

Article

Reproduction of the Androgenetic Population of the Asian *Corbicula* Clam (Bivalvia: Cyrenidae) in the Northern Dvina River Basin, Russia

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Abstract: The *Corbicula* clam is one of the most successful invaders of aquatic ecosystems and has invaded all continents except Antarctica. The natural dispersion of *Corbicula* seems to be limited by low winter temperatures that fall below the lower lethal temperatures (0 to +2 °C). However, *Corbicula* can be found in colder regions, taking refuge in waters heated by thermal power plants. The purpose of this investigation was to study the gonadal histology, reproductive cycle, and the seasonal changes of shell size structure of the *Corbicula* clam populations in the warm water discharge of the Arkhangelsk thermal power plant (Northwest Russia). Samples were collected monthly from January 2017 to December 2018 and processed using traditional histological and morphological techniques. The number of reproductive periods varied from year to year. It was established that the *Corbicula* clam has a continuous reproduction period which may be adaptive in unstable environmental conditions. This reproductive strategy is probably aimed at increasing the reproductive success of the population. Our data expand the understanding of reproductive features of the *Corbicula* clam in harsh environmental conditions. These results could be applied to control, monitoring, and management measures.

Keywords: *Corbicula*; invasive species; reproduction; Northwest Russia



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1. Introduction

The genus *Corbicula* consists of estuarine or freshwater clams native to Asia, Africa, and Australia that are able to reproduce sexually and asexually (androgenetic lineages) [1–4]. Asexual *Corbicula* lineages have been introduced into freshwater ecosystems across the globe for almost a century and are considered a major aquatic invader, mainly due to their negative environmental and economic consequences [5,6]. *Corbicula* can affect hydrology, biogeochemical cycling, and biotic interactions through several mechanisms with wide-ranging impacts on individuals and ecosystems [7–10]. Hence, the features of reproduction and specificity of the life cycle of *Corbicula* should receive more attention in order to develop monitoring and management measures [11]. Furthermore, the knowledge on the reproductive dynamics of an invasive species is considered a key tool for planning and implementing control strategies [12].

Androgenetic *Corbicula* have a widespread distribution across Asia and multiple invasive populations in Europe, North America, and South America [4,13]. The limit for dispersion of the *Corbicula* clam is defined by lower winter temperatures [6,7]. However, global warming can favor the success of invasive species [14–16]. In addition, *Corbicula* can be found in colder regions where they find refuge in waters heated by thermal power plants, which may provide them with favorable habitats [17–23].

The great invasive potential of *Corbicula* is associated with the presence of a wide range of reproductive strategies [12]. Thus, the ability of *Corbicula* to reproduce clonally

through androgenesis, rapid maturation, and high fecundity is the main contribution to their invasive success [5,24], but it is likely that the most important factor is androgenetic reproduction [5]. The unreduced spermatozoa of androgenetic *Corbicula* are capable of both cross- and self-fertilization [4,25]. The unreduced spermatozoa from one genetic lineage can also fertilize the eggs of another lineage. As a result, there is the combination of the nuclear genome of the first lineage with the mitochondrial genome of the second lineage, which is a phenomenon known as “egg parasitism” [26]. In addition, this process enables a mixing of different nuclear genomes “nuclear genome capture” when the maternal nuclear genome is incompletely extruded, whereby the offspring inherits a hybrid genome [4,24].

The features of reproduction and life cycle of both native and invasive populations of the *Corbicula* spp. have been the focus of studies since the 1970s [12,21–24]. At the same time, the gonadal cycle of *Corbicula* spp. remains poorly studied to date [19]. An important aspect in such studies is the influence of environmental factors, such as water temperature, on reproduction. The potential relationship between temperature and life span may be relevant to forecast future distribution patterns of *Corbicula*, as well as develop management strategies [6]. Several studies have demonstrated that water temperature and food availability may influence reproduction and growth of *Corbicula* [23,27–30]. The latter three works cited demonstrated that there is a positive correlation among spawning frequency, number of offspring, and the concentration of chlorophyll *a* in water. The life span of *Corbicula* spp. and the number of annual reproductive periods vary from ecosystem to ecosystem and may be related to water temperature and food resources available in a particular ecosystem [29,31,32]. It was established that *Corbicula* is incubated by the larvae of the inner demibranchs [33]. The released juveniles are small (around 250 µm), completely formed, and have a D-shaped form [9]. A review of data in the literature indicates that *Corbicula* reproduces mainly twice a year: from spring to summer and from late summer or early fall to late fall [7,17,29]. Following their release, juveniles anchor themselves to sediments, vegetation, or hard surfaces, and maturation occurs within 3 to 6 months [33]. According to French and Schloesser [34], low water temperature may limit the success of *Corbicula* in a river, by reducing growth, delaying the onset of sexual maturity and reproduction, and causing heavy overwinter mortality in the first year of life. Denton et al. [35] and Cataldo and Boltovskoy [32] found that temperature has the greatest influence on the onset of reproduction, and an elevated temperature stimulates an increase in the fecundity of *Corbicula* [36].

In 2015 *Corbicula* was discovered in the heated waters of the Arkhangelsk Thermal Power Plant (TPP) in Northwest Russia [20]. The TPP discharge waters flow into the Yuras River, a tributary of the Severnaya Dvina River (one of the largest rivers in Northwest Russia, with exceptional economic importance for the region). Two distinct morphotypes (Rlc and R) were distinguished on the basis of morphological characteristics (i.e., shell shape, size, external and internal coloration, sculpture, and umbo position), corresponding to forms that have been described previously [25]. The morphotype R has well-marked concentric ridges, round and broad shell shape, and larger sizes. The external shell coloration is dark, and the internal coloration is white with purple marks [37]. The Rlc morphotype is similar to form R, but the shell size is small and the external coloration is light while the internal coloration is yellow-white [20]. We observed a discrepancy between the mtDNA sequences and morphology for all individuals, indicating the presence of cryptic hybrids between *Corbicula* lineages [20].

At the same time, the reproduction features and gonadal cycle of this *Corbicula* clam population remain incompletely understood. The goals of this study were to describe the gonadal histology, reproductive cycle, and the seasonal changes of shell size structure of the population of the *Corbicula* clam in the warm water discharge of the Arkhangelsk thermal power plant. We assumed that *Corbicula* would have appropriate reproductive features in harsh environmental conditions. Our data expand our understanding of reproductive features of the *Corbicula* clam in unstable environmental conditions. These results can be applied to the development of control, monitoring, and management measures.

2. Materials and Methods

2.1. Study Area

This study was conducted in the Arkhangelsk Oblast (i.e., a political subdivision in Northwest Russia), specifically, the Severnaya Dvina River basin, which is characterized by a stable freeze-up regime with an ice cover duration of 144–185 days [38]. The freezing of the rivers starts in late October/early November and finishes in April and May [38]. The specimens of *Corbicula* form R were collected in a manmade channel of the Arkhangelsk TPP (N 64°34′28.88″, E 40°34′59.06″) (Figure 1A,B) located in the industrial zone on the right bank of the Kuznechikha River, a tributary of the Severnaya Dvina River. The channel length is 3.5 km with depths up to 2 m. Warm waste waters from the channel flow into the River Juras, another tributary of the Severnaya Dvina River. Hydrochemical parameters of wastewater of the Arkhangelsk thermal power plant were presented in a previous paper [20]. The conductivity is 269.8 $\mu\text{S}/\text{cm}$, dissolved oxygen is 7.6 mg/L, and pH is 7.8. High concentrations of Ca_2^{2+} and SO_4^{2-} ions were recorded [20].

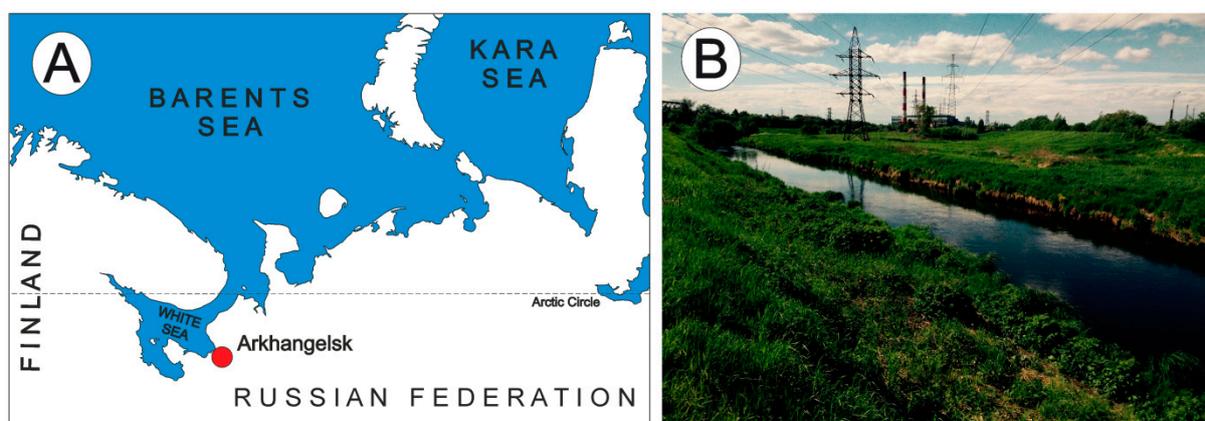


Figure 1. Map of the study area: (A) location map of Arkhangelsk City; (B) view of the Arkhangelsk Thermal Power Plant (TPP) channel. Photo BespalayaYu.V.

2.2. Field Sampling

Monthly sampling of *Corbicula* form R began in January 2017 and continued until December 2018, excluding July 2017, as well as January, June, and October 2018. Samples were collected at three sites along the channel. Five to 10 replicates were collected at each station using a rectangular hand net (dimensions 0.28 m \times 0.5 m, mesh size 200 μm , sampling area of 0.14 m^2). In total, the collection included 966 individuals in 2017 and 630 individuals in 2018.

Samples were washed using a hydrobiological sieve (mesh size 0.56 mm), fixed in 96% alcohol in the field, and transported to the laboratory for further study.

The water temperature was measured using iButton temperature data loggers (Thermochron, Maxim Integrated, San Jose, CA, USA) with an interval of 240 min during the period of February 2017–December 2018.

2.3. Morphological and Anatomical Studies

In total, 1596 clams were studied. The specimens of *Corbicula* were measured for length (L) to the nearest 0.1 mm using dial calipers and a Leica M165C stereomicroscope. In accordance with the size threshold [25,34], sampled specimens were subdivided into mature individuals (shell length of >6 mm) and juveniles (shell length of <6 mm). Information in the literature indicates that *Corbicula* starts to reproduce when shell length reaches 6–10 mm [9,39].

The size structure of the population was analyzed according to the following size classes (shell length): small individuals (1–10 mm), medium individuals (11–25 mm), and

large individuals (26–40 mm) [40]. We divided the group size class of 1–10 mm into size classes of 1–5 mm and 6–10 mm in order to distinguish juvenile and mature individuals. The size distribution was plotted on a frequency histogram.

The gills of specimens for incubating juveniles were investigated. The lengths of larvae were measured using a microscope (Axio Lab.A1; Carl Zeiss, Oberkochen, Germany). Photographs of gills with larvae were obtained using a microscope with a digital camera (AxioCam ICc 5; Carl Zeiss, Oberkochen, Germany).

2.4. Histological Examination

A histological examination was performed on the gonads of five randomly selected mature specimens (average shell length of 15 mm), sampled monthly from January 2017 to December 2018 [41,42]. Tissues were dehydrated through a graded alcohol series and embedded in paraffin. Histological sections with a thickness of 6 μm were made using a rotary microtome (HM 325; Thermo Scientific, Waltham, MA, USA). The sections were stained with Mayer's hematoxylin and eosin (H&E) double stain for examination under a light microscope (Axio Lab.A1; Carl Zeiss, Oberkochen, Germany). To assess the stage of development of gonads and the stages of growth and development of oocytes, we used the classification proposed by Morton [43] and Juhel et al. [44]. The number and the length of oocytes were measured in 100 individuals sampled monthly from January 2017 to December 2018 using a microscope (Axio Lab.A1; Carl Zeiss, Oberkochen, Germany). Only those oocytes showing conspicuous nucleoli were considered [12].

2.5. Statistical Analyses

Differences in the number of oocytes in the follicles of *Corbicula* clams between seasons were estimated using the Mann–Whitney *U* test and the PAST program [45]. The significance of seasonal changes of shell size structure was estimated using Kruskal–Wallis (multiple comparisons) tests and the PAST program. Differences in the mean temperatures of water in October–November in 2017 and 2018 were estimated using the Mann–Whitney *U* test.

3. Results

3.1. Habitat Characteristics

In the study period, the lowest water temperature was recorded in November 2018 (+4.5 °C), and the highest was recorded in August 2018 (+34.5 °C) (Figure 2). Water temperature in the manmade channel of the Arkhangelsk TPP increased from May to September (Figure 2). Water in the channel did not freeze during the winter.

In 2017, the channel water temperature varied from 14 to 32.5 °C (mean 25.9 ± 3.5 °C) in summer and from 6 to 19 °C (mean 8.9 ± 2 °C) in winter. In 2018, the water temperature varied from 11 to 34.5 °C (mean 26.6 ± 4 °C) in summer and from 4.5 to 16 °C (mean 8.8 ± 2.2 °C) in winter (Figure 2). The settlements of *Corbicula* clams were confined to the silty-clay and gravel ground patches of 0.65–1.1 m in depth.

3.2. Shell Length Structure and Brooding

Through shell length analysis, the seasonal changes of shell size structure of the population were recorded (Figure 3A,B). In 2017, from January to March, small individuals with shell length 1–10 mm prevailed in the population. From April to June, medium-sized individuals dominated (11–15 mm). Lastly, between August and December, individuals with shell length 16–20 mm prevailed in the population (Kruskal–Wallis test: $H = 258.6$, $df = 2$, $p < 0.0001$). In 2018, from February to April, individuals with shell length 26–40 mm dominated the population. In the period from May to August, individuals with shell length 16–20 mm were most common. From September to December, individuals with shell length 16–20 and 21–25 mm prevailed (Kruskal–Wallis test: $H = 60.72$, $df = 2$, $p < 0.0001$).

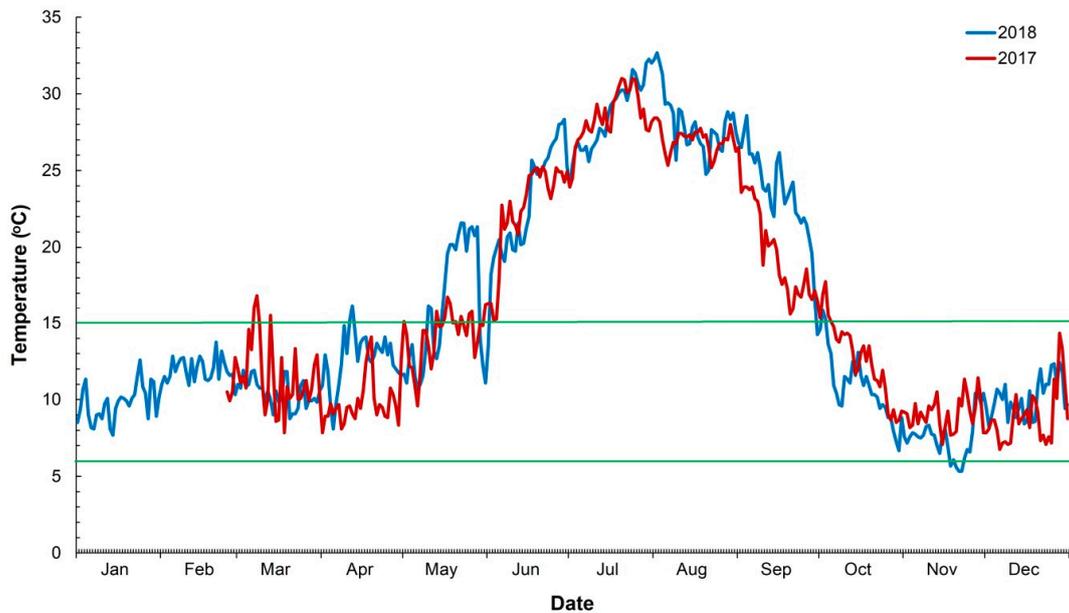


Figure 2. The mean water temperature in the manmade channel of the Arkhangelsk Thermal Power Plant (TPP). The green lines indicate the range of minimum temperature for breeding *Corbicula* sp. from +6 to +15 °C [7].

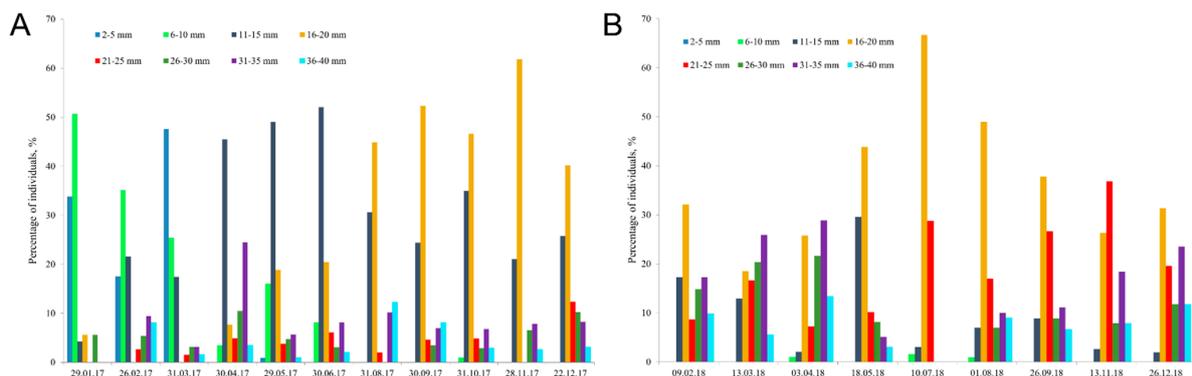


Figure 3. Seasonal changes of shell size structure in the *Corbicula* morphotype R population. Axes correspond to the eight size classes in accordance with shell length intervals. The juvenile individuals belong to a size class with shell length of 2–5 mm. (A) 2017, (B) 2018.

Specimens of *Corbicula* form R (Figure 4A–C) with incubated larvae in their gills were found in June and September 2017 (Figure 4D–G). Larvae were found in inner demibranchs and had a D-shape form (Figure 4H). The length of larvae in summer ranged from 181 to 275 μm (with an average length of $233.0 \pm 11.6 \mu\text{m}$, $\pm\text{SD}$; $N = 150$), and the length of larvae in the fall ranged from 156 to 306 μm (with an average length of $234.4 \pm 28 \mu\text{m}$, $\pm\text{SD}$; $N = 100$). We found no pregnant individuals in the samples in 2018. Presumably, the release of juveniles in 2017 occurred from late May–June to August and from September to November. In 2018, the release of juveniles was probably from June to August.

3.3. Gonad Histology

According to our data, histological sections of gonads indicated that clams showed reproductive activity throughout the year. Histological changes in hermaphroditic gonads in 2017 and 2018 are shown in Figure 5A–P. Previtellogenic and early vitellogenic oocytes were usually present and scattered along the acinus wall, where clusters of spermatocytes and spermatids were also present. The *Corbicula* form R is a simultaneous hermaphrodite. Each acinus had regions of oogenic and spermatogenic tissue. The spermatogenic regions

were usually located in the terminal portion of the acinus along the edge of the visceral mass. According to our results, the mean mature oocyte size (\pm SD) was $113.8 \pm 12.9 \mu\text{m}$.

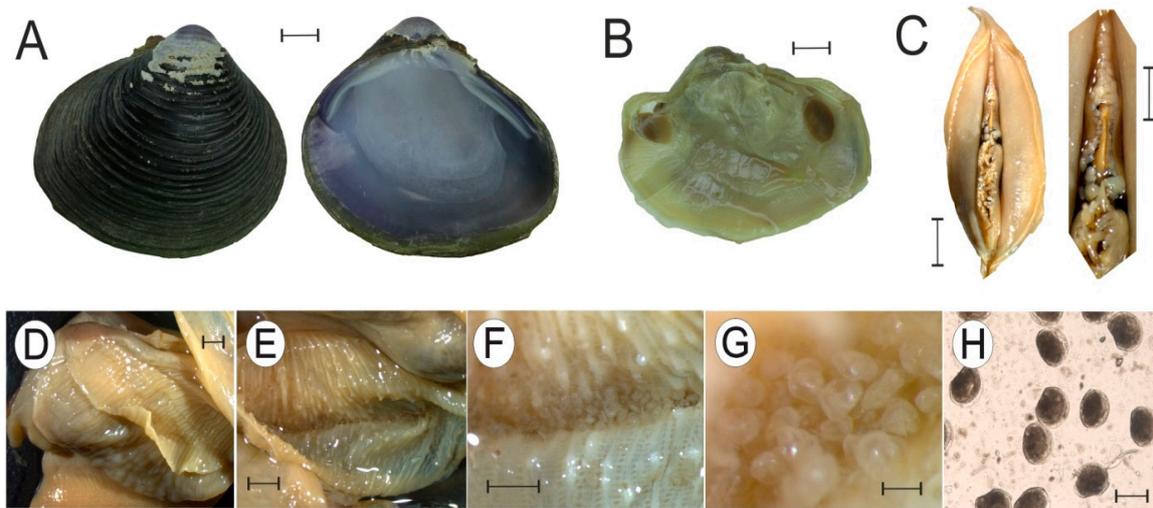


Figure 4. Shell morphology, anatomy, and larvae of *Corbicula* form R: (A) external and internal view of shell, left valve; (B) anatomy of soft body; (C) siphons morphology; (D) general view of gills; (E) gills of the incubating specimens; (F) larvae in the outer demibranch; (G) larvae inside of gill; (H) larvae D-shaped configuration.

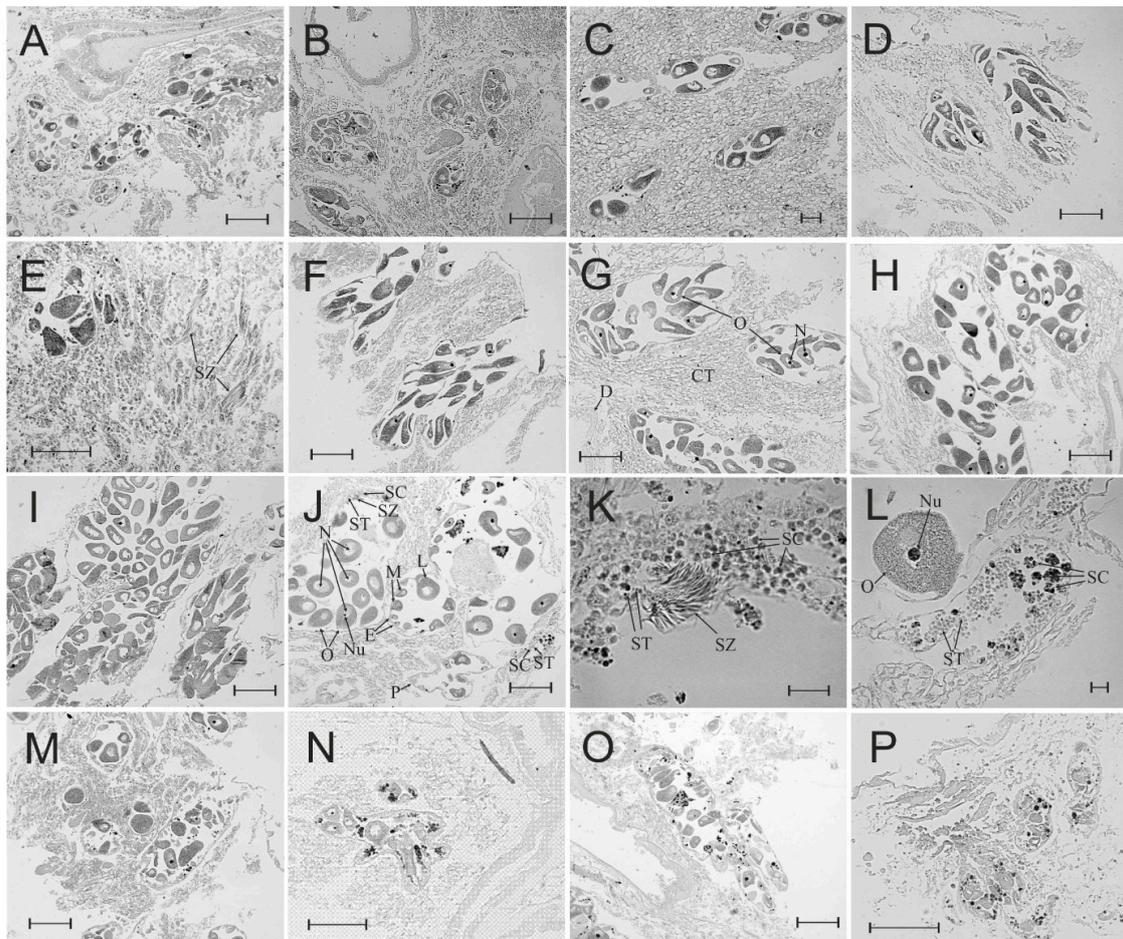


Figure 5. The gonads of hermaphroditic specimens of *Corbicula* form R at different stages of their reproductive cycle in 2017

and 2018. The state of the gonad in the final reproduction stage, showing a small number of advanced gametes: (A) 22 December 2017; (B) 26 December 2018; (C) 26 February 2017; (D) 9 February 2018. The state of gonad at the beginning of the spawning season, showing an increase in the number of advanced gametes: (E) 30 April 2017; (F) 3 April 2018; (G) 29 May 2017; (H) 18 May 2018. The state of the gonad in the first peak of the spawning season, showing a large number of advanced gametes: (I) 30 June 2017; (J) 1 August 2018. (K) Spermatocytes, spermatids, and sperm were typically in the terminal region of the ascini (1 August 2018). (L) Ascinus with advanced oocytes and developing spermatocytes (1 August 2018). The state of the gonad in the autumn months: (M) 30 September 2017; (N) 26 September 2018; (O) 28 November 2017; (P) 13 November 2018. Legend: O—oocyte, CT—connective tissue, N—nucleus, Nu—nucleolus, SC—spermatocytes, ST—spermatids, SZ—sperm, pre—(P), early—(E), mid—(M), and late—(L) vitellogenic oocytes. Scales: (A–J), (M–P) = 0.2 mm; (K,L) = 0.02 mm.

During the study period, the histological conditions of the gonad changed. In December–March 2017–2018, the gonads were in the final reproduction stage, showing a small number of advanced gametes, and we also observed oocytes in atresia (Figure 5A–D). The state of the gonads at the beginning of the spawning season (April–May) showed an increase in the number of advanced gametes (Mann–Whitney U test: $p = 0.005$) compared with December–March (Figure 5E–H). The period of active breeding occurred during the warmest period from June to the August (Figure 5I–L). The second peak of breeding occurred in the fall (Figures 3 and 5M,O).

In 2018, the beginning of the reproductive period occurred in April (Figure 5F,H) and continued until August (Figure 5J–L). The histological conditions of the gonad in the fall indicated that gametogenesis was reduced during this period (Figure 5N,P). The number of oocytes in the follicles in late September 2018 decreased significantly (Mann–Whitney U test: $p = 0.02$) (Figure 5N); in November, oocytes were not detected (Figure 5P).

4. Discussion

4.1. Reproduction and Influence of Water Temperature

In this study, we expanded our preliminary data that focused on the estimated shell size structure of the *Corbicula* form R, obtained from June 2015 to September 2016 [20]. We previously established that *Corbicula* form R is apparently characterized by one reproductive period (during the warm season) [20].

Research conducted during 2017–2018 on the analysis of gonad conditions, shell size structure, and period of incubated larvae by *Corbicula* clams indicated that, in 2017, the population of *Corbicula* form R had a continuous reproduction period with two clear peaks (in June and in September–November) (Figure 3, Figure 4D–F and Figure 5M,O). In 2018, the recorded seasonality corresponded to one generation in that year (i.e., per year), with reproduction starting in April and continuing throughout the summer (Figures 3B and 5F,H,J–L). Despite the fact that, during the present study, no pregnant individuals were found in the samples, the shell size structure of the population and gonad histology suggested that the breeding season started at the beginning of spring (Figure 3A,B and Figure 5F,H). Previous studies indicated that the number of reproductive periods per year depends on habitat conditions [29,31,46], with differences among years and even at the same site [9]. Furthermore, some studies concluded that *Corbicula* reproduces twice a year: one occasion in the spring going through the summer and the other occasion starting in late summer and going through the fall [9,29]. However, some studies found only one reproductive period [28,31,32,35]. There were three major reproductive peaks in populations of *Corbicula* recorded in the New River (Glen Jean, VA, USA) and in Santa Catalina stream (Buenos Aires Province, Argentina), with differences among years even in the same site [12,46]. The fluctuations in the number of reproductive events may be related to water temperature and nutritional availability [28,29,31,46]. According to Rajagopal, et al. [29], the minimum temperature for reproduction of *Corbicula* clams ranges from +6 to +15 °C. Therefore, the water temperature in the channel in 2017 from January to December generally satisfied the environmental requirements of *Corbicula* [7] and did not fall below the limits established for *Corbicula* (Figure 2). During the study period in 2018, the mean water temperature on

some days was below the lower limits for *Corbicula* reproduction (Figure 2). The mean water temperature in October and November in 2017 was significantly higher than in 2018 (Mann–Whitney U test: $p < 0.001$). When the temperature in a man-made channel of the Arkhangelsk TPP decreased below 6 °C, it is likely that spawning of *Corbicula* clams did not occur. We presume that a decrease in mean water temperature in October and November 2018 below the lower limits for *Corbicula* reproduction was one of the reasons for the lack of a spawning event in the fall. In the present study, potential seasonal periodicities in food availability were not investigated for *Corbicula* clams; however, the influence of this factor cannot be excluded.

The size of mature oocytes varies between species of genus *Corbicula* and from population to population [12]. In the present study, the mature oocyte mean size for *Corbicula* form R was 113.8 µm (min–max: 84–138 µm). According to the results of the work by Cao et al. [12], the mature oocyte mean size for *C. fluminea* was 102 µm, whereas, in accordance with Park and Chung [47], it was 150–170 µm. The mean mature oocyte size for *C. leana* was reported as 110–130 µm and that for *C. japonica* was reported as 70 µm [42].

4.2. Reproductive Strategies and Gonadal Histology

As mentioned above, *Corbicula* clams are characterized by a wide range of reproductive strategies, allowing them to invade new habitats and spread rapidly [1–3,5,25,48]. In addition, some populations of *Corbicula* clams are characterized by year-round gametogenesis, thus permitting their capability to respond rapidly throughout the year to suitable environmental conditions by spawning [12,49,50].

Therefore, we assume that the continuous reproduction of *Corbicula* clams may be adaptive in unstable environmental conditions, with the aim of increasing the reproductive success of the population. A similar reproductive strategy was found in another invasive species, *Sinanodonta woodiana*, in the cooling water of the Cieply Channel of the “Dolna Odra” power plant (DOPP) [51]. In their study, Labecka and Domagala [51] concluded that the continuous reproduction of *S. woodiana* may undoubtedly contribute to an increase in the size of the mussel population and colonization success in this species.

Nevertheless, we found oocytes in atresia (Figure 5A–D). It is well known that spawning does not empty the gonad entirely [52]. The residual oocytes degenerate within the gonad and the debris are cleared by macrophage hemocytes [53]. The presence of oocytary atresia may have been caused by a limited capacity of the follicle and a control mechanism governing the number of cells [54]. Lastly, it may have been a result of the response to environmental or contaminating stress conditions [52,53,55]. Baba et al. [41] observed oocyte atresia in *Corbicula japonica* and concluded that, in years which are unfavorable for spawning, oocyte atresia occurs in mature gonads of individuals after the season. Atretic cells have also been described for Unionidae mussels [51,54,56] and marine bivalves [52,53]. We found oocytes in atresia only in December–February 2017–2018 when *Corbicula* clams were at the final reproduction stage (Figure 5A–D). The observed atresia is likely the result of a self-cleaning process at the end of a gametogenic cycle in preparation for the next cycle. However, this issue would require additional research.

5. Conclusions

This study provides new data on the reproduction of *Corbicula* clam in the manmade channel of Arkhangelsk Thermal Power Plant (Severnaya Dvina River basin) in Northern European Russia. It was established that *Corbicula* form R has a continuous reproduction period. Our histological data indicate that advanced gametes were present year-round in *Corbicula* form R. The number of reproductive periods varied from year to year. In 2017, the population of *Corbicula* form R had two peaks: one in June and one in late August; in 2018, there was one generation (i.e., one per year). We presume that a decrease in the mean water temperature in October and November 2018 below the lower limits for *Corbicula* reproductions was one of the reasons for clams not spawning in autumn. Continuous

reproduction of *Corbicula* clams may be adaptive in unstable environmental conditions, aimed at increasing the reproductive success of the population.

We assume that the temperature factor does not allow *Corbicula* to settle in the water-courses of Severnaya Dvina River basin because the rivers are characterized by a stable freeze-up regime and, therefore, water temperature here is below the permissible limit for reproduction and growth of *Corbicula* clams. The next research step will include the examination of reproductive features of *Corbicula* clams over a wide geographical range, while gathering information on the native and endemic *Corbicula* populations.

Author Contributions: Y.V.B. conceptualized the paper. Y.V.B., O.V.A., A.V.K., A.R.S. and O.V.T. conducted field research and collected samples. A.V.K. performed the histological studies. O.V.A. created the figures. Y.V.B. and A.V.K. wrote the paper, with input from O.V.A. All authors have read and agreed to the published version of the manuscript.

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