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**Title:** Communal pair spawning behaviour of vendace (*Coregonus albula*) in the dark

**Year:** 2018

**Version:** Accepted version (Final draft)

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**Please cite the original version:**

Karjalainen, J., & Marjomäki, T. (2018). Communal pair spawning behaviour of vendace (*Coregonus albula*) in the dark. *Ecology of Freshwater Fish*, 27(2), 542-548.

<https://doi.org/10.1111/eff.12368>

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

2

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7

## 8 **Abstract**

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

25

26 **Running headline:** Spawning behavior of communal spawning coregonid

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

29

30 **Introduction**

31

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

41

42 Mating is rarely random in nature, and most fish species have refined mating systems, from  
43 strict monogamy to polyandry and polygyny (Taborsky 1994). The vendace (*Coregonus*  
44 *albula*) is a short-lived, small-sized, cold-water adapted schooling species (Karjalainen et al.  
45 2016) that is supposed to spawn in groups, but the actual mating system of this species, like  
46 many other group-spawning fishes, has not previously been described in detail. Vendace  
47 typically spawn in the littoral or sublittoral zones of lakes in the autumn, with hatching of the  
48 larvae taking place close to ice-break in the following spring, up to 6 months later (Urpanen  
49 et al. 2005). Contrary to the closely related whitefish (*Coregonus lavaretus*) which has  
50 breeding tubercles, neither vendace male or female have distinct secondary sexual  
51 characteristics. The whitefish is presumed to perform some kind of pre-spawn mate choice,  
52 because the size of the breeding tubercles correlates positively with offspring fitness  
53 (Wedekind et al. 2001; Wedekind et al. 2007; Huuskonen et al. 2011). Despite the inter-  
54 sexual selection and tendency for pair spawning behavior of whitefish, polygamous matings  
55 probably also occur (Rudolfson et al. 2008).

56

57 Our *first aim* was to document the courtship and mating of vendace under experimental  
58 conditions by non-intrusive monitoring of the natural behavior. Our hypothesis, based on the

59 previous information and local knowledge of fishermen, was that vendace has communal  
60 group spawning, typical of pelagic schooling planktivores such as Clupeidae (Mank & Avise  
61 2006). We also aimed to observe whether vendace has single or multiple pair spawning. Our  
62 *second aim* was to examine at what time of the day the spawning occurs. Earlier results from  
63 test fishing and movements on the spawning grounds (Lahti 1992; Heikkilä et al. 2004)  
64 suggested that the mating occurs at night, and our hypothesis was that mating activity is  
65 associated with the level of illumination. Our *third aim* was to examine the mortality rate of  
66 vendace after spawning. Many other salmonid species have high mortality after spawning  
67 (Belding 1934; Quinn 2005; Jonsson & Jonsson 2011) and based on the occasional non-  
68 documented observations of local fishermen and the small proportion of repeated spawners in  
69 the populations (Karjalainen et al. 2016), we hypothesized that post-spawning mortality of  
70 vendace is high. Finally, we discuss how the observed spawning behavior potentially affects  
71 the lake-wide distribution of vendace eggs and larvae.

72

73

#### 74 **Material and methods**

75

76 Vendace were caught by seine net from the oligotrophic Lake Southern Konnevesi (62°30′–  
77 62°40′N, 26°20′–26°44′E, Central Finland, area 120 km<sup>2</sup>, mean depth 13 m; Karjalainen et  
78 al. 2016) on two different occasions. The first shoal was caught in October 2015 (reared in  
79 tank 1, number of fish in the tank in the beginning of the study period n = 283) and two other  
80 shoals in October 2016 (tanks 2, n = 195 and tank 3, n = 225). Seining was carried out near a  
81 spawning site known to a local commercial fisherman. Fish were collected gently by a bucket  
82 from the seine net, underwater and fish were loaded to a transport tank for transporting them  
83 to the nearby Konnevesi Research Station. The water into the experimental tanks was piped  
84 from Lake Konnevesi and included zooplankton and other invertebrates at low, natural  
85 densities. Further, in both years fish were fed commercial dry feed for salmonid fishes and  
86 the fish caught in 2015 eagerly ate the dry feed during the growing season and grew normally  
87 but their feeding ceased in the autumn before spawning. The fish caught in autumn 2016 did  
88 not eat dry feed to a large extent or at all before the spawning period but the surviving  
89 individuals began to eat the dry feed soon after the spawning period. Fish caught in 2015

90 served as a test group which had long acclimation period to the rearing conditions before  
91 spawning and went through the annual maturation period in captivity.

92

93

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

106

107 The study period started on October 13, 2016 when fish were caught and arrived at the  
108 research station and ended on December 16, 2016. The spawning period started on October  
109 26 (Oct 26 to 27 was night 1) and ended on November 5 (night 11). Further, we continued  
110 monitoring of the fish that survived the study period until April 10, 2017. The bottoms of the  
111 tanks were checked every morning during the study period for laid eggs which were siphoned  
112 from the tanks if observed. The tank bottoms were visually checked also in the evening  
113 before lights were turned off to observe eggs from possible daytime spawning. Fertilization  
114 rate (% of fertilized eggs) of eggs laid in the tanks and gathered by siphoning was determined  
115 by microscopy for the samples taken from tank 3 where the video recordings occurred.  
116 Samples were taken after nights 4, 6, 7, 8 and 10 of the spawning period. The total number of  
117 eggs laid during one dark period was counted at night 6 to estimate the number of spawning  
118 rises with egg release during the dark period.

119

120 Video recordings of the spawning were carried out during nights 2 and 6 (on October 27–28  
121 and October 31–November 1) during the spawning period in tank 3. Video recording started  
122 before lights were turned off and continued two hours after the lights were turned on. The  
123 camera system in tank 3 comprised of three cameras and a video recorder (Kalatel Calibur  
124 DVMRE-4). The bottom and top horizontally viewing cameras were Ikegami ICD-47 black  
125 & white CCD with waterproof chambers, and the surface camera with a vertical field of  
126 vision from the water surface to the bottom of the tank was a Tracer TS-6030HPSC. One  
127 horizontally viewing camera on the bottom was used in tanks 2 and 3. During the dark period  
128 of the experiment, the tanks were illuminated by infrared illuminators (one Eneo IRLED-  
129 402E 850 nm/30 W per tank) attached above the tanks.

130

131 The number of spawning rises (the rise of two mating fish side by side from the bottom shoal  
132 towards the surface of the tank), number spawning rises with egg release and number of eggs  
133 released per spawning rise were counted for the tank 3 during night 6 from the first observed  
134 spawning rise to the end of the dark period (from October 31 at 20:04 to November 1 at  
135 07:45). All events (spawning rise and/or egg release) were counted from the field of vision of  
136 the top horizontally viewing camera, which covered approximately one third of the top water  
137 layer of the tank. The video recordings were examined by eye and the events were counted  
138 for a 30-minute period at hourly intervals. Altogether nine 30-minute periods were examined  
139 for night 6. It was not possible to record data blind because our study involved focal animals  
140 in the tanks.

141

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

150

151 Distribution of the newly-hatched vendace larvae in the littoral zone of Lake Konnevesi in  
152 1999–2011 was determined immediately after the ice-out by a random stratified-sampling  
153 procedure with bongo-nets (500 µm mesh) attached in front of a jet-powered motor boat  
154 (Karjalainen et al. 1998; Urpanen et al. 2009). Altogether samples were taken in 1020  
155 sampling plots from four zones in the littoral area: zone 1 bottom depth 0–0.5 m, zone 2 0.5–  
156 1 m, zone 3 1–2 m and zone 4 2–4 m and in 129 sampling plots in the pelagic area (bottom  
157 depth >4 m). The sample volume of each tow was measured by a flowmeter. Annually, the 20  
158 littoral and 10 pelagic sampling plots were randomly picked, and thus the sampling locations  
159 varied from year to year.

160

161

## 162 **Results**

163

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

170

171 The spawning behavior was intensively monitored in tank 3 during night 6 of the spawning  
172 period. When the lights were switched off, within a few minutes vendace formed a shoal near  
173 the tank bottom and active, mature individuals started mating (Fig 2A, Online Resource 1).

174 The first spawning rise was detected 21 minutes after the lights were switched off.

175 Occasionally, a female and male pair darted from the bottom shoal up towards the surface  
176 side by side with synchronized movements; i.e. a pair performed a spawning rise which  
177 ended near the surface and, if successful, the female released eggs at the end of the spawning  
178 rise (Supporting information S1). Only 2 %, (three out of 183 observed spawning rises)  
179 included more than two individuals (i.e. three fish). In at least one of these three-fish events  
180 the third individual clearly separated from the spawning rise before egg release (Supporting

181 information S2). During the dark period, there was also another shoal near the surface  
182 comprising of rather passive individuals which seemed to rest or did not take part in the  
183 spawning during that night. We were not able to reliably measure the number of fish in the  
184 top and bottom shoals or movement between them. Clearly, many fish dived immediately  
185 after spawning rise back to the bottom shoal but few of them seemed to be passive and stay  
186 longer in the top shoal.

187

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

192

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

209

210 Post-spawning mortality of mature individuals in every tank was high (Fig 4), the mean  
211 proportional mortality for the whole study period being 56 % (SE = 7). Before the spawning



212 period the mean mortality was only 1 % (SE = 1). The mortality started to increase 2 to 6  
213 days after spawning ceased. Most of the fish (95 % of all died fish) died during 40-days  
214 period after spawning. We observed the fish in tanks until April 10, 2017 and the mortality  
215 stayed low (3 %, SE=1) during whole winter after the 65-day study period. Males seemed to  
216 have higher mortality after spawning than females. In tanks 2 and 3, the proportion of  
217 females was 57 % before the study period but after the study period it was 62 % and 61 %  
218 respectively in these tanks. In tank 1, the proportion of females was even higher (Table 1).

219

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

225

226

## 227 **Discussion**

228

229 Our observations under laboratory conditions showed that vendace exhibit communal group  
230 spawning, typical of pelagic schooling planktivores, but that within the group they engage in  
231 pair mating behavior and not mass spawning as e.g. clupeids (Haegele & Schweigert 1985;  
232 Mank & Avise 2006). Both males and females spawn several times during the spawning  
233 period. They also have potential to spawn several times at each night (the estimated mean  
234 number of the spawning rises per female was 150) but it remained unclear how individual  
235 fish performed night by night during the spawning period. As the fish were not individually  
236 marked, we cannot rule out the possibility of permanent pairing between certain male and  
237 female individuals, but according to video recordings it appears more likely that individual  
238 fish spawned with several partners. The partner choice may be random and triggered by  
239 simultaneous excitement during random encounter. However, despite their polygamy  
240 vendace may still select mates, since egg release did not take place during every spawning  
241 rise. Intersexual selection and pairing has been proposed as an important component affecting

242 the embryonic and larval survival of coregonids (Wedekind et al. 2007; Huuskonen et al.  
243 2011) and the importance of mate choice certainly needs further experimental studies. In  
244 vendace also, despite the alleged random mating, cryptic female choice (Gasparini & Pilastro  
245 2011) after egg release may be an important element in the reproductive system of this  
246 schooling species, for example in reducing inbreeding depression (Jokinen 2015). Our  
247 finding that vendace can go through the annual maturation in captivity and perform spawning  
248 behavior under experimental conditions opens opportunities for future research. The  
249 fertilization rate of eggs in our experiment (68 %) corresponds to the proportion of fertilized  
250 eggs pumped from the spawning areas of vendace in four Finnish lakes (from 37 to 87 %,  
251 Karjalainen et al. 2015). Thus, fertilization success under our experimental conditions was  
252 similar to the natural fertilization success of vendace.

253

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

261

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

268

269 In agreement with our third hypothesis, the spawning stress seems to be a potential  
270 component of mortality regulating the duration of life span of vendace individuals.  
271 Considerable post-spawning mortality is typical of the life history strategies of many fishes in  
272 the family Salmonidae (Belding 1934; Quinn 2005; Jonsson & Jonsson 2011), some of them

273 being semelparous (*Onchorhynchus* spp.). Natural mortality caused by factors other than  
274 predation, is not well understood for fishes in general although the age-specific estimates of  
275 natural mortality are essential components of population models (Gislason et al. 2010;  
276 Nielsen et al. 2012). The natural mortality of many species has been shown to increase with  
277 age (Gislason et al. 2010; Nielsen et al. 2012; Uriarte et al. 2016), despite the fact that  
278 predation mortality typically decreases with size (age), and senescence processes, including  
279 high stress caused by spawning, have been proposed to be important factors causing the  
280 increase in mortality after maturation (Caputo et al. 2002; Nielsen et al. 2012). The natural  
281 mortality of vendace in nature has been estimated very rarely because it requires information  
282 on true (not only proportional) fish abundances and catches. Valkeajärvi (1983) and  
283 Marjomäki & Huolila (1994) have supported the increase in natural mortality with age based  
284 on quantitative lake specific data. From the population demography, male fish have been  
285 shown to typically have higher mortality than females (Bunnell et al. 2012; Nilssen et al.  
286 2012). For vendace, already Järvi (1920) pointed out that the proportion of males decreased  
287 strongly with age in seine catch samples, from 69 % in age 1+ to 26 % in age 4+. His large  
288 data set from more than 30 lakes (e.g. Järvi 1950) and various later studies (e.g. Lehtonen  
289 1981) confirm this tendency, thus implying to higher mortality in males than females.  
290 Bunnell et al. (2012) concluded that the underlying mechanisms of sex-specific difference in  
291 mortality of bloater (*Coregonus hoyi*) include sex-specific differences in age at maturity,  
292 growth rate and activity or behavior during the spawning period. Even though vendace males  
293 had higher mortality than females, both sexes encountered significant post-spawning  
294 mortality which seems to be an important component affecting population dynamics and the  
295 future spawning stock structure. Karjalainen et al. (2016) reported that only 16–60% of  
296 females in Finnish lakes were repeat spawners. However, naive (often age of 1+) and repeat  
297 (age of 2+ or older) female spawners did not differ in their offspring productivity, except that  
298 larger individuals, despite their age, had higher fecundity (Karjalainen et al. 2016).

299

300 Depending on their reproductive strategy, different fish species aim to aggregate or disperse  
301 the eggs and larvae in their reproductive habitat (Taborsky 1994; Leis et al. 2016). Some  
302 species aggregate eggs in nests (Wootton 1999; Pampoulie 2001; Jonsson & Jonsson 2011) or  
303 in specific substrata (Wootton 1999; Haegele & Schweigert 1985), but many, especially  
304 pelagic species, disperse both eggs and larvae widely around the potential nursery areas (Leis  
305 et al. 2013; Pacariz et al. 2013). Vendace larvae have been observed to disperse lake-wide to

306 both littoral and pelagic zones (Fig 5, Karjalainen et al. 2002). Similarly, the density of eggs  
307 in the spawning ground is low: the mean density of eggs in four Finnish lakes was 8 eggs m<sup>-2</sup>  
308 (SD = 10, n = 29, min = 0.1 max = 35; recalculated from reports by Väisänen et al. 1994;  
309 Valkeajärvi et al. 2001; Huuskonen 2005). The observed spawning behavior with small egg  
310 batches and spawning rises in the dark have the potential to promote dispersal of early stages.  
311 If spawning shoals in lakes move around the spawning ground, the eggs of an individual  
312 female may spread around a broad bottom area during the spawning period which can last  
313 several days. Direct observations of spawning shoal movements in lakes are needed to verify  
314 this assumption. Due to the long egg incubation time (up to six months from October to May)  
315 without protection, the dispersal of eggs seems to be a strategy to decrease the mortality by  
316 predators with the type III functional response (Holling 1959) preying visually, but also by  
317 vertebrate predators which can also be active at night (Karjalainen et al. 2015). On the other  
318 hand, the strategy of spawning in darkness may serve to protect against visually feeding  
319 fishes (most of the fishes in boreal lakes) that would potentially feed on the spawning  
320 vendace themselves (e.g. perch, brown trout) and/or on their eggs (e.g. perch, ruffe).

321

### 322 **Acknowledgments**

323 We thank Janne Koskinen, Risto Latvanen and Jyrki Raatikainen for their invaluable  
324 assistance in fish care and in experimental work, Tuula Väänänen for the help with fish  
325 samples, Prof. Roger Jones for the kind check of the English and three anonymous reviewers  
326 for their helpful comments. This study was supported by North Savonia Centre for Economic  
327 Development, Transport and the Environment.

328

### 329 **Conflict of interest**

330 The authors declare that they have no conflict of interest.

331

### 332 **Ethical approval**

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

335

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- 452

453 **Supplementary material**

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

456

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

459

460

461 **Figure captions**

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

464

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

467

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

473

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

477

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

481

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

486

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

487

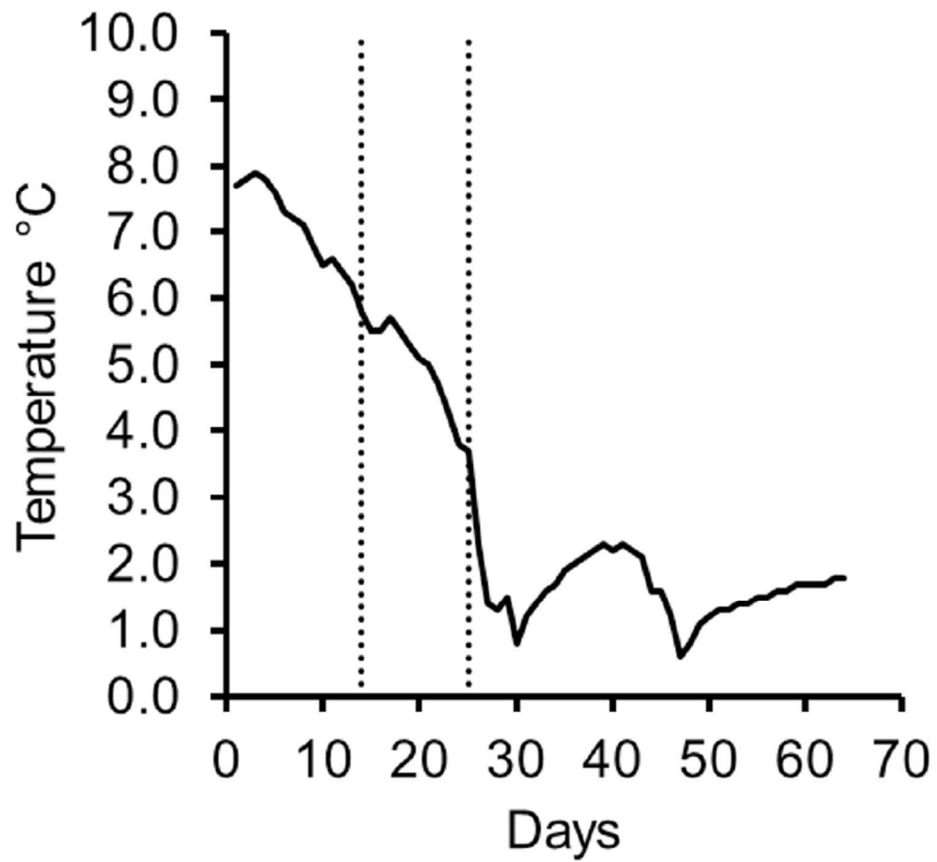


Fig. 1. Water temperature during the experimental period. The spawning episode (11 nights) was represented by the vertical dotted lines.

64x59mm (300 x 300 DPI)

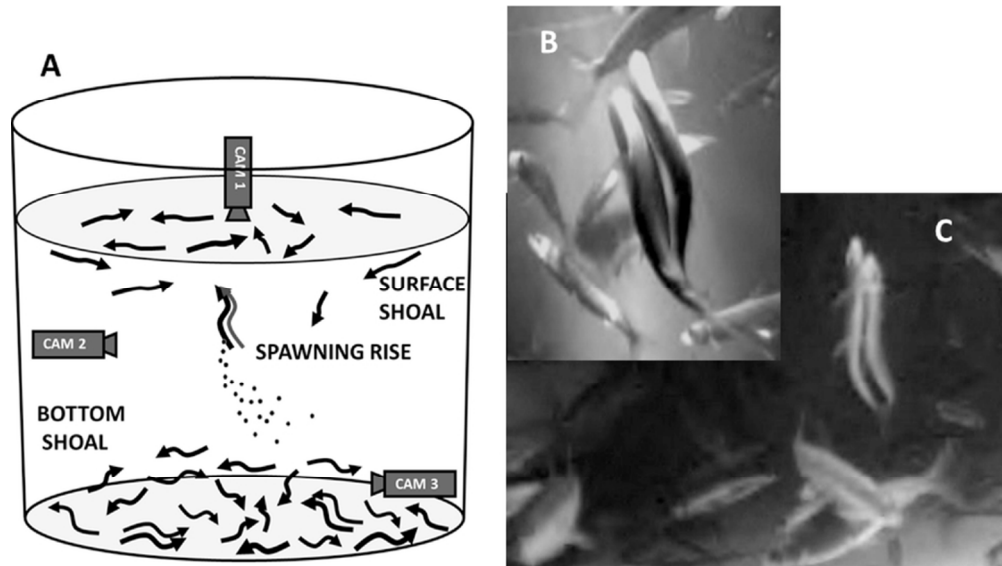


Fig. 2. A) General pattern of the spawning shoal and behavior of vendace. Spawning rise in the B) top side (camera 2) and C) bottom side camera (camera 3) view (photo J Karjalainen).

80x45mm (300 x 300 DPI)

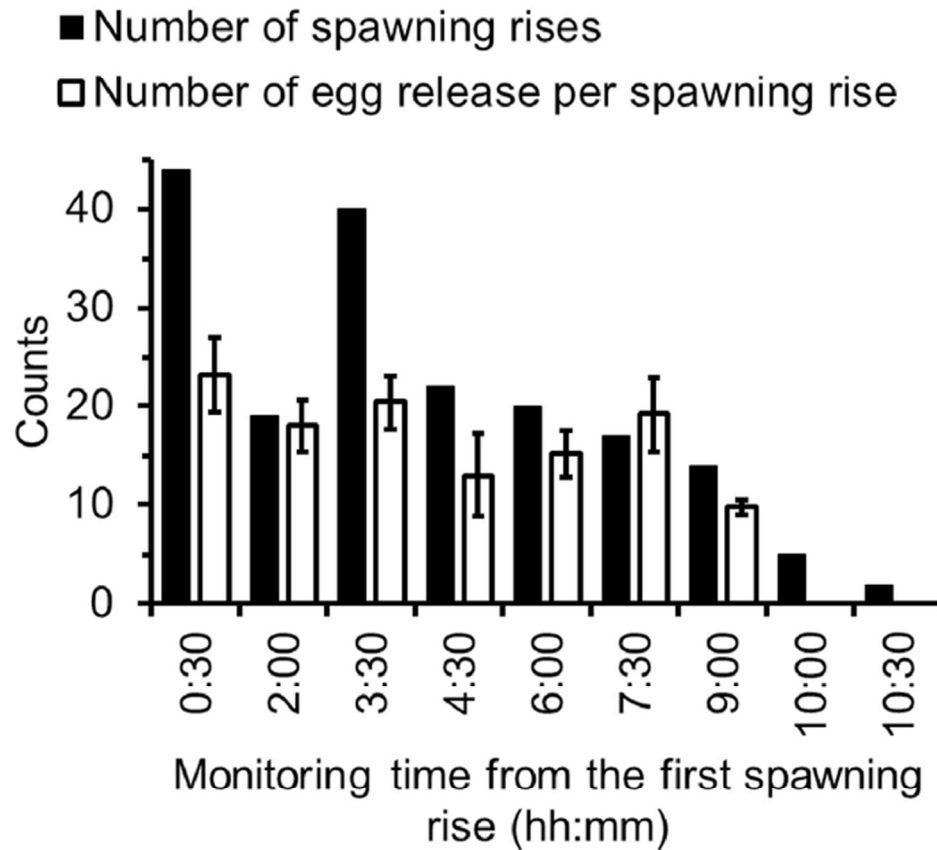


Fig. 3. Mean number of spawn rises (black bar) and eggs laid per a spawn rise (open bar) for the 30-minutes observation periods during one dark period (from 31 October at 20:04:00 to 1 November at 07:45:00) in the spawning episode. Vertical lines in the egg release bars represent the standard errors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

62x56mm (300 x 300 DPI)

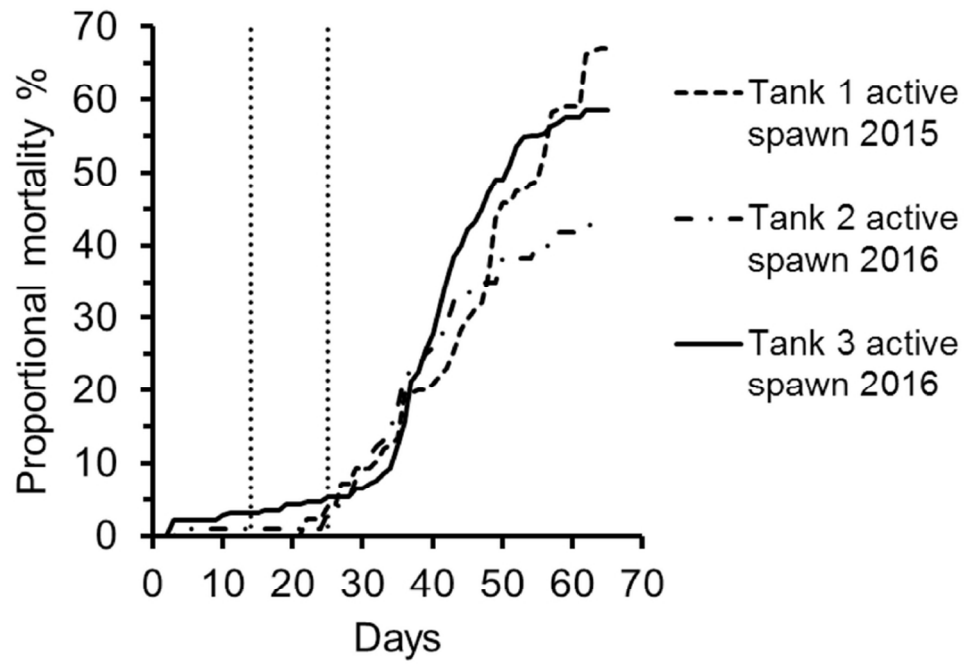


Fig. 4. Cumulative relative mortality (%) of mature vendace individuals before, during and after the spawning episode. The spawning episode (11 nights) was represented by the vertical dotted lines.

79x56mm (300 x 300 DPI)



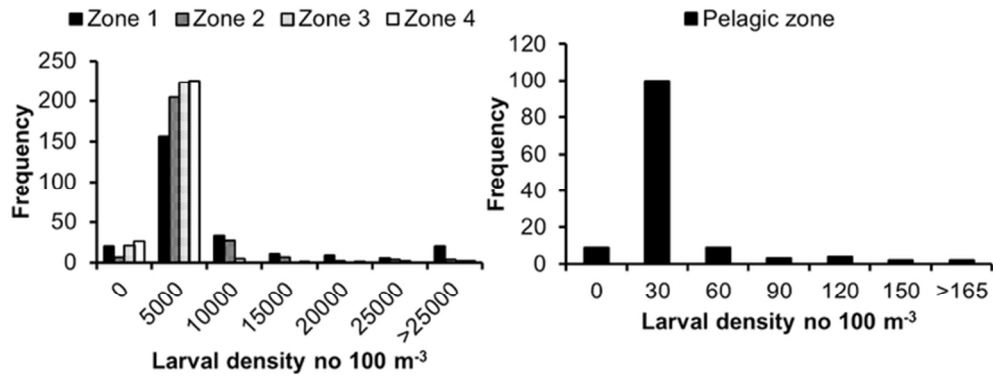


Fig. 5. Frequency distributions of newly-hatched vendace densities (no. 100 m<sup>-3</sup>) in the different A) littoral (n=1020) and B) pelagic (n=129) sampling locations in Lake Konnevesi in 1999-2011.

63x26mm (300 x 300 DPI)