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Paper

Argulus foliaceus (Crustacea: Branchiura) infestation in common carp (*Cyprinus carpio*) from South Sulawesi, Indonesia

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Abstract

Parasites represent a major constraint in pond-based aquaculture, as their presence can lead to substantial fish mortality and associated economic losses. This study investigated the extent of *Argulus* infestation in cultured common carp (*Cyprinus carpio*) reared in a freshwater hatchery in South Sulawesi Province, Indonesia. Two host groups were examined: broodstock (n = 60; 1091.2 ± 58.16 g) and fingerlings (n = 150; 19.6 ± 0.82 g). Identification of *Argulus* specimens was conducted using morphological examination complemented by molecular analyses. Parasite prevalence and mean intensity were quantified, and Spearman's rank correlation was applied to determine the relationship between fish body weight and infestation severity. Both morphological and molecular evidence confirmed that the *Argulus* specimens infesting carp in this study were *Argulus foliaceus*. Fish body weight was significantly correlated with infestation intensity ($P < 0.01$), with broodstock exhibiting markedly higher prevalence and mean intensity than fingerlings. Preferred attachment sites differed between life stages: the base of the pectoral fins in broodstock and the body surface in fingerlings. These findings indicate that host life stage and body size strongly influence the severity and spatial pattern of *A. foliaceus infestations* in common carp. The outcomes provide a scientific basis for developing management guidelines to reduce the incidence and spread of *Argulus* in aquaculture systems.

Keywords

Argulus, Infestation, Host, Fish, Aquaculture

Introduction

Aquaculture serves to enhance food availability for human populations by complementing the exploitation of wild fish stocks in natural ecosystems (Fry et al., 2016). The common carp (*Cyprinus carpio*) is a major freshwater aquaculture species, cultivated through a range of production systems. According to the Ministry of Marine Affairs and Fisheries (2019), carp production in Indonesia was projected to increase from 697,384 tonnes in 2020 to 749,224 tonnes in 2021, with expansion targeted across several regions. South Sulawesi is among the provinces with considerable potential for carp aquaculture, supported by the presence of research centres engaged in the production of fingerlings and broodstock. Notably, Gowa District ranks as the second-largest producer of carp in South Sulawesi by volume (Gowa Regency Bureau of Statistics, 2017). In addition, community-based aquaculture initiatives and small-scale backyard hatcheries have been established to supply fingerlings for grow-out operations. Despite this growth, disease remains a significant constraint on carp farming, with parasitic infestations by *Argulus* spp. (fish lice) constituting a substantial cause of mortality and economic loss.

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Argulus spp. are ectoparasites within the subclass Branchiura that infest freshwater, brackish water, and marine fishes. Approximately 153 species of *Argulus* (fish lice) have been documented worldwide (Poly, 2008). *Argulus foliaceus* is among the species most commonly associated with infections and disease in freshwater fish (Pekmezci et al *.,* 2011), owing to its low host specificity and notable adaptability to extreme environmental conditions (Alsarakibi et al *.,* 2014). The suckers located on the mouth tube, together with the stylet, facilitate attachment to the host; the stylet pierces the host's skin, while the mouth tube enables feeding on bodily fluids. This mode of attachment and feeding results in tissue damage that predisposes fish to secondary infections caused by bacteria (Bandilla, 2007), fungi (Singhal et al *.,* 1990), and viruses (Nofal & Abdel-Latif, 2017). Such infections may contribute to weight loss, impaired physiological condition, and, in severe cases, mortality of the host fish (Pekmezci et al *.,* 2011).

Substantial economic losses associated with *Argulus* infestations have been well-documented across the aquaculture industry. Mortality attributable to *A. foliaceus* has been reported in numerous carp farms in Türkiye (Pekmezci et al., 2011). In aquaculture settings, infestations reduce production efficiency and increase maintenance costs. For instance, losses exceeding USD 1,400 per hectare per year have been attributed to *Argulus* infestation in carp farms in India (Sahoo et al *.,* 2013). In managed environments for public use or commercial fisheries, infestations can also reduce the aesthetic quality of fish, negatively influencing consumer preference and leading to decreased revenue, as observed in Stillwater trout recreational fisheries in the United Kingdom (Taylor et al *.,* 2006).

In Indonesia, numerous cases of *Argulus* infestation have been reported, although many additional occurrences are likely to have gone undocumented. In Aceh Province, a high prevalence of *Argulus* has been recorded in *Tor tambra* aquaculture ponds as well as in wild fish populations (Muchlisin et al *.,* 2014). Infestations involving several fish species, including *Cyprinus carpio*, *Carassius auratus*, and *Carassius auratus auratus*, have been documented in aquaculture ponds in Central Java (Kismiyati et al *.,* 2018). In Sulawesi, *Argulus* lice have been observed on *Anguilla marmorata* from Lake Poso (Amrullah et al *.,* 2019). Collectively, these reports indicate that *Argulus* infestation is a relatively common occurrence in Indonesia, underscoring the need for further studies to determine its extent and potential impact on national aquaculture.

The present study examined *Argulus* infestation in common carp (*C. carpio*) fingerlings and broodstock at an aquaculture facility in South Sulawesi. The primary aim was to enhance understanding of infestation patterns in relation to fish size and life stage by quantifying parasite abundance and identifying preferred attachment sites on the host. Furthermore, the *Argulus* species infesting carp in Sulawesi warrants species-level identification to support accurate diagnosis and management. The findings from this study will contribute to improved knowledge of the potential risks posed by *Argulus* infestation and inform strategies for the prevention and control of parasitic outbreaks in common carp and other susceptible fish species.

Materials and methods

Study site and fish sampling

This study was conducted from March to August 2019 at a freshwater hatchery in South Sulawesi, Indonesia. Broodstock common carp were stocked at a density of approximately 1 fish m^{-2} and maintained for up to one year, after which broodstock were routinely replaced with new individuals. At the time of sampling, broodstock had been reared for approximately six months, with partial water exchange conducted every two months. Common carp fingerlings were stocked at a density of approximately 6 fish m^{-2} and reared for approximately three months, after which the fish were either sold for consumption or transferred to candidate broodstock ponds for further rearing as future broodstock. Fingerlings were subjected to monthly water exchange prior to sale or transfer. Common carp (*Cyprinus carpio*) comprising 60 broodstock (1091.2 ± 58.16 g) and 150 fingerlings (19.6 ± 0.82 g) were obtained from the hatchery. The sampled specimens were caught from the holding tanks and pond using scoop nets and placed in separate buckets containing water from their respective habitats. While on-site, each specimen was measured (total length in cm), weighed (g), and screened for the presence of *Argulus* fish lice in the hatchery laboratory. To determine parasite attachment sites, the fish body was divided into four regions: head, fins, gills, and body surfaces. Each area was carefully inspected for the presence of parasites. *Argulus* individuals were removed using sterilised tweezers, which had been soaked in 70% ethanol to prevent cross-contamination. All collected parasites were preserved in 70% ethanol in labelled vials according to host identification (Patra et al *.,* 2016). Samples were transported to the Fish Parasite and Disease Laboratory at Hasanuddin University for further morphological and molecular analyses.

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Morphological identification of Argulus

Each preserved *Argulus* specimen was placed on a clean glass slide with a drop of 10% KOH (Kennedy, 1979). The body structures and organs were subsequently examined and measured under a microscope (Kruss MBL2000; A. Krüss Optronic GmbH, Hamburg, Germany) equipped with ocular and stage micrometres at 10×, 40×, 100×, and 150× magnification. A calibrated microscope (Olympus CX31; Olympus Corporation, Tokyo, Japan) was then used to evaluate morphological and morphometric characteristics, which were compared with the identification keys provided by Rushton-Mellor (1994).

Deoxyribonucleic Acid (DNA) Extraction and Polymerase Chain Reaction (PCR) Amplification

Genomic DNA was extracted from three *Argulus* specimens taken from each fish, randomly selected from both fingerlings and broodstock, using Qiagen DNeasy Blood and Tissue Kits (Qiagen, Hilden, Germany) in accordance with the manufacturer's instructions. DNA fragments of approximately 1800 base pairs (bp) of the 18S rRNA gene were amplified from each *Argulus* specimen by PCR (Labcycler PCR system, SensoQuest, Göttingen, Germany) using a universal eukaryotic primer set: the forward primer ERIB1 (5´-ACC TGG TTG ATC CTG CCA G-3´) and the reverse primer ERIB10 (5´-CTT CCG CAG GTT CAC CTA CGG-3´) (Patra et al., 2016). A 20 µL PCR mixture was prepared, comprising 1 µL of each primer, 10 µL of Taq DNA polymerase, 7 µL nuclease-free water, and 1 µL of template DNA. The amplification protocol consisted of an initial denaturation at 95°C for 5 minutes, followed by 35 cycles of denaturation at 95°C for 30 seconds, primer annealing at 51°C for 30 seconds, and extension at 72°C for 60 seconds, with a final extension at 72°C for 5 minutes. The PCR products were verified by electrophoresis on a 1.5% agarose gel containing 0.5 µg/mL GelRed in 1× Tris–acetate–EDTA (TAE) buffer at 120 V for 40 minutes, and visualised using an MUV-series UV transilluminator (Major Science, California, USA). Amplicons of approximately 1800 bp were subsequently sent to 1st BASE Asia (Singapore), via PT Genetika Science Indonesia (Jakarta), where amplicon purification and Sanger sequencing were performed.

Sequence similarity search and phylogenetic analysis

Although DNA was extracted from three *Argulus* specimens, only two samples yielded high-quality sequences suitable for submission to NCBI GenBank. The nucleotide sequence data generated in this study, based on the 18S rRNA gene, were deposited in the National Centre for Biotechnology Information (NCBI) GenBank under the accession numbers MW375604 and MW375605. Homologous *Argulus* sequences were retrieved from GenBank using the BLAST search tool implemented in Molecular Evolutionary Genetics Analysis (MEGA) version X (Kumar et al., 2018). The sequences incorporated into the phylogenetic analysis included JQ740819 for *A. foliaceus* from *Carassius auratus* in Iran, KF747861 for *A. foliaceus* from an unidentified host in China, KM597744 for *A. siamensis* from *Labeo rohita* in India, and the two sequences obtained in this study (*A. foliaceus* from *Cyprinus carpio*). *Chonopeltis australis*, from *Labeo capensis*, in Africa (accession number MT274324) was used as the outgroup for tree construction. Sequence alignment and phylogenetic analyses were performed in MEGA X. Evolutionary relationships between the study samples and reference sequences were inferred using the Maximum Likelihood method with the Kimura 2-parameter substitution model (Kimura, 1980), and nodal support was assessed using 1,000 bootstrap replicates.

Argulus Infestation

The prevalence and mean intensity of *Argulus* infestation were calculated following the procedure outlined by Bush et al. (1997). Prevalence was defined as the proportion of examined fish infected with *Argulus*, while mean intensity referred to the average number of *Argulus* individuals per infected fish, calculated as the total number of parasites recorded divided by the number of infected hosts. To assess the significance of the relationship between fish weight and the mean intensity of *Argulus* infestation, Spearman's rank correlation coefficient was computed using GraphPad Prism version 8.0.2.

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Water Quality Parameters

Water quality parameters were assessed at monthly intervals in both the broodstock and fingerling ponds from which the fish specimens were collected. The parameters measured included water temperature, pH, dissolved oxygen (DO), and five-day biochemical oxygen demand (BOD_5), following the Indonesian standards for aquaculture water quality (Indonesian Government, 2001). Temperature and pH were recorded in situ during sample collection using a digital pH meter (Hanna HI98129), which also provided temperature readings. Water samples for DO analysis were fixed in the field by adding 2 mL of NaOH, 2 mL of KI, and 2 mL of $MgCl_2$ to 100 mL of pond water in a Winkler bottle. Samples designated for BOD_5 analysis were placed in 100 mL Winkler bottles and stored in a fiber glass container for transport to the Productivity and Water Quality Laboratory. DO and BOD_5 were determined using the Winkler titration method (United States Environmental Protection Agency, 1997). DO was measured on the same day as sample collection, whereas BOD_5 was measured after a five-day incubation period.

Results

Morphological characteristics

The morphological characteristics of the *Argulus* specimens were examined using the identification key for the genus *Argulus* provided by Rushton-Mellor (1994). The mean body dimensions of the examined specimens (n = 10) were 9.2 ± 1.7 mm in length and 4.9 ± 1.2 mm in width. The carapace was oval, dorsoventrally flattened, and covered most of the thoracic region, extending to the posterior margin of the swimming legs but not reaching the abdomen (Figure 1). The cephalic region was triangular and bore two compound eyes. Ventrally, the cephalon displayed two pairs of appendages equipped with hooks and spines. The suckers were supported by sclerites arranged in rib-like formations, consisting of 5–6 sclerites anteriorly and 6–7 posteriorly. The basal plate was triangular, sharply pointed, and equipped with a posterior spine. The thorax consisted of four segments, each bearing four pairs of swimming legs. In males, the copulatory structures partially overlapped the third and fourth pairs of swimming legs, and the anterior abdomen tapered posteriorly to a pointed terminus. The spermathecae were elliptical and did not extend to the posterior margin of the abdomen. The morphological traits observed in specimens from common carp closely correspond to those described for *Argulus foliaceus* in Rushton-Mellor (1994). Diagnostic features consistent with *A. foliaceus* included the presence of a socket and copulatory peg on the third and fourth swimming legs (Figure 1). However, minor variation in sclerite number was recorded, ranging from 5 to 9. The basal sclerite was elongate, whereas the remaining sclerites were small and oval, positioned alternately along the internal rib margin.

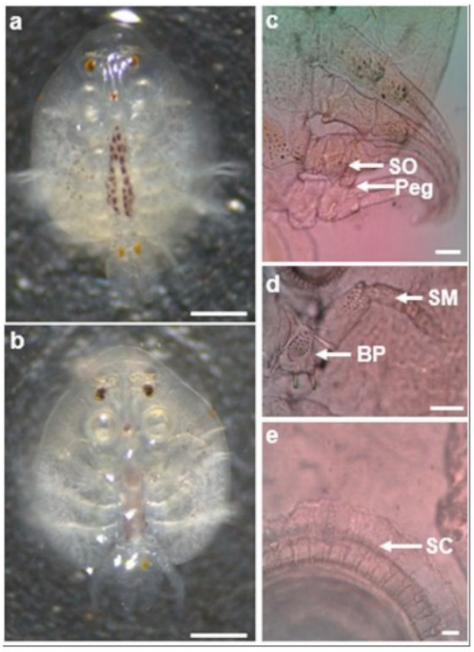

Figure 1. *Argulus foliaceus* male. a. Dorsal view, b. Ventral view, c. Copulatory organ (socket, SO and peg), d. Second maxilla (SM) and basal plate (BP), e. Sclerite (SC). Scale bar: a, b = 1 mm; c = 400 µm; d = 200 µm; e = 50 µm.

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Genetic Analysis

The identification of the *Argulus* specimens as *A. foliaceus* was confirmed through molecular analysis. The two 18S rRNA sequences generated in this study exhibited 99–100% similarity to *A. foliaceus* sequences available in GenBank, specifically KF747861 (from an unidentified host in China) and JQ740819 (from *Carassius auratus* in Iran) (Figure 2; Tables I and II). Maximum Likelihood analysis revealed two closely related haplotypes among the *A. foliaceus* specimens collected from *C. carpio* (Tables I and II). The resulting phylogenetic tree demonstrated that the *A. foliaceus* sequences from this study clustered within the same well-supported clade as *A. foliaceus* from China and Iran, supported by a bootstrap value of 99%. In contrast, *A. siamensis* from India formed a distinct, well-separated clade (Figure 2). Nucleotide polymorphisms identified in the 18S rRNA sequence alignment further confirmed the high degree of similarity between *A. foliaceus* in this study and reference sequences from Iran and China (Table II). Pairwise genetic distance analysis (Table I) indicated a close relationship between *A. foliaceus* in this study and those from Iran (0.000–0.002) and China (0.028–0.030). In contrast, substantially larger genetic distances were observed between the *A. foliaceus* sequences and the closest congeneric species, *A. siamensis* (0.069–0.085), thereby corroborating the species-level identification.

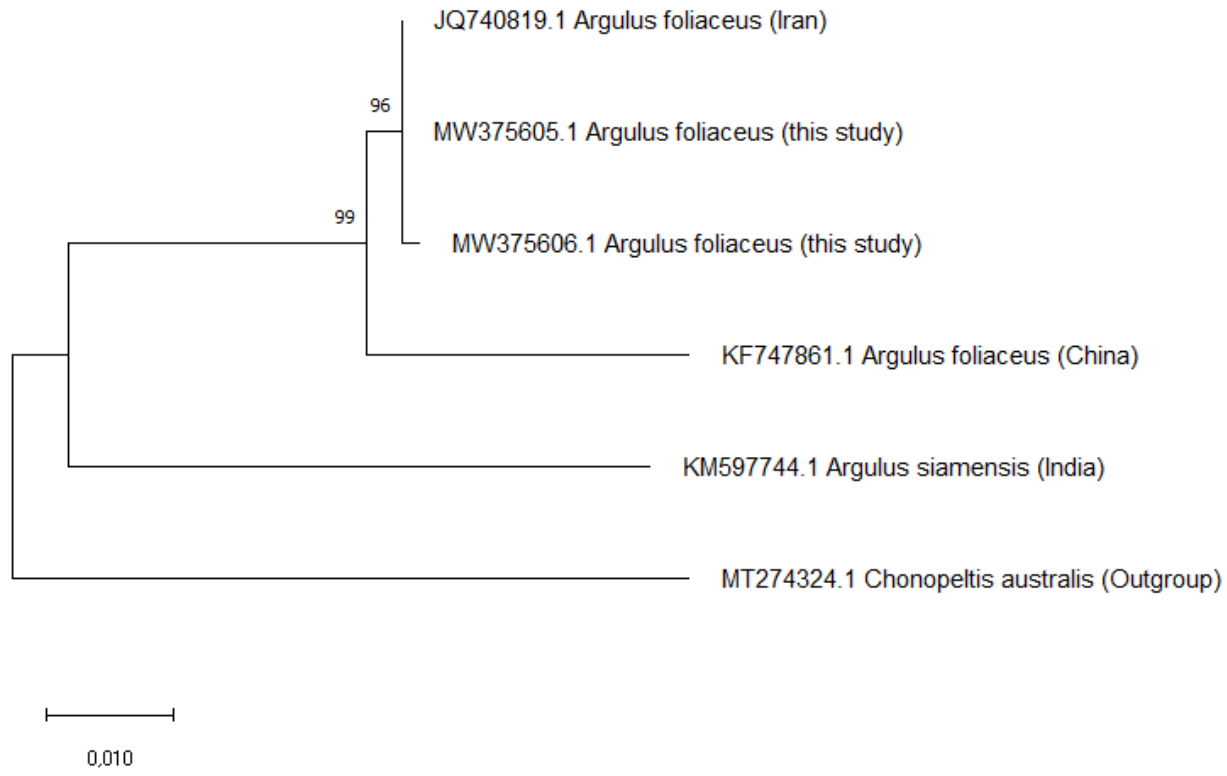

Figure 2. Phylogenetic relationship of *Argulus foliaceus* from this study (accessions MW375605 and MW375606) with the most closely related *Argulus* sequences in the NCBI GenBank. The phylogenetic tree was generated using the Maximum Likelihood method with the Kimura-2 parameter model (Kimura, 1980) and the numbers on the branches of the tree represent bootstrap values.

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No	Accession number	Species	Host	Locality	1	2	3	4	5	6
1	MT274324	*Chonopeltis australis* (Outgroup)	*Labeo capensis*	Africa	-					
2	KM597744	*Argulus siamensis*	*Labeo rohita*	India	0.110	-				
3	JQ740819	*Argulus foliaceus*	*Carassius auratus*	Iran	0.085	0.069	-			
4	KF747861	*Argulus foliaceus*	Unknown	China	0.082	0.085	0.028	-		
5	MW375605	*Argulus foliaceus*	*Cyprinus carpio*	this study	0.086	0.071	0.000	0.028	-	
6	MW375606	*Argulus foliaceus*	*Cyprinus carpio*	this study	0.085	0.072	0.002	0.030	0.002	-

Table I. Pairwise genetic distance of Argulus foliaceus from this study and closely related species using Kimura-2 parameter model based on a 1,800 bp fragment of the 18S rRNA gene.

Specimens	**Polymorphic sites in the 18S rRNA gene region of *Argulus* sequences**																
	76	**77**	**78**	**751**	**866**	**901**	**924**	**940**	**1005**	**1070**	**1183**	**1184**	**1208**	**1209**	**1210**	**1219**	**1220**
JQ740819	G	A	C	-	-	A	-	-	G	-	-	-	T	-	-	-	-
KF747861	A	G	A	G	G	A	A	G	G	G	C	G	G	C	G	C	C
MW375605	G	A	C	-	-	A	-	-	G	-	-	-	T	-	-	-	-
MW375606	G	A	C	-	-	G	-	-	A	-	-	-	T	-	-	-	-
	1221	**1222**	**1223**	**1229**	**1233**	**1236**	**1237**	**1240**	**1242**	**1246**	**1248**	**1249**	**1250**	**1251**	**1254**	**1256**	**1258**
JQ740819	-	-	-	T	T	T	G	G	G	T	T	C	T	G	T	A	T
KF747861	G	T	C	G	G	G	C	A	A	G	C	T	G	C	C	T	C
MW375605	-	-	-	T	T	T	G	G	G	T	T	C	T	G	T	A	T
MW375606	-	-	-	T	T	T	G	G	G	T	T	C	T	G	T	A	T
	1261	**1265**	**1269**	**1270**	**1271**	**1276**	**1277**	**1278**	**1280**	**1281**	**1284**	**1288**	**1290**	**1292**	**1294**	**1295**	**1296**
JQ740819	G	A	A	C	G	C	C	T	T	C	G	A	T	G	C	A	G
KF747861	A	G	C	A	C	A	T	A	C	A	A	G	G	A	G	-	-
MW375605	G	A	A	C	G	C	C	T	T	C	G	A	T	G	C	A	G
MW375606	G	A	A	C	G	C	C	T	T	C	G	A	T	G	C	A	G

Table II. Nucleotide sequence alignment showing polymorphic sites in the 18S rRNA gene for Argulus foliaceus from this study and GenBank accessions.

Distribution and abundance of A. foliaceus on the host body

Based on the examination of 60 broodstock and 150 fingerling common carp, the broodstock exhibited consistently higher levels of infestation than the fingerlings. Both the prevalence and mean intensity of *A. foliaceus* were greater in broodstock across all sampling months (Table III). Spearman's Rank Correlation Coefficient analysis demonstrated a significant positive correlation between host body weight and the intensity of *A. foliaceus* infestation ($P < 0.01$; Figure 3). The correlation coefficient ($r = 0.625$) indicates a strong positive association between infestation intensity and host size. Notably, the heaviest fish (1,522 g) harboured the greatest number of *A. foliaceus* individuals.

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Host	Fish Weight (g)	No. of Fish Examined	No. of Fish Infected	No. of *Argulus*	Parasite Prevalence (%)	MI (X ± SE)
March						
Broodstock	1269.20±564.71	10	10	125	100	12.5 ± 4.0
Fingerlings	38.72±19.22	25	12	20	48	1.67 ± 0.2
April						
Broodstock	1069.80±326.46	10	10	82	100	8.2 ± 3.4
Fingerlings	43.01±36.71	25	9	13	36	1.44 ± 0.2
May						
Broodstock	922.38±341.24	10	3	7	30	2.33 ± 0.7
Fingerlings	15.46±4.91	25	0	0	0	0
June						
Broodstock	595.81±349.36	10	3	9	30	3.0 ± 0.6
Fingerlings	15.57±4.32	25	0	0	0	0
July						
Broodstock	1027.80±318.28	10	9	37	90	4.11± 0.8
Fingerlings	17.07±4.68	25	0	0	0	0
August						
Broodstock	1294.90±511.59	10	9	39	90	4.33± 0.8
Fingerlings	13.85±4.58	25	0	0	0	0

Table III. Prevalence (%) and intensity of Argulus foliaceus infestation in carp (Cyprinus carpio) broodstock and fingerlings. Notes: Prevalence = % of fish examined that were infected with Argulus. Mean intensity = average of the total number of Argulus/fish examined, including parasites found on head, fins, and body. Abbreviations: MI = mean intensity, SE = standard error, X= mean

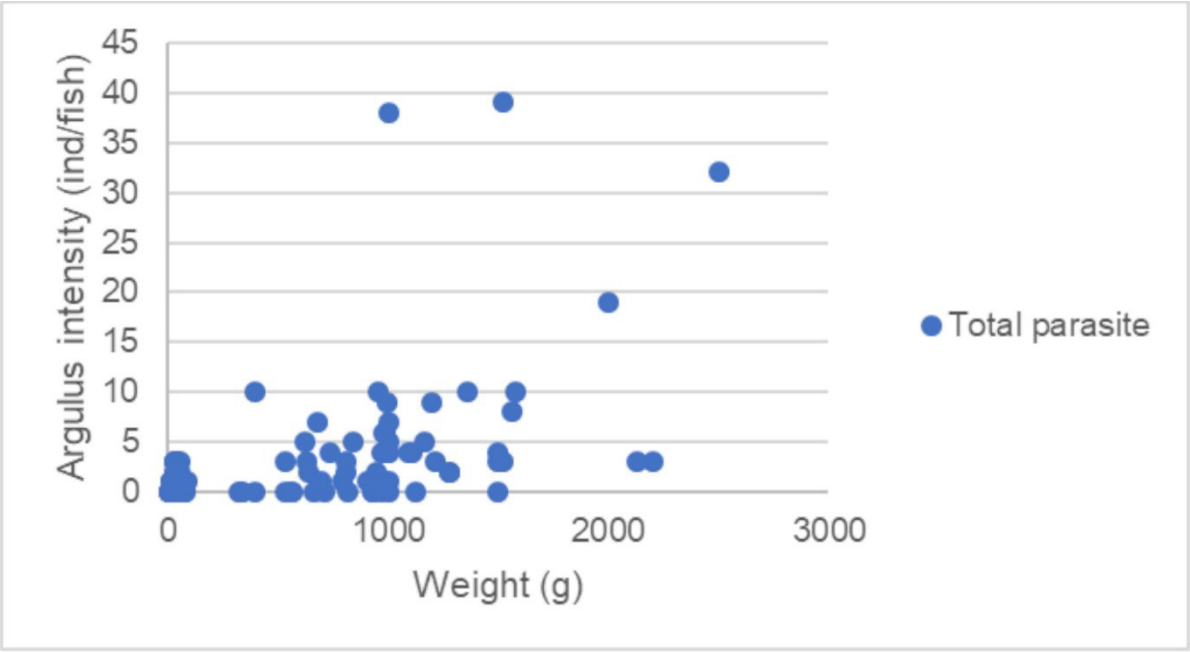

Figure 3. Correlation between the intensity of *Argulus foliaceus* infestation and body weight of the host *Cyprinus carpio*. The data points represent the number of Argulus/individual fish examined (n = 210), which include the total number of parasites found on head, fins, and body from broodstock (n = 60) and fingerlings (n = 150). Note that A. foliaceus was not detected on gills.

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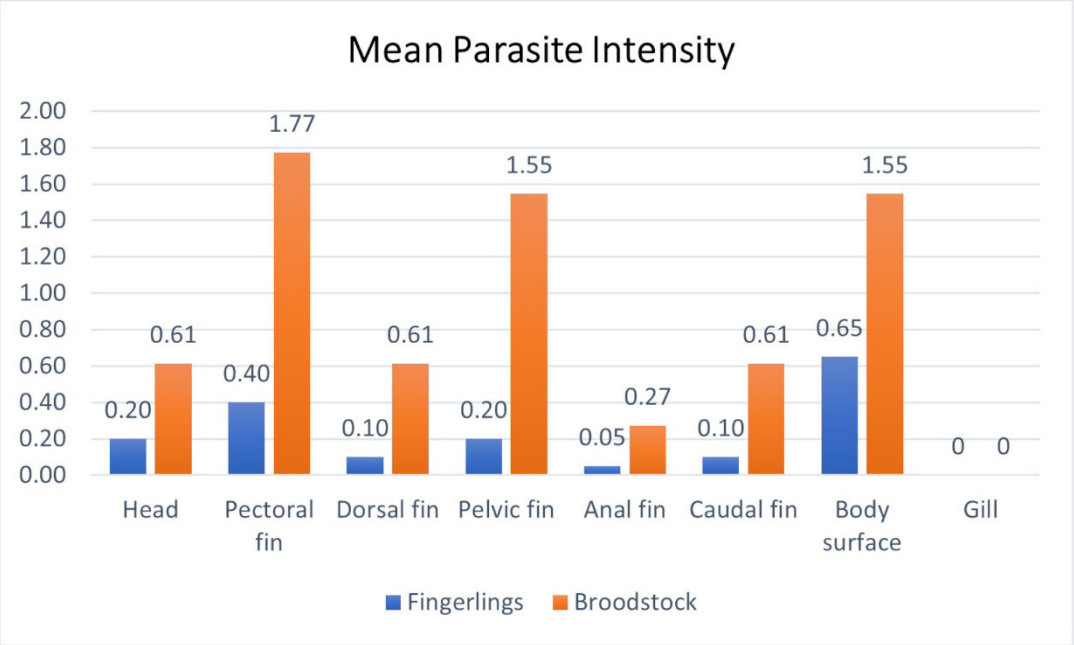

Figure 4. Microhabitat of *Argulus foliaceus* in carp (*Cyprinus carpio*) broodstock (n = 60) and fingerlings (n = 150). The mean intensity of parasite infestation for each microhabitat is the average number of *Argulus* present on each body part of individual host fish examined.

Water quality

Water quality parameter values were generally within the standard ranges established by the Indonesian Government for freshwater aquaculture (Indonesian Government, 2001) (Table IV). Dissolved oxygen (DO) and temperature remained within acceptable limits throughout the sampling period. However, the pH values in both the broodstock and fingerling ponds were relatively high (8.60 and 9.24, respectively), and on several occasions exceeded the Class III water quality threshold for freshwater fish culture. In the broodstock ponds, BOD_5 levels complied with the recommended standard (≤ 6 ppm), whereas the BOD_5 value recorded in the fingerling pond (6.42 ppm) slightly surpassed the upper permissible limit.

Site/source	Temperature(°C)	pH	DO(ppm)	BOD_5(ppm)
Broodstock pond	28.2-31.6	8.60	6.50	5.12
Fingerling pond	28.5-31.5	9.24	7.21	6.42
Water quality standard[a]	-	6-9	>3	≤6
Range tolerated by *Argulus foliaceus*[b]	10-43	4-7	2.9-10.5	0.9-6.04

Table IV. Water quality parameters in carp (Cyprinus carpio) broodstock and fingerling ponds infested with Argulus foliaceus. Notes: a Water quality standards for freshwater fishponds in Indonesia as required by Indonesian Government Regulation No. 82 of 2001, b Alsarakibi et al., 2014. Abbreviations: DO = dissolved oxygen; BOD5 = five-day biochemical oxygen demand.

Discussion

Based on the integrative taxonomic approach combining classical morphology with phylogenetic analyses employed in this study, the parasites collected from pond-raised carp in South Sulawesi, Indonesia, were conclusively identified as *Argulus foliaceus.* Initial presumptive identification was determined through morphological examination, which strongly corresponded with diagnostic descriptions of *A. foliaceus*. This identification was subsequently verified using molecular phylogenetic analyses, which confirmed that the specimens belonged to *A. foliaceus* and exhibited close genetic affinity to conspecific sequences reported from Iran.

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Our findings indicate that both the prevalence and mean intensity of *A. foliaceus* infestation were consistently higher in broodstock than in fingerlings. Patterns of attachment across body regions highlighted clear site preferences. In broodstock, the pectoral fins were the most frequently colonised locations, whereas in fingerlings the body surface served as the principal site of attachment (Figure 4). Attachment to the pectoral fins may confer hydrodynamic protection, reducing the likelihood of detachment during active swimming. Conversely, regions such as the head, dorsal, anal and caudal fins—being more exposed to water flow—supported fewer parasites. In fingerlings, smaller body size likely restricts fin surface area, making the body surface more favourable for parasite settlement. The behavioural ecology of carp further supports these trends: fingerlings, which swim actively in upper water layers, may experience fewer attachment events, while the more sedentary broodstock provide greater opportunities for parasite settlement. A significant positive correlation between host body mass and infestation intensity suggests that body size is a strong predictor of susceptibility to *A. foliaceus*. Larger individuals present a greater surface area and a wider range of microhabitats available for parasite attachment and feeding. Similar relationships between parasite burden and host size have been reported previously (Walker et al., 2011). However, it should be noted that differences in husbandry practices between broodstock and fingerlings may also have contributed to the observed infestation patterns. Broodstock were maintained at lower stocking densities but for longer residence periods, whereas fingerlings were reared at higher densities for shorter durations prior to sale or transfer to candidate broodstock ponds. Additionally, the frequency of water exchange differed between groups. These management-related factors may have influenced exposure duration and transmission dynamics of *A. foliaceus*. Therefore, the observed association between host body size and infestation severity should be interpreted with caution, as environmental and husbandry variables may act as confounding factors alongside host size.

Several morphological adaptations of *Argulus* contribute to its parasitic success. The dorsoventrally flattened body and extensive carapace reduce hydrodynamic drag, helping the parasite remain attached during host movement (Walker et al., 2004). Ventral appendages including modified antennae, hooked structures, suckers and stylets facilitate secure attachment and efficient feeding. These features also allow *Argulus* to move across the host's surface, enabling exploitation of various attachment sites (Mikheev et al., 2015). The mobility and versatility of *Argulus* thus enhance its capacity to colonise diverse microhabitats across the host body.

Environmental factors likely contributed to infestation severity. Water temperature in both broodstock and fingerling ponds frequently exceeded 29°C, a range favourable for carp growth but also conducive to argulid reproduction, development and transmission (Karvonen et al., 2013). Although dissolved oxygen levels remained within optimal limits for carp, pH values were relatively high occasionally exceeding recommended thresholds which may indirectly affect host susceptibility. While *A. foliaceus* tolerates wide pH variation, stressful environmental conditions can compromise host immunity, thereby facilitating parasitic establishment. BOD_5 in the fingerling pond slightly exceeded recommended limits, which may indicate a degree of organic pollution; although this is unlikely to directly affect *Argulus*, suboptimal water quality could impair host resistance.

Overall, this study demonstrates that host size and life stage significantly influence infestation prevalence, intensity and site preference of *A. foliaceus* in common carp. Environmental parameters, particularly temperature and water quality, may further modulate host–parasite interactions. Heavy infestation can compromise host health by damaging skin tissues, promoting secondary infections, and disrupting osmoregulatory functions (Steckler & Yanong, 2012). The insights gained here provide an important basis for improved surveillance, prevention and management strategies for *Argulus* infestations in Indonesian aquaculture systems.

Conclusion

The *Argulus* specimens collected from *C. carpio* were identified as *A. foliaceus* based on both morphological characteristics and molecular analyses, the latter confirming a close genetic relationship with *A. foliaceus* previously reported from *C. auratus* in Iran. The prevalence and mean intensity *of A. foliaceus* infestation were consistently higher in carp broodstock than in fingerlings. The preferred attachment sites also differed between life stages: pectoral fins were the primary site of attachment in broodstock, whereas the body surface was most frequently colonised in fingerlings. These differences in prevalence and infestation severity are likely associated with variations in host life stage, as fingerlings and broodstock differ substantially in body size and behaviour, which in turn affects their susceptibility and response to parasitic infestation. Water quality conditions and pond management practices may also have influenced the severity and potential spread of *A. foliaceus* within the aquaculture system. Infected fish are capable of transmitting the parasite to healthy individuals, particularly under intensive culture conditions where close proximity and environmental stress may facilitate parasite propagation.

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Ethical approval

This research was conducted with the approval of the Hasanuddin University Health Research Ethics Committee for the use of experimental animals in research (Protocol No. 13720093017). All procedures undertaken in this study complied with the Animal Ethics Guidelines issued by the Ministry of Health of the Republic of Indonesia.

Conflict of interest

The authors declare no conflicts of interest.

Author Contributions

Conceptualization: AA, HA, DVB; Methodology: AA, SS, DKS; Formal analysis: AA, SS, DKS; Investigation: AA, SS, DKS; Writing original draft preparation: AA; Writing, review and editing: AA, HA, DVB; Visualization: AA; Supervision: HA, DVB; Project administration: AA, HA; Funding acquisition: HA, AA. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement

The datasets generated in this study are available from the corresponding author or the first author upon reasonable request.

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