Influence of abiotic factors on incubation of Baikal omul eggs in the Selenga River (Lake Baikal Basin)

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Abstract. Abiotic factors affecting the choice of spawning sites for the Baikal omul (Coregonus migratorius) in the Selenga River over 27 years were studied. A total of 3,450 samples were collected using the Dulkeit scraper in Decembers of 1987-2014, at 24 transsections in the Selenga River channel over a total length of 410 km. At each sampling site we recorded omul egg density, substrate particle size, water depth, water flow velocity, and ice thickness. Omul eggs were found mainly on hard substrates (sand, gravel, pebbles, and pebble-cobbles combinations). Omul has been found to avoid spawning at depths less than 1.5 m and greater than 6.0 m. Water velocity and ice thickness did not strongly influence the choice of site. Omul eggs were found at flow rates of 0.05-0.7 m/s with a maximum at 0.1 m/s.

1. Introduction
Lake Baikal is the oldest, deepest, and largest freshwater lake in the world. The Selenga River, the main tributary of Lake Baikal, is 1,453 km long and provides 50% of its surface runoff [1]. The Selenga basin covers 447,000 km², of which 33% is in Russia (figure 1A). The water discharge in the downstream of the river is 28 km³ per year. The Selenga is a large stream with the highest fishery value in the Baikal region.

Despite the great importance of omul as a valuable commercial species [3-8], information about its spawning habitat is minimal. Baikal omul, Coregonus migratorius (Georgi, 1775), is an endemic whitefish of Lake Baikal. Its adult length is 30-60 cm, weight – 0.25-1.5 kg. In the recent past, the share of omul in the annual fish catch in Lake Baikal accounted for 55-60% [5, 9]. In the 21st century, this share is falling [2].

The omul spends most of its life cycle in the lake and spawns in rivers. The most important spawning rivers are the Selenga, Upper Angara, and the Barguzin; each accounting for 0.4-5.7 million spawning fish annually [10-12]. Spawning migration in the Selenga runs from late August to early September and is completed within 1.5 months [10]. Typical spawning sites are 20-570 km upstream of the lake’ tributaries, including the Mongolian-Russian border, which is 410 km upstream of the Selenga [2, 13, 14]. The spawning generally occurs in the second half of October. An incubation period lasts 180-200 days. The larvae hatch in April-May of the following year and migrate into the lake by the second week of May [6].

The research presented here was conducted from 1987 to 2014. The data were collected as part of a long-term monitoring project of Baikal omul spawning structures, that ran from 1984 to 2021. This monitoring program investigated abiotic factors for spawning site selection, including substrate types, water depth, water velocity and ice thickness.
2. Material and methods
The Selenga River. 80–85% of the Selenga’s annual discharge occurs from April to September, 12-14% – from October to November. Within Russia, the open-water flow rate is high (up to 4 m/s) due to a channel slope of 0.34‰. During summer floods, water is very turbid, 540-1,100 g/m$^3$. In mid-September, the water level gradually decreases, and water is cleared due to a cessation of surface runoff. Freezing occurs in mid-November and lasts about 140 (150-170) days. Under the ice, the Selenga carries clear water all winter until early spring. The water temperature is around 0 °C, being 0.2 °C from late October to early November and in the second half of April. In spring, the temperature rises steadily, reaching a maximum in mid-summer, in July [15, 16].

Egg Sampling. Sampling was conducted annually in December, shortly after the end of omul spawning, when the ice on the river was thick enough for safe work. The average ice thickness was 0.44 m at the beginning of the glacial period and 1.00 m at the end from 1987 to 2012. A total of 3,450 samples were taken at 24 transects along the length of the river within 20-410 km from the mouth. Transects were established at intervals of 15-20 km, and each covered the entire width of the river (figure 1B). At each transect, holes were drilled in the ice to collect samples. The number of holes in the ice on each transect varied from 6 to 11 (usually 10). The holes followed a two-row staggered pattern (e.g., to make 10 holes, two rows of five holes were made along the axis of the transect, spaced ~10-30 m apart).

Egg samples were collected using a Dulkeit circular scraper, 0.196 m$^2$ [2]. Each sample was collected using one and a half scraper turns against the current. For sampling omul eggs, substrates were treated with 15-20% NaCl solution (heated with a blowtorch on a specially equipped sled) with subsequent washing of floating fractions through 2 sieves with a mesh size of 780 µm. Counting of eggs was made immediately after draining the samples on a sieve, separately for live transparent eggs, and for dead white eggs [2].

Figure 1. Lake Baikal and the Selenga River basin. Box A shows the sites where HPPs were planned within the Selenga River basin. Box B shows the sites where transects for collecting eggs of Baikal omul were established.

Water temperature was not measured due to inoperability of the instrument in harsh winter conditions and accumulation of anchor ice on submerged devices. Ice thickness (m), water depth (m), and substrate characteristics were recorded for each hole. The type of substrate was determined visually as follows: 1 – silt, sand; 2 – sand (coarse and fine-grained); 3 – silt, gravel, sand; 4 – gravel, pebble, sand; 5 – gravel, cobbles, sand; 6 – cobbles. Substrates were classified according to the size of particles: sand – 0.1-2 mm; gravel – 2-10 mm; pebbles or round stones – 1-10 cm, and cobbles – over 10 cm.
The river discharge was measured in 1999, 2005, 2007, 2008 and 2009 years (161, 110, 218, 40 and 10 measurements respectively) using a ‘Flowmeter-0.06/120/70’ at a depth of one meter below the ice.

The systematic errors when using a Dulkeit scraper for egg collection were evaluated in experiments carried out in December 1989 [2]. The highest error values were observed for sandy (sand, fine gravel, ±10%) and rocky substrates (gravel and stones, ±13%). The former occurred because the scraper caused eddy currents, and the latter – because collecting eggs in stones is the most difficult compared to other substrates. Errors were also noted in gravel/pebble substrates (1-3%).

To select a sampling site, we compared the frequency distributions of the physical characteristics with the number of eggs observed at locations with similar characteristics. For example, the frequency distributions of the six substrate categories were compared with the number of eggs observed for each category. To calculate the relative proportions of eggs in each category, the number of eggs for an individual category was divided by the frequency of the category.

These relative values were compared with the mean number of eggs in all categories to determine which categories had more or fewer eggs than the mean. Data from spawning grounds only (excluding data outside spawning grounds, without eggs) were used to calculate average egg counts. Because the substrate types were categorical, ANOVA tests were performed to determine differences in egg counts between substrate types. To remove null values from the count data, one was added to each, and then the data were normalized by logarithmic (ln) transformation for use in the ANOVA test. Tukey’s HSD tests of all pair-wise comparisons were used to determine which substrates differed in egg counts.

### 3. Results

**Substrate types.** During this ice period, a mixture of gravel, pebbles, and sand dominates the Selenga’s riverbed, accounting for 81% of the study area, while coarse rocks, pebbles, and sand accounted for 5-6% of the area, and sands and silts – 6% and 2% of the area respectively.

The maximum mean number of eggs (~39% of the total mean) was observed on gravel-stony grounds (substrate 5), which occupied 16% of the spawning area. On gravel-pebble grounds (substrate 4), which occupied ~70% of the spawning grounds, was slightly less ~33%. Even fewer eggs (~17%) were observed on stony grounds (substrate 6), which occupied ~4%. On substrates 1–3 (silt, sand, silted gravel) that occupied ~2-6% of spawning grounds, the average number of eggs varied from 1% to 7%. Substrates 1-3 predominate within 20 km of the Selenga River delta, and are less common upstream to Ulan-Ude (153 km). At the time of sampling in December, three times fewer (8%) dead eggs were found on hard substrates (substrate 4-6) than on grounds with a soft component (substrate 1-3 – 27%; table 1).

There was a statistically significant difference in the number of eggs observed among the six substrate types: \( p = 0.0000 \) for a Kruskal-Wallis ANOVA test, while \( H = 70.5, df = 5 \) and \( n = 2,850 \). Egg densities for substrates 1 and 2 were significantly different from those for substrates 4 and 5. Moreover, the egg density for substrate 3 was significantly different from the egg density for substrate 5.

**Water velocity** was measured only during 1999, 2005, 2007-2009 low-water years. Five years were unusually dry, and river flow was 0.01-1.12 m/s. South and north of Ulan-Ude, the river velocity was 0.01-1.12 m/s, on average 0.31-0.40 m/s. Using combined flow velocity data from 1999-2007 did not reveal a preference for omul for egg-laying depending on this factor. Eggs were found at a flow rate of 0.05 m/s in the amount of 9%. The largest number (30%) was observed at a flow of 0.1 m/s, while at 0.2-0.7 m/s the density was lower and varied from 4 to 14%, averaging 9%. At higher flow rates (0.8-1.2 m/s), the number of eggs was almost five times lower (2%; table 1). Single year data (e.g. 2007), showed similar results. Eggs were found at a flow rate of 0.05 m/s (15%), with maximum number (33%) at 0.1 m/s. As the speed increased from 0.2 to 0.7 m/s, the number of eggs gradually decreased from 15% to 5%, and at 0.8 m/s and above no eggs were found at all (table 1).
Table 1. Mean number of omul eggs (pcs/m²) in the Selenga River in 1987–2014 in accordance with the main abiotic factors.

| Substrate Code | Live Eggs | Dead Eggs | Sum | Live Eggs | Dead Eggs | Sum |
|----------------|-----------|-----------|-----|-----------|-----------|-----|
| S1             | 1.14 ± 0.54 | 0.30 ± 0.23 | 1.44 ± 0.60 | 16 | 3.96 ± 3.00 | 0.00 | 3.96 ± 3.00 |
| S2             | 8.8 ± 2.37 | 2.0 ± 0.77 | 10.8 ± 2.94 | 1.0 | 8.43 ± 1.98 | 1.96 ± 1.01 | 10.39 ± 2.53 |
| S3             | 3.16 ± 1.01 | 2.53 ± 0.61 | 5.69 ± 1.51 | 1.5 | 28.28 ± 6.84 | 2.95 ± 0.65 | 31.23 ± 7.40 |
| S4             | 45.08 ± 3.95 | 4.15 ± 0.44 | 49.23 ± 4.20 | 2.0 | 34.18 ± 5.77 | 3.63 ± 0.51 | 45.21 ± 6.05 |
| S5             | 54.59 ± 9.32 | 4.14 ± 0.67 | 58.74 ± 11.55 | 2.5 | 31.02 ± 11.07 | 3.63 ± 0.51 | 34.65 ± 11.56 |
| S6             | 23.11 ± 10.92 | 2.25 ± 0.82 | 25.36 ± 11.55 | 3.0 | 49.71 ± 7.46 | 5.13 ± 1.17 | 54.84 ± 8.40 |

| V1             | 19.09 ± 12.31 | 1.63 ± 1.18 | 20.72 ± 12.33 | 0.1 | 34.32 ± 17.27 | 4.38 ± 2.12 | 38.70 ± 19.30 |
| V2             | 63.47 ± 18.32 | 5.60 ± 1.66 | 69.07 ± 19.42 | 0.2 | 61.43 ± 10.44 | 10.03 ± 2.01 | 71.46 ± 11.56 |
| V3             | 15.22 ± 7.52 | 0.99 ± 0.50 | 16.21 ± 7.82 | 0.3 | 81.08 ± 11.57 | 10.19 ± 1.77 | 91.27 ± 12.96 |
| V4             | 22.12 ± 6.89 | 2.14 ± 0.72 | 24.26 ± 7.46 | 0.4 | 62.47 ± 9.38 | 6.69 ± 1.35 | 69.16 ± 10.00 |
| V5             | 30.24 ± 10.63 | 1.09 ± 0.33 | 31.34 ± 10.78 | 0.5 | 109.84 ± 13.00 | 10.52 ± 2.17 | 120.35 ± 13.69 |
| V6             | 24.29 ± 6.89 | 1.44 ± 0.62 | 25.73 ± 7.11 | 0.6 | 87.20 ± 22.29 | 7.81 ± 1.89 | 95.01 ± 23.56 |
| V7             | 9.13 ± 3.82 | 0.28 ± 0.20 | 9.41 ± 3.86 | 0.7 | 82.38 ± 22.65 | 5.31 ± 1.68 | 87.69 ± 23.85 |
| V8             | 13.39 ± 8.45 | 1.64 ± 1.25 | 15.04 ± 9.64 | 0.8 | 131.92 ± 36.40 | 12.56 ± 6.19 | 144.47 ± 41.32 |
| V9             | 0.80 ± 0.80 | 0.00 | 0.80 ± 0.80 | 0.9 | 159.21 ± 40.65 | 7.83 ± 1.80 | 167.04 ± 41.75 |
| V10            | 9.00 ± 5.51 | 3.00 ± 1.84 | 12.00 ± 7.35 | 1.0 | 126.80 ± 32.62 | 5.00 ± 1.42 | 131.81 ± 33.10 |
| V11            | 1.50 ± 1.50 | 0.00 | 1.50 ± 1.50 | 1.1 | 38.28 ± 30.49 | 0.00 | 38.28 ± 30.49 |
| V12            | 2.89 ± 2.89 | 0.72 ± 0.72 | 3.61 ± 2.90 | 1.2 | 33.93 ± 17.46 | 0.87 ± 0.87 | 34.80 ± 17.30 |
| V13            | 0.00 | 0.00 | 0.00 | 1.3 | 92.66 ± 22.29 | 2.61 ± 2.61 | 95.27 ± 23.28 |

| h | 1.50 ± 1.50 | 0.00 | 1.50 ± 1.50 | 1.1 | 38.28 ± 30.49 | 0.00 | 38.28 ± 30.49 |

Water depths. Throughout the study, water level in the Selenga decreased from October to March by an average of 50-180 cm (AIS GMVO). The minimum number of eggs was found at depths from 0.5 to 1.5 m (3%), then at depths from 1.5 to 3.5 m the number of eggs gradually increased from 7% to a maximum of 14%. At depths from 4 to 5 m, the number of eggs was at the same level, averaging up to 12-13%, and in deeper sites (6 m), the number of eggs was 7%. Depths more than 6 m are uncommon for the Selenga River and were rarely encountered in the sampled transects (table 1).

Ice thickness. River ice thickness was 0.2-0.5 m at most sites throughout the survey, although we have not found a strong correlation between the omul preference and ice thickness (table 1).

4. Discussion

Foreign studies of whitefish spawning grounds are mainly related to lakes [17]; data on omul spawning grounds in rivers are mainly qualitative [18-21]. For example, spawning of the whitefish Coregonus clupeaformis was detected for the first time in 80 years and viable eggs and larvae were collected in the Detroit River [21]. In 2005-2016, whitefish eggs were found in large numbers in the St. Clair – Detroit River system in places with high flow rates, but their presence was not associated with either depth, flow rates or artificial spawning substrates [18]. In 2017-2018, 30-625 live eggs of C. clupeaformis were collected in Lake Michigan tributaries at depths of 1.1-2.0 m, with a flow rate of 0.3-1.0 m/s. The survival rate of its eggs was highest at temperatures not exceeding 2 °C [20].

In the Ob River tributaries in the Urals, whitefish spawning grounds are located in lowland and foothill areas with a flow of at least 0.3-0.5 m/s, with a maximum concentration of 600 eggs/m² [22]. Yudanov I [23] found winter survival of Siberian whitefish C. sardinella eggs in the Gulf of Ob on spawning grounds that were frozen to the bottom. However, the larvae that hatched in spring were quite viable despite their development in ice and in the absence of oxygen. Other studies have shown...
that whitefish eggs in embryogenesis are capable to develop normally within the frazil ice, in the 'pagon' conditions, which is explained by the low respiratory activity – 0.12 and 0.95 mg O₂/litre per hour per 1,000 eggs in Oct and Apr, respectively [4, 22]. In March 2021 BaikalNIRO employees discovered the omul eggs incubation in the Bolshaya Rechka River (southern shore of Baikal). They found, that the omul eggs incubation occurred in the 'pagon' conditions (within the ice), when there is no runoff in the riverbed. In the Baikal basin, studies of omul egg distribution were carried out mainly at the spawning grounds of small rivers in 1920-1980.

Eggs were found on coarse-grained substrates, at a depth of 0.3-1.7 m, at a flow rate of 0.8-2.8 m/s, with a density of 2,000 to 11,000 pcs/m². Most live eggs (98%) were observed in areas with an average flow rate (34%). The highest loss of eggs was observed on muddy substrates, in areas with a low flow (up to 100%). Following spawning, the eggs were found to roll downstream; their stickiness appears within 20-30 min. Drifting with the turbulent flow of water, the eggs lie behind the rocks on the underside and stick to them. As a result, the spawning eggs lie about 5 km from the spawning places, on the lower side of the rifts, in the upper part of the backwaters. The area of spawning grounds was 80-160 thous. pcs/m², and ~50% of them were subjected to freezing and drying out due to the ice build-up and falling water levels. The egg survival rate of was ~5% [2].

In the lower Selenga River, about 10-35 km upstream from Baikal, omul spawned for one year mainly on a pebble-sand substrate, at a depth of 1.4-4.0 m, but this habitat was not used the following year. In 1965-1973, the distance of spawning migration of omul in the Selenga typically varied from 20 to 153 upstream from Baikal. In only a few years, this distance exceeded 153 km. Later, spawning of omul was recorded up to 570 km upstream [2, 5, 13, 14, 24, 25].

Until 1984, egg samples were obtained using a 20 cm wide toothed hydrobiological scraper with the long sieve bag. Samples were obtained by dragging the scraper along the bottom at a distance of ~1 m. The samples were placed in a bucket, then passed through a sieve-screen in a warm room and disassembled. Omul eggs and macrozoobenthos rose to the surface of a salt solution of 15-20%.

Samples were routinely collected from 5 ha control plots of 25 pcs. It was noted that the catching ability of such scrapers varies depending on the substrate and the flow rate. In the upper reaches of the Kichera mountain river with high flow velocities and large stony substrates, the scraper captured 2% while in the middle reaches – 15%. In contrast, in the lower reaches with a decelerated flow rate and sand-gravel substrates, the capture was 70%. Further, factors that affected egg eliminations in spawning substrates in the Kichera and Selenga Rivers were determined: removal from spawning grounds (2-4%), mortality from freezing (2%), and destruction by benthic invertebrates (10-29%) and by fishes (6-7%) [14, 26].

Spawning Site Selections. According to M Voronov [14], the primary abiotic factors that omul uses to select spawning sites are substrate and water velocity. Moreover, in some parts of the Selenga, substrates constantly shift due to high velocities and anthropogenic disturbances; these areas are not used by omul for spawning, or, if they are, the eggs are pulled off the substrates and die [14].

In our studies, omul eggs on grounds with a soft component (substrates 1 and 3, silt, sand, silted gravel) were found in minimal quantities; these substrates contain silt, unsuitable for incubation of omul eggs, since they can sink into silt, and die. Similarly, substrate 2 (sand), is an unreliable substrate for the long omul incubatory period due to its high mobility. It can be assumed that the presence of eggs on substrates 1-3 is associated with their accidental drift during omul spawning or their demolition during incubation. Omul spawns mainly on hard grounds (substrates 4-6), where the dead eggs are 3.5 times less than on grounds with a soft component. It should be noted that the results of sampling on substrates 5 and 6 (gravel, stones, sand) can be significantly underestimated and contain a higher error value (46%) due to the difficulties of sampling with a scraper on stony grounds (table 1).

Underwater video (2008) showed omul eggs after spawning had occurred. The eggs have lost an initial stickiness have become covered with sand and were heavier than water in regards to specific gravity. The eggs rotated in vortex flows in a suspended state behind various irregularities on the river bottom, e.g., large and small stones, and sand deposits. Some eggs became attached to large boulders and rocks, while others lied motionless in deep places and shelters. Washing samples from sandy
grounds showed that on the sandy surface, omul eggs were not visible, although live eggs were present; 10-12 eggs were noted in two samples. These observations noted the development of parts of eggs in the sand-covered state.

Our studies have not revealed a clear preference for omul spawning sites depending on the water velocity. Eggs were absent in areas with a flow rate below 0.01 m/s, it is probable that speeds of less than 0.01 m/s were too low, and eggs were covered with silt and died. Eggs were found mainly at flow velocities of 0.05-0.7 m/s with a maximum at 0.1 m/s, at such values, an average of 6% of the laid eggs died by the time of sampling. At speeds exceeding 0.7 m/s, almost three times as many eggs died, 17%, this is most likely due to the flushing of eggs in such habitats. The main omul spawning grounds in the Selenga are also the locations with the lowest riverbed slopes; as a result, the omul prefers regions with lower average flow rates and thicker ice than other regions. Omuls reach these areas and wait to spawn because it is easier for them to wait where the flow is weaker.

In addition, omul avoid certain depths. The Selenga watershed receives most of its precipitation in the summer, as winters are cold and dry. This causes water levels in the Selenga to drop continuously from the time it freezes until spring (early April). By the time omul eggs were sampled in December for the present study, water levels had fallen from the high flow of the summer by ~50-180cm ([15]; data of AIS GMVO; A Bazov). When a water level drop is combined with ice thickness, a large number of eggs lay at depths of less than 100-50 cm are likely to die from freezing. Omul have adapted to these seasonal changes in water levels and generally lay their eggs at depths of greater than 100 cm in the central channel of the river, and prefer sites at depths of 150 cm or greater.

Despite the water temperatures decreases to ~0 °C in winter [15], there is no complete freezing of the Selenga riverbed. Thus, in a long subglacial period, omul eggs are successfully incubated in a significant underwater habitat during 5-6 months from November to April. The reliability of such a shelter is due to a significant decrease in the flow rate and temperature, as well as an increase in water transparency and a relatively favourable O2 regime. This decrease determines the protective habitat functions, the metabolism of aquatic organisms, potential eggs consumers, is minimal at such low temperatures. Ice cover formation can also be explained by a reliable protective shelter for eggs from external atmospheric influences; the average ice thickness in the river during the study was 0.5 m (0.1-1.5 m), and often reached 2 m near the shore by spring.

Thus, all the studied factors, depth, substrate, flow velocity, and ice thickness in various combinations determine the spawning sites of Baikal omul. Despite the water temperature was not measured in our studies, it can be assumed that the incubation temperature of omul eggs in the Selenga River is ~0 °C (data of the AIS GMVO [15]).

Since gravel, pebbles, stones, and sand, occupy almost the entire underwater river habitat, they are the spawning ground of Baikal omul in the Selenga. The potential capacity of this substrate was much higher in the past; the average numbers ~40-50 eggs/m2, were calculated based on the average population size of 1.5 million producers. Meanwhile, in the 19th century, the populations were much higher, up to 10 million producers [2], therefore, this substrate could be a spawning area with a proportionally higher average eggs number, ~250-350 eggs/m2. Those substrates are common throughout the Selenga riverbed during the subglacial period in Russia, and are highly likely common in its Mongolian part. The hydropower plants (HPPs) construction in the Selenga basin in Mongolia may have a significant negative impact on the Baikal omul spawning area. For example, even one or two potential HPPs are operated in the Selenga basin in Mongolia, its low winter water flow on the border with Russia will increase by 2-3 times, which will lead to an increase in the discharge of the heated water into the riverbed [4]. An increase in the egg incubation temperature can lead to earlier larvae hatching and their subsequent death in non-optimal habitats. An increase in the flow rate can cause the eggs to be washed off the substrate, or buried by sediments from the HPPs discharge waters. For these reasons, the disappearance of the omul might happen, which would have an extremely negative impact on the entire ecosystem.
5. Conclusion
A combination of abiotic conditions is necessary for the successful incubation of Baikal omul eggs in the Selenga riverbed. Omul eggs are incubated mainly on grounds made of a mixture of sand, gravel, pebbles, or cobblestones. Eggs are found in minimal quantities on combinations of silt, sand, gravel, and cobbles. In addition, omul eggs are distributed mainly at depths from 1.5 to 6.0 m. Omul eggs occur at current velocities of 0.05-0.7 m/s with a maximum at 0.1 m/s. At a current velocity of 0.7 m/s and greater, omul eggs are found in minimal numbers.

Construction of an HPP in Mongolia can lead to a rapid decrease in the survival rate of omul eggs during the long winter from early November to early April. Moreover, the implementation of HPP projects in combination with global climate warming as well as other anthropogenic disturbances will result in the extinction of the omul, the cold-loving endemic of Lake Baikal, which will undoubtedly affect the entire ecosystem.

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