Ann. Zool. Fennici 58: 129–140 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 August 2021

Spawning behaviour of whitefishes (Coregonidae)

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Received 31 July 2020, final version received 26 Feb. 2021, accepted 28 Jan. 2021

Semenchenko, S. & Smeshlivaya, N. 2021: Spawning behaviour of whitefishes (Coregonidae). — *Ann. Zool. Fennici* 58: 129–140.

We observed, photographed, and recorded (video and audio) spawning of five whitefish species — *Coregonus migratorius* (Baikal basin), *C. peled*, *C. tugun*, *C. pidschian*, *C. muksun* (the Ob basin) — in the spawning devices. All species spawned in autumn in the dark and the spawning period lasted 10–30 days. Individual fish spawned several times during the night and the spawning behaviour consisted of three, cyclically repeated phases: courtship, mating and recovery. Spawning occurred in male–female (with males to be initiators) or male–male combination, and took place either in the water column or near the water surface. A mating act consisted of a rhythmic parallel movement of the fish swimming side by side with the synchronous release of the gametes. Three types of mating acts were observed: vertical (from bottom to top), horizontal and combined including both vertical and horizontal movements. The male in the spawning pair moved forward towards the female by the length of its head; it rhythmically struck the back of the female's abdomen by bending the caudal peduncle. Depending on the species and size of the fish, the mating act lasted for 0.3–3 s within 0.3–2 m. The frequency of rhythmic body collisions was on average 17 Hz for *C. migratorius* and *C. pidschian*, while for *C. tugun* and *C. peled* it was 25–27 Hz. An egg batch released during the mating act amounted to about 90 eggs for *C. tugun* and 290–370 for *C. peled*, which corresponded to 1%–6% of the total fecundity of a female. A female participated in 20–100 mating acts during 1–3 nights. Eggs cannibalism was also observed. During spawning, eggs were widely dispersed across the spawning area, which may be regarded as an adaptation aimed at increasing survival rate during embryogenesis.

Introduction

Knowledge of the ethological and ecological aspects of fish reproduction is important for rational exploitation of fish, their artificial reproduction and sustainable aquaculture development. Whitefishes (Coregonidae) are of significant commercial importance in northern Eurasia and North America. However, the spawning behaviour of most species in this family has not been studied in detail except for *Coregonus migratorius* (Tyurin & Sosinovich 1937, Seleznev 1942), *C. lavaretus* (Fabricius & Lindroth 1953) and *C. albula* (Karjalainen & Marjomäki 2017).

Editor-in-charge: Juha Karjalainen

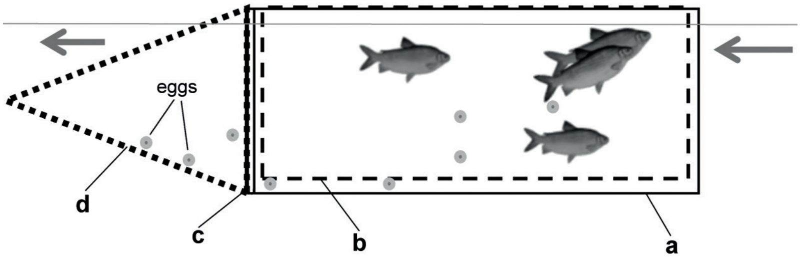

Fig. 1. Side-view diagram of a tray-type device (L × W × H: 6.0 × 2.0 × 1.2 m; effective vol. 10 m^3) for collecting whitefish eggs during natural spawning in river conditions: (**a**) frame (the side walls and the bottom are covered with tarpaulin or made of aluminium sheets, and the end walls are covered with metal mesh); (**b**) cage made of a stock canvas; (**c**) end frame; and (**d**) pyramidal nylon net (mesh size 1.2 mm) for collecting eggs. The arrows indicate direction of the current.

In Russia, an ecological method for collecting whitefish eggs for artificial reproduction has been developed and used commercially in the Baikal and Ob basins. In this method, fish are placed in spawning devices that enable collection of fertilized eggs for incubation (Dzyumenko 1984, Dzyumenko & Semenchenko 1987, Semenchenko 2014, Litvinenko 2016). In addition, this method provides a unique opportunity to study the spawning behaviour of whitefishes. Spawning is a complex behaviour of sexually mature fish aimed at fertilizing eggs and distributing them in space. Mating is an interaction between mature fish, resulting in the release of gametes into the environment. Apart from mating, spawning also includes courtship, i.e. selection of partners, and recovery of mates during the interval between mating acts.

The aim of our study was to characterise spawning of whitefishes based on our own observations and available data.

Material and methods

We carried out observations of the spawning process (courtship, mating, and the recovery phase after mating) of five species of Siberian whitefishes: *C. migratorius*, *C. peled* (riverine and lacustrine), *C. tugun*, *C. pidschian*, *C. muksun* (Table 1). Apart from the lacustrine form of *C. peled*, all other studied species occur and spawn in rivers. To this end we photographed and recorded (video and audio) the fish during spawning in the spawning devices used for egg collection. We also either measured ourselves or acquired existing data on fish body (standard) length, total body mass, female fecundity, as well as start and end of spawning, its durations and water temperature during this period.

Mature individuals of *C. migratorius*, riverine *C. peled*, *C. pidcshian* and *C. tugun* were caught from natural spawning stocks during the migration period. Before spawning, the fish were held in net cages for 7–50 days. *Coregonus muksun* and lacustrine *C. peled* were reared to maturity in cages on commercial dry feed in Lake Volkovo.

In 1984–1993, 1998–2002 and 2000–2002, observations of the spawning behaviour of *C. migratorius*, riverine *C. peled* and *C. tugun*, respectively, were carried out in tray-type devices (Fig. 1; *see* also Dzyumenko & Semenchenko 1987) placed in the river (flow 0.1–0.2 m s^{-1}) using pontoons. In this device, water flow flushes the eggs downstream towards the end of the device and into the pyramidal collection net. The numbers of mature *C. migratorius*, *C. tugun* and riverine *C. peled* individuals placed in one tray-type device were 2000–3000, 3000–10 000 and 1000–2400, respectively.

As of 2003, spawning of *C. peled*, *C. tugun*, *C. pidcshian* and *C. muksun*, was monitored also in cage-type devices constructed for lacustrine conditions (Fig. 2). In such device (installed using pontoons in a lake or in an oxbow lake), the cage for keeping spawning fish is placed inside the outer cage made of synthetic net (mesh size 1.0–1.4 mm). The eggs gathering at the bottom of the device are pumped through the hose to container. We used the devices of the following sizes (W × L × H): 4.0 × 4.0 × 3.0 m (effec-

Table 1. Whitefish body (standard) length (min–max, cm), total body mass (min–max, g) and fecundity (min–max eggs per female) of the fish, as well as the duration and timing of the spawning period and temperature conditions.

Species/sex	Observation period	Total number of measured fish	Body length (cm)	Body mass (g)	Fecundity (eggs per female)	Spawning		
						start date range	duration (days)	temp. range (max–min) (°C)
C. migratorius[1]	1984–1993					1 Oct–5 Oct	23–28	6.0–0.2
Female		258	29.0–31.2	290–390	7700–10800			
Male		312	28.3–29.0	240–335				
C. tugun[2]	2000–2004, 2013–2016					27 Sep–4 Oct	9–18	7.6–0.2
Female		345	10.6–12.2	15–24	900–2400			
Male		304	10.3–12.1	11–20				
C. peled riverine[2]	1998–2011, 2013–2017					4 Oct–16 Oct	17–27	6.9–0.2
Female		768	29.6–33.1	387–596	19900–44100			
Male		646	28.3–32.1	295–478				
C. peled lacustrine[3]	2017–2019					15 Nov–5 Nov	23–31	1.8–0.9
Female		94	27.4–30.8	343–560	12040–21380			
Male		108	27.2–30.2	320–448				
C. pidschian[2]	2004–2006, 2009–2013					7 Oct–14 Oct	13–18	7.1–0.9
Female		258	27.9–29.7	268–360	11200–17500			
Male		276	27.2–29.7	222–338				
C. muksun[3]	2017–2019					3 Nov–5 Nov	15–23	2.5–0.7
Female		75	44.4–47.8	1567–2011	50900–66500			
Male		83	43.2–46.6	1420–1845				

Locations: [1)] Ina River (53°42´N, 109°58´E), a tributary of the Barguzin River in the Baikal basin, as well as the Bolsherechensky hatchery (51°58´N, 106°19´E); [2)] Rakhtynya fish farm (63°39´N, 61°49´E) on the Lyapin River, a tributary of the Severnaya Sosva River in the Ob basin. [3)] Lake Volkovo (58°01´N, 68°49´E).

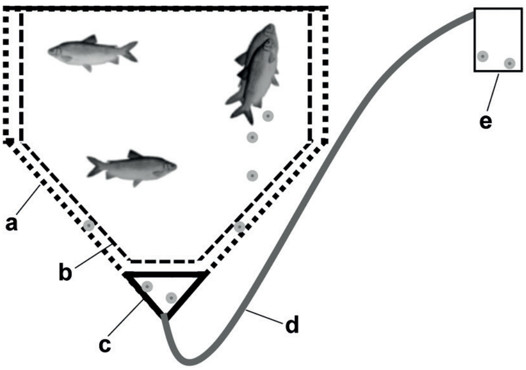

Fig. 2. Side-view of a cage-type device for collecting whitefish eggs during natural spawning in the absence of flow: (**a**) outer cage made of fine-mesh synthetic material, (**b**) inner cage, (**c**) pyramidal metal tip with a pipe, (**d**) hose, and (**e**) container for collecting eggs.

tive vol. 32 m^3) for *C. tugun*; 6.4 × 6.4 × 3.7 m (effective vol. 86 m^3) for riverine *C. peled* and *C. pidschian*; and 7.0 × 7.0 × 5.5 m (effective vol. 184 m^3) for C. *muksun*. There was no spawning substrate in the devices. In one cage-type device, there were 3000–4500, 1500–3000 and 400–1000 mature individuals of *C. peled*, *C. pidschian* and *C. muksun*, respectively.

In each case, the numbers of males and females in one device were nearly equal. Pituitary-gland injections to stimulate maturation were not performed.

During the spawning season, eggs were collected from the devices usually every day in the morning or afternoon, and their amount was assessed by the volume and weight method. The spawning start date in each season was the date when by the first batch of eggs was collected. The egg fertilization rate was determined daily at the middle-celled morula stage by lateral microscopy (Chernyaev 1962).

In 2011–2019, we took photographs and recorded the spawning fish from above the water surface with Canon EOS 600D and 650D cameras (EF-S 18–135 mm lens). Video recordings were done at natural illumination (twilight) of 1–20 lux, and flash photography was used to take pictures in the evening and at night. Photographs and video recordings of *C. migratorius* spawning were taken by I. N. Taradanov in 2018 and 2019. A total of 589 photographs and 213 videos were analysed. In a pair of spawning fish, we identified females by the characteristic shape of their abdomens. It was possible to identify the sex of a fish in only 30% of photographs.

To assess whether eggs were released during a mating act, in 2015 and 2017, at 20:00 and 06:00 hrs we observed spawning *C. peled* (20 pairs) as this species spawns in the water column near the surface making such observations and species identification possible. To this end, we looked for eggs in the spawning zone of a pair immediately after the completion of the mating act by illuminating the water with a pocket flashlight for 1–3 s. This was done during 20 mating acts, and there were 4440 observations in total.

As during a mating act, fish generate specific sounds, we evaluated the spawning activity (mating acts per minute) from sound recordings of mating acts in the spawning device between 16:00 and 07:00 hrs. The recordings were made by the second author on 15–29 October 2016 for *C. peled* and 6–8 October 2015 for *C. tugun* with an Olympus Digital recorder VN-732PC equipped with a microphone and placed above the spawning device. When analysing the audio recordings, we compared them with a parallel video recording of spawning made in the evening. Fifteen-minute sections of audio recordings were analysed and mating acts in each 3 minutes were counted, and the average number of acts per minute was calculated.

To assess the amount of light at which the first mating act took place after dusk, in October 2015, 2016 and 2017 we measured the illumination above the water surface in the spawning device every 10 min between 16:00 and 20:00 hrs with a TKA-LUX light meter.

The number of eggs released during one mating act (egg batch) by *C. tugun* and *C. peled* females was determined by counting from the photographs of the spawning area taken 2–3 s after the act's completion. Those photographs were taken by us in 2015 and 2016 from above the water surface with Canon EOS 600D or 650D equipped with a flash immediately after the mating act near the side of the spawning device was observed. We assumed that all eggs were released into the device and none got outside. The photographs were displayed on the computer screen, and counting was done by sequentially highlighting the eggs.

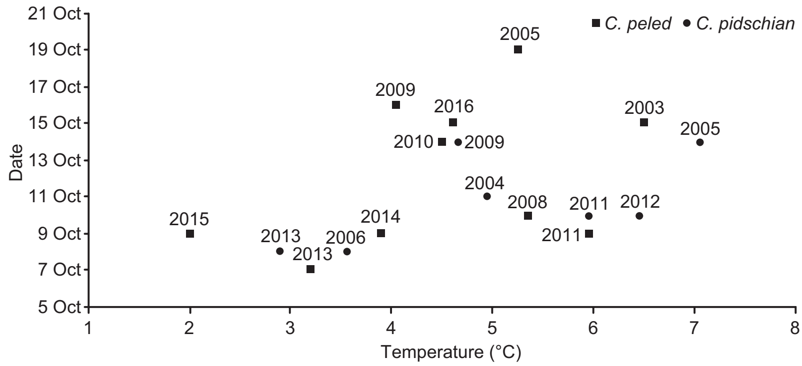

Fig. 3. Water temperature on the dates of the start of spawning of whitefishes at the "Rakhtynya" fish farm in 2003–2016.

In addition to the above, the number of eggs released by *C. peled* during one mating act was estimated by direct counting three times in 2016 as follows: the number of eggs collected from the device in one day was divided by the total number of mating acts and multiplied by the proportion of mating acts associated with egg release. To estimate the total number of mating acts for that day, summed the mean numbers of mating acts for 15-min intervals of audio recordings of spawning.

The duration of mating acts and the distance the fish swam during one mating act were estimated from video clips using the Pinnacle Studio programme. When scaling the image, we used the average length of the fish. We also determined the frequency of fish collisions during the mating act from audio recordings, by counting sound peaks.

Results

The length of the spawning period was between 10 and 30 days, and mass spawning usually lasted for 7–15 days at water temperatures below 4 °C (Table 1).

Riverine coregonids spawned between the end of September and the end of November in the following order: *C. tugun*, *C. migratorius*, *C. pidschian*, *C. peled*, *C. muksun*. Water temperatures at which spawning commenced varied among species and ranged from 7.6 to 0.2 °C (Table 1). Differences in water temperatures at the beginning of *C. peled* and *C. pidschian* spawning periods were 4.0–4.5 °C (Fig. 3). For example, the "early" spawning of *C. peled* on 9 October in 2013 and in 2011 began at 2 °C and 6 °C, respectively. In general, spawning of the riverine *C. peled*, *C. migratorius* and *C. pidschian* ended 3–7 days after the waterbody became frozen over, while spawning of *C. muksun* started at the same time. Spawning of the lacustrine form of *C. peled* was observed in November–December.

In all studied species, spawning behaviour of males was observed 2–5 days before the appearance of females with ripe gametes. During this period, male–male mating pairs were frequently observed in spawning devices. During the mass spawning period, approximately 70%–100% of all observed *C. peled* mating acts were male–female, and about 95% them were associated with egg release (Fig. 4). Paired contacts of males became more frequent at the end of the spawning period.

During the spawning period, mating acts were observed every day, but with different frequency at different times of the day. The threshold illumination and time of the beginning of spawning varied among the studied species and depending on the timing of the spawning period. For example, *C. pidschian* began to spawn earlier than other species — during sunset with natural illumination at the water surface within 240–480 lux, while *C. peled* began spawning 30–60 min after the sunset when illumination decreased to 14–55 lux. *Coregonus tugun* usually began to spawn in the evening at about 1–19 lux.

According to our audio recording and visual observations, the spawning activity increased steadily reaching maximum 1–2 hours after its beginning at 0.5–1.0 lux and < 0.4 lux at the water surface for *C. peled* and *C. tugun*, respec-

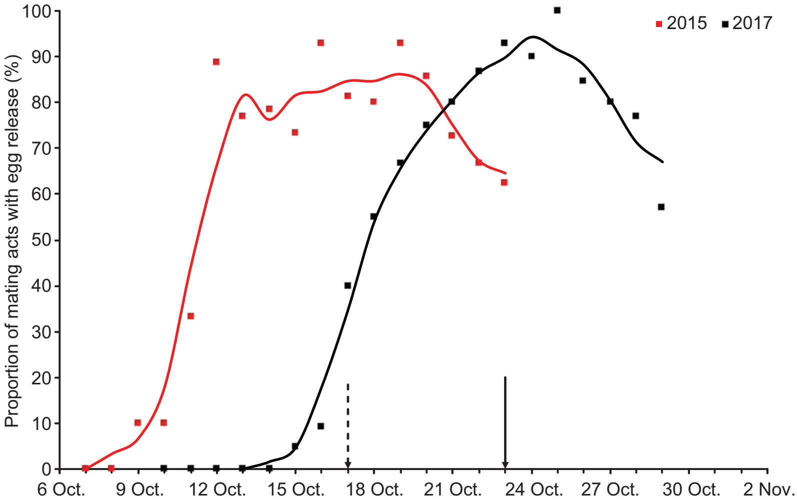

Fig. 4. Proportions of *Coregonus peled* spawning acts with egg release during the spawning period in the Rakhtynya fish farm in the years with the early (2015) and late (2017) spawning. The curves were made using moving averages of three consecutive values. Each symbol shows an average value of two series of observations at 20:00–22:00 hrs and 06:00 hrs including 20 mating acts. The arrows show the dates of the maximum daily egg collection from experimental devices.

tively, and then fluctuated throughout the night (Figs. 5 and 6). Spawning ceased about 1 hour before dawn or at early dawn. Most of the eggs were released before 02:00–03:00 hrs. An increase in the intensity of spawning was seen in the predawn hours for *C. tugun* (Fig. 6). The duration of *C. peled* continuous spawning activity was observed to reach 14 hours.

One–two hours before spawning, we observed an increase in swimming activity in a group of mature fish. The fish were rising to the surface and moving vigorously as if they were chasing each other.

The following phases during spawning were distinguished: (1) courtship (selection of partners), (2) mating with possible release of eggs, and (3) recovery. Those three phases were cyclically repeated during the entire spawning period.

Males were the initiators of spawning behaviour. During the courtship phase, the male was positioned behind the female — its head was at the level of the female's anus (Fig. 7). Females not ready to spawn actively avoided the contact with males during courtship. Upon meeting ready-to-spawn individuals, the courtship turned into a mating act.

The mating act was a complex spatiotemporal process which consisted of rhythmic collision of bodies of a pair of mature fish during their parallel forward movement with the synchronous release of gametes. Normally, a pair of whitefish participated in a mating act. In three photographs (less than 1% of the total number), however, we noted spawning interaction of possibly three *C. peled* fish, and in one video, we observed three *C. pidschian* individuals of undetermined sex engaged in a mating act. Group spawning behaviour was never observed in *C. migratorius*, *C. tugun* and *C. muksun*.

As exemplified by *C. peled*, in a spawning pair, the male was positioned ahead of the female by approximately the length of its head (Fig. 8), and its caudal peduncle near the anus of the female. The male stimulated release of the eggs by rhythmically stroking the posterior part of the female's abdomen with the anterior part of the caudal peduncle while releasing the milt (Fig. 9). The female performed reciprocal synchronous oscillatory movements releasing an egg batch. During mating, a female can swim either on male's right or left. At the end of a mating act, the female usually slowed down, and the male moved forward, after which mating fish separated.

A mating act was accompanied by a characteristic drumming sound generated by frequent collision of fish bodies. The analysis of audio recordings revealed that the sound frequency of impacts averaged 27–29 Hz for *C. tugun* and *C. peled*, and about 17 Hz for *C. migratorius* and *C. pidschian* (Table 2). The duration of a mating act in whitefishes varied from 0.2 to 5 s, lasting on average 0.3 s in *Coregonus tugun*, 1–2 s in *C. peled* and *C. pidschian*, and 2–4 s in *C.*

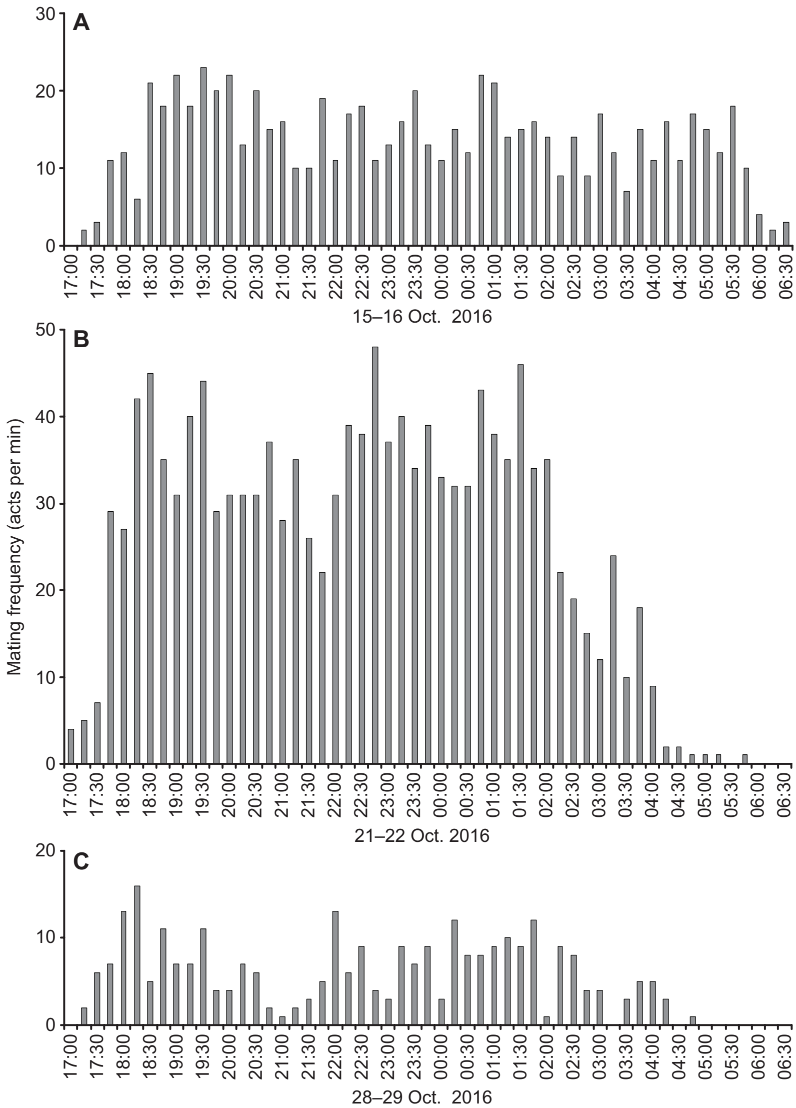

Fig. 5. Dynamics of mating frequency (mating acts per min) in *Coregonus peled* observed in the spawning devices and based on the analysis of audio recordings. — **A**: Beginning of the spawning period. — **B**: Mid-phase of the spawning period. — **C**: End of spawning the period

migratorius. The distance swam by a spawning pair while in direct contact was on the average 0.4 m in *C. tugun*, and 1.4 m in *C. peled* and *C. pidschian*. The average speed of a pair was about 1 m s^{-1}, and jumps out of water were also observed.

Table 2. Characteristics of the whitefish mating act based on the analysis of video and audio recordings.

Species	Number of eggs per batch		Distance (m) covered during one mating act		Mating act duration (s)		Mate collision frequency (Hz)	
	mean ± SD	*n*	mean ± SD	*n*	mean ± SD	*n*	mean ± SD	*n*
C. migratorius	–	–	1.86 ± 1.20	6	3.15 ± 2.04	4	16.8 ± 4.2	4
C. peled	368 ± 198	13	1.41 ± 0.49	6	1.35 ± 0.54	13	24.6 ± 6.8	30
C. tugun	93 ± 40	8	0.39 ± 0.11	5	0.30 ± 0.09	10	26.6 ± 2.0	4
C. pidschian	–	–	1.36 ± 0.34	6	1.40 ± 0.26	9	17.5 ± 0.7	3

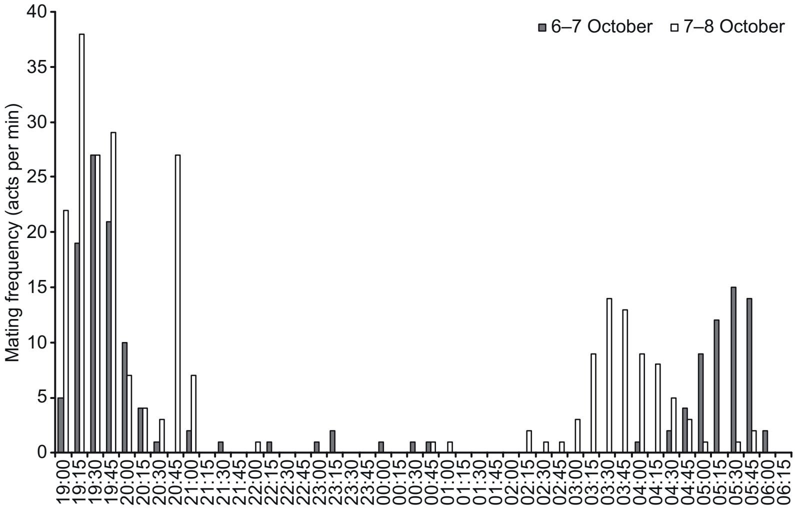

Fig. 6. Dynamics of *Coregonus tugun* mating on 6–8 October 2015 observed in the spawning devices and based on the analysis of audio recordings.

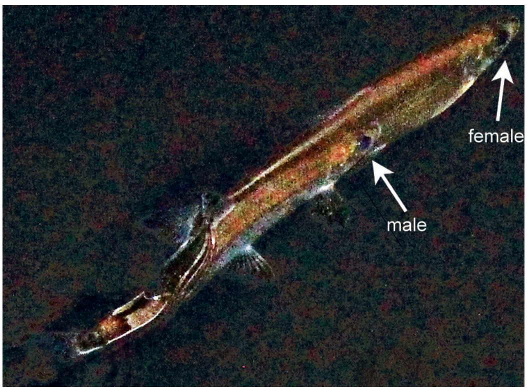

Fig. 7. *Coregonus tugun* courtship phase. Photographed on 7 Oct. 2015.

It was possible to distinguish three types of mating acts in terms of the movement of a pair:

1. Vertical (*C. pidschian*, *C. muksun*, *C. tugun*): the predominant vector of movement was from bottom to top. When reaching the surface, a pair separated while turning over to one side or upside down. Some pairs did not reach the surface.
2. Horizontal (*C. migratorius*, *C. peled*; Fig. 8): a pair moved along the water surface, and commenced a mating act immediately after the courtship phase while maintaining the direction of movement.
3. Combined (*C. migratorius*, *C. tugun*, *C. muksun*): a pair began to move towards the

Fig. 8. Leading position of the male in relation to the female in the spawning pair of *Coregonus peled*. Photographed on 17 Oct. 2011 (left) and 21 Oct. 2013 (right).

surface and, after reaching it, moved horizontally in a straight line for some time or arced with turning over.

It should be noted that the movement of a spawning pair from the surface towards the bottom was not observed. A spawning pair always moved towards the surface, releasing eggs and milt at the surface with slowly settling eggs forming a widening trail at an angle of approximately 30° (Figs. 10 and 11).

The number of eggs released in a single batch varied between species ranging from 142 to 900 (mean ± SD = 368 ± 198) in *C. peled* and from 45 to 173 ((mean ± SD = 93 ± 40) in *C. tugun*. (Table 2). In one egg batch, *C. peled* and *C. tugun* released 1.1%–1.4% and 6%, respectively, of the total egg number. As the mean ± SD female fecundity in *C. tugun* (*n* = 46) was 1550 ± 136 eggs, and in *C. peled* (*n* = 40) 26 900 ± 1897 eggs (*n* = 40), *C. tugun* and *C. peled* females have to participate in approximately 17 an 73–93 mating acts, respectively, to release all mature eggs.

The observed whitefish spawning behaviour usually ensured a high fertilization rate of eggs. According to our long-term data, in case of industrial collection of *C. migratorius* and *C. peled* eggs by an ecological method during the spawning season 2019, the average fertilization rates in *C. migratorius* and *C. peled*, *C. pidschian* and *C. muksun* were 88%–93%, 88%–93%, 76%–83% and 85%, respectively.

Fig. 9. Interaction of *C. muksun* male (left) and female (right) during the mating act. Photographed on 7 Nov. 2018.

Fig. 10. Horizontal type of a *Coregonus tugun* pair movement. A trail of eggs (arrow) visible behind the spawning. Photographed on 8 Oct. 2016.

Fig. 11. *Coregonus muksun* pair that have completed the mating act by turning their belly towards water surface (view from above). Photographed on 7 Nov. 2018.

Discussion

Pair spawning observed in Siberian whitefishes, is also typical for other European coregonids, the common whitefish (*C. lavaretus*) (Fabricius & Lindroth 1953) and the vendace (*C. albula*) (Karjalainen & Marjomäki 2017). Participation of three vendace mates in a spawning was recorded in less than 2% of acts (Karjalainen & Marjomäki 2017). Based on Seleznev's (1942) description of Baikal *C. migratorius* spawning, Reshetnikov and Bogdanov (2011), and Chernyaev (2017) concluded that in whitefish typically two males and one female participate in spawning. Moreover, it is argued that during a mating act, a male holds a female by the pectoral fins with its mouth, but we did not observe this in our study. We also did not recorded a single spawning interaction which would involve two males and one female as described by Seleznev (1942). However, we often observed a *C. pidschian* spawning pair being followed by a third individual eating released eggs, which in poor lighting conditions could be mistaken for two males participating in spawning.

Annual fluctuation in the timing of the spawning period within ten days is typical for each population. Previously, it had been considered that spawning begins when the water temperature reaches a certain threshold value but our observations indicated that it seems to be triggered by date rather than by water temperature alone.

Our observations confirmed that whitefishes spawn mainly in the dark (Tyurin & Sosinovich 1937, Eckmann 1991, Karjalainen & Marjomäki 2017) which is probably an adaptation. It is known that whitefishes consume their own eggs (Tyurin & Sosinovich 1937, Ventling-Schwang & Müller 1991). We found up to 400 eggs in the stomachs of *C. migratorius* and *C. pidschian* males caught from an experimental device, and about 20 eggs in the stomach of *C. tugun*. We also observed yellow-orange faeces from digested eggs in all species. According to Tyurin (1937), the proportion of eggs consumed by *C. migratorius* in the Kichera River was up to 5% of the individual fecundity. It is known that whitefishes locate prey visually and do not feed in complete darkness (Volkova 1971, Dabrowski & Jewson 1984). Therefore, spawning of whitefishes under low illumination is probably aimed at reducing eggs consumption by both parental individuals and other fish (Eckmann 1991). However, a considerable part (up to 20%) of the daily spawning activity still occurs during the period with illumination exceeding the threshold value for successful feeding of whitefish (3–10 lx; Volkova 1971), which makes egg cannibalism possible. The question arises as to why this group of fish has not evolved to spawn in darkness? It is assumed that egg cannibalism is an adaptation that reduces mates' death from after-spawning exhaustion, and thus ensures polycyclic reproduction of the population (Rohwer 1978, Skurdal 1985). In addition, it can be assumed that limited egg cannibalism is aimed to compensate for energetic costs of milt production and long-term participation of males in spawning in conditions of food shortage in the breeding grounds.

We recorded partial asynchrony in the spawning activity of males and females. According to our observations, male gametes mature 2–3 weeks earlier than those of females (Smeshlivaya & Semenchenko 2015) which may be associated with conditions in the spawning devices that differ from natural environment. In particular, in the devices for collecting eggs, fish stocking density was probably higher than at the natural spawning sites.

According to our observations, whitefish males are nonselective in choosing the object

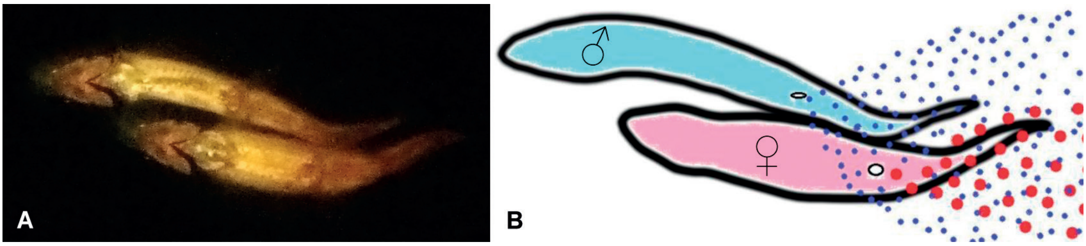

Fig. 12. (**A**) Position of the bodies of the male and female *Coregonus tugun* during the mating act, and (**B**) spatial interaction between eggs and milt.

with which they engage in spawning behaviour. In addition to females ready to spawn, they can choose another male of the same species, an inanimate object with a smooth surface (*see* Dzyumenko & Semenchenko 1987), or an individual (male or female) of different species.

The position of fish bodies during a mating act is an important element of spawning behaviour which ensures a more complete encounter of eggs and milt during the act (Fig. 12). Due to the leading position of a male in a pair of fish, each egg enters the milt trail immediately after it is released which increases the probability of fertilization. This interaction of mates is also typical in vendace (Karjalainen & Marjomäki (2017).

Since we did not mark fish, we cannot confirm repeated spawning of one female with different males (polygamy) but considering low sexual selectivity in whitefish males and high number of mates in the experimental device or at a spawning site it is the most probable assumption.

We were unable to estimate the duration of spawning activity of a females. Nevertheless, we can assume that a female releases all eggs within one to three nights. Dzyumenko and Semenchenko (1987) observed a *C. pidschian* pair in a tray-type device for collecting eggs completing spawning during three nights. A female released most of the eggs (70% of the total number) during the first night of spawning, with the next two portions released during two following nights being approximately equal.

Unlike in many other groups of fish, whitefishes spawn in the absence of specific spawning substrate (Dzyumenko 1984) which was also confirmed in this study. Presence of water current is also not a mandatory condition for spawning of whitefishes that normally breed in rivers. In our study, riverine C. *peled*, *C. tugun* and *C. muksun* successfully spawned in cage-type devices with no current. In such devices mating pairs usually moved in an organized manner along the perimeter of the cage, which probably compensates for the lack of current.

During the spawning period, we did not observed aggression between individuals nor territorial competition which is typical, for example, in salmonids (Fabricius & Lindroth 1953). Thus, the density of mates at spawning sites or in breeding devices is limited only by the amount space needed to complete all elements of spawning behaviour.

We can conclude that whitefish (1) spawn mainly in the dark; (2) pair spawning is typical; (3) a spawning pair moves up to the water surface or along the surface; (4) a male occupies the leading position in a spawning pair, moving forward relative to a female by approximately the length of a head; (5) physical contact in a spawning pair associated with the release of gametes occurs through rhythmic collision of a caudal-peduncle anterior part of a male and the posterior pre-anal part of the female abdomen; (6) a female releases eggs repeatedly in portions of 1%–6% of its individual fecundity; and (7) spawning cannibalism is observed in whitefish. Scattering of eggs during spawning has an adaptive nature and is aimed at increasing the survival rate of embryos during long incubation period by, amongst the others, reducing the probability of detection and consumption by potential predators (Ivlev 1961). It also improves embryo survival by enabling better respiration and reducing the probability of *Saprolegnia* moulds damage by decreasing the contact between live and dead eggs.

Acknowledgments

We express our gratitude to all numerous participants of expeditions on the river Inu and river Lyapin, as well as fish farmers of the "Volkovo" fish farm who provided the invaluable technical assistance in carrying out these studies. In addition, we are grateful to I. N. Taradanov, specialist of the Tyumen branch of the Research Institute of Fishery and Oceanography of the Russian Federation for provided video footage of the *C. migratorius* spawning.

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