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Communal pair spawning behavior of vendace (*Coregonus albula*) in the dark

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Abstract

Mating in nature is rarely random and most fish species have refined mating systems. The vendace (*Coregonus albula*) is a short-lived, small-sized, cold-water adapted pelagic schooling species that is known to spawn in groups, but the actual mating system of this species, like many other group-spawning fishes, has not been described in detail. Vendace typically spawn in the littoral or sublittoral zones of lakes in late autumn and the hatching of larvae occurs close to ice-break in the following spring. In our large study lake, vendace larvae were caught in 93 % of 1149 random sampling locations lake-wide. We examined the courtship and mating of vendace under experimental conditions by non-intrusive observation of the natural behavior, to clarify whether spawning activity is associated with illumination and to assess the post-spawning mortality of vendace. Here we describe and document in detail for the first time the spawning behavior of vendace: they spawn in the dark and females release a small portion of their eggs (on average 1 % of mean total individual fecundity) when the female and male, side by side, dart from near the bottom up towards the surface, i.e. perform a spawning rise. Males and females had several spawning rises (on average 1200). Our results showed high post-spawning mortality (56 %). The spawning stress seems to be a potential component of mortality regulating the life span duration of vendace.

Running headline: Spawning behavior of communal spawning coregonid

Keywords: coregonid, egg, fertilization, fish, larvae, mating strategy, schooling, spawning rise

Introduction

The ultimate basis for the management of natural resources and the conservation of endangered as well as commercially exploited species is a comprehensive knowledge of the life cycle characteristics and important reproductive traits of the species. These properties essentially regulate the productivity of commercially exploited fish species and unknown aspects of their reproductive biology may jeopardize the ecologically sustainable use of valuable resources. A high proportion of inland fish catches in Europe and North America consists of coregonid fishes (Ebener et al. 2008; Marjomäki et al. 2016) and, despite their intensive utilization, many key questions of their biology, such as what kind of mating system they have and how they spawn, are still unknown.

Mating is rarely random in nature, and most fish species have refined mating systems, from strict monogamy to polyandry and polygyny (Taborsky 1994). The vendace (*Coregonus albula*) is a short-lived, small-sized, cold-water adapted schooling species (Karjalainen et al. 2016) that is supposed to spawn in groups, but the actual mating system of this species, like many other group-spawning fishes, has not previously been described in detail. Vendace typically spawn in the littoral or sublittoral zones of lakes in the autumn, with hatching of the larvae taking place close to ice-break in the following spring, up to 6 months later (Urpanen et al. 2005). Contrary to the closely related whitefish (*Coregonus lavaretus*) which has breeding tubercles, neither vendace male or female have distinct secondary sexual characteristics. The whitefish is presumed to perform some kind of pre-spawn mate choice, because the size of the breeding tubercles correlates positively with offspring fitness (Wedekind et al. 2001; Wedekind et al. 2007; Huuskonen et al. 2011). Despite the inter-sexual selection and tendency for pair spawning behavior of whitefish, polygamous matings probably also occur (Rudolfsen et al. 2008).

Our *first aim* was to document the courtship and mating of vendace under experimental conditions by non-intrusive monitoring of the natural behavior. Our hypothesis, based on the previous information and local knowledge of fishermen, was that vendace has communal group spawning, typical of pelagic schooling planktivores such as Clupeidae (Mank & Avise 2006). We also aimed to observe whether vendace has single or multiple pair spawning. Our *second aim* was to examine at what time of the day the spawning occurs. Earlier results from test fishing and movements on the spawning grounds (Lahti 1992; Heikkilä et al. 2004) suggested that the mating occurs at night, and our hypothesis was that mating activity is associated with the level of illumination. Our *third aim* was to examine the mortality rate of vendace after spawning. Many other salmonid species have high mortality after spawning (Belding 1934; Quinn 2005; Jonsson & Jonsson 2011) and based on the occasional non-documented observations of local fishermen and the small proportion of repeated spawners in the populations (Karjalainen et al. 2016), we hypothesized that post-spawning mortality of vendace is high. Finally, we discuss how the observed spawning behavior potentially affects the lake-wide distribution of vendace eggs and larvae.

Material and methods

Vendace were caught by seine net from the oligotrophic Lake Southern Konnevesi (62°30′–62°40′N, 26°20′–26°44′E , Central Finland, area 120 km^2, mean depth 13 m; Karjalainen et al. 2016) on two different occasions. The first shoal was caught in October 2015 (reared in tank 1, number of fish in the tank in the beginning of the study period n = 283)) and two other shoals in October 2016 (tanks 2, n = 195 and tank 3, n = 225). Seining was carried out near a spawning site known to a local commercial fisherman. Fish were collected gently by a bucket from the seine net, underwater and fish were loaded to a transport tank for transporting them to the nearby Konnevesi Research Station. The water into the experimental tanks was piped from Lake Konnevesi and included zooplankton and other invertebrates at low, natural densities. Further, in both years fish were fed commercial dry feed for salmonid fishes and the fish caught in 2015 eagerly ate the dry feed during the growing season and grew normally but their feeding ceased in the autumn before spawning. The fish caught in autumn 2016 did not eat dry feed to a large extent or at all before the spawning period but the surviving individuals began to eat the dry feed soon after the spawning period. Fish caught in 2015 served as a test group which had long acclimation period to the rearing conditions before spawning and went through the annual maturation period in captivity.

The water volume in the cylindrical tanks was 1.3 m^{-3} and tank diameter and water height was 137 and 91 cm, respectively. While the fish were in captivity, the photoperiod was adjusted weekly to mimic field conditions. During the spawning period the dark:light rhythm was 16:8 hours, with illumination provided by day light lamps. The illuminance (lx) during the dark period was 0.02 (SD 0.01), 0.05 (SD 0.01) and 0.01 (SD 0.01) above the water surface in tanks 1, 2 and 3, respectively, and during the light period 427 (SD 50), 274 (SD 55) and 226 (SD 120) in tanks 1, 2 and 3, respectively. Thus, at night the illuminance in our study was slightly lower than the natural illuminance in general at full moon with clear sky (range from 0.03 to 0.15 lx, Fraser & Metcalfe 1997) and slightly higher than the illuminance in cloudy nights regardless of moon type (<0.01 lx, Fraser & Metcalfe 1997). Water temperature in the tanks followed the natural temperature of water piped from Lake Konnevesi into the tanks and was measured daily (accuracy 0.1°C).

The study period started on October 13, 2016 when fish were caught and arrived at the research station and ended on December 16, 2016. The spawning period started on October 26 (Oct 26 to 27 was night 1) and ended on November 5 (night 11). Further, we continued monitoring of the fish that survived the study period until April 10, 2017. The bottoms of the tanks were checked every morning during the study period for laid eggs which were siphoned from the tanks if observed. The tank bottoms were visually checked also in the evening before lights were turned off to observe eggs from possible daytime spawning. Fertilization rate (% of fertilized eggs) of eggs laid in the tanks and gathered by siphoning was determined by microscopy for the samples taken from tank 3 where the video recordings occurred. Samples were taken after nights 4, 6, 7, 8 and 10 of the spawning period. The total number of eggs laid during one dark period was counted at night 6 to estimate the number of spawning rises with egg release during the dark period.

Video recordings of the spawning were carried out during nights 2 and 6 (on October 27–28 and October 31–November 1) during the spawning period in tank 3. Video recording started before lights were turned off and continued two hours after the lights were turned on. The camera system in tank 3 comprised of three cameras and a video recorder (Kalatel Calibur DVMRE-4). The bottom and top horizontally viewing cameras were Ikegami ICD-47 black & white CCD with waterproof chambers, and the surface camera with a vertical field of vision from the water surface to the bottom of the tank was a Tracer TS-6030HPSC. One horizontally viewing camera on the bottom was used in tanks 2 and 3. During the dark period of the experiment, the tanks were illuminated by infrared illuminators (one Eneo IRLED-402E 850 nm/30 W per tank) attached above the tanks.

The number of spawning rises (the rise of two mating fish side by side from the bottom shoal towards the surface of the tank), number spawning rises with egg release and number of eggs released per spawning rise were counted for the tank 3 during night 6 from the first observed spawning rise to the end of the dark period (from October 31 at 20:04 to November 1 at 07:45). All events (spawning rise and/or egg release) were counted from the field of vision of the top horizontally viewing camera, which covered approximately one third of the top water layer of the tank. The video recordings were examined by eye and the events were counted for a 30-minute period at hourly intervals. Altogether nine 30-minute periods were examined for night 6. It was not possible to record data blind because our study involved focal animals in the tanks.

Mortality of mature individuals (age > 1 years) was recorded daily and dead fish were removed from the tanks and stored at -20°C for determination of their size, sex and age. A random sample of mature fish was also taken from the shoals before and after the study period. Age was determined from the scales and total length, wet body mass, gonad mass and fecundity of females were measured. Total number of fish in each spawning shoal before the spawning period was counted and the mortality expressed as cumulative relative mortality (%) for each tank. There was small number of immature fish (less than 10 individuals per tank) in the tanks and they were excluded from the mortality calculations.

Distribution of the newly-hatched vendace larvae in the littoral zone of Lake Konnevesi in 1999–2011 was determined immediately after the ice-out by a random stratified-sampling procedure with bongo-nets (500 µm mesh) attached in front of a jet-powered motor boat (Karjalainen et al. 1998; Urpanen et al. 2009). Altogether samples were taken in 1020 sampling plots from four zones in the littoral area: zone 1 bottom depth 0–0.5 m, zone 2 0.5–1 m, zone 3 1–2 m and zone 4 2–4 m and in 129 sampling plots in the pelagic area (bottom depth >4 m). The sample volume of each tow was measured by a flowmeter. Annually, the 20 littoral and 10 pelagic sampling plots were randomly picked, and thus the sampling locations varied from year to year.

Results

The spawning of fish started in tanks 2 and 3 at the same time when the water temperature decreased below 6°C (Fig 1) and the spawning period lasted for 11 nights. Laid eggs were found daily on the bottom of the tanks with active spawning shoals. The fish caught in October 2015 and reared in tank 1 for a year at Konnevesi Research Station started their spawning 4 days later than the fish caught in October 2016. Spawning activity and behavior of fish caught in 2015 was similar to the fish caught in 2016.

The spawning behavior was intensively monitored in tank 3 during night 6 of the spawning period. When the lights were switched off, within a few minutes vendace formed a shoal near the tank bottom and active, mature individuals started mating (Fig 2A, Online Resource 1). The first spawning rise was detected 21 minutes after the lights were switched off. Occasionally, a female and male pair darted from the bottom shoal up towards the surface side by side with synchronized movements; i.e. a pair performed a spawning rise which ended near the surface and, if successful, the female released eggs at the end of the spawning rise (Supporting information S1). Only 2 %, (three out of 183 observed spawning rises) included more than two individuals (i.e. three fish). In at least one of these three-fish events the third individual clearly separated from the spawning rise before egg release (Supporting information S2). During the dark period, there was also another shoal near the surface comprising of rather passive individuals which seemed to rest or did not take part in the spawning during that night. We were not able to reliably measure the number of fish in the top and bottom shoals or movement between them. Clearly, many fish dived immediately after spawning rise back to the bottom shoal but few of them seemed to be passive and stay longer in the top shoal.

In strict contrast to the dark period, under daylight vendace formed distinct schools in all tanks; individuals swam sedately oriented in in the same direction in a coordinated manner against the slow current in the circular tanks. No tendency for mating behavior or egg release was observed in the daytime.

During night 6, the maximum frequency of spawning rises occurred at the beginning of spawning (Fig 3); the activity decreased during the night and ended totally when the lights were switched on. Females released an average of 18 eggs (SD = 9) per successful spawning rise (Fig 3). The number of eggs released was also highest at the beginning of the spawning period. During night 6, 183 spawning rises were detected by the video recordings, so interpolation for the whole of night 6 indicates 477 rises performed within the vision field of the top camera. However, the top camera did not cover the whole volume of the tank. The number of the mature fish was 225. Thus, several male and female individuals performed more than one spawning rise per night. After night 6, 21 600 eggs were siphoned from the bottom of the tank, and this total number of eggs divided by the mean number of eggs per egg release as detected by the video recordings (18 eggs) indicates 1200 spawn rises with egg release. The mean fecundity of females was 2700 eggs per female (SD= 600, n=27) in tanks 2 and 3 at the beginning of the study period. Thus, to release all its eggs, an average female should perform at least 150 rises during the spawning season. The fertilization rate of the eggs was 63, 81, 74, 54 and 68 % during nights 4, 6, 7, 8 and 10, respectively. The mean fertilization rate was thus 68 % (SE = 5 %) for the whole spawning period in tank 3.

Post-spawning mortality of mature individuals in every tank was high (Fig 4), the mean proportional mortality for the whole study period being 56 % (SE = 7). Before the spawning period the mean mortality was only 1 % (SE = 1). The mortality started to increase 2 to 6 days after spawning ceased. Most of the fish (95 % of all died fish) died during 40-days period after spawning. We observed the fish in tanks until April 10, 2017 and the mortality stayed low (3 %, SE=1) during whole winter after the 65-day study period. Males seemed to have higher mortality after spawning than females. In tanks 2 and 3, the proportion of females was 57 % before the study period but after the study period it was 62 % and 61 % respectively in these tanks. In tank 1, the proportion of females was even higher (Table 1).

The distribution of newly-hatched vendace larvae in the littoral and pelagic area of Lake Konnevesi showed that immediately after the ice-out vendace larvae were dispersed widely around the lake (Fig 5). Only in 83 of the 1149 random sampling locations (7 %) no larvae were caught. Although in some littoral locations the density of larvae was occasionally high (up to 2600 larvae m^{-3}), densities were mostly below 50 m^{-3}.

Discussion

Our observations under laboratory conditions showed that vendace exhibit communal group spawning, typical of pelagic schooling planktivores, but that within the group they engage in pair mating behavior and not mass spawning as e.g. clupeids (Haegele & Schweigert 1985; Mank & Avise 2006). Both males and females spawn several times during the spawning period. They also have potential to spawn several times at each night (the estimated mean number of the spawning rises per female was 150) but it remained unclear how individual fish performed night by night during the spawning period. As the fish were not individually marked, we cannot rule out the possibility of permanent pairing between certain male and female individuals, but according to video recordings it appears more likely that individual fish spawned with several partners. The partner choice may be random and triggered by simultaneous excitement during random encounter. However, despite their polygamy vendace may still select mates, since egg release did not take place during every spawning rise. Intersexual selection and pairing has been proposed as an important component affecting the embryonic and larval survival of coregonids (Wedekind et al. 2007; Huuskonen et al. 2011) and the importance of mate choice certainly needs further experimental studies. In vendace also, despite the alleged random mating, cryptic female choice (Gasparini & Pilastro 2011) after egg release may be an important element in the reproductive system of this schooling species, for example in reducing inbreeding depression (Jokinen 2015). Our finding that vendace can go through the annual maturation in captivity and perform spawning behavior under experimental conditions opens opportunities for future research. The fertilization rate of eggs in our experiment (68 %) corresponds to the proportion of fertilized eggs pumped from the spawning areas of vendace in four Finnish lakes (from 37 to 87 %, Karjalainen et al. 2015). Thus, fertilization success under our experimental conditions was similar to the natural fertilization success of vendace.

Spawning started soon after the lights were switched off and activity was intense for 9 hours. The maximum intensity of spawning occurred at the beginning of the dark period. Vendace can prey on zooplankton at a light level of 0.05 lx (Ohlberger et al. 2009) and start visual feeding already at light levels about 0.007 lx (Gjelland et al. 2009). Thus, vendace could to some degree observe partners during the spawning in our tanks with active spawning at light levels 0.01–0.05 lx. Interestingly, despite light levels potentially sufficient for feeding we did not observe any attempts to prey upon the eggs released by females.

The tank bottom was plastic and not covered by any natural lake bottom substratum, which did not prevent the intense spawning activity in the tanks. In nature, vendace spawn on hard bottoms such as sand or gravel (Lahti 1992; Valkeajärvi et al. 2001). Further, the morphology of littoral slope and water color are important for the lake-wide distribution of vendace spawning areas (Karjalainen et al. 2002; Heikkilä et al. 2006). In humic waters vendace spawn in shallower areas than in clear-water lakes (Heikkilä et al. 2006).

In agreement with our third hypothesis, the spawning stress seems to be a potential component of mortality regulating the duration of life span of vendace individuals. Considerable post-spawning mortality is typical of the life history strategies of many fishes in the family Salmonidae (Belding 1934; Quinn 2005; Jonsson & Jonsson 2011), some of them being semelparous (*Onchorhynchus* spp.). Natural mortality caused by factors other than predation, is not well understood for fishes in general although the age-specific estimates of natural mortality are essential components of population models (Gislason et al. 2010; Nielsen et al. 2012). The natural mortality of many species has been shown to increase with age (Gislason et al. 2010; Nielsen et al. 2012; Uriarte et al. 2016), despite the fact that predation mortality typically decreases with size (age), and senescence processes, including high stress caused by spawning, have been proposed to be important factors causing the increase in mortality after maturation (Caputo et al. 2002; Nielsen et al. 2012). The natural mortality of vendace in nature has been estimated very rarely because it requires information on true (not only proportional) fish abundances and catches. Valkeajärvi (1983) and Marjomäki & Huolila (1994) have supported the increase in natural mortality with age based on quantitative lake specific data. From the population demography, male fish have been shown to typically have higher mortality than females (Bunnell et al. 2012; Nilssen et al. 2012). For vendace, already Järvi (1920) pointed out that the proportion of males decreased strongly with age in seine catch samples, from 69 % in age 1+ to 26 % in age 4+. His large data set from more than 30 lakes (e.g. Järvi 1950) and various later studies (e.g. Lehtonen 1981) confirm this tendency, thus implying to higher mortality in males than females. Bunnell et al. (2012) concluded that the underlying mechanisms of sex-specific difference in mortality of bloater (*Coregonus hoyi*) include sex-specific differences in age at maturity, growth rate and activity or behavior during the spawning period. Even though vendace males had higher mortality than females, both sexes encountered significant post-spawning mortality which seems to be an important component affecting population dynamics and the future spawning stock structure. Karjalainen et al. (2016) reported that only 16–60% of females in Finnish lakes were repeat spawners. However, naive (often age of 1+) and repeat (age of 2+ or older) female spawners did not differ in their offspring productivity, except that larger individuals, despite their age, had higher fecundity (Karjalainen et al. 2016).

Depending on their reproductive strategy, different fish species aim to aggregate or disperse the eggs and larvae in their reproductive habitat (Taborsky 1994; Leis et al. 2016). Some species aggregate eggs in nests (Wootton 1999; Pampoulie 2001; Jonsson & Jonsson 2011) or in specific substrata (Wootton 1999; Haegele & Schweigert 1985), but many, especially pelagic species, disperse both eggs and larvae widely around the potential nursery areas (Leis et al. 2013; Pacariz et al. 2013). Vendace larvae have been observed to disperse lake-wide to both littoral and pelagic zones (Fig 5, Karjalainen et al. 2002). Similarly, the density of eggs in the spawning ground is low: the mean density of eggs in four Finnish lakes was 8 eggs m^{-2} (SD = 10, n = 29, min = 0.1 max = 35; recalculated from reports by Väisänen et al. 1994; Valkeajärvi et al. 2001; Huuskonen 2005). The observed spawning behavior with small egg batches and spawning rises in the dark have the potential to promote dispersal of early stages. If spawning shoals in lakes move around the spawning ground, the eggs of an individual female may spread around a broad bottom area during the spawning period which can last several days. Direct observations of spawning shoal movements in lakes are needed to verify this assumption. Due to the long egg incubation time (up to six months from October to May) without protection, the dispersal of eggs seems to be a strategy to decrease the mortality by predators with the type III functional response (Holling 1959) preying visually, but also by vertebrate predators which can also be active at night (Karjalainen et al. 2015). On the other hand, the strategy of spawning in darkness may serve to protect against visually feeding fishes (most of the fishes in boreal lakes) that would potentially feed on the spawning vendace themselves (e.g. perch, brown trout) and/or on their eggs (e.g. perch, ruffe).

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Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

International, national and institutional guidelines for the care and use of experimental animals were followed.

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Supplementary material

Supporting information S1. Electronic supplementary material for video showing the spawning behavior of vendace (*Coregonus albula*).

Supporting information S2. Electronic supplementary material for video showing the spawning behavior of vendace (*Coregonus albula*).

Figure captions

Fig. 1. Water temperature during the study period. The spawning period (11 nights) was represented by the vertical dotted lines.

Fig. 2. A) General pattern of the spawning shoal and behavior of vendace. Spawning rise in the B) top side (camera 2) and C) bottom side camera (camera 3) view (photo J Karjalainen).

Fig. 3. Mean number of spawn rises (black bar) and eggs laid per a spawn rise (open bar) for the 30-minutes observation periods during one dark period (from 31 October at 20:04:00 to 1 November at 07:45:00) in the spawning period. Vertical lines in the egg release bars represent the standard errors of the mean. All events have been counted from the field of vision of the top side camera.

Fig. 4. Cumulative relative mortality (%) of mature vendace individuals before, during and after the spawning period. The spawning period (11 nights) was represented by the vertical dotted lines.

Fig. 5. Frequency distributions of newly-hatched vendace densities (no. 100 m^{-3}) in the different A) littoral (n=1020) and B) pelagic (n=129) sampling locations in Lake Konnevesi in 1999-2011.

Table 1**.** Mean total length (mm ± standard error SE) and wet body mass (g) of mature fish in tanks 1-3 (T1-T3). Fish in the tank 1 were caught in 2015 and in the Tanks 2 and 3 in 2016. Samples were taken before (B) and after the study period (A). Total number of mature females and males in the spawning shoals in the beginning of the study period is also given.

Tank	Total length ± SE	Wet mass ± SE	N	Total number of mature fish
T1 B female	139.8±4.1	146.9±11.5	11	-
T1 B male	135.3±4.8	136.4±24.0	7	-
T1 A female	137.3±2.3	153.3±13.9	54	215
T1 A male	140.1±2.0	160.6±4.3	3	9
T2&3 B female	143.0±1.3	208.3±6.3	27	-
T2&3 B male	140.7±1.6	172.8±6.2	20	-
T2 A female	139.0±2.9	148.0±7.4	39	112
T2 A male	137.1±1.3	137.4±4.0	24	83
T3 A female	142.0±1.3	151.4±4.2	46	162
T3 A male	136.0±1.0	141.2±4.0	30	120

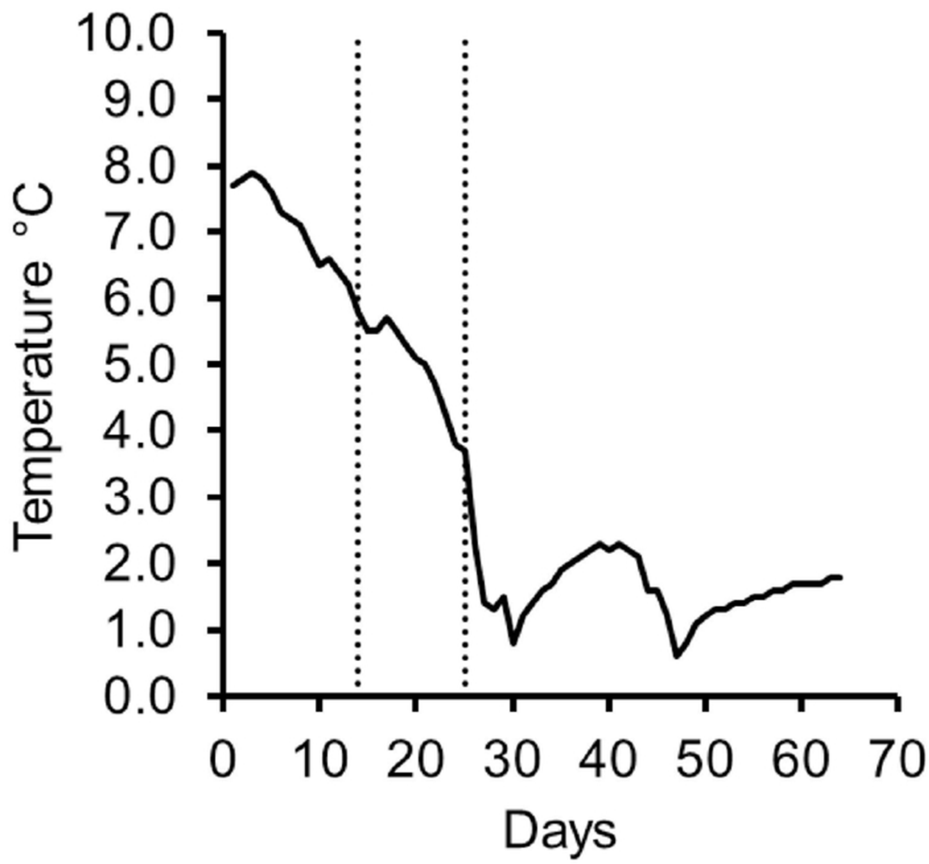

Fig. 1. Water temperature during the experimental period. The spawning episode (11 nights) was represented by the vertical dotted lines.

64x59mm (300 x 300 DPI)

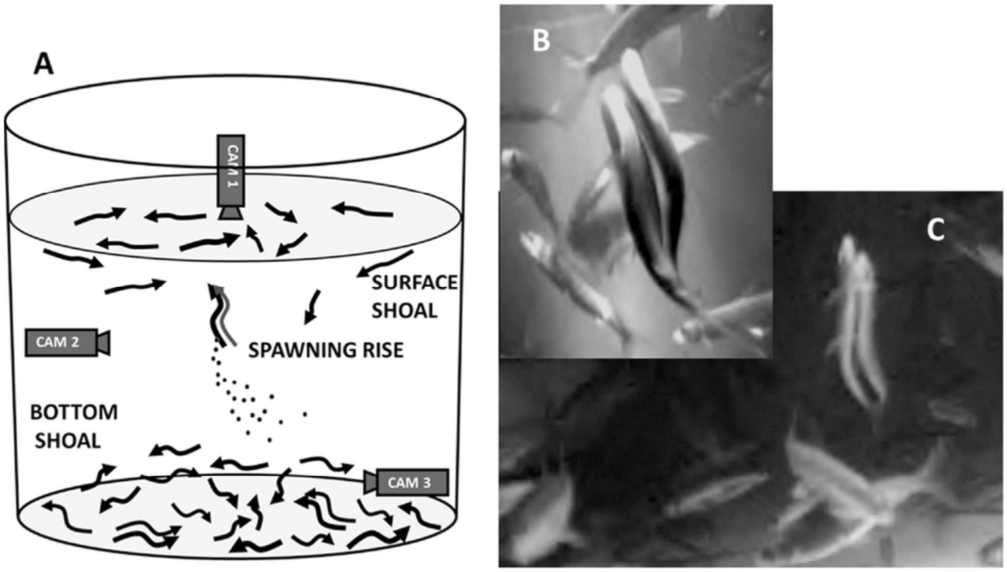

Fig. 2. A) General pattern of the spawning shoal and behavior of vendace. Spawning rise in the B) top side (camera 2) and C) bottom side camera (camera 3) view (photo J Karjalainen).

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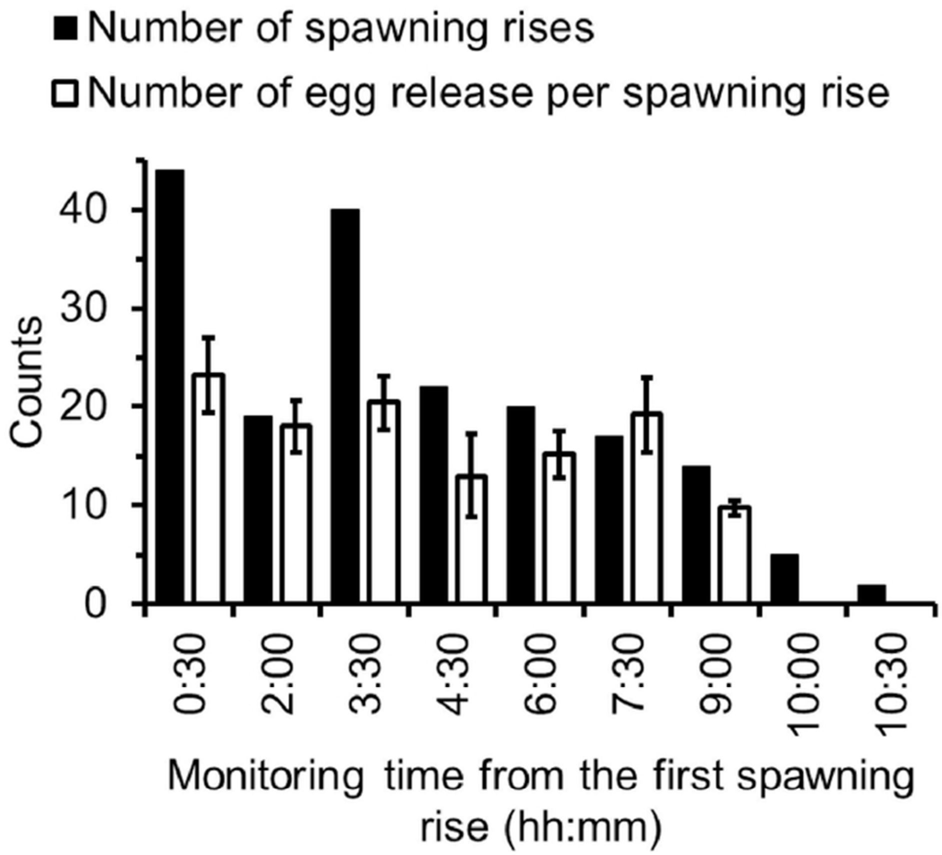

Fig. 3. Mean number of spawn rises (black bar) and eggs laid per a spawn rise (open bar) for the 30-minutes observation periods during one dark period (from 31 October at 20:04:00 to 1 November at 07:45:00) in the spawning episode. Vertical lines in the egg release bars represent the standard errors of the mean. All events have been counted from the field of vision of the top side camera.

62x56mm (300 x 300 DPI)

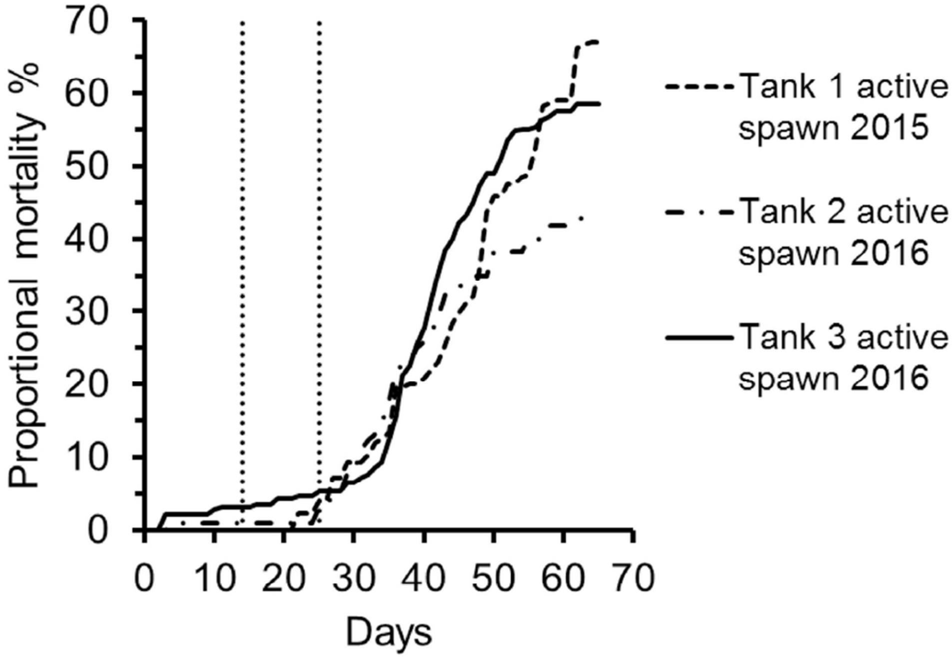

Fig. 4. Cumulative relative mortality (%) of mature vendace individuals before, during and after the spawning episode. The spawning episode (11 nights) was represented by the vertical dotted lines.

79x56mm (300 x 300 DPI)

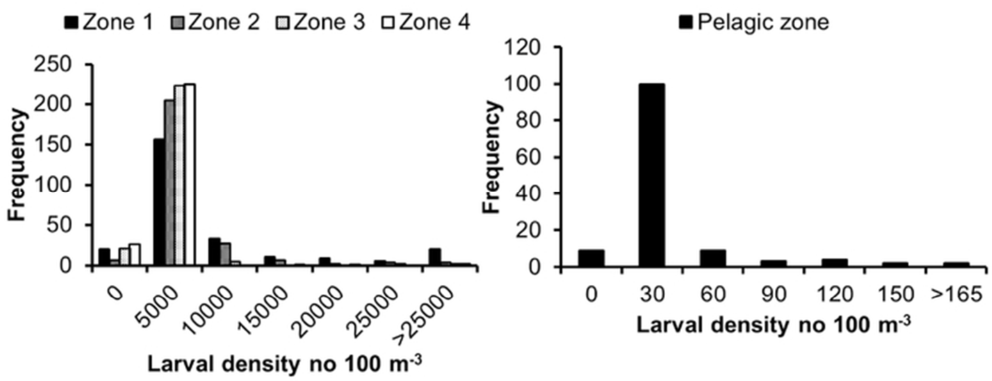

Fig. 5. Frequency distributions of newly-hatched vendace densities (no. 100 m-3) in the different A) littoral (n=1020) and B) pelagic (n=129) sampling locations in Lake Konnevesi in 1999-2011.

63x26mm (300 x 300 DPI)