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Interactions of Organisms Associated with the Mollusc *Nodularia douglasiae* in a floodplain lake of the Razdolnaya River (Primorsky Region, Russia)

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Abstract—The interactions among organisms in the system "mollusk *Nodularia douglasiae* (Unionidae)—fish embryos *Acheilognathus chankaensis* (Acheilognathidae)—mites *Unionicola* sp. (Unionicolidae)" were studied in an artificial floodplain lake of the Razdolnaya River (Primorsky Region, Russia). Prelarvae of the Khanka bitterling *A. chankaensis* developed in April–June in the inner gills of *N. douglasiae*. During the same period, glochidia were brooded in the outer gills of the mussels, but concurrent development of fish embryos and glochidia in the same mollusk was not observed. Four stages of the bitterling prelarval life cycle were identified. It was established that these prelarvae are not parasites but use the mussels as a shelter. Eggs of the mite *Unionicola* sp. were found in both gills of *N. douglasiae* during the autumn, with nymphs appearing only by April–June of the following year. In controlled experiments, attacks by *Unionicola* sp. on slow-moving *A. chankaensis* embryos were documented, indicating a trophic three-way interaction in the "*Nodularia*—bitterling—mite" system. A scheme of multilateral relationships is proposed, in which bivalve mollusks play a central role as incubators for brooding their own glochidia and for the reproduction of *A. chankaensis* and *Unionicola* sp.

Keywords: *Nodularia douglasiae*, glochidia, *Acheilognathus chankaensis* embryos, *Unionicola*, symbiosis, trophic links

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INTRODUCTION

It is well known that bitterlings of the family Acheilognathidae reproduce by utilizing large bivalve mollusks of the order Unionida: male and female bitterlings deposit their gametes into the gills of the mussels, where the fish embryos develop to the fry stage. In this way, the juvenile bitterlings gain protection from predators and favorable conditions for their development. In turn, the mollusks attach their parasitic glochidial larvae to fish. Initially, glochidia develop in the outer gills of the mussels and, after completing their development, are released by the maternal individual onto passing fish. Using byssal threads and spines, the glochidia attach to the gills and skin of the fish. During the parasitic phase on the fish, the glochidia feed on the host's tissues, and after completing the formation of the juvenile mussel, they drop to the bottom of the water body and transition to a free-living mode of life. These mutualistic relationships facilitate the brooding of offspring for both groups of animals, and for the mollusks, they also ensure colonization of distant habitats through the mobility of fish.

Extensive research has been conducted on the reproductive relationships between unionid mussels and acheilognathid bitterlings, where each organism participates in brooding the offspring of the other. These studies have covered the Russian Far East [1–4], China [5, 6], South Korea [7, 8], and Japan [9–11]. A certain difficulty in studying the interactions between bitterlings and bivalve mollusks has been their insufficient taxonomic resolution. For bivalve mollusks, it has been shown that the subfamily Unioninae in the south of the Russian Far East, outside the Amur River basin, is represented by two species: *Nodularia douglasiae* (Gray, 1833) and *Middendorffinaia mongolica* (Middendorff, 1851), while the subfamily Anodontinae is represented by *Buldowskia suifunica* (Lindholm, 1925) and *Sinanodonta schrenckii* (Lea, 1870) [12–14, and others]. The taxonomic position of the Far Eastern bitterlings has also remained confusing

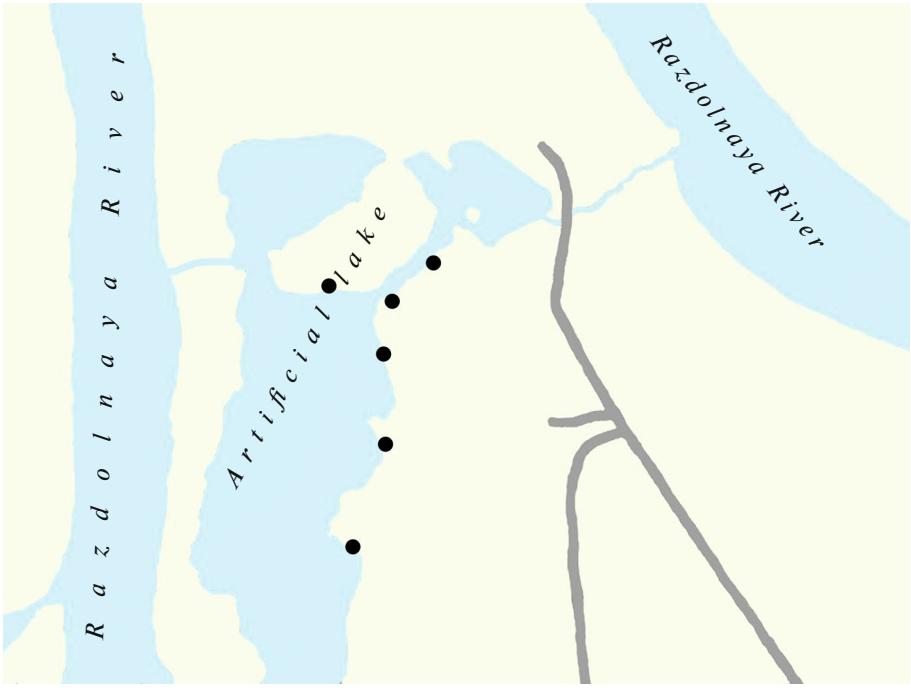


Fig. 1. Artificial floodplain lake in the Razdolnaya River basin near the village of Razdolnoye. Dots indicate the sampling sites of *Nodularia douglasiae* mollusks.

until recently. Among the Acheilognathidae in the Russian Far East, representatives of the genera *Acanthorhodeus*, *Acheilognathus*, *Rhodeus*, and *Tanakia* have been recorded. In the south of Primorsky Region, the common bitterling *Rhodeus sericeus* (Pallas, 1776) and the Khanka spiny bitterling *Acheilognathus chankaensis* (Dybowski, 1872) are registered [15–17], which are weakly distinguishable morphologically and are indistinguishable at the prelarval stage.

Some groups of aquatic invertebrates—mites, leeches, insect larvae—constantly found in the mantle cavity of mollusks can be components of various types of symbiosis with Far Eastern Unionidae [4, 18–20, and others]. At the same time, the number of studies devoted to the precise localization of these symbionts within the host, their parasitic conditions, or their participation in trophic relationships, etc., is limited. Given that the infestation of mollusks by invertebrates can be high, a more detailed study of the interrelationships of these aquatic organisms—both with the host mollusks and with other symbionts, including Acheilognathidae and Unionicolidae—is necessary.

The aim of our research was to study the interactions of prelarvae of the Khanka spiny bitterling *Acheilognathus chankaensis* and water mites *Unionicola* sp. with bivalve mollusks *Nodularia douglasiae* inhabiting a semi-enclosed floodplain lake of the Razdolnaya River. Special attention was paid to the relationships among symbionts associated with the mollusks, including trophic interactions.

MATERIAL AND METHODS

The study was conducted in an artificial lake (a former sand quarry) located in the floodplain of the Razdolnaya River (Nadezhdinsky District, Primorsky Region), with coordinates 43°34′ N, 131°53′ E (Fig. 1). The lake is approximately 500 m long, and its width in the central part is about 200 m. During medium and high water levels, the lake connects to the river via a narrow channel. The substrate near the shore is sandy or sandy-silty, becoming silty at depths exceeding 0.7–1 m. Water pH is typically around 7.5, and carbonate hardness is approximately 3.0.

Initial collections of bivalve mollusks, conducted in May 2022 (sample No. 16 [14]), showed that the lake is inhabited by two unionid species, *Nodularia douglasiae* and *Buldowskia suifunica* (Fig. 2), with the majority of collected *N. douglasiae* being infected with prelarvae of Acheilognathidae (species identification of mollusks was performed by V.V. Bogatov). The population of *B. suifunica* at the time of observation was represented by single individuals, while the population of *N. douglasiae* in the coastal zone had a relatively high density, reaching 180–200 ind./m^2 or more in some coastal areas. In addition, a high proportion of newly recruited *N. douglasiae* was observed everywhere, accounting for 10–15% of the total bivalve abundance [14].

For parasitological examination of *N. douglasiae*, mollusk collections were carried out in May–June 2023, as well as in April, May, June, September, and



Fig. 2. Shells of *Nodularia douglasiae* (a) and *Buldowskia sujfunica* (b). Photo by V.V. Bogatov.

October 2025. Additionally, in May 2023 and 2025, 5 and 8 specimens of *B. suifunica* were collected, respectively. Mollusks were collected manually, using a hydrobiological toothed dredge, or with rakes having elongated teeth. In total, the mantle cavities of 294 specimens of bivalve mollusks were examined. A total of 219 prelarvae of *A. chankaensis* were counted from the gills of *N. douglasiae*. Bitterling embryos were absent in all *B. suifunica* specimens. Identification of fish embryos was performed using molecular genetic analysis [21]. The obtained sequences of *A. chankaensis* were deposited in the GenBank database under accession numbers PV820667–PV820689. ZooBank registration: urn:lsid:zoobank.org:act:733A2CD0-D21A-4FA0-8E39-B4A95-8953D7F. Specimens with the designation ACH are part of the zoological collection of the Department of Aquatic Bioresources and Aquaculture, Far Eastern State Technical Fisheries University.

In the mantle cavity and gills of the mollusks, in addition to counting *A. chankaensis* embryos, associated invertebrates were recorded; among these, mites of the genus *Unionicola* were the most abundant. Chironomid larvae and leeches were occasionally observed in the mollusks.

At the end of October 2025, five adult bitterlings *A. chankaensis* were captured in the lake using collapsible traps; two of these were infected with seven mature nematodes *Philometroides strelkovi* Vismanis & Yunchis, 1994, localized under the skin of the head.

In May 2023, to identify the life cycle stages of *A. chankaensis* prelarvae and their capacity for autonomous development, observations were conducted on five bitterling embryos measuring 4 mm, previously extracted from the gills of *N. douglasiae* and subsequently maintained individually in Petri dishes (12 cm diameter) at a water temperature of 20–25°C. Daily recordings were made of the preservation or decline of locomotor function, yolk sac reduction, and the development of external morphological features: pigmentation, fin fold, mouth opening, and eyes. The experiment lasted 28 days.

The prevalence of *N. douglasiae* infection by bitterling prelarvae was assessed in 2023 based on a random sample of 15 mollusks and in 2025 based on a random sample of 100 mollusks, expressed as the percentage of infected mollusks relative to the total number examined. In early October 2025, a similar assessment of *N. douglasiae* infestation by *Unionicola* sp. mites was conducted based on a random sample of 40 mollusks. Additionally, standard parasitological indices were calculated: the ratio of the total number of bitterling prelarvae (and separately mites) to the number of infected mollusks (mean intensity of infection), as well as to the total number of both infected and uninfected mollusks (abundance index).

RESULTS

It was established that in the studied water body, glochidial larvae were brooded in the outer gills of *Nodularia douglasiae* from April to the first half of June (Fig. 3a). During the same period, *A. chankaensis* embryos developed in the inner gills of the mussels (Fig. 3b), and concurrent development of glochidia and fish embryos in the same mollusk was not observed. The main infection indices of *N. douglasiae* by bitterling embryos in May 2023 and May 2025 were as follows: prevalence was 73.3 and 15.5%, mean intensity was 6 and 11 (range 4–7 and 7–15), and the abundance index of bitterling prelarvae was 4.9 and 1.7, respectively.

Observations on the metamorphosis and behavior of *A. chankaensis* prelarvae, extracted from the mollusk gills and maintained individually in Petri dishes, allowed us to distinguish the following four key stages of the embryonic life cycle:

Stage 1. Body shape is an elongated ellipse. Total length including the larval tail is 3.92–3.93 mm, maximum body height is 0.81–0.87 mm; body height to length ratio is 20.6–22.2%. Height of the anterior head

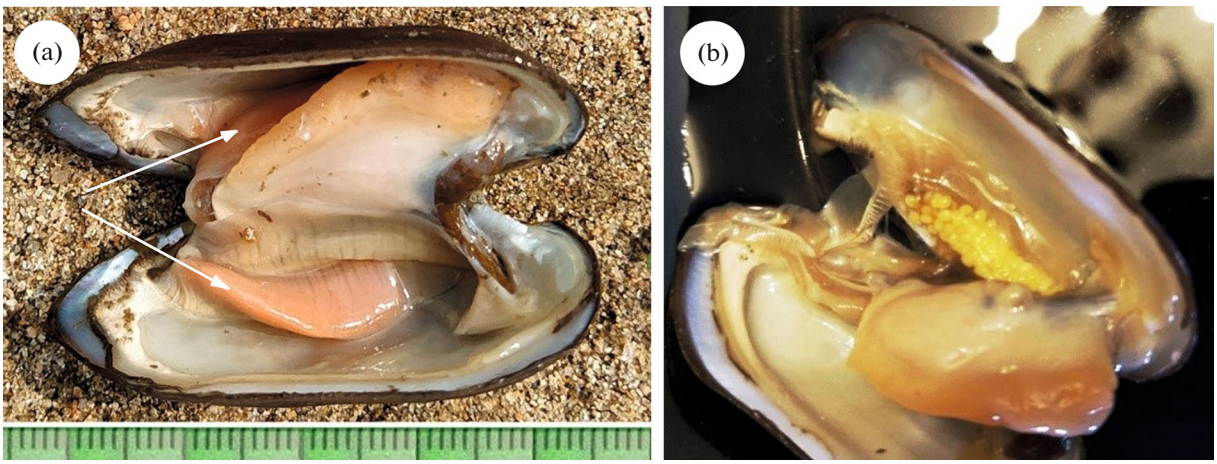


Fig. 3. *Nodularia douglasiae*: internal view, with glochidia in the outer gills (shown by arrows) (a) and with *A. chankaensis* larvae in the inner gill (b). Photo by V.V. Bogatov.

region is 0.58–0.66 mm; head height to maximum body height ratio is 0.67–0.82. The larval tail is transparent and approximately half the body length; tail length from the posterior body margin is 1.25–1.81 mm, height at the base is 0.33–0.34 mm, height at the margin is 0.12–0.25 mm; the tail margin is rounded. The ratio of tail base height to tail length is 0.18–0.27; body length without tail is 2.11–2.38 mm; tail base height to body height ratio is 0.38–0.42%; tail length to body length ratio is 0.53–0.86. The notochord rudiment height in the middle part of the tail is 0.09–0.11 mm. The entire internal space of the body is opaque and filled with the yolk sac (Fig. 4a).

Stage 2. During the first week, a reduction in the yolk sac is observed, head contours begin to form, tail length decreases by approximately 50%, initial formation of the caudal fin is evident, and the body acquires a spindle-shaped form (Fig. 4b). Embryo movement is accomplished by progressive wave-like motions along the walls of the Petri dish.

Stage 3. During the second week of observation, the yolk sac is reduced to approximately two-thirds of its original size, and the spindle-shaped body form is retained (Fig. 4c). Formation of the optic cups and initial differentiation of head structures are noted. The caudal part of the fin fold continues to regress, with signs of differentiation appearing. Locomotor activity is represented by occasional low-amplitude forward movements.

Stage 4. During the third week of the experiment, the yolk sac is reduced to 25–33% of its original size, and body elongation becomes pronounced. Pigmentation of the optic cups (melanin deposition) is observed, and the caudal fin acquires a delta shape with rounded edges (Fig. 4d). Locomotor activity is maintained but with reduced amplitude compared to the previous week.

By the end of the third week to the middle of the fourth week of the experiment (day 25), embryo survival was 40% (2 out of 5 specimens).

In early October 2025, 47 adult mites (Fig. 5a) were collected from *N. douglasiae* individuals infected with mites. The prevalence of mollusk infection was 60%, the mean intensity of infection was approximately two mites per mollusk (range 1–7), and the abundance index was 1.2. Each bivalve mollusk infected with mature mites simultaneously contained *Unionicola* sp. eggs in both gills (Fig. 5b). Thus, *N. douglasiae* proved to be an incubator not only for brooding its own glochidia and *A. chankaensis* embryos but also for water mites of the genus *Unionicola* sp. Intermediate larval stages of the mites (protonymphs, deutonymphs, tritonymphs) were not found at the time of examination; however, they were abundantly recorded in the mollusks during the spring–summer period.

In May 2025, during controlled 24-hour experiments, we documented rare cases of attacks by *Unionicola* sp. mites, extracted from the mollusk gills, on relatively slow-moving *A. chankaensis* prelarvae (Fig. 5c). These observations suggest the possibility of active use of bitterling embryos by mites as a food source. This trophic relationship is indirectly supported by the frequently observed concentration of mite nymphs in the area where bitterling embryos are localized (Fig. 5d).

DISCUSSION

The data obtained show that the infection rate of *N. douglasiae* by fish prelarvae was notably lower in 2025 compared to 2023, which appears to be related to the catastrophic flood in August 2023 caused by Typhoon Khanun [22]. The entire valley of the Razdolnaya River was flooded for an extended period, which may have led to fish moving from the lake to

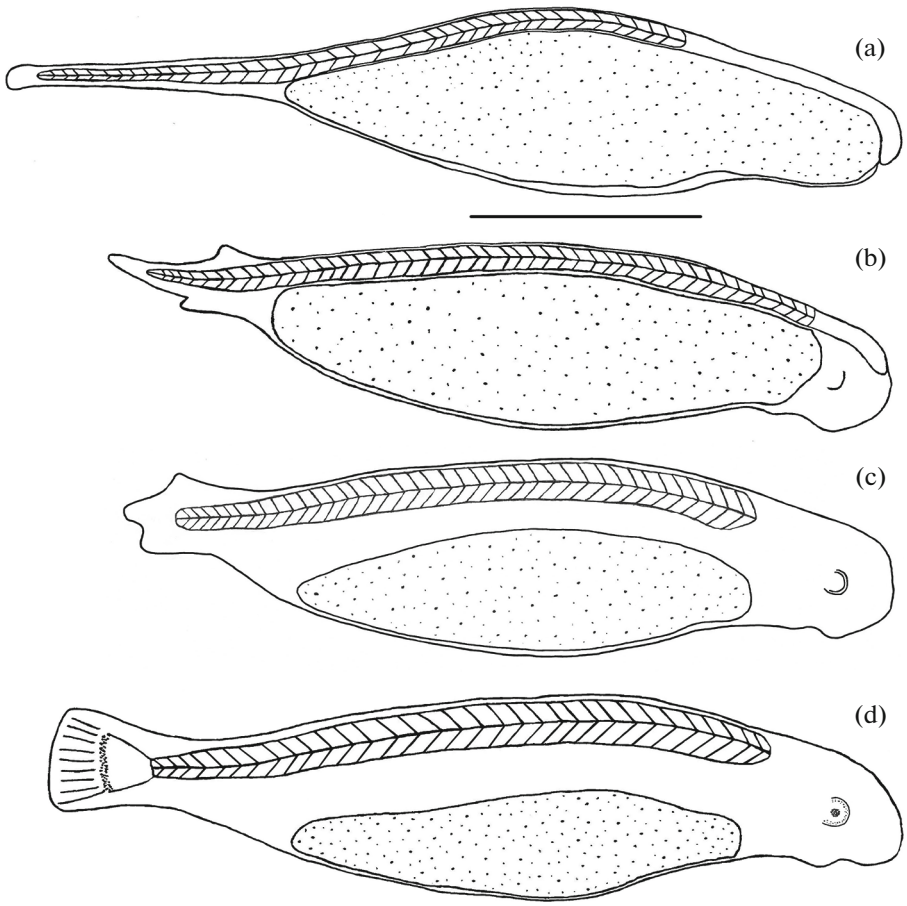


Fig. 4. Schematic representation of the developmental stages of *Acheilognathus chankaensis* larvae: start of the experiment (a), after one week (b), after two weeks (c), and after three weeks (d) of the experiment. Scale bar: 100 μm.

other floodplain areas, while the mussel population density remained stable.

Comparison of our data on the early developmental stages of *A. chankaensis* during cultivation outside the host mollusk with the results of observations on embryo development in closely related bitterling species revealed similar morphogenetic dynamics. In particular, the embryonic period of *A. chankaensis* established by us at 3–4 weeks is consistent with the encapsulation periods known for other bitterling species within bivalve mollusks [4, 23]. Based on the experimental cultivation of *A. chankaensis* prelarvae, as well as numerous reports from Russian and international sources [1–3, 5, 7, 9–11, 21, 24, 25], it can be considered proven that bitterling larvae act as symbionts in relation to mollusks, using these invertebrates as shelters. No behavioral or mobility impairments have been observed to date in mollusks infected with juvenile bitterlings under natural conditions.

Thus, experimental cultivation of bitterling prelarvae outside *N. douglasiae* allowed, on the one hand, the first characterization of the early life cycle stages of *A. chankaensis* and, on the other hand, demonstrated the ability of these fish embryos to develop independently of the mollusks. In other words, *A. chankaensis* embryos use the mollusk gills not as parasites but as symbionts, primarily as a shelter, which evidently significantly increases their survival under natural conditions.

Among the invertebrates associated with *N. douglasiae*, mites of the genus *Unionicola* predominated, and the main infection indices of mollusks by mites were comparable to those for bitterling embryos. It should be noted that in addition to our observations, extensive data are available on the infestation of unionids by mites of this genus in Amur Oblast [26] and Tyumen and Sverdlovsk Oblasts [27]. In particular, V.A. Stolbov and K.P. Voronova [27] described the infestation of unionids by mites in Lakes Krugloe and Kuchak (Tyumen Oblast) during the summer period. The infestation rates of mollusks by different mite developmental stages differed significantly between the two lakes; however, the prevalence and mean intensity of infection for adult mites in Lakes Krugloe and Kuchak were lower than those for adults from the studied lake in the Razdolnaya River basin.

We also found high infestation of both gills of *N. douglasiae* by eggs of the water mite *Unionicola* sp.

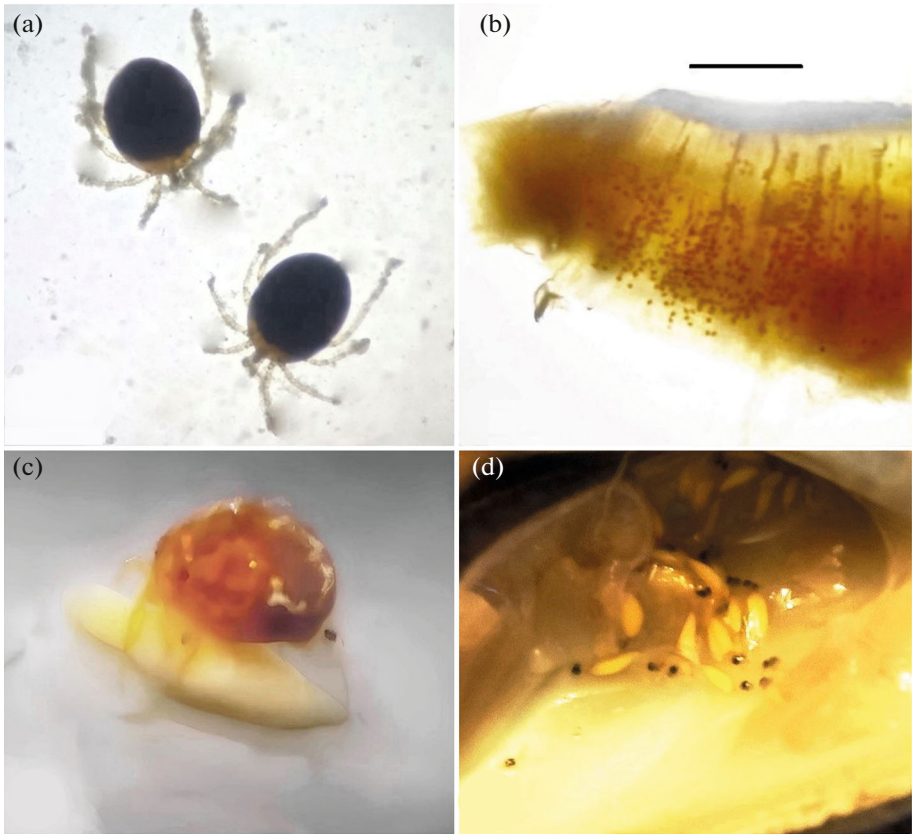


Fig. 5. Water mites parasitizing *Nodularia douglasiae*: a – female *Unionicola* sp. mites; b – gill of *N. douglasiae* infected with *Unionicola* sp. mite eggs (scale bar: 5 mm); c –adult *Unionicola* sp. mite attacking a free embryo of *Acheilognathus chankaensis*; d – concentration of a group of mite nymphs in the area where *A. chankaensis* embryos are localized. Photos by K.S. Vainutis (a, b, c, May 2025) and V.V. Bogatov (d, 08.06.23).

during the autumn period, when the mollusk gills are free of glochidia and bitterling embryos. The emergence of mite nymphs was observed in late April to early June of the following year, coinciding with the development of bitterling embryos in the mollusk gills. During the same calendar period, in June 2024, E.M. Saenko [4] also recorded mite nymphs in mollusks from Lake Lotos (Razdolnaya River basin, Ussuriysk Urban District).

The active attacks by adult *Unionicola* sp. mites on slow-moving *A. chankaensis* prelarvae observed in controlled experiments suggest a previously unrecognized three-way trophic interaction in the "mollusk–bitterling–mite" system. Since *Unionicola* mites are traditionally considered parasites of unionids, their predation on bitterling prelarvae expands the ecological role of these invertebrates. Our observations are supported by studies by V.F. Matveev and C. Martinez [28], who documented facultative predation by water mites on small slow-moving organisms. Furthermore, some water mites, including *Unionicola*, may exhibit opportunistic predation on fish eggs and larvae. There are also several reports of predatory behavior of water mites toward fish [28–30]. Therefore, when studying the interactions of symbionts associated with mollusks, the potential direct impact of mites on the survival of *A. chankaensis* embryos should be taken into account.

Recently, in experiments on freshwater Unionida from the Lake Biwa basin (Japan) and bitterlings *Acheilognathus rhombeus*, cases of feeding on bitterling eggs and embryos by parasitic leeches associated with mollusks were investigated [31, 32]. Furthermore, using the example of the spring-spawning bitterlings *Tanakia limbata* (Temminck & Schlegel, 1846) and *T. lanceolata* (Temminck & Schlegel, 1846), it was shown that female bitterlings during spawning prefer mollusks uninfected by leeches or those with lower infestation density, which, for *T. limbata*, was confirmed both by observations of bitterling spawning and by dissection of mollusks [32]. Apparently, the strategy of protecting the new generation of bitterlings by laying eggs in mollusks that are uninfected or lightly infected with parasites and not occupied by developing glochidia ensures the stable existence of aquatic organisms associated with bivalve mollusks. The egg deposition by *Unionicola* sp. in mollusk gills observed

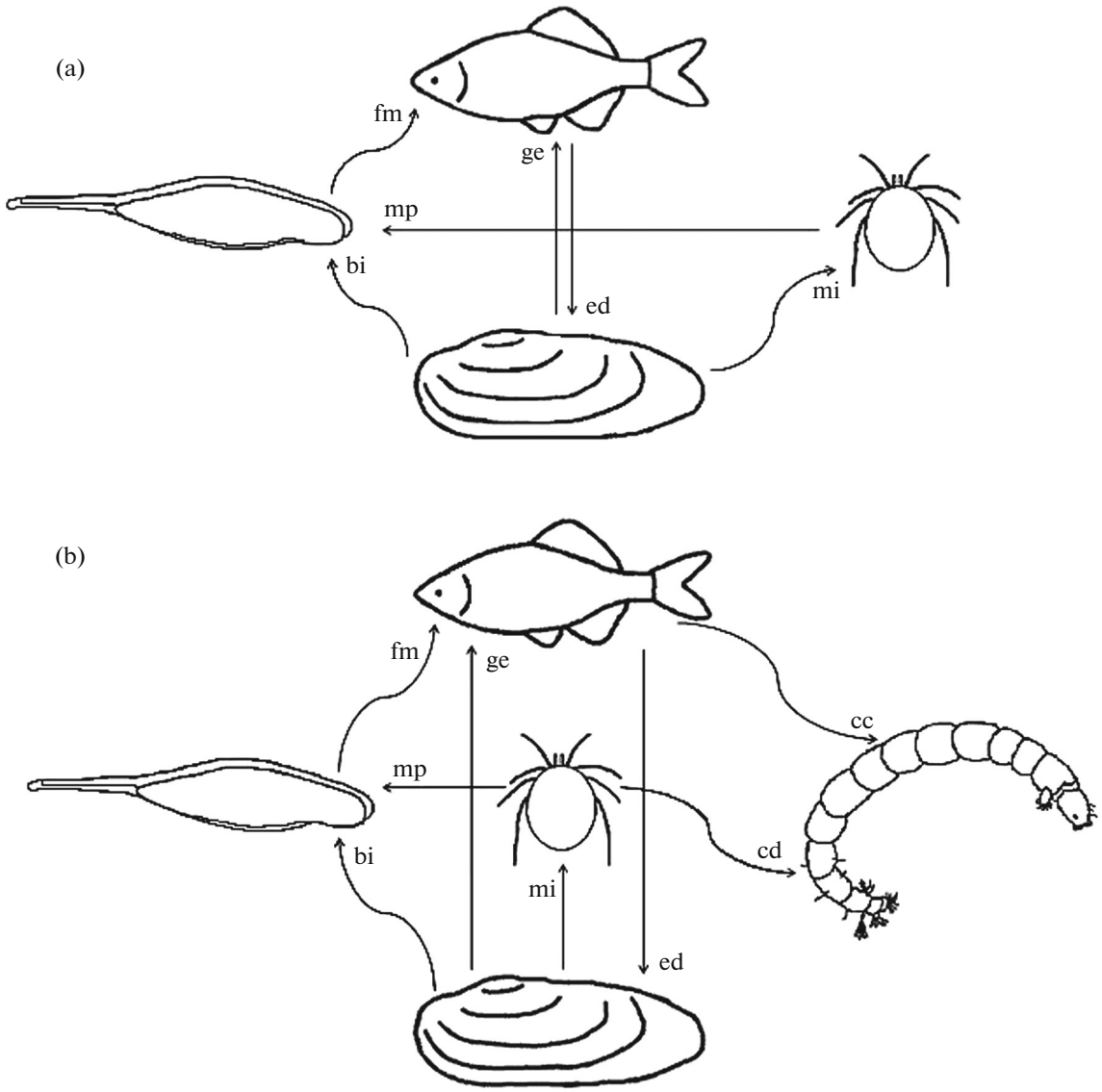


Fig. 6. Variants of the most probable interactions in the artificial floodplain lake of the Razdolnaya River basin. a – tripartite (three-way) interaction. b – hypothetical quadripartite (four-way) interaction. Abbreviations: fm – fish maturation; bi – bitterling incubation; ed – egg deposition; ge – glochidia encystment; mi – mite incubation; mp – mite predation; cc – chironomid consumption; cd – mite dispersal via chironomids.

by us in autumn may also be an example of adaptation of predatory mites for more successful reproduction.

It is evident that the network of relationships between interacting aquatic organisms can be of varying complexity. In particular, the trophic three-way interaction in the "mollusk–fish–mite" system we identified implies complex but stable relationships among the three species. The mutual infection of fish and mollusks by each other's larvae reflects reciprocal brood care. The mollusk also serves as a natural incubator for mite eggs and a substrate for their larvae, which in the adult stage may leave the host or reside within it. In the latter case, adult mites are capable of hunting bitterling larvae or parasitizing mollusk tissues (Fig. 6a).

More complex, multipartite interactions involving four or more species of aquatic organisms are also possible. Although we did not study the role of chironomids in these interactions, their inclusion in the interaction scheme could provide a four-way interaction. All previously described relationships are retained, but additional predator–prey relationships emerge between chironomid larvae, mites, and adult bitterlings (Fig. 6b). Importantly, chironomid larvae can act primarily as phoretic carriers for parasitic mites [26, 33–35] and likely facilitate mite dispersal not only within a single water body but also between different water bodies, while simultaneously serving as prey for bitterlings [36, 37].

To the interaction schemes proposed above, the nematode *Philometroides strelkovi*, found on adult bitterlings, could be added, which would potentially reveal a more complete system of relationships between adult fish and mollusks, their glochidia, and some invertebrates, as well as with parasites. Considering that for the nematode *P. strelkovi* only one type of interaction is available—parasitism on fish—the definitive hosts for these parasites could include not only *A. chankaensis* but also the sharpbelly (*Hemiculter leucisculus*) recorded in the studied floodplain lake, given previous data on their association with *P. strelkovi* in the Luchegorsk Reservoir [38].

CONCLUSIONS

In a model artificial floodplain lake of the Razdolnaya River (Primorsky Region, Russia), the interactions between embryos of the Khanka bitterling *A. chankaensis* and water mites *Unionicola* sp. with the bivalve mollusk *N. douglasiae* and with each other were investigated. The study showed that *A. chankaensis* prelarvae developed in the inner gills of the mollusks in April–June. During the same period, glochidia were brooded in the outer gills of *N. douglasiae*, but concurrent development of fish embryos and glochidia in the same mollusk was not observed. It was experimentally demonstrated that bitterling prelarvae were capable of developing outside the mollusk body. Therefore, in nature, *A. chankaensis* embryos use the mollusks primarily as a shelter, which significantly increases their survival. Under experimental conditions, four stages of the bitterling prelarval life cycle were observed during development within the gills of *N. douglasiae*, after which the mature larvae leave the mantle cavity of the mollusks.

In autumn, eggs of the mite *Unionicola* sp. were found in large numbers in the gills of *N. douglasiae*. Adult mites either inhabited the mantle cavity of the unionids throughout the year or continued their life activities in open water. The detection of mite eggs in *N. douglasiae* during the period when the mollusk gills were free of bitterling embryos and glochidia confirms the existence of stable parasite–host relationships in the Unionidae–*Unionicola* system, which is consistent with literature data. In controlled experiments, attacks by *Unionicola* sp. on slow-moving *A. chankaensis* prelarvae were documented, indicating a trophic three-way interaction in the "*Nodularia*—bitterling—mite" system. The presence of chironomid larvae in the mantle cavity of the mollusks suggests the possible dispersal of mites via insects.

The proposed schemes of multilateral relationships emphasize the central role of bivalve mollusks as incubators not only for their own glochidia but also for the reproduction of *A. chankaensis* and *Unionicola* sp., as well as a habitat for some insect larvae, leeches, and other invertebrates.

AUTHOR CONTRIBUTION

Vainutis K.S.—sampling and field data processing, study of bitterling prelarval development, preparation of illustrations, interpretation of results, writing—original draft.

Bogatov V.V.—conceptualization and study design, sampling, interpretation of results, preparation of illustrations, writing—review & editing, supervision.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

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ETHICAL STANDARDS

The authors adhered to ethical standards in handling live invertebrates and fishes.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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