



Life Cycle Development of *Anacanthorus spathulatus* and *Notozothecium janauachensis* (Monopisthocotyla), Parasites of the Gills of *Colossoma macropomum* (Osteichthyes: Serrasalminidae) Raised in Glass Aquariums in the Peruvian Amazon

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Abstract

Introduction This study describes the life cycle development of two monopisthocotyls gill parasites, *Anacanthorus spathulatus* Kritsky, Thatcher & Kayton, 1979 and *Notozothecium janauachensis* Belmont-Jégu, Domingues & Martins, 2004 (Monopisthocotyla), infecting *Colossoma macropomum* (Cuvier, 1816) reared under controlled aquarium conditions in the Peruvian Amazon.

Materials and Methods Twenty naturally infected fingerlings were collected from a fishpond and maintained in glass aquariums under controlled conditions. Fish showing typical clinical signs of monopisthocotyls infestation were selected. Eggs were obtained from adult parasites isolated from the gill arches and monitored using stereomicroscopy and light microscopy to characterize embryonic development, oncomiracidium morphology, and early post-hatching stages. Additional gill samples were processed to mean study juvenile, subadult, and adult morphology.

Results In *A. spathulatus*, development from egg to hatching oncomiracidium required approximately 72 h, followed by an active swimming phase of approximately 10 h before loss of cilia and immobilization. In contrast, *N. janauachensis* completed embryonic development in approximately 48 h, with free-swimming oncomiracidia remaining active for about 12 h. In both species, a sequence of well-defined developmental stages was documented, including egg (time 0), early and advanced embryo, fully developed oncomiracidium with four ocelli and ciliation, early and developing juvenile, subadult, and adult forms, accompanied by progressive differentiation of the haptor and copulatory complex.

Conclusions This study provides a detailed morphological and temporal characterization of the life cycles of *A. spathulatus* and *N. janauachensis* under experimental conditions, identifying critical windows of larval infectivity. These findings contribute to a better understanding of host–parasite dynamics and provide essential information for the development of monitoring and control strategies for monopisthocotyls infections in *C. macropomum* aquaculture in the Peruvian Amazon.

Keywords Monopisthocotylans · Oncomiracidium · Tambaqui · Host–parasite relationships

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Introduction

The Peruvian Amazon is one of the regions with the greatest availability of water resources and fish diversity in the world, making it an ideal setting for the development of fish farming. The extensive network of rivers, lakes, and streams, together with stable tropical climatic conditions and high primary productivity, favor the cultivation of native species of high economic and social value. Among these, *Colossoma macropomum* (Cuvier, 1816) popularly

known in Peru as gamitana, stands out for its rapid growth, good feed conversion, high market acceptance, and ability to adapt to intensive and semi-intensive farming systems. In addition, its predominantly frugivorous diet and tolerance to variations in water quality position it as a strategic species for strengthening food security, generating income in rural communities, and diversifying aquaculture production in the region. In this context, the sustainable exploitation of the fish farming potential of the Peruvian Amazon, with an emphasis on *C. macropomum*, presents itself as a key opportunity for local economic development and the conservation of native aquatic resources [1].

Fish in fish farming systems are highly vulnerable to parasitic infestations due to high stocking densities, handling stress, and often suboptimal environmental conditions, which favor the transmission and establishment of various groups of parasites. Among these, gill monopisthocotyls are particularly relevant due to their direct life cycle, high host specificity, and high reproductive capacity, which allows parasite loads to increase rapidly in ponds and intensive systems. These parasites attach themselves to the gills, causing mechanical and tissue damage, alterations in gas exchange, increased mucus production, and, in severe infestations, significant mortality, especially in juvenile stages [2]. Detailed knowledge of the life cycle of monopisthocotyls including their egg, infective larva (oncomiracidium), and adult stages is essential for designing effective management and control strategies, such as treatment synchronization, improved biosecurity practices, and the implementation of preventive measures that reduce infection pressure in farming systems [2].

In farming systems of *Colossoma macropomum*, significant health problems have been associated with infestations by gill monopisthocotyls. These parasites attach firmly to the gill epithelium using specialized haptor structures, causing epithelial hyperplasia, lamellar fusion, excessive mucus production, and impaired gas exchange. These pathological effects compromise respiratory function and overall physiological performance, leading to reduced growth, increased susceptibility to secondary infections, and, in severe infections, mortality, particularly in fry and juvenile stages, resulting in significant economic losses in aquaculture [3]. In this context, understanding the life cycle and developmental biology of monopisthocotylean is essential for aquaculture, as it provides key information to identify transmission dynamics, optimize treatment timing and effectiveness, and implement preventive management strategies. This knowledge contributes to improving fish health and the sustainable production of native species such as *C. macropomum*. Therefore, the present study aimed to (i) describe the embryonic and postembryonic development of *A. spathulatus* and *N. janauachensis* under controlled

laboratory conditions, (ii) compare the developmental chronology between both species, and (iii) identify critical infective windows relevant to parasite transmission and aquaculture management.

Materials and Methods

Twenty *C. macropomum* fingerlings (9.5 ± 2.5 cm total length and 12.6 ± 3.2 g weight) were collected from a fish-pond in the “Instituto de Investigaciones de la Amazonía Peruana” (IIAP) in Iquitos, Loreto-Peru ($3^{\circ}49'01.81''$ S $73^{\circ}19'15.54''$ W). After collecting, the fish were transported alive in plastic bags with oxygen to the “Laboratorio de Parasitología y Sanidad Acuicola” and were maintained in a 100 L glass aquarium with constant water flow. The fish were fed *Ad libitum* once a day on extruded commercial feed containing 45% crude protein (Aquatech[®]). Water quality parameters were monitored using a multiparameter probe (Hanna Instruments[®], HI 9829). Total ammonia nitrogen (TAN) concentration averaged 4.0 mg/L, while the concentration of unionized ammonia (NH₃), which represents the toxic fraction, was estimated at 0.05 mg/L based on water temperature and pH values. These levels were inside acceptable limits for tropical fish culture and are not considered stressful for *Colossoma macropomum*. Additionally, dissolved oxygen, pH, and conductivity were maintained within optimal ranges throughout the experimental period.

Some fish showed signs of parasitism. The operculum's frequent opening and “flashing” are the two common behaviors that make up the clinical manifestations of infestation by monopisthocotyls. These behaviors indicate the irritating process of itching caused by parasite feeding and moving. The fish remain swimming with the shoal and feed normally during this period. Animals presenting frequent opening of the operculum and “flashing” were sampled to study the eggs, and the embryonic development of the oncomiracidia.

During the period when fish were kept, the wastewater from the 100 L glass aquarium was filtered to investigate the presence of eggs. For this, a 20 µm net was coupled to the overflow pipe to filter the discharge water. After thirty minutes of filtration, the filtered contents were observed via stereomicroscopy (Zeiss Stemi 305). These eggs were used for the experiments of Sect. 2.4 since we already knew the stages of egg development.

Fish were sacrificed by means of medullary sectioning. The gills were excised and placed in a Petri dish with water to visualize monopisthocotyls with eggs inside them. Once the parasites were located, they were separated with stylets and placed on slides with a drop of water until the egg was expelled, which occurred after 10 to 15 min. The monopisthocotyl parasites were identified as *Anacanthorus*

spathulatus Kritsky, Thatcher & Kayton, 1979 and *Notozothecium janauachensis* Belmont-Jégu, Domingues & Martins, 2004. The main taxonomic feature used for identifying *A. spathulatus* were absence of anchors and bars in the haptor, a copulatory complex consisting of the male copulatory organ (MCO), which is spatula-shaped, and the accessory piece, which is rod-shaped. Together, they resemble tweezers (Fig. 1). *Notozothecium janauachensis* was identified

by the presence of a pair of prominent ventral anchors, approximately four times longer than the dorsal anchors. The ventral bar is elongated and robust, with a small antero-medial projection. The dorsal bar is thin and small. The copulatory complex consists of the MCO, which is a thin, short, comma-shaped tube, and the accessory piece, which is a small rod articulated at the base of the MCO (Fig. 2).



Fig. 1 *Anacanthorus spathulatus* Kritsky, Thatcher & Kayton, 1979 from the gills of *Colossoma macropomum* (Cuvier, 1816). (A) Whole parasite, ventral view. (B) Copulatory complex. (C) Egg

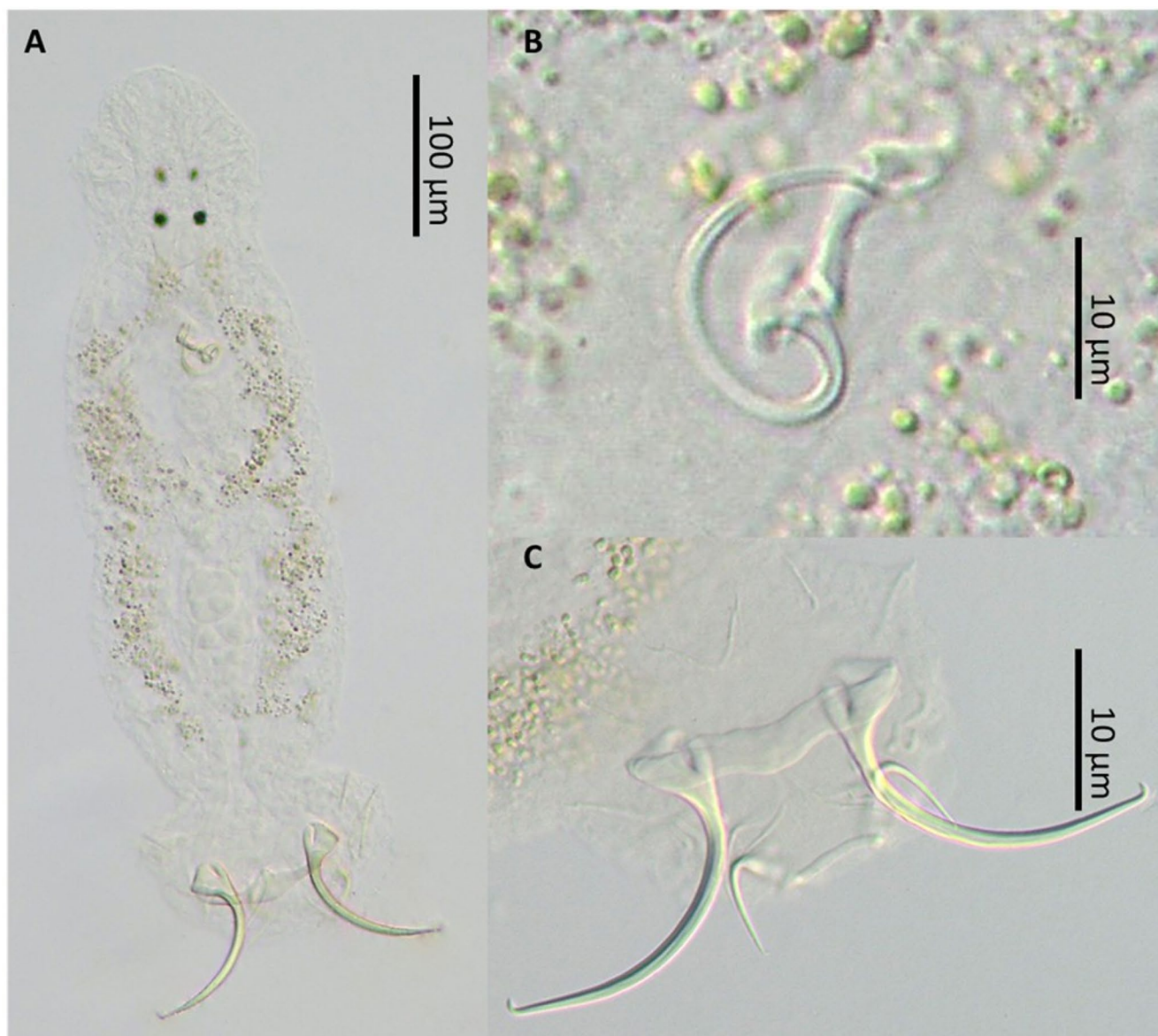


Fig. 2 *Notozothecium janauachensis* Belmont-Jégu, Domingues & Martins, 2004 from the gills of *Colossoma macropomum* (Cuvier, 1816). (A) Whole parasite, ventral view. (B) Copulatory complex. (C) Haptor

The expelled eggs were individually transferred to glass slides with a drop of filtered and aerated freshwater and covered with coverslips. From the moment the egg was expelled by the adult parasite, this point was defined as time 0 h post-oviposition. The term hatching was used exclusively to refer to the moment when the fully developed oncomiracidium emerged from the egg. Fifteen eggs of *Anacanthorus spathulatus* were observed, each serving as a replicate, as did eggs of *Notozothecium janauachensis*. The eggs were kept at room temperature, without manipulation of the physicochemical variables. The temperature was monitored daily and ranged between 27 ± 1 °C, corresponding to the optimal temperature range for monopistocotylan embryonic development. An 8 h light photoperiod, equivalent to

the time spent in the laboratory, followed by 16 h of darkness, was used. The eggs were kept in filtered water (previously aerated for 24 h) and monitored daily until hatching. Additionally, the main physicochemical parameters of the water were monitored. Dissolved oxygen was maintained at 5.2 ± 0.5 mg/L, pH at 7.0 ± 0.2 , conductivity at 80.4 ± 5 µS/cm, and the concentration of non-ionized ammonia was kept below 0.02 mg/L. These values were obtained using Hanna multiparameter probe.

Daily observations were made using a stereomicroscope (Zeiss Stemi 305) and a compound microscope. To prevent desiccation and maintain stable osmotic conditions, a small volume of fresh water was added daily using a sterile syringe. Morphological changes during embryonic

development were documented by photomicrography with a Leica DM 3000 LED microscope equipped with a Flexacam i5 digital camera. After hatching, live oncomiracidia were observed with a light microscope to describe their morphology, assess their swimming behavior, ciliary activity, and survival time until complete loss of cilia and cessation of movement.

The other stages of development following the hatching of the oncomiracidium larva (juvenile and adult) were not monitored; however, they could be seen in the sample of processed gills. Some gill arches were placed in vials containing heated water (approximately 68 °C). Each vial was vigorously shaken, and 96% ethanol was added. The content of each vial was examined using a dissecting microscope and parasites were removed from the gills or sediments using dissection needles. Sample was observed under stereoscope. Monopisthocotylan specimens were cleared in Hoyer's medium for the study of sclerotized structures (4).

Results

The incubation period of *Anacanthorus spathulatus* eggs ranged from 70 to 74 h, with a mean of 72.0 ± 1.4 h ($n=15$). In contrast, eggs of *Notozothecium janauachensis* hatched between 46 and 50 h, with a mean incubation time of 48.0 ± 1.4 h ($n=15$).

For *A. spathulatus*, the development of the oncomiracidium larva from egg to hatching occurred in approximately 72 h. The oncomiracidium larva then swims actively until, after 10 h, it begins to lose its cilia, at which point it becomes immobile. The following was observed in the developmental stages of the *A. spathulatus* life cycle:

Stage A – Adult with egg inside (Fig. 3A).

Stage B – Egg (Time 0): oval structure, with a regular outline and a relatively thick, homogeneous wall. The internal content appears to be a poorly differentiated cell mass, with no defined organs. No appendages or attachment structures are yet visible (Fig. 3B).

Stage C – Embryo inside the egg / pre-oncomiracidium (30 h post egg extrusion - hpe): the wall of the “egg” remains clearly defined, but the internal content is no longer a homogeneous mass: lighter and denser areas appear, corresponding to the of embryonic organization. The internal contour begins to become somewhat asymmetrical, a sign that the anterior-posterior axis of the future larva is forming (Fig. 3C).

Stage D – Advanced embryo/oncomiracidium in formation (48 hpe): more irregular and flattened shape, differentiated from the simple oval capsule of B. An

anterior and posterior region can be distinguished, with a somewhat reniform or pyriform body. The cytoplasm shows vacuoles and areas of varying density, indicating tissue differentiation. In this stage, the primordia of ocelli and attachment structures (hooks) usually begin to become individualized (Fig. 3D).

Stage E – Oncomiracidium (free larva) (72 hpe): body clearly separated from the original envelope, with a defined outline, flatter and somewhat elongated. A wider, rounded anterior region and a somewhat narrower posterior region can be identified. Four small pigmented spots (ocelli) can be distinguished in the anterior region. The integument appears clearer, indicating that the larva is fully formed and ready to emerge from the egg. In this stage, cilia can be seen in the anterior, middle, and posterior parts of the body. Hooks can also be seen on the haptor (Fig. 3E).

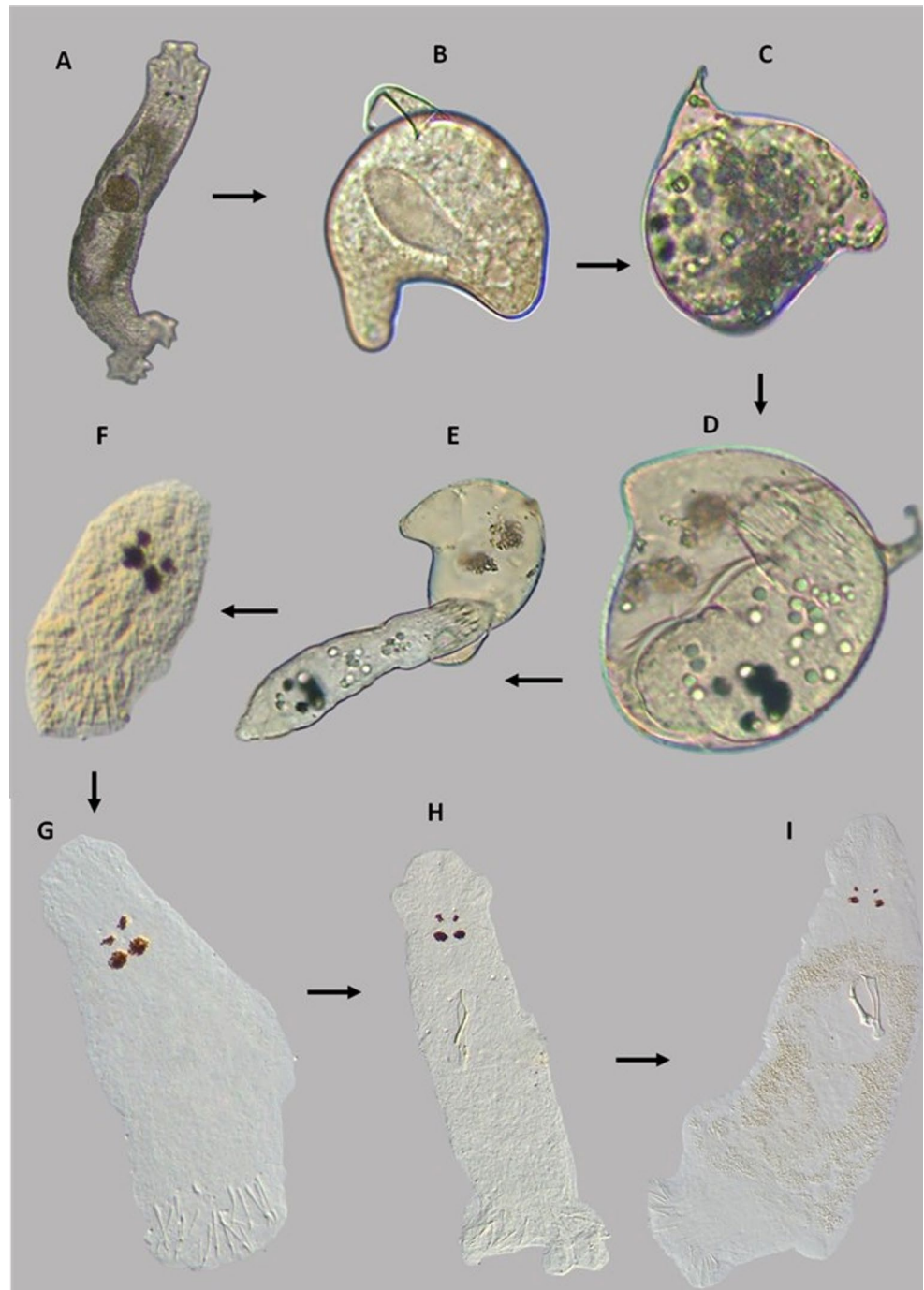
Stage F – Juvenile (post-hatching) (82 hpe): elongated body, larger than in previous stages, but still relatively simple in appearance. The anterior ocelli are now clearly distinguishable, with the anterior pair smaller than the posterior pair. The posterior end of the body begins to show a slight expansion where the haptor will form, although no complex armor is yet visible. The interior is poorly differentiated, with no clearly distinguishable bulky organs (Fig. 3F).

Stage G – Developing juvenile: shows greater body elongation and a more defined outline. The ocelli are still clearly visible; the anterior region is well defined, although the cephalic lobes are not clearly differentiated. At the posterior end, the haptor appears as a wider, somewhat lobed area with 14 distinguishable hooks. A more complex internal organization begins to be apparent (denser areas in the central position of the body (Fig. 3G).

Stage H – Subadult: the body is even more elongated, with proportions very close to those of an adult. The haptor is clearly differentiated from the rest of the body, bilobed, with a wider base and 14 hooks distributed in seven pairs. The copulatory complex has a male copulatory organ and an accessory piece in formation. The body lacks vitellaria. The internal parenchyma has lighter and darker areas, reflecting the progressive development of the digestive and reproductive systems, although still without the large gonadal development typical of adults (Fig. 3H).

Stage I – Adult: body completely elongated and fusiform, with thicker integument and an opaquer appearance. Haptor is well developed, clearly distinguishable from the trunk. Denser parenchymatous structures occupy a large part of the internal volume, indicative of the complete development of the copulatory complex

Fig. 3 Life cycle of *Anacanthorus spathulatus* Kritsky, Thatcher & Kayton, 1979 from the gills of *Colossoma macropomum* (Cuvier, 1816). (A) Adult specimen with egg inside. (B) Egg (Time 0). (C) Embryo inside egg (30 hpe). (D) Advanced embryo (48 hpe). (E) Oncomiracidium (72 hpe). (F) Juvenil post hatching (82 hpe). (G) Developing juvenile. (H) Subadult. (I) Adult



typical of the species. Presence of vitelline distributed from approximately the level of the pharynx to the beginning of the haptor (Fig. 3I).

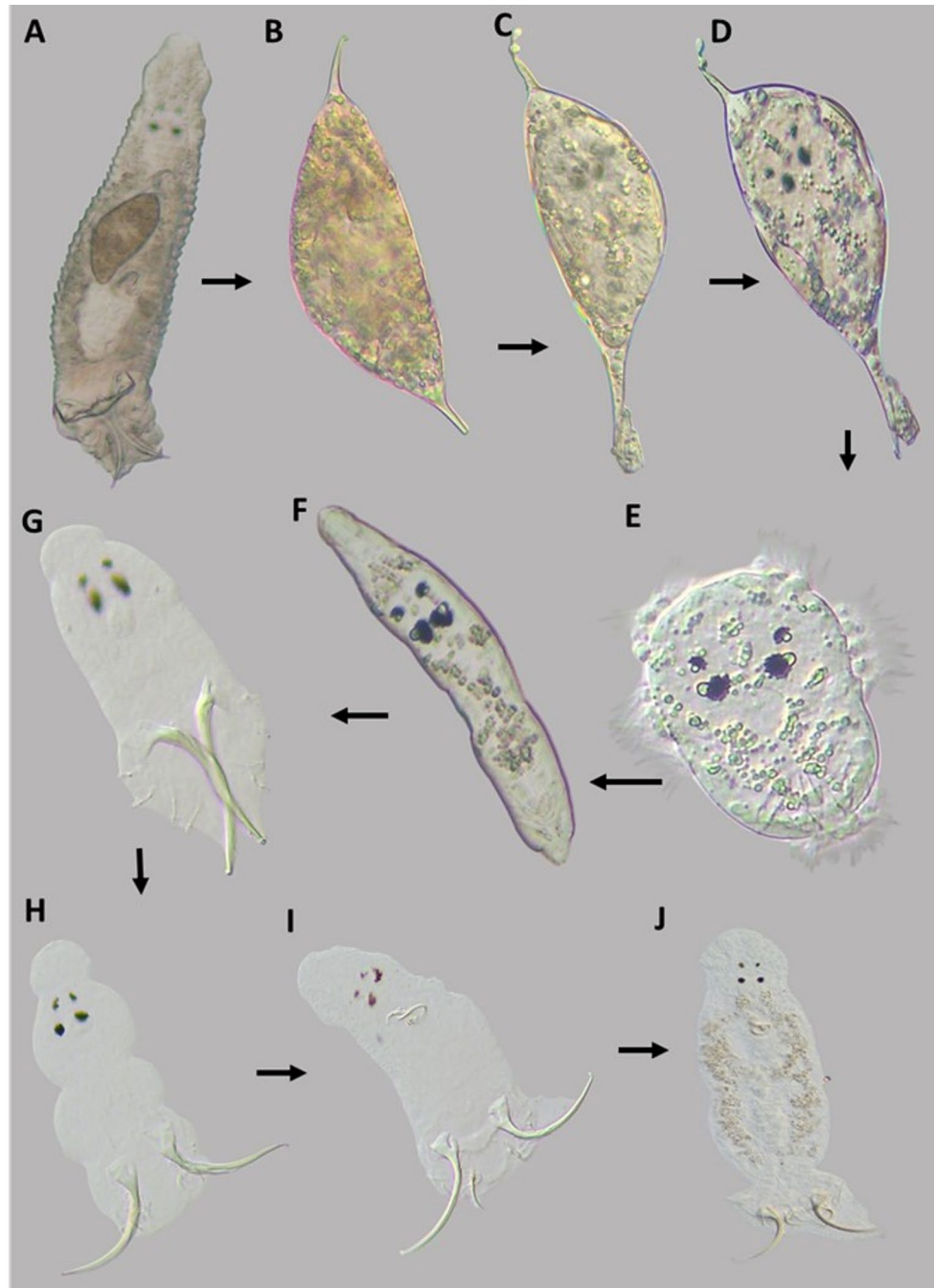
Regarding the development of *N. janauachensis*, the development of the oncomiracidium larva from the egg stage to hatching occurred in approximately 48 h. The oncomiracidium larva then swims actively until, after 12 h, it begins to lose its cilia, at which point it becomes immobile. The

following was observed in the developmental stages of the life cycle of *N. janauachensis*:

Stage A – Adult with egg inside (Fig. 4A)

Stage B – Egg (Time 0): elongated oval shape, with well-defined, relatively thick walls. Homogeneous internal content, with no recognizable organs. There is still no clear differentiation between anterior and

Fig. 4 Life cycle of *Notozothecium janauachensis* Belmont-Jégu, Domingues & Martins, 2004 from the gills of *Colossoma macropomum* (Cuvier, 1816). (A) Adult specimen with egg inside. (B) Egg (Time 0). (C) Embryo inside egg (24 hpe). (D) Advanced embryo (36 hpe). (E) Oncomiracidium (48 hpe). (F) Oncomiracidium losing cilia (60 hpe). (G). Early juvenile. (H). Developing juvenile. (I). Subadult. (J). Adult



posterior poles. It presents two polar filaments at both ends (Fig. 4B).

C – Early embryo in the egg (24 hpe): oval in shape. The internal content is no longer uniform: areas of different density appear (granular cytoplasm, vacuoles). An anterior-posterior axis begins to form, with one end slightly narrower and the other slightly more rounded. The egg continues to function as a clearly visible protective envelope (Fig. 4C).

D – Advanced embryo/pre-oncomiracidium (36 hpe): the embryo occupies almost the entire cavity of the egg,

with an elongated and slightly curved shape. The interior is heavily vacuolated and granular, typical of a metabolically very active embryo. A broader anterior region and a more pointed posterior region are already recognizable. The outline of the future larval body is clearly defined within the capsule. The ocelli begin to differentiate (Fig. 4D).

E – Oncomiracidium (48 hpe): body with a clearer outline. Fusiform and slightly curved shape, with a wider anterior end. The ocelli are distinct, with the anterior pair being smaller than the posterior pair. The interior

shows abundant vacuoles and inclusions; the integument is somewhat more defined. They have cilia on the anterior, middle, and posterior parts of the body. It is possible to differentiate some haptor attachment structures, such as hooks (Fig. 4E).

F – Oncomiracidium losing cilia (60 hpe): Body more flattened and somewhat oval, with a well-defined outline. The interior has numerous clear vacuoles and granules. A slightly wider anterior region and a more rounded posterior region can be distinguished. This stage corresponds to the short-lived free-living larva, responsible for finding and attaching itself to the host. The cilia on the larvae's body can be seen, which gradually detach, making swimming difficult (Fig. 4F).

G – Early juvenile (with incipient haptor): elongated body, with a narrow anterior region and two pairs of clearly visible ocelli. The posterior end forms a clearly differentiated, wider haptor, from which a pair of large, curved hooks protrude. Seven pairs of hooks are observed distributed around the haptor. The rest of the body is still relatively simple, with homogeneous parenchyma and few distinguishable internal structures (Fig. 4G).

H – Developing juvenile (more robust haptor): slightly more voluminous body, with a more “bulging” silhouette in the middle region. Ocelli remain clear. The haptor appears larger and more complex, with a pair of well-developed ventral anchors pointing outward. Hooks are visible, but not yet bars. The copulatory complex is not visible (Fig. 4H).

I – Subadult: more elongated and fusiform body, approaching adult proportions. Ocelli clearly marked and well positioned in the cephalic region. Haptor well defined, with a pair of ventral anchors, a pair of dorsal anchors, a ventral bar, a dorsal bar, and seven pairs of hooks. The copulatory complex can be seen, which is still developing and has not yet reached its final form (Fig. 4I).

J – Adult (final stage): elongated, slender body with clear integument and regular contours. Anterior region with two pairs of intensely pigmented ocelli, standing out against the background. Dense vitelline distributed throughout the body, from the pharynx to the beginning of the peduncle. Fully formed copulatory complex, fully formed and functional haptor structures (Fig. 4J).

Discussion

The present study provides a detailed analysis of the life cycle development of *A. spathulatus* and *N. janauachensis*, two monopisthocotylans parasitizing the gills of *C.*

macropomum under controlled aquarium conditions. Life cycle characterization of monopisthocotylans remains a cornerstone for understanding transmission dynamics and infection risk in aquaculture systems, particularly in tropical environments where elevated temperatures and high host densities favor rapid parasite proliferation [4–6].

Clear interspecific differences in embryonic development were observed. Eggs of *A. spathulatus* required approximately 72 h to hatch, whereas *N. janauachensis* completed embryogenesis within approximately 48 h. Comparable variation has been reported among monopisthocotylans infecting neotropical freshwater fishes, suggesting that developmental timing is largely species-specific, although modulated by environmental factors such as temperature, dissolved oxygen and water quality [7–9]. In tropical aquaculture systems, shorter incubation periods may enhance population turnover, increasing infection pressure and the likelihood of epizootic outbreaks [10–11].

The oncomiracidium stage exhibited a limited infective lifespan in both species, remaining actively motile for approximately 10 h in *A. spathulatus* and up to 12 h in *N. janauachensis*. This short free-swimming period is consistent with the general life history pattern of gill monopisthocotyls and has been described as a critical bottleneck for successful transmission [12–13]. Nevertheless, in intensive aquaculture systems, host proximity and continuous availability of susceptible juveniles may compensate for this limitation, facilitating rapid attachment and reinfection [5, 6, 14].

Morphological observations revealed progressive differentiation of the haptor and copulatory complex throughout post-larval development. In *N. janauachensis*, early development of robust ventral anchors suggests a highly efficient attachment strategy, which may contribute to increased persistence on the branchial epithelium. Similar associations between haptor morphology and pathogenic potential have been reported for monopisthocotyls infecting a variety of cultured fishes [13, 15, 16]. In *C. macropomum*, such attachment efficiency is particularly relevant given the severe branchial alterations previously reported, including epithelial hyperplasia, lamellar fusion and excessive mucus production, which compromise respiratory efficiency and growth performance [3, 17].

The methodological approach adopted in this study, based on direct observation of egg extrusion and daily monitoring of embryonic development under controlled conditions, proved effective for accurately describing ontogenetic progression. Similar approaches have been widely applied in monopisthocotyl life cycle studies and allow reliable correlation between developmental timing and morphological differentiation [7, 18]. However, it must be acknowledged that aquarium-based experiments may not fully reflect

conditions in pond or cage systems, where temperature fluctuations, organic matter accumulation, microbial activity and hydrodynamics may affect egg viability and larval survival [11, 14].

The lack of continuous experimental monitoring of post-hatching juvenile and adult stages under controlled conditions represents a limitation of the present study. Nonetheless, the identification of these stages in gill samples allowed completion of the ontogenetic sequence for both species. Future studies incorporating controlled infestation trials could provide quantitative estimates of attachment success, growth rates and fecundity, contributing to population models and risk assessment frameworks for monopisthocotyl outbreaks in *C. macropomum* aquaculture [5, 19].

From an applied perspective, the findings have direct implications for health management in Amazonian aquaculture. Knowledge of species-specific hatching times and infective windows allows improved synchronization of antiparasitic treatments, reducing reinfection from newly hatched larvae present in the environment [2, 11]. Integrated management strategies combining optimized stocking densities, improved water quality, routine parasitological monitoring and biosecurity measures are increasingly recognized as essential for sustainable disease control in tropical aquaculture [1, 6, 17].

Finally, considering the growing importance of *C. macropomum* as a key food and economic resource in the Peruvian Amazon, studies addressing the biology and transmission dynamics of its major parasites are crucial for sustainable production. Integrating parasitological knowledge into routine management practices is fundamental for minimizing economic losses, improving animal welfare and strengthening the resilience of Amazonian aquaculture systems in the face of emerging health challenges [1, 20].

Conclusions

The life cycle development of *Anacanthorus spathulatus* and *Notozothecium janauachensis* revealed species-specific differences in embryonic incubation time under controlled conditions. *Notozothecium janauachensis* exhibited faster hatching, which may increase transmission efficiency, particularly in high-density aquaculture systems. The oncomiracidium stage showed a limited infective lifespan, emphasizing the importance of host proximity for successful infestation. Rapid morphological differentiation of the haptor suggests an early acquisition of attachment capacity to the gills of *Colossoma macropomum*. These findings provide valuable information for aquaculture management, particularly for optimizing the timing of antiparasitic treatments by targeting early developmental stages before

parasite establishment. Furthermore, knowledge of the developmental chronology contributes to improving epidemiological forecasting and implementing preventive strategies to reduce parasite transmission and production losses in intensive tambaqui farming.

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Author Contributions the study was designed by GAMM, RNFA, HADP; Collection of parasites was performed by ANPV, SPQ; Laboratory tests were performed by GAMM, RNFA, HADP, and CTCG. The manuscript was written by GAMM, RCG, JYA and subsequently revised by all other authors.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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