawrence River) was also lower during the years with low water level and aquatic vegetation biomass (Massicotte *et al.*, 2015), and water level, dissolved oxygen, and temperature were the primary variables affecting the density of larvae of dourado (*Salminus brasiliensis* (Cuvier)) in the Ivinheima River (Rosa *et al.*, 2019).

In our more detailed modeling to reveal the factors affecting European whitefish egg survival in Tehinselkä, the spawning stock biomass was not found to have any compensatory density-dependent effect on the survival of eggs which implies direct proportionality between whitefish spawning stock and larval density. Very little is known about the density-dependent effects during the egg incubation of Coregonines. The data for Lake Konnevesi vendace imply compensation (Marjomäki *et al*., 2021) but the spawner and egg densities are likely two to three orders of magnitude higher

than those for European whitefish there. No evidence was found for hypothesis 3) that water level variables and/or vendace stock regulate the survival of whitefish larvae during the period before hatching (from the development of reproductive products, spawning, fertilization, and over-wintering of the eggs to hatching). Vendace population abundance has been found to be negatively associated with whitefish recruitment at age 2+ years in Tehinselkä (Valkeajärvi *et al*., 2012) but judging from our results, this negative effect must occur after whitefish hatching. The abundance of the age groups of whitefish targeted by fishing is influenced by various factors, including unpredictable environmental factors, the abundance of vendace, as well as the quantity and quality of whitefish fishing (selective fishing based on size and whitefish forms). The negative correlation between vendace and European whitefish stock indices (Valkeajärvi *et al.,* 2012) can, in some cases, be attributed to a statistical bias: higher likelihood of whitefish going undetected by fishers when caught alongside a large vendace catch compared to situations with smaller vendace catches. Furthermore, migration of a larger proportion of the whitefish population into trawling areas may occur when vendace density is low, and pelagic zooplankton density is high (Svärdson, 1976). The exact impact of these factors on the indices remains unknown.

Based on the results, we cannot exclude the possibility that water level fluctuations greater than those observed during the study period could negatively affect European whitefish larvae production. Our study analyzed only the water levels in autumn, minimum in spring, and wintertime water level changes (Δh) during the period from spawning to the hatching of whitefish eggs and provides no information on the later and indirect effects of regulation or the other factors which may be important drivers of larval density and coregonid recruitment. The wide confidence intervals in the annual larval density estimates indicate that the estimates are rough, but they represent the best currently available information. In the future, the estimation method could be improved by considering the effect of changes in catchability as larvae grow and accounting for the temporal peak dynamics of larval hatching within a collecting time (3-week) window.

5 Conclusions

The studied water level variables were not found to have any direct effects on the density of European whitefish larvae or survival of whitefish eggs from spawning to hatching that would have an impact on the fishery. Some other environmental, biological, and/or ecological local factors or interactions regulate the survival of the eggs or larvae in lakes. The abundance of vendace is known to be one of the factors regulating European whitefish population size (Valkeajärvi *et al.,* 2012), but the abundance of vendace population did not affect the survival of whitefish larvae in the period before hatching in Tehinselkä, so the negative effect of vendace on whitefish recruitment must occur during the period after hatching. However, it is important to note that this study does not provide information on the indirect effects of water level regulation, such as the impact on whitefish nursery areas, food resources, or competitors and predators that can affect whitefish growth and mortality after hatching and during the juvenile stage. It should also be noted that our northern study lakes are shallow, with only moderate water level regulation and large, shallow littoral zones. The results should be cautiously applied to lakes with different climates, lake morphometry, intensity of water level regulation, and habitat use and spawning behavior of whitefish.

Acknowledgments

We thank all those who have been involved in the whitefish larvae collection fieldwork over the past twenty years, as well as the technical staff at the University of Jyväskylä. Special thanks are also due to commercial fishermen in Tehinselkä, special researcher Pentti Valkeajärvi (RKTL), and the Fisheries Center of Häme for providing valuable monitoring material and CPUE data from Tehinselkä in Päijänne. We are also grateful for their support to our sponsors and financiers: the Centres for Economic Development, Transport, and the Environment (ELY Centres) of Southeast Finland (formerly Southeast Finland Environmental Center), Southern Savo and Northern Savo, the CORNET project, the TUKALA project of the European Maritime and Fisheries Fund (EMFF).

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contribution statement

TV: data collection, data analysis, and interpretation, manuscript writing, TM: study conception and design, data collection, data analysis and interpretation, supervision, reviewing, TR: data collection, and reviewing, JK: study conception and design, data collection, supervision, reviewing.

Supplementary material

Figure S1. Water level change during winter, Δh (cm), and sliding mean (3 years) in regulated Tehinselkä and Ruotsalainen, unregulated Southern Konnevesi, and moderately regulated Puula. Negative Δh = a decrease in water level.

Figure S2. Time series of standardized ln(D + 1)-transformed whitefish larval density and corresponding linear trendlines in Päijänne Tehinselkä, Southern Konnevesi, and Puula in the years 2000–2022 and Ruotsalainen in the years 2008–2022. The linear trend was significant only in Puula (p = 0.019) (Tab. 2).

Table S1. Correlation between the time series from different study areas for the water level in spring (hm_y, on white background) and water level in autumn ($h_{Nov15\ y-1}$, on gray background). Pearson correlation coefficients (r), risk levels (p) according to the one-tailed hypothesis (H1: positive correlation) and the number of observations (n). Statistically significant correlation coefficients are in **bold**.

Table S2. Correlation between the time series from different study areas for interannual variation in wintertime water level changes (Δh). Pearson correlation coefficients (r), risk levels (p) according to the one-tailed hypothesis (H1: positive correlation), and number of observations (n). Statistically significant correlation coefficients are in **bold**.

Table S3. Sampling dates by study area from 2000 to 2022.

Table S4. Whitefish larval sampling scheme in the littoral and pelagic zones of the study lakes. Samples were collected in 4 strata in the littoral zone and one pelagic stratum in two vertical sampling depths. In the sublittoral zone there were differences in depth limits: [1)] Ruotsalainen [2)] Tehinselkä [3)] Southern Konnevesi [4)] Puula. In the strata with bottom depth > 2 m, the lower limit of whitefish distribution was assumed to be 2 m from the surface.

Table S5. The water volume of sampling strata in the study lakes. For all strata with a bottom depth ≥ 2 m, the volume of the 0–2 m layer for the surface was included in the stratum volume.

Table S6. Significant mean differences in the ln(D + 1)-transformed larval density time series between the years. 2-ANOVA, multiple comparison: Tukey HSD. Mean difference and risk levels (p) according to the two-tailed hypothesis (H1: average larval densities are different) and 95 % confidence interval (CI).

Table S7. Parameter estimates, standard errors of the mean (s.e.), and significance (p) for linear (3a) and compensatory Ricker (5a) models fitted to the Päijänne Tehinselkä basin whitefish larval density–spawning stock data in 2000–2022. α = constant survival, β = compensatory density dependent mortality. One-tailed H1: $\alpha, \beta > 0$.

Table S8. Parameter estimates, standard errors of the mean (s.e.) and significance (p) for linear (3b) model including environmental factors fitted to Päijänne Tehinselkä basin larval density-spawning population data 2000–2022. $\varphi 1$ = effect of wintertime water level change (Δh), $\varphi 1.1$ = effect of water level in autumn ($h_{Nov15\ y-1}$), $\varphi 1.2$ = effect of water level on spring (hm_y) and $\varphi 2$ = effect of vendace population, **year y**, age groups 1+ and older. One-tailed H1: $\alpha, \beta, \varphi 1 > 0, \varphi 2 < 0$.

Table S9. Parameter estimates, standard errors of the mean (s.e.) and significance (p) for linear (3b) model including environmental factors fitted to Päijänne Tehinselkä basin larval density-spawning population data 2000–2022. $\varphi 1$ = effect of wintertime water level change (Δh), $\varphi 1.1$ = effect of water level in autumn ($h_{Nov15\ y-1}$), $\varphi 1.2$ = effect of water level on spring (hm_y) and $\varphi 2$ = effect of vendace population, **year y-1**, age groups 1+ and older. One-tailed H1: $\alpha, \beta, \varphi 1, \varphi 2 > 0$.

Table S10. AICc analysis for different combinations of model 5b including the constant survival α, the compensatory density-dependent mortality β (Ricker 1954) and different non-correlated environmental factors fitted to Päijänne Tehinselkä basin larval density in year y. Data from the years 2000–2022. X = variable included in the model, Δh = wintertime water level change, $h_{Nov15\ y-1}$ = water level in Autumn y–1, hm_y = minimum water level in spring y, Ven y-1 = vendace population (ages 1+ and older) index in year y-1 and Ven y = vendace population (ages 1+ and older) index in year y, AICc = Akaike (1973) Information Criterion corrected for small sample sizes, ΔAICc = AICc – min(AICc), and wi = Akaike weight, the probability that the model is the best among the whole set of considered models.

The Supplementary Material is available at https://www.limnology-journal.org/10.1051/limn/2024019/olm.

References

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov BN. and Csáki F. (eds.), Proceedings of the 2nd International Symposium on Information Theory, Akadémiai Kiadó, Budapest, 267–281. Republished in: Kotz S, Johnson NL. ;1 1992. (eds.), Breakthroughs in Statistics Vol. I, New York: Springer-Verlag pp. 610–624.

Berezina NA, Terentjev PM, Zubova EM, Tsurikov SM, Maximov AA, Sharov AN. 2024. Seasonal diet changes and trophic links of cold-water fish (Coregonus albula) within a northern lake ecosystem. *Animals* 14: e394.

Brabrand Å, Koestler AG, Borgstrøm R. 2002. Lake spawning of brown trout related to groundwater influx. *J Fish Biol* 60: 751–776.

Bitz-Thorsen J, Häkli K, Bhat S, Præbel K. 2020. Allochrony as a potential driver for reproductive isolation in adaptive radiations of European whitefish ectomorphs. *Ecol Freshw Fish* 29: 40–49.

Carmignani JR, Roy AH. 2017. Ecological impacts of winter water level drawdowns on lake littoral zones: a review. *Aquat Sci* 79: 803–824.

Cunningham KE, Dunlop ES. 2023. Declines in lake whitefish larval densities after dreissenid mussel establishment in Lake Huron. *J Gt Lakes Res* 49: 491–505.

Eckmann R, Rösch R. 1998. Lake constance fisheries and fish ecology. *Adv Limnol* 53: 285–301.

Eckmann R. 2013. A review of the population dynamics of coregonids in European alpine lakes. *Ad Limnol* 64: 3–24.

Glatting G, Kletting P, Reske SN, Hohl K, Ring C. 2007. Choosing the optimal fit function: comparison of the Akaike information criterion and the *F*-test. *Med Phys* 34: 4285–4292.

Heikinheimo-Schmid O, Huusko A. 1987. Kemijärven kalatalouden nykytila ja ehdotukset kalakantojen hoitotoimenpiteiksi. *RKTL, kalantutkimusosasto. Monistettuja julkaisuja* 69: 1–21, (in Finnish).

HERTTA version 5.7. Open database of Finnish Environmental Institute. Available at: https://wwwp2.ymparisto.fi/scripts/hearts/welcome.asp. (in Finnish).

Hirsch PE, Eloranta AP, Amundsen P, Brabrand Å, Charmasson J, Helland IP, Power M, Sánchez-Hernández J, Sandlund OT, Sauterleute JF, Skoglund S, Ugedal O, Yang H. 2017. Effects of water level regulation in alpine hydropower reservoirs: an ecosystem perspective with a special emphasis on fish. *Hydrobiologia* 794: 287–301.

ISY. 2002. Decision of the Environmental Permit Authorities of Eastern Finland, 20.12.2002. Register number: 2002/19 (YHy).

Kahilainen K, Østbye K. 2006. Morphological differentiation and resource polymorphism in three sympatric whitefish *Coregonus lavaretus* (L.) forms in a subarctic lake. *J Fish Biol* 68: 63–79.

Kahilainen K, Patterson WP, Sonninen E, Harrod C, Kiljunen M. 2014. Adaptive radiation along a thermal gradient: preliminary results of habitat use and respiration rate divergence among whitefish morphs. *PLoS ONE* 9: e112085.

Karjalainen J. 1992. Effects of different preservation methods on total length and weight of larval vendace (*Coregonus albul* (L.)). *Nordic J Freshw Res* 67: 88–90.

Karjalainen J, Helminen H, Hirvonen A, Sarvala J, Viljanen M. 1992. Identification of vendace *(Coregonus albula (L.)*) and whitefish (Coregonus lavaretus) larvae by the counts of myomeres. *Hydrobiologia* 125: 167–173.

Karjalainen J, Ollikainen S, Viljanen M. 1998. Estimation of the year-class strength of newly hatched fish larvae in Finnish lakes—how sampling design can influence abundance estimations? *Hydrobiologia Special Issues Adv Limnol* 50: 73–80.

Karjalainen J, Keskinen T, Pulkkinen M, Marjomäki TJ. 2015. Climate change alters the egg development dynamics in cold-water adapted coregonids. *Environ Biol Fishes* 98: 979–991.

Karjalainen J, Tuloisela M, Nyholm K, Marjomäki TJ. 2021. Vendace (Coregonus albula) disperse their eggs widely during spawning. *Ann Zool Fennici* 58: 141–153.

Kerätär K, Visuri M, Hellsten S, Ulvi T, Liekonen E, Kiviniemi M, Heikinheimo O, Marttunen M. 2003. Säännöstelyn vaikutukset Kemijärven kalatalouteen. *Lapin ympäristökeskuksen moniste* 48: 1–54, (in Finnish).

KHO. 2006. Decision of the Supreme Administrative Court, 27.2.2006. Register number: 2754/1/04, 3639/1/04, 3640/1/04 ja 3641/1/04.

Kuriqi A, Pinheiro AN, Sordo-Ward A, Bejarano MD, Garrote L. 2021. Ecological impacts of run-of-river hydropower plants-current status and future prospects on the brink of energy transition. *Renew Sustain Energy Rev* 142: e110833.

Linløkken AN, Sandlund OT. 2016. Recruitment of sympatric vendace (*Coregonus albula*) and whitefish (*C. lavaretus*) is affected by different environmental factors. *Ecol Freshw Fish* 25: 652–663.

Marjomäki TJ, Huolila M. 2001. Long-term dynamics of pelagic fish density and vendace (Coregonus albula (L.)) stocks in four zones of a lake differing in trawling intensity. *Ecol Freshw Fish* 10: 65–74.

Marjomäki TJ, Auvinen H, Helminen H, Huusko A, Sarvala J, Valkeajärvi P, Viljanen M, Karjalainen J. 2004. Spatial synchrony in the inter-annual population variation of vendace (Coregonus albula (L.)) in Finnish inland waters. *Ann Zool Fennici* 41: 225–240.

Marjomäki TJ, Valkeajärvi P, Keskinen T, Muje K, Urpanen O, Karjalainen J. 2021. Towards sustainable commercial vendace fisheries in Finland: lessons learned from educating stakeholders for management decision-making based on imprecise monitoring data. *Advanc Limnol* 66: 25–46.

Marttunen M. 1992. A system model for the effects of lake regulation on European whitefish stocks. *Pol Arch Hydrobiol* 39: 885−894.

Marttunen M, Hellsten S, Kerätär K, Tarvainen A, Visuri M, Ahola M, Huttunen M, Suomalainen M, Ulvi T, Vehviläinen B, Väntänen A, Päiväniemi J, Kurkela R. 2004. Kemijärven säännöstelyn kehittäminen − yhteenveto ja suositukset. *Lapin − ja Suomen Ympäristökeskuksen raportti, Suomen ympäristö* 718: 70–96, (in Finnish).

Massicotte P, Bertolo A, Brodeur P, Hudon C, Mingelbier M, Magnan P. 2015. Influence of the aquatic vegetation landscape on larval fish abundance. *J Great Lakes Res* 41: 873–880.

Michaletz PH. 1997. Factors affecting abundance, growth, and survival of age-0 gizzard shad. *Trans Am Fish Soc* 126: 84–100.

Mills KH, Chalanchuk SM, Allan DJ, Bodaly RA. 2002. Abundance, survival, condition, and recruitment of lake whitefish (Coregonus clupeaformis) in a lake subjected to winter drawdown. *Adv Limnol* 57: 209–219.

Müller R. 1992. Trophic state and its implications for natural reproduction of salmonid fish. *Hydrobiologia* 243/244: 261–268.

Pulkkinen K, Valtonen ET, Niemi A, Poikola K. 1999. The influence of food competition and host specificity on the transmission of *Triaenophorus crassus* (Cestoda) and *Cystidicola farionis* (Nematoda) to *Coregonus lavaretus* and *Coregonus albula* (Pisces: Coregonidae) in Finland. *Int J Parasitol* 29: 1753–1763.

Puranen M, Ranta T. 2017. Päijänteen Tehinselän yleisveden siika- ja muikkuseuranta 2011- 2016. *Hämeen kalatalouskeskuksen raportti* 11/2017: 5–7, (in Finnish).

Raitaniemi J, Malinen T, Nyberg K, Rask M. 1999. The growth of whitefish in relation to water quality and fish species composition. *J Fish Biol* 54: 741–756.

Ricker WE. 1954. Stock and recruitment. *J Fish Res Board Can* 11: 559–623.

Rosa RR, Silva JC, Bialetzki A. 2019. Long-term monitoring of potamodromous migratory fish larvae in an undammed river. *Mar Freshw Res* 71: 384–393.

Salojärvi K. 1992. Compensation in whitefish (Coregonus lavaretus L. s.l.) populations in Lake Oulujärvi, Northern Finland. *Finn Fish Res* 13: 31–48.

Sandlund OT, Gjelland KØ, Bøhn T, Knudsen R, Amundsen P-A. 2013. Contrasting population and life history responses of a young morph-pair of European whitefish to the invasion of a specialised Coregonid competitor, vendace. *PLoS ONE* 8: e68156.

Senlu Y, Yujun Y, Qi L, Qiyoung L, Kebing C. 2022. A review on effects of human activities on aquatic organismsin the Yangtze River Basin since the 1950s. *River* 1: 104–119.

Sutela T, Mutenia A. 2001. Kirjallisuuskatsaus pohjoisten tekojärvien kalataloudesta. *Kala- ja riistaraportteja* 214: 1–23, (in Finnish).

Sutela T, Mutenia A, Salonen E. 2002. Relationship between annual variation in reservoir conditions and year-class strength of peled (*Coregonus peled*) and whitefish *(C. lavaretu*). *Hydrobiologia* 485: 213–221.

Svärdson G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. *Rep Inst Freshw Res Drott* 55: 144–171.

Svärdson G. 1979. Speciation of scandinavian coregonus. *Rep Inst Freshw Res Drott* 57: 1–95.

Urpanen O, Huuskonen H, Marjomäki TJ, Karjalainen J. 2005. Growth and size-selective mortality of vendace (Coregonus albula (L.)) and whitefish (C. lavaretus L.) larvae. *Boreal Environ Res* 10: 225–238.

Urpanen O, Marjomäki TJ, Viljanen M, Huuskonen H, Karjalainen J. 2009. Population size estimation of larval coregonids in large lakes: stratified sampling design with a simple prediction model for vertical distribution. *Fish Res* 96: 109–117.

Urpanen O. 2011. Spatial and temporal variation in larval density of coregonids and their consequences for population size estimation in Finnish lakes. *Jyväskylä Stud Biol Environ Sci* 222: 1–49.

Urpanen O, Marjomäki TJ, Keskinen T, Karjalainen J. 2012. Features of intercohort cannibalism of Vendace (*Coregonus albula* (L.)) under laboratory conditions. *Mar Freshw Behav Physiol* 45: 177–184.

Valkeajärvi P, Riikonen R, Keskinen T. 2001. Siian kutusyvyys ja säännöstelyn vaikutus siikaan Päijänteessä. *Kala- ja riistaraportteja* 232: 1–25, (in Finnish).

Valkeajärvi P, Marjomäki TJ, Raatikainen M. 2012. Vendace and whitefish stocks in Lake Päijänne in 1985–2010. *Riista- ja kalatalous − Tutkimuksia ja selvityksiä*, 3/2012: 1–35, (in Finnish, English abstract) http://urn.fi/URN:ISBN:978-951-776-882-5

Valkeajärvi P. 1987. On the species and growth of whitefish (*Coregonus lavaretus* L. *s.l.*) in Lake Päijänne. *Biol Res Rep Univ Jyväskylä* 10: 133–145.

VHO. 2004. Decision of the Administrative Court of Vaasa, 9.9.2004, Register number: 00490-00496/03/8150.

Vuorio K, Järvinen M, Moilanen S, Kotamäki N, Bilaletdin Ä. 2015. Water level regulation in winter triggers fouling of fishing nets by the diatom Aulacoseira islandica in a boreal lake. *Boreal Env Res* 20: 587–602.

Väänänen T, Marjomäki TJ, Karjalainen J, Ranta T. 2022. Päijänteen ja Konnivesi-Ruotsalaisen säännöstelyn kalataloudellinen tarkkailu: Siian poikastuotantoon kohdistuva seuranta jakson 2018–2022 seurantatulokset sekä koko seurantajakson 2008–2022 loppuraportti. University of Jyväskylä, 23 p. (in Finnish).

Wahl B, Löffler H. 2009. Influences on the natural reproduction of whitefish (*Coregonus lavaretus*) in Lake Constance. *Can J Fish Aquat Sci* 66: 547−556.

Winfield IJ, Fletcher JM, James JB. 2004. Modelling the impact of water level fluctuations on the population dynamics of whitefish (*Coregonus lavaretus* (L.)) in Haweswater, U.K. *Ecohydrol Hydrobiol* 4: 409–416.

Waterinfo.fi, 4.12. 2023. Research-based information on water issues for the website is produced by the Finnish Environment Institute, the ELY Centres, the Finnish Meteorological Institute, and the Flood Centre in collaboration with water sector expert organisations. https://www.vesi.fi/teemasivu/vesistojen-saannostely/

Zubova EM, Kashulin NA, Terentyev PM, Denisov DB, Valkova SA, Cherepanov AA, Postnova SV, Melekhin AV. 2023. Foraging morphology and diet divergence of European whitefish (Coregonus lavaretus) in water courses of Murmansk region. *Limnologica* 99: e126053.

Cite this article as: Väänänen T, Marjomäki TJ, Ranta T, Karjalainen J. 2024. The effect of water level changes on the density of newly hatched European whitefish (*Coregonus lavaretus* (L.)) larvae in unregulated and regulated lakes. *Int. J. Lim.* 60: 23.