

# Vendace (*Coregonus albula*) disperse their eggs widely during spawning

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Depending on their reproductive strategy, different fish species either aggregate or disperse eggs and larvae in their reproductive habitat. Because yolk-sac larvae of vendace (*Coregonus albula*) disperse widely across the littoral and pelagic zones of boreal lakes, it is unclear where the exact spawning and egg incubation locations are. Vendace egg and larvae densities were studied in Lake Southern Konnevesi to clarify its spawning strategy. In autumn 2019, 1–2 weeks prior to spawning, 500 egg samplers were installed in five depth zones in 20 sampling plots. Fertilized eggs were found in 18 plots. The mean density of eggs was 74 eggs m<sup>-2</sup> and the mean fertilization rate 85%. During spawning, vendace dispersed their offspring throughout the lake. The sampling-plot-specific egg density in autumn 2019 did not correlate with larval density in the spring next year. The reproduction strategy of vendace reduces the effects of high spatial and temporal fluctuation in their reproduction and nursery habitats.

## Introduction

Reproductive strategies of different fish species vary from attentive parental care of offspring to broadcast spawning in which high numbers of eggs and sperm released into the surrounding environment are left unattended (Wootton 1997). Most fish species are broadcast spawners and especially in unpredictably variable environment, such strategy guarantees that at least some of the newly hatched larvae encounter conditions favourable for survival and growth. Lambert and Ware (1984) suggested a “continuum of reproductive strategies with ‘bet hedging’ at one extreme and an “all at once” egg release at the other”.

Karjalainen and Marjomäki (2018) discovered that autumn-spawning vendace (*Coregonus*

*albula*) is a batch spawner which seems to have the bet-hedging reproductive strategy in space and time, where larvae and presumably also eggs are allocated widely into different habitats around lakes (Karjalainen *et al.* 2019). In long-term monitoring of vendace larvae in Finnish lakes, it was found that only 4%–15% of the random sampling plots in the littoral zone did not contain vendace larvae, and the simulation results from an egg distribution model supported the hypothesis that the spawning of vendace in Lake Southern Konnevesi occurs in littoral and sub-littoral zones across the entire lake (Karjalainen *et al.* 2019). In boreal, oligotrophic, large lakes with fragmented morphology and complex shoreline, weather-induced conditions (winds, currents, water level, water temperatures, ice conditions), water quality and

predation between spawning in autumn to hatching in spring vary spatially unpredictably from year to year. The bet-hedging strategy mitigates the effects of high spatial and temporal fluctuations on the offspring survival and consequently, inter-annual population fluctuation.

Egg abundance monitoring of coregonids is used to study location of spawning areas (Amidon *et al.* 2019), spawning time (Irvine *et al.* 2017), egg density and mortality (Nissinen 1972, Viljanen 1980, Žuromska 1982, Ventligen-Schwank & Müller 1991, Müller 1992), and spawning stock size (Wahl & Löffler 2009). In coregonid spawning, eggs released by females and possibly fertilised by males sink towards the bottom sediment. To collect the eggs from the bottom, both active and passive sampling methods can be used. Different kind of pumping systems with a salt-water sampling chamber (Nissinen 1972), sled (Stauffer 1981) or suction nozzles (Tiitinen 1982, Viljanen 1988) have been developed and successfully used. Towed dredges have been useful in deep lakes, even to the depth of 250 m (Müller 1992, Wahl & Löffler 2009). Bagenal and Nellen (1989) reported that “eggs of whitefish *C. lavaretus* have been collected by a SCUBA diver with a pipette from a sandy bottom, and this method could be made quantitative”. Active sampling of coregonid eggs is a slow and laborious process, which can be carried out mainly in restricted areas or in areas where spawning is known to happen. The information obtained is often relative catch per unit effort and the sampling is possible only at relatively hard bottoms. Passive samplers such as egg mats (Roseman *et al.* 2011, 2012) are lowered to the bottom in the potential sampling areas before spawning. They provide quantitative density estimates (e.g. eggs m<sup>-2</sup>).

In this study, we developed a new passive egg sampler with removable egg-collecting net bag. It is a smaller device compared with the traditional passive egg mat with a greater surface area, and practical in field without large vessels.

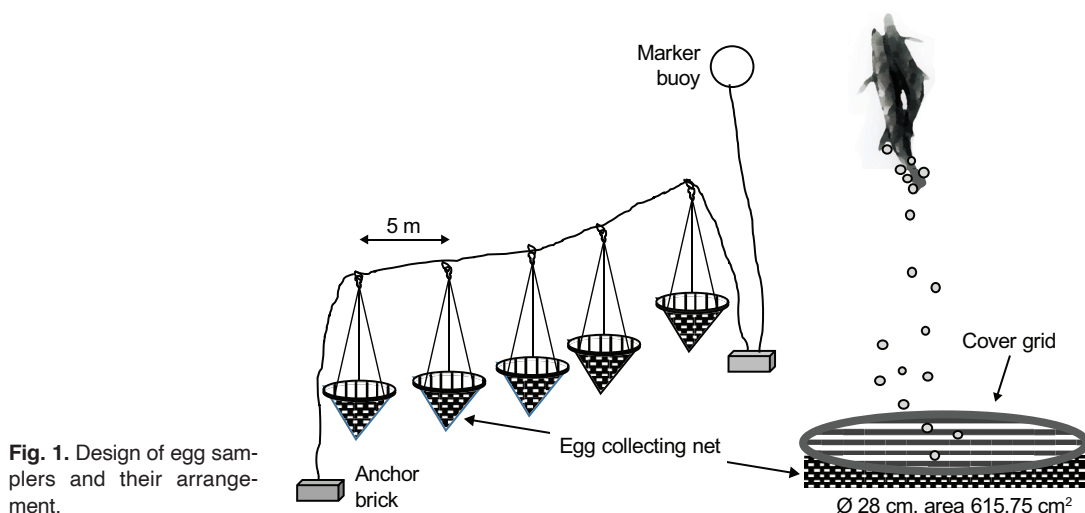
Detailed information on spawning behaviour of vendace in nature, movements of spawning shoals, spawning site fidelity, distribution of spawning areas, and subpopulation structure is still lacking. By developing new methodology and a sampler for coregonid egg sampling and analysing the distribution of vendace eggs

in a boreal lake together with long-term larval sampling protocol (Urpanen *et al.* 2009), we examined the reproductive strategy and dispersion patterns of early life stages in coregonids. We hypothesized that (1) vendace disperse their eggs during spawning across the entire lake, and (2) the within-sampling-plot egg density correlates with the density of newly hatched larvae in spring. We also aimed to determine the fertilization rate of eggs caught by the egg samplers and estimate the survival of embryos during the egg incubation as well as total population fecundity and spawning stock size of vendace, which would deepen the body of knowledge for coregonid fisheries management.

## Material and methods

The egg distribution and location of spawning areas of vendace were studied in Lake Southern Konnevesi (henceforth Lake Konnevesi; 62°37'N, 26°27'E; area 12 000 ha). This lake, located in central Finland, is oligotrophic (total P < 10 µg l<sup>-1</sup>) and oligohumic–mesohumic (colour 25–35 mg Pt l<sup>-1</sup>) with a productive population of vendace and its commercial fishery (Karjalainen *et al.* 2016b, Marjomäki *et al.* 2020). The mean biomass of vendace was 22 kg ha<sup>-1</sup> in 2004–2007 (Karjalainen *et al.* 2016b). Vendace is a small pelagic planktivore (typically < 20 cm in length) with short life-span (typically < 5 years). Major part of the cohort reaches its sexual maturity at the age of 2 summers (Karjalainen *et al.* 2016b).

In mid-October 2018 and 2019, 1–2 weeks prior to the expected spawning, egg samplers (Fig. 1) were set according to stratified sampling design in potential spawning areas in Lake Konnevesi and left there for 23–30 days (in 2019, first samplers set on 14 October and last taken out on 14 November). A sampler was comprised of a plastic rim with a cover grid and an egg-collecting net bag. The diameter and area of a sampler were 28 cm and 615.7 cm<sup>2</sup>, respectively (Fig. 1). The gab width of the grid was 5 mm and eggs sunk through the grid into the egg-collecting net (mesh size 0.2 mm). In Lake Konnevesi, the diameter of fertilized vendace eggs is < 2 mm (first author's unpubl. data). The



**Fig. 1.** Design of egg samplers and their arrangement.

net bag was under the grid when the sampler was on the bottom. Eggs were flushed to the cod end of the net bag during lifting of the sampler. In 2018, 50 samplers were lowered to the bottom at one spawning plot (plot 11) and in 2019, 500 samplers were placed in 20 sampling plots. Of those plots, 15 were selected from 20 regular and randomly located littoral larval-vendace monitoring plots (Karjalainen *et al.* 2019). Five regular monitoring plots (3, 12, 13, 17, 19) were excluded and replaced with 5 extensive sampling plots (30, 35, 43, 71, 73). Selection criteria for the five extensive sampling plots were: (1) in extensive larval sampling in 2016 and 2017 (20 regular and 60 extensive sampling plots), newly hatched vendace larvae were observed in those plots, (2) the egg distribution back-casting by the 3-D hydrodynamic model (Karjalainen *et al.* 2019) showed that due to their remote locations, the larvae caught from these sampling plots should have hatched in nearby spawning areas.

A row of egg samplers contained originally five samplers attached to a rope with 5-m distance between samplers. In each plot, 4–9 sampler rows were installed in 4–5 depth zones: 0–3, 3–6, 6–9, 9–12, and 12–15 m bottom depth (see Appendix). In eight plots, the water depth was < 12 m. In 2018, only the depth zones 3–6 and 9–12 were sampled in one plot (plot 11). Numbers of rows and depth zones depended on the littoral depth in the sampling area, and in the plots with low density of newly hatched larvae

in 2016 and 2017, extra rows were installed in order to obtain at least some sampled eggs from these plots. The depth of water was monitored by an echo sounder.

The timing of spawning was monitored by gill net fishing in three plots (11, 21 and 71). In each plot, mature and ripe females and males were caught. The end of the spawning season was ascertained from the degree of ripeness (ripe, running ripe and spent) of fish caught from the spawning-monitoring plots and water temperature: spawning was assumed to cease when the water temperature dropped below 4 °C (Karjalainen & Marjomäki 2018). In 2019 in four plots, the water temperature was between 4.1–4.6 °C on the day of lifting the samplers. On the lifting day in plot 11, water temperature was 4.4 °C and 75% of females and all males were in the category “spent”. Only one female was ripe and all running ripe females had already laid major part of their eggs.

The autumn 2019 was cold and Konnevesi started to freeze up during the egg sampling period. Due to the ice cover in plot 20, 5 rows of samplers could not be lifted. Further, 3 rows of samplers disappeared during the sampling period. During sampler lifting it was also noticed that 1–3 samplers in some rows were in incorrect positions (i.e. upside down or tilted), hence these samplers were excluded from the data. The total numbers of the sampler rows and samplers in the analysis were 92 and 441, respectively

(see Appendix). In 2018, 36 of 50 samplers were lifted and included in the analysis.

Immediately after lifting, the net bags of samplers were detached from the cover grids, packed individually in plastic bags, placed in styrofoam boxes and transported to the laboratory within 2–4 hours after lifting. Each net bag was separately and carefully flushed into a sieve with 500  $\mu\text{m}$  mesh. Then the sieve contents were flushed into a white bowl where eggs were counted and their fertilization rate was determined.

In each sampling plot, one temperature logger (Hobo UA00108) was attached with a cable tie to an anchor brick of the sampler row located in the depth zone of 3–6 m. The logger recorded bottom water temperature ( $^{\circ}\text{C}$ ) each hour between the setting and lifting days of samplers, i.e. for 23–30 days. In 2019, there were 20 loggers in total, and 19 of those were recovered while one was lost. The data from those loggers were used in this study.

For intercalibration purposes, all 19 loggers removed from the lake, were placed for about two weeks in one bucket with cold (lake) water flowing through where they measured the temperature hourly. The temperatures measured by every logger in the field were corrected by subtracting from the daily average temperature the logger-specific mean deviation value (range of logger-specific deviation values was from  $-0.26$  to  $+0.26$ ). The deviation values were obtained by (1) calculating the mean value for all loggers exposed to the same temperature in the bucket and (2) subtracting the logger-specific temperature from that mean. The deviation value for each logger was the mean of the logger-specific deviations during the calibration period.

In spring, samples of larvae were taken from the littoral zone of each plot using a stratified-sampling procedure (Urpanen *et al.* 2009). The sampling depths (lower-depth limit) were 0–0.5 m, 0.5–1 m, 1–2 m and 2–4 m. In the shallow littoral zone (0–0.5 m), samples were taken with a tube net pushed by a wader, and in the remaining depths ( $> 0.5$  m) using engine-powered boat with Bongo nets attached in front. In both cases, the mesh size of the net was 500  $\mu\text{m}$ . In the spatial analysis in this study, only samples taken from the uppermost sampling layer of 0–30 cm were used because in Finnish

lakes, the majority of vendace larvae (over 70%) aggregates soon after hatching near the water surface (Urpanen *et al.* 2009). Thus, the density in this sampling layer serves as a sufficient index of total density. The volume sampled by each tow was measured by a flowmeter and larvae density was expressed as individuals  $100\text{ m}^{-3}$ . Estimates of the average larval density (indiv.  $100\text{ m}^{-3}$ ) in the samples from the four sampling zones were used as indices of density in each plot. The average larval population density (indiv.  $\text{ha}^{-1}$ ) and 95% confidence limits for the entire lake were estimated according to Urpanen *et al.* (2009) by resampling (bootstrap): 5000 random samples of 20 littoral and 10 pelagic plots were drawn from the original plot data and average density was then estimated based on their data.

Slope of the littoral zone in the larvae and egg sampling plots was calculated from the slope raster data (resolution 5 m), which was created with the planar method of the Slope tool of Spatial Analyst extension in ESRI ArcGIS Desktop 10.5.1 (ESRI 2011). The tool determines the slope (in degrees) from an elevation surface raster as the maximum rate of change in the value from a cell to its immediate eight neighbouring cells, using the average maximum technique (Burrough & McDonnell 1998). The elevation surface for the calculation of the slope was a mosaic raster constructed from an open-source elevation model (source National Land Survey of Finland) and a bathymetry map processed using TIN surface analysis from the depth contour data (source Finnish Environment Institute) that was before the TIN analysis transformed into N2000 height values. The mean slope value was extracted for every larval sampling plot area, which was determined as a minimum bounding area that enclosed all the samplers in the plot with a further 50-m buffer around the enclosing area. The areas of the sampling plots varied between 5900 and 80 675  $\text{m}^2$ .

To estimate the total egg abundance (estimate of population fecundity) and larval abundance in spring, the total area of each depth zone used in the egg and larval sampling in the lake was extracted from raster bathymetry with Raster Calculator tool in ESRI ArcGIS Desktop 10.6.1. The raster bathymetry used in the area calculations of the sampling depth zones was processed

in ESRI ArcGIS Desktop 10.5.1 from digitized navigational chart depth contours (source Finnish Environment Institute 2017) with TIN surface analysis which result was further rasterised to 5-m resolution.

The effect of depth zone on egg density and fertilization rate were analysed using the independent samples Kruskal-Wallis test. Samples from the different depth zones were pooled. Egg density in each sampler in a row was considered an independent estimate of density as no significant correlation was found between densities in adjacent samplers. Differences in egg density among the depth zones were tested with the Conover post-hoc test (Conover 1999). The effect of littoral slope on egg density at different depths was studied by (1) dividing the plots into three slope categories (gentle  $< 4^\circ$ , moderate  $4^\circ\text{--}8^\circ$  and steep  $> 8^\circ$ ), and (2) comparing egg densities at different depths among slope categories. Pearson's correlation coefficient was used to evaluate dependencies between cooling rate of water and fertilization rate (arcsine-transformed) in the sampling plots, as well as to evaluate dependencies between egg density and larval density in spring 2020 and mean larval density in 2011–2019 (egg and larval densities  $\log_{10}(x + 1)$ -transformed) (Karjalainen *et al.* 2019). Differences in fertilization rate among sampling plots was evaluated with a Kruskal-Wallis test. Samples from different depth zones in each sampling plot were pooled.

Total egg abundance, an estimate of population fecundity (total number of eggs laid) was calculated by multiplying the average egg number in each depth zone by the total area of that depth zone, and then summing the numbers of eggs in all depth zones. The egg numbers in the depth zones 15–18 m and 18–21 m which were not sampled, were extrapolated based on the linear decrease rate ( $7.73 \text{ eggs m}^{-1}$ ) of the egg density from the depth zone 6–9 m to the depth zone 12–15 m. The 95% confidence limits of the mean density was estimated by resampling (bootstrap): 5000 random samples from 20 plots were drawn from the original sampling plot data and total egg abundance re-estimated based on the data from those samples.

The mean relative fecundity of vendace female (eggs  $\text{g}^{-1}$ ) and sex ratio was determined from the random seine sample of 123 females

and 92 males collected in October 2019 before the spawning season. The number of mature females ( $\text{kg ha}^{-1}$ ) in the spawning stock (age 1+ and older, age determined from scales) was estimated by dividing the estimate of the total number of eggs in the lake by the relative mean fecundity of females (eggs  $\text{g}^{-1}$ ), and dividing the result by 1000. The spawning stock density ( $\text{kg ha}^{-1}$ ) was estimated by dividing the number of females by their proportion in the above-mentioned population sample, then multiplying this result by the mean weight of a spawner and dividing it by the lake area ( $12\,000 \text{ ha}$ ). The egg-density-based estimate of the spawning stock was compared with an independent estimate derived from the vendace fisheries monitoring data (Marjomäki *et al.* 2014, 2020). The fisheries-based estimate was based on first estimating the fishing mortality ( $F_h$ ) per one unit of effort, trawling hour ( $f, \text{h}^{-1}$ , a function of the area swept by trawl in an hour: width of the trawl  $\times$  speed,  $\text{ha h}^{-1}$ ), estimate of aggregation of adult vendace in pelagic trawling areas and estimate of catchability of trawl ( $q$ , proportion of vendace caught from swept area) (Marjomäki *et al.* 2005). The estimate of the mean spawning biomass (SB) during late summer (ls) is thus:

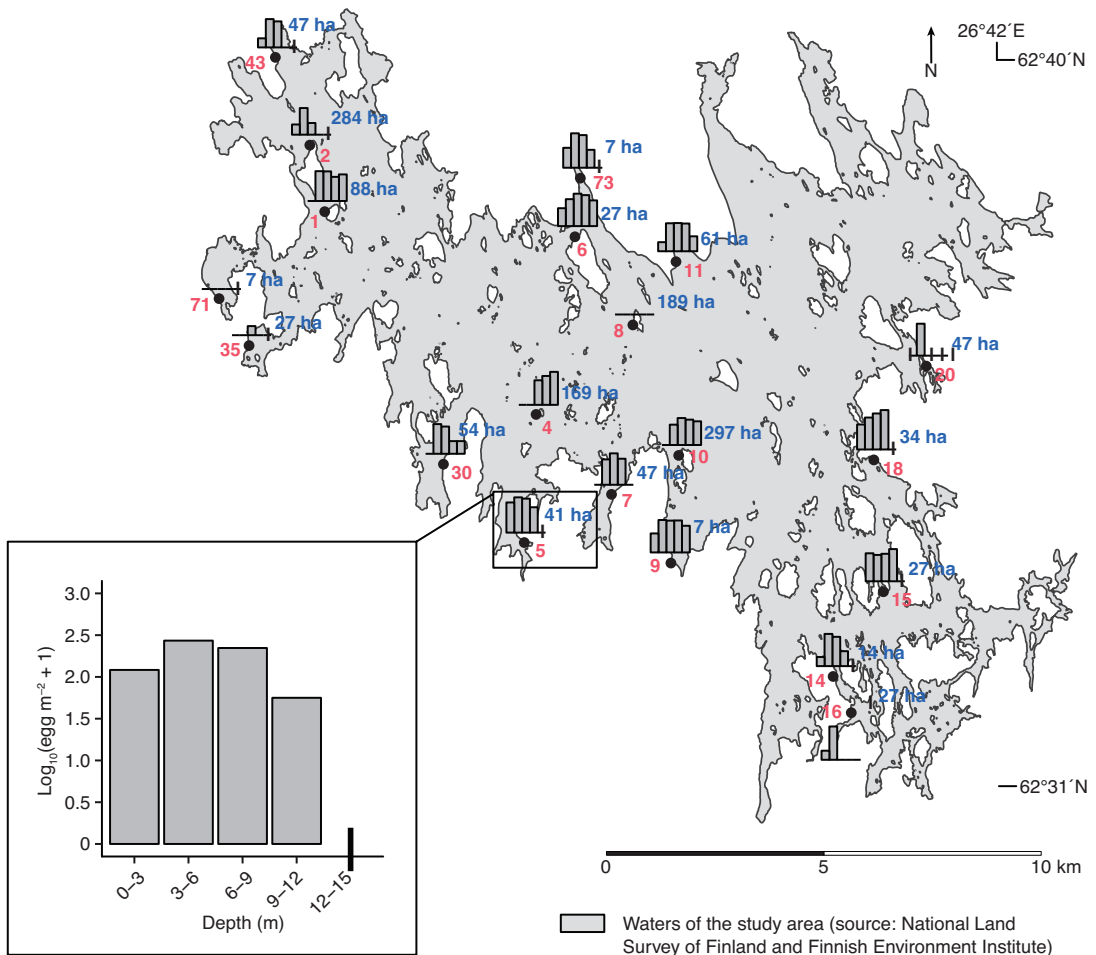
$$\text{SB}_{\text{ls}} = \text{YPUE}_{\text{ls}} / F_{\text{h,ls}}$$

where the YPEU is yield per unit effort =  $Y \text{ (kg) / effort (h)}$ . The spawning biomass during the spawning period was further extrapolated from this using an estimate of the total mortality from late summer to the spawning period. The 95% confidence limits for the SB estimate were calculated by defining distributions describing our assessment of the probability of different values of the input variables and then recalculating the SB estimate 10 000 times using random input-values from these distributions.

## Results

Fertilized vendace eggs were found in 18 out of the 20 sampling plots (Fig. 2). Also, samplers in 4 out of 5 selected, remote sampling plots (plots 30, 35, 43, 73) contained vendace eggs. No eggs were found in plots 8 and 71, but in the





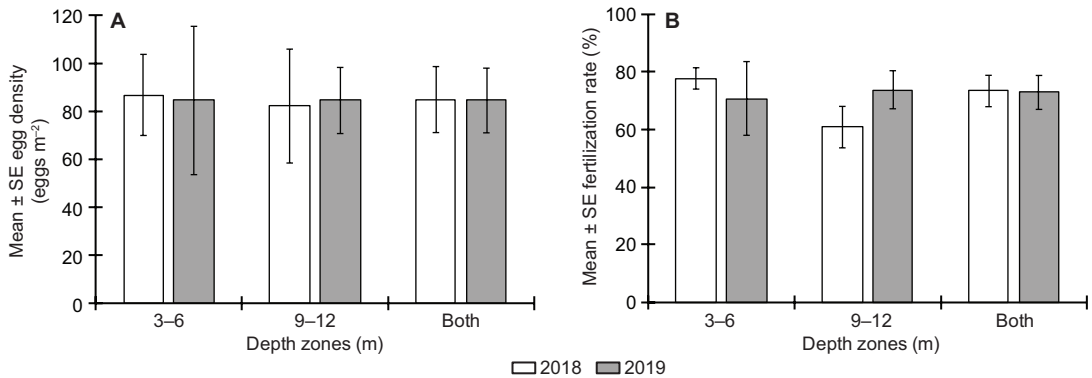
**Fig. 2.** Vendace egg densities (eggs m<sup>-2</sup>, log<sub>10</sub>(x + 1)-transformed) in the 20 sampling plots in the five depth zones (0–3, 3–6, 6–9, 9–12, 12–15 m) in Lake Konnevesi in autumn 2019. No bars = no eggs, I = no samplers in the depth zone. Numbers in red are sampling plot numbers and numbers in blue are estimated larval hatching areas (ha) in 2016 according to the models in Karjalainen *et al.* (2019).

latter plot some running ripe vendace females and males were caught by gill nets during the spawning monitoring fishing. Altogether 2014 vendace eggs and 2 European whitefish (*Coregonus lavaretus*) eggs were caught by the samplers and of those, 1693 vendace eggs were fertilized. The overall (all samplers) mean  $\pm$  SD density of vendace eggs was  $74 \pm 113$  ( $n = 441$ ) eggs m<sup>-2</sup>.

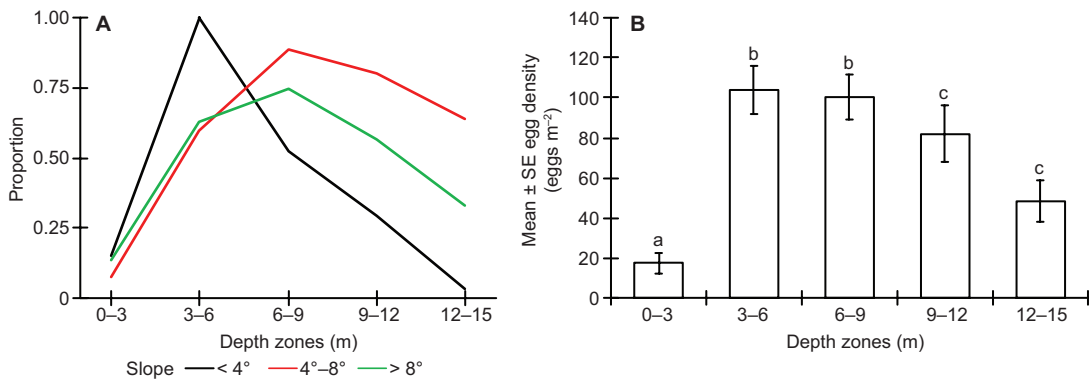
In plot 11, the egg sampling was performed in the years 2018 and 2019, and the egg densities and fertilization rates of eggs (%) were similar in both years (Fig. 3). In 2018 and 2019, the mean egg  $\pm$  SE densities were  $85 \pm 14$  per m<sup>2</sup> and  $84 \pm 13$  per m<sup>2</sup>, respectively, and fertilization rates  $73\% \pm 5\%$  and  $73\% \pm 6\%$ , respectively (Fig. 3).

The eggs distribution among the depth zones varied among sampling plots (Figs. 2 and 4A). If the littoral slope was steep ( $> 8^\circ$ ), the egg density was higher also at greater depths ( $> 9$  m), while in the spawning areas with a gentle littoral slope ( $< 4^\circ$ ), it was the highest in the depth zone of 3–6 m (Fig. 4A). In all, egg density differed significantly among the depth zones (Kruskal-Wallis test:  $\chi^2_4 = 80.04$ ,  $p < 0.001$ ). According to the Conover post-hoc test ( $p < 0.05$ ), the egg densities in the shallowest and deepest zones differed significantly from each other and from those at the depth zones of 3–6 and 6–9 m (Fig. 4B).

In 2019, the mean  $\pm$  SD fertilization rate of eggs in all plots taken together was  $85\% \pm 24\%$



**Fig. 3.** (A) Mean  $\pm$  SE density (eggs m<sup>-2</sup>) of vendace eggs, and (B) mean  $\pm$  SE fertilization rate (%) in two depth zones and for both zones together in sampling plot 11 in Lake Konnevesi in autumns 2018 and 2019.



**Fig. 4.** (A) Proportion of vendace eggs in the three slope categories (< 4°, 4°–8°, > 8°) relative to the maximum mean density observed in the depth zone 3–6 m in the slope category < 4°, and (B) mean  $\pm$  SE egg density (eggs m<sup>-2</sup>) in the five depth zones in all 20 sampling plots in Lake Konnevesi in autumn 2019; different letters above the bars indicate significant difference between the depths (Conover pairwise tests,  $p < 0.05$ ).

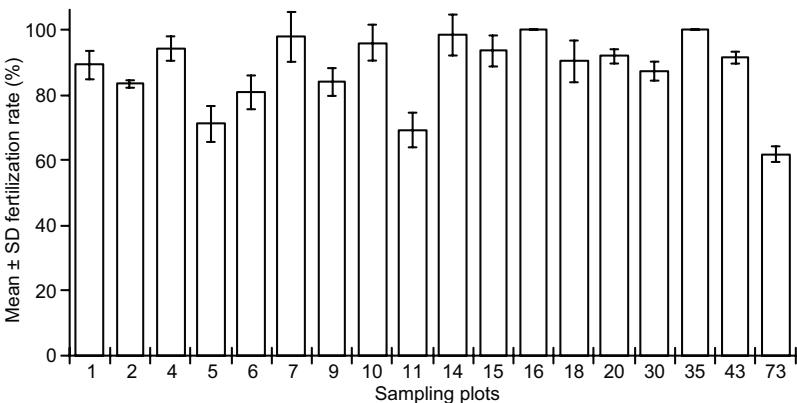
( $n = 266$ ). Fertilization rate differed significantly among plots (Kruskal-Wallis test:  $\chi^2_{17} = 64.99$ ,  $p < 0.001$ ), being the lowest, 62%, in plot 73 and the highest, 100%, in plots 16, 43 (Fig. 5). Fertilization rate did not differ between the depth zones (Kruskal-Wallis test:  $\chi^2_4 = 3.80$ ,  $p = 0.433$ ) (Fig. 6). In spawning plots, fertilization rate correlated negatively with water cooling rate ( $^{\circ}\text{C d}^{-1}$ ) (Pearson's  $r = -0.504$ ,  $p = 0.039$ ). Thus, in the sampling plots where the water temperature decreased more rapidly, the fertilization rate seemed to be higher than in the plots with slow cooling of the water.

Sampling-plot-specific mean egg density in autumn 2019 did not correlate with larval density index in spring 2020 (Pearson's  $r = 0.281$ ,  $n = 20$ ,  $p = 0.231$ ), nor did long-term mean larval density estimates (2011–2019) with egg density

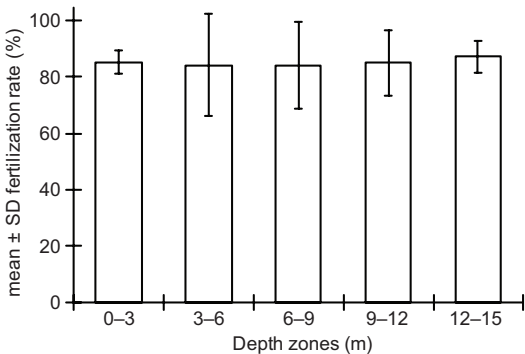
(Pearson's  $r = 0.341$ ,  $n = 20$ ,  $p = 0.141$ ). Furthermore, sampling-plot-specific fertilization rate in 2019 did not correlate with larval density in 2020 (Pearson's  $r = -0.264$ ,  $p = 0.290$ ,  $n = 18$ ).

We estimated the total number of vendace eggs laid in Lake Konnevesi to be  $5.9 \times 10^9$  (95%CL =  $3.7 \times 10^9$ – $7.7 \times 10^9$ ) (Table 1), thus the mean egg density per hectare of lake surface (12 000 ha) was 490 000. The mean larval density in 2020 was 17 700 indiv. (95%CL = 11 000–27 000) and thus, a rough estimate of mortality during egg incubation was 3.5% (95%CL = 2.1%–6.7%). When the loss due to unsuccessful fertilization (15%) is accounted for, the survival estimate of embryos during the incubation was 4.2%.

Mean  $\pm$  SD individual and relative fecundities of vendace females were  $1308 \pm 56$  eggs



**Fig. 5.** Mean  $\pm$  SD fertilization rates (%) of vendace eggs in the 20 sampling plots in Lake Konnevesi in autumn 2019.



**Fig. 6.** Mean  $\pm$  SD fertilization rate (%) of vendace eggs in the five depth zones in Lake Konnevesi in autumn 2019.

per female and  $114 \pm 2$  eggs  $\text{g}^{-1}$ , respectively. The estimated density of spawning females was  $4.3 \text{ kg ha}^{-1}$  ( $372 \text{ indiv. ha}^{-1}$ ), thus considering the proportion of mature females (57.2% females of total 215 fish) in the seine sample,

total density estimate of the spawning stock was  $7.6 \text{ kg ha}^{-1}$  ( $691 \text{ indiv. ha}^{-1}$ ). The mean  $\pm$  SD fresh weights of mature females and males were  $11.6 \pm 0.3 \text{ g}$  (mean  $\pm$  SD length  $117.5 \pm 1.1 \text{ mm}$ ) and  $10.0 \pm 0.3 \text{ g}$  (mean  $\pm$  SD length  $115.7 \pm 1.2 \text{ mm}$ ), respectively.

Discussion

In egg sampling in Lake Konnevesi, the vendace eggs were found distributed across the entire lake as could be expected based on our earlier egg distribution backcasting from larval distribution by the 3-D hydrodynamic model (Karjalainen et al. 2019). Also most of the remote locations where the potential hatching areas predicted by the model were small (areas of the potential hatching in blue in Fig. 2) harboured vendace eggs. Thus, our results confirm the hypothesis that vendace disperse their offspring across the

**Table 1.** Area of the depth zones (0–3, 3–6, 6–9, 9–12, 12–15 m), mean density of eggs (eggs  $\text{m}^{-2}$ ) in the depth zones, total number of eggs in the depth zone, and the proportion of eggs in each depth zone. \* extrapolated according to the decrease of density between depth zones of 6–9, 9–12 and 12–15.

Depth zone	Area ( $\text{km}^{-2}$ )	Mean egg density (eggs $\text{m}^{-2}$ )	Number of eggs $\times 10^6$	Proportion of eggs (%)
0.0–3.0	21.53	17.3	371	6.4
3.0–6.0	19.04	103.9	1978	34.0
6.0–9.0	13.52	100.4	1358	23.4
9.0–12.0	16.98	82.1	1394	24.1
12.0–15.0	12.75	48.4	617	10.6
15.0–18.0	7.33	*25.2	185	1.3
18.0–21.0	9.59	*2.0	19	0.3
Total	100.74		5922	100.0



entire lake already during spawning. The reproduction strategy of vendace stabilizes the effects of high environmental and temporal variability in their habitats. However, the spatial and temporal scales of spawning behaviour of an individual female are still unclear: it is not known whether a female lays eggs within one spawning area (i.e. corresponding one sampling plot in this study) or whether it disperses the eggs widely in space and time, and moving from one site to another or several sites within one spawning season or in different years. In terms of fitness, females benefit from producing offspring of variable phenotypes (e.g. egg size) in unpredictable environments (Crean & Marshall 2009). In vendace, this “dynamic bethedging” may occur when a female mates with several males and produces offspring having different hatching time and size (Karjalainen *et al.* 2015). Both hatching time and size of vendace have been observed to be affected by both parents (Karjalainen *et al.* 2016a).

In eight Finnish lakes (Table 2), the egg densities in the known spawning areas of vendace varied from 0 to 915 eggs per m<sup>2</sup>, and the inter-annual and inter-lake variation was high. The density of eggs was higher in autumn immediately after spawning season than in spring before hatching. Furthermore, considerable between-year variability has been observed e.g., in Lake Puruvesi during the high spawning stock period the density in autumn was 34 eggs per m<sup>2</sup>, and during the low stock period with only 6 eggs per m<sup>2</sup> (Nissinen 1972). In six lakes where the

samples were collected by saltwater sampler and different kind of pump systems from the well-known spawning areas of the vendace, the mean egg density in autumn was 42 eggs per m<sup>2</sup>. In Lake Konnevesi, the mean density was 74 eggs per m<sup>2</sup> (range 0–747 eggs per m<sup>2</sup>) and thus, well in range of other Finnish lakes. However, the egg density and population fecundity in our study may have been underestimated, thus, they are the minimum estimates of abundance. Firstly, in some areas of the lake, spawning might still have continued when the samplers were lifted. However, based on the spawning monitoring by net fishing we assume that this had a minor effect on our estimates. Secondly, in the samplers, there were some small bullheads (*Cottus gobio*), ruffe (*Gymnocephalus cernua*) and potential predatory benthic invertebrates i.e. amphipods (Amphipoda), larvae of odonates (Odonata) and caddisflies (Trichoptera) which may prey on eggs. In 7 out of 441 samplers, we found 1–3 empty egg shells per sampler (total 10 shells in all). Although we excluded from the analysis the samplers found to be out of order (21 of 500 i.e. 4.2%), it was obviously not possible to inspect the catchability of all samplers. Lowered catchability can be expected if a sampler is tilted or sinks partly into soft sediment. In deeper sampling zones, one should use a remotely operated underwater vehicle to check whether the samplers are set correctly, which would make setting of the rows of samplers very slow. Uncertainties in area estimates of different depth zones cause

**Table 2.** Density of vendace eggs in Finnish lakes in autumn after the spawning season and spring before hatching of larvae.

Lake	Sampling season	Years	Sampling method	Mean ± SE egg density (eggs m <sup>-2</sup> )	Source
Puruvesi	Autumn	1964–1971	saltwater	27 ± 11	Nissinen 1972
	Spring	1964–1971	saltwater	9 ± 3	Nissinen 1972
Oulujärvi	Autumn	1968–1971	saltwater	26 ± 5	Nissinen 1972
	Spring	1968–1971	saltwater	6 ± 1	Nissinen 1972
Lappajärvi	Autumn	1978–1980	pump	146 ± 40	Tiitinen 1978
	Spring	1978–1981	pump	11 ± 3	Tiitinen 1978
Onkamojärvi	Spring	1979–1980	pump	70 ± 7	Viljanen 1980
Suomunjärvi	Spring	1979–1980	pump	9 ± 2	Viljanen 1980
E Pyhäjärvi	Autumn	1979–1980	pump	38 ± 15	Viljanen 1980
Päijänne	Autumn	2000	pump	8 ± 2	Valkeajärvi <i>et al.</i> 2001
Koitere	Autumn	2004	pump	9 ± 2	Huuskonen 2005

uncertainties in estimates of mean egg density and population fecundity. We approximated that only the slopes connected to the shoreline of mainland and islands were potential spawning areas of vendace and not the ridges of comparable depths in the pelagic area. Additional sampling effort is needed to clarify the detailed egg distribution of vendace in different types of lakes.

In Lake Konnevesi, relatively high number of eggs was caught in the deep sublittoral zone ( $> 9$  m). Heikkilä *et al.* (2006) approximated by test fishing that the depth of water in the spawning area in Lake Konnevesi varied from 1.5 to 13.5 m. We successfully sampled eggs in the depth zone of 12–15 m and, based on the decrease rate of the egg density with depth, extrapolated that the depth zone of 18–21 m very likely harbours still a small amount of eggs.

Egg incubation conditions in the sublittoral zone differ from the conditions in the shallow littoral. The temperature during winter incubation period is higher than that in the shallow areas (Karjalainen *et al.* 2015) and in spring when the eggs in the littoral zone are exposed to solar radiation while the eggs in the sublittoral zone are in the dark. Differences in both temperature and light conditions between egg incubation areas affect the larval hatching and shape the hatching time window of the larvae.

The bottom substrate in the egg sampling areas varied: mud, sand, granules, pebbles and cobbles were observed. In the sandy substrate, isoetids (*Isoetes* sp., *Lobelia* sp.) were common and in many plots, currents and waves had transported decomposing plant debris into the samplers. Bottom currents may also transport eggs and, especially in the plots where the littoral slope is steep, eggs can be washed down to the deeper part of the sublittoral zone. Due to their high lipid content eggs seem to float on top of the bottom sediment and they do not sink easily to the bottom substrate.

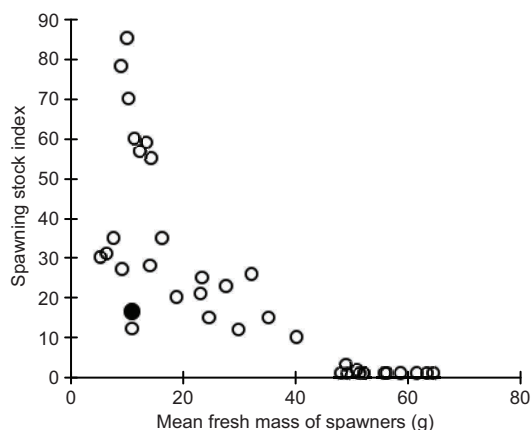
There was no correlation between egg density in autumn 2019 and index of density of newly hatched vendace in spring 2020 although the between-site variability in both variables was considerable. Karjalainen *et al.* (2019) showed that the larvae continue to disperse after hatching. Newly hatched vendace larvae are not

very strong swimmers and can be carried long distances by wind-induced currents. Depending on the characteristics of the spawning area larvae can either remain in that area or disperse: spawning areas with steep slopes and shores of islands in the middle of basins retain larvae less efficiently than the sheltered bays and straits. Karjalainen *et al.* (2019) observed hotspots in larval densities, i.e., areas where from year to year larval densities were higher than those elsewhere. Several years of egg sampling is needed to find out if any similar patterns in the spawning and egg incubation areas exist.

Marjomäki (2003) concluded that the typical survival of vendace eggs from spawning to hatching is a few percent and emphasised that the inter-annual variability is high. For example, Viljanen (1988) estimated that in 1980–1983 in two Finnish lakes (Suomunjärvi and Onkamojärvi) the survival from eggs to newly hatched larvae was 2.6%–4.1% and 12.4%–72.9%, respectively. Karjalainen *et al.* (2016b) estimated earlier that in Lake Konnevesi the egg survival during winter was 2% (SD = 2). Our current estimate (4.2%) which was based on the quantitative estimates of both population fecundity and larval abundance, thus, matches well with the earlier findings. Wahl and Löffler (2009) found strong positive correlation between egg abundance and number of spawning fish in Lake Constance, and calculated that the mortality of whitefish eggs was 6% d<sup>-1</sup> and thus, survival of eggs was 0.4% during the whole 90-day incubation period in that lake.

Our spawning stock estimate for autumn 2019 (7.6 kg ha<sup>-1</sup>) was nearly the same as our other estimate of spawning stock in autumn 2019 (5.7 kg ha<sup>-1</sup>, range 4.3–8.1 kg ha<sup>-1</sup>) calculated from the commercial catch statistics using the method of Marjomäki *et al.* (2005). In Lake Konnevesi, the density of vendace spawning stock in 2019 was moderate: the spawning stock index in that year was at the same level as the median index of spawning stock (median index = 18) (Marjomäki *et al.* 2020) during the monitoring period 1980–2019 (Fig. 7).

The new egg sampler developed for coregonid eggs functioned well: the sampler is relatively easy to build, reasonably practical to use in the field without need for large vessels, and



**Fig. 7.** Spawning stock index (from Marjomäki *et al.* 2020) in relation to the fresh mass (g) of spawners in Lake Konnevesi in 1980–2019. The black dot indicates the stock index which is based on the population fecundity estimated from the egg density in the lake in autumn 2019.

it produced good estimates of egg densities in different kind of shores. We lost only 3% of the samplers, 4% remained under the ice but they were found later in spring, and 4.2% of the samplers were not in working order when lifted. The measured egg abundance was well in line with the larval density and showed > 95% egg mortality during the winter incubation. Likewise, our spawning stock estimate was at the same level as the estimate made independently from the commercial catch statistics. In all, novel results of the lake-wide spawning behaviour of vendace were documented in our study.

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**Appendix.** Location of sampling plots in Lake Konnevesi, number of sampler rows, number of samplers in working order, depth zone sampled, mean temperature during sampling, water cooling rate, mean littoral slope, mean egg density, mean fertilization rate in 2019 and larval density in 2020.

Plot	Lat. °N	Long. °E	No. of rows	No. of samplers in working order	Depth zone (m)	Mean temp. (°C)	Water cooling rate (°C d <sup>-1</sup> )	Mean slope	Egg density per m <sup>2</sup>	Fertilization rate (%)	Larvae density (indiv. ha <sup>-1</sup> )
1	62.634328	26.398176	5	23	0–15	5.48	–0.195	11°	67	89.6	1465
2	62.648264	26.387896	4	17	0–12	5.22	–0.175	2°	19	65.6	32214
4	62.592854	26.494639	5	25	0–15	6.13	–0.167	5°	67	94.6	448
5	62.565942	26.488452	5	24	0–12	6.10	–0.164	3°	188	70.7	355
6	62.629733	26.510891	5	25	0–15	6.00	–0.175	10°	91	83.1	2952
7	62.576396	26.527991	5	22	0–15	5.96	–0.185	6°	53	97.8	313
8	62.611185	26.536887	5	21	0–15	6.30	–0.169	19°	0	–	1339
9	62.5625	26.553189	5	25	0–15	6.33	–0.158	9°	115	82.5	221
10	62.584562	26.557906	5	24	0–15	6.77	–0.172	14°	39	96.2	327
11	62.624399	26.556729	9	45	0–15	6.73	–0.153	3°	58	72.4	2585
14	62.539011	26.62831	4	20	0–12	5.72	–0.184	7°	71	98.9	1487
15	62.556537	26.649677	4	20	0–12	6.11	–0.166	9°	98	94.2	4340
16	62.531294	26.636207	4	19	0–12	5.26	–0.177	4°	50	100.0	5353
18	62.583755	26.645445	4	20	0–12	6.06	–0.174	5°	260	90.2	8654
20	62.603258	26.668496	1	6	0–15	6.36	–	3°	160	91.8	768
30	62.582555	26.451813	5	26	0–15	4.59	–0.174	10°	40	91.1	1521
35	62.665894	26.375599	5	24	0–12	5.38	–0.173	6°	1	100.0	2108
43	62.665953	26.37801	4	18	0–15	6.77	–0.170	2°	39	93.3	6137
71	62.616579	26.352226	4	17	0–12	5.91	–0.140	2°	0	–	20
73	62.641651	26.512667	4	20	0–12	5.96	–0.159	6°	114	67.6	22752