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Freshwater Gastrotrichs as Prey: First Documented Evidence of Cyclopoid Copepod Predation

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Abstract

Gastrotrichs (Phylum Gastrotricha) are widespread and species-rich components of benthic and periphytic communities, where they are thought to contribute substantially to food-web functioning by linking the microbial loop to higher trophic levels through their feeding on detritus, bacteria, microalgae, and fungi and serve as prey for larger animals. Despite the well-recognized role as primary consumers, their position as potential prey remains largely unresolved, with documented predators so far restricted to carnivorous protists. Here, we report the first documented case of metazoan predation on a freshwater gastrotrich, in which a cyclopoid copepod actively captures and partially consumes a chaetonotid species. The interaction was first detected under minimally disturbed conditions and subsequently replicated in controlled experimental settings. Predation was documented through in vivo video recordings and supported by species-level identification of both predator and prey. These findings expand the currently recognized trophic interactions involving freshwater gastrotrichs and provide new insight into their ecological role within aquatic food webs.

Keywords: Gastrotricha; Cyclopoida; Copepoda; meiofauna; benthos; predator-prey interaction; freshwater ecosystem; trophic ecology; optimal foraging

1. Introduction

Gastrotricha is a phylum of microscopic benthic invertebrates found in virtually all aquatic ecosystems. To date, more than 900 species have been described, divided into two orders: Macrodasyida (ca. 380 species), occurring mainly in marine and brackish environments, and Chaetonotida (ca. 520 species), inhabiting both marine and freshwater habitats [1–7]. Despite their diversity and widespread distribution, gastrotrichs remain relatively understudied, particularly with regard to their ecological role [8].

Current evidence suggests that gastrotrichs, like other meiofaunal taxa, play a key role in aquatic food webs by linking the microbial loop to higher trophic levels. This interpretation is supported by gut content analyses, which typically reveal microalgae and biodetritus, the latter likely enriched with bacteria and likely microfungi [1,9–11] (Figure 1). In contrast, their role as prey remains poorly understood.

Based on the available literature, reports of predation on gastrotrichs are scarce and largely anecdotal, involving amoebas [12], heliozoans [13], and cnidarians [12]. To date, the only well-documented case is a photographic record of a dileptid ciliate engulfing a specimen of the marine species *Paraturbanella teissieri* Swedmark, 1954 [14]. Within this context, we report the first documented instance of predation on a freshwater gastrotrich by a metazoan.

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This study is part of a large Italian biodiversity project (NBFC – National Biodiversity Future Center) and falls under the mission of Spoke 3, focusing on terrestrial and freshwater biodiversity, representing the sixth contribution dealing with freshwater gastrotrichs [2,5,15–17].

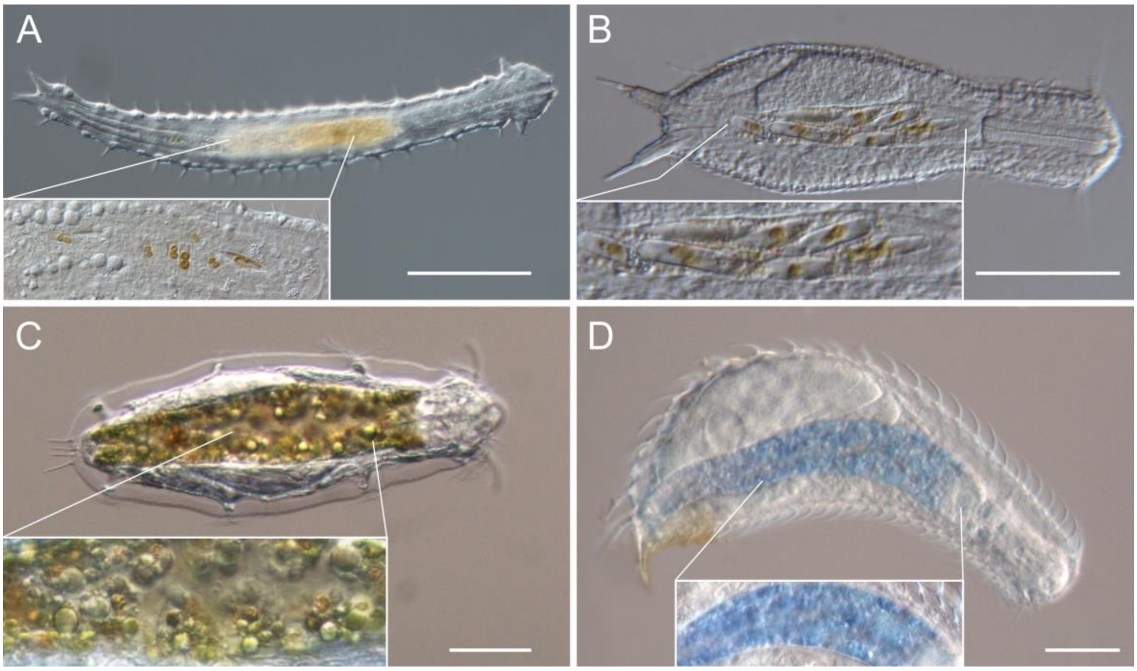

Figure 1. – Gastrotrich diversity across habitats, highlighting their role as primary consumers at the base of aquatic food webs. (A) Turbanella sp., a marine interstitial macrodasyidan; (B) Xenotrichula intermedia, a marine interstitial chaetonotidan; (C) Kijanebalola devestiva, a planktonic freshwater chaetonotidan; (D) Chaetonotus cf. gastrocyaneus, an epibenthic freshwater chaetonotidan. In panels A–C, both main images and insets reveal gut contents composed of diatoms and biodetritus, reflecting microphagous feeding. In (D), the gut displays a characteristic bluish coloration, indicating ingestion of cyanobacteria. Scale bars: (A) 100 μm; (B–D) 50 μm. Differential interference contrast (DIC) microscopy.

2. Material and Methods

2.1. Study Site and Sampling

The material examined in this study was collected in February 2026 from a small pond known as “Stagno del Drago” (“Dragon’s Pond”) (Figure 2), located at approximately 250 m a.s.l. within the mesophilous oak-dominated woodland of the protected area “Oasi di Bianello”, Quattro Castella, in the province of Reggio Emilia, Italy (44°37′35.71″ N; 10°28′7.06″ E). The site is an artificial pond, originally used as a livestock watering basin and later renaturalized. At full capacity, it covers an area of about 75 m^2, although it is subject to partial desiccation during summer. The pond is surrounded by arboreal vegetation dominated by oak species and hosts amphibians such as *Pelophylax* sp., *Rana dalmatina* Fitzinger, 1839, *Bufo viridis* (Laurenti, 1768), and *Triturus carnifex* (Laurenti, 1768) [18]. At the time of sampling, the water surface was entirely covered by common duckweeds. Sampling was carried out by collecting bottom sediment using a plankton net with a 29 μm mesh size [16,19]. The collected material, consisting of detritus, water, and small amounts of plant debris, was stored in two 500 mL plastic jars and transported to the laboratory in Modena. There, samples were maintained under controlled conditions (18 °C; 12 h light/dark cycle) and examined for gastrotrichs within ten days of collection.

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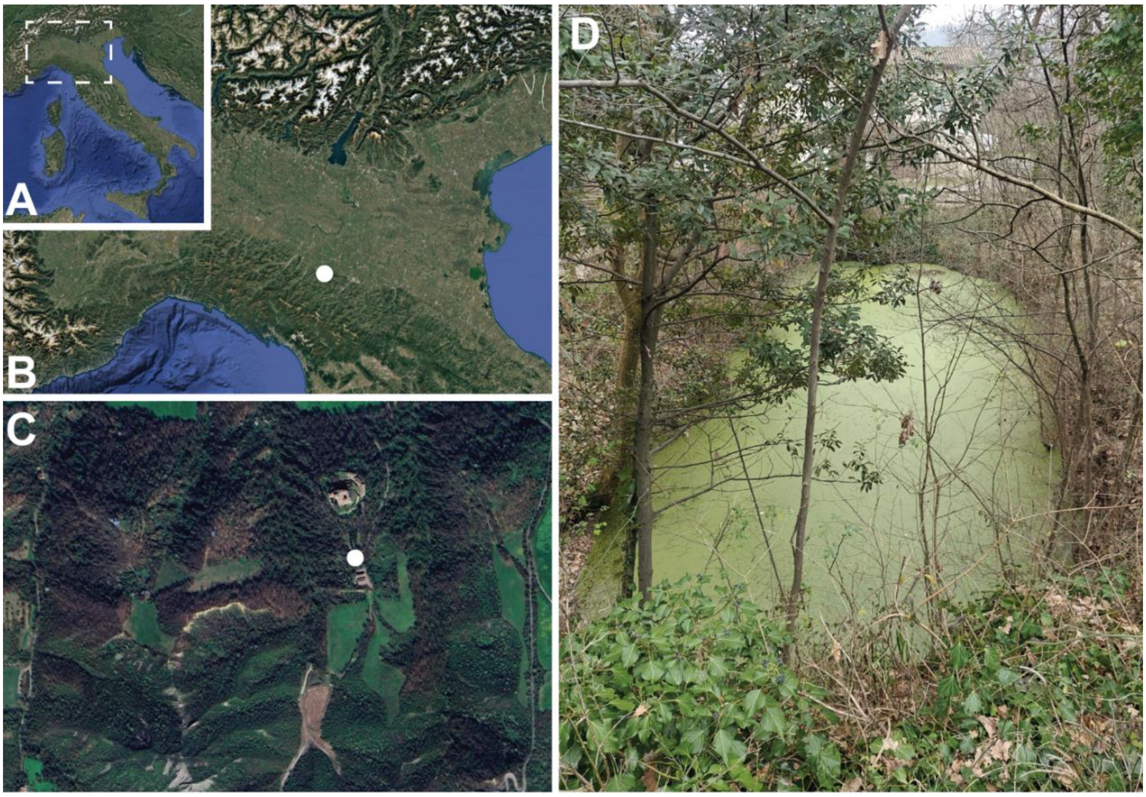

Figure 2. – Sampling site. (A) Map of Italy, with a white dashed square indicating the area enlarged in B. (B) Satellite view of northern Italy, with the sampling area marked by a white dot. (C) Aerial view of the "Oasi del Bianello" protected area, with the sampling site indicated by a white dot. (D) Photograph of the sampling biotope.

2.2. Sample Processing and Predation Documentation

Small subsamples (approximately 15 mL) of water and sediment mix were transferred to Petri dishes (9 cm in diameter) and observed under a Wild M8 stereomicroscope in search for gastrotrichs. During the examination of a Petri dish, a cyclopoid copepod was observed preying on a gastrotrich specimen identifiable as belonging to the genus *Polymerurus*, based on its large size and long, segmented furca. To confirm that this interaction was not incidental, we conducted a series of controlled predation experiments in which pairs of the two organisms were placed together in an observation chamber created ad hoc (see below). For these experiments, several specimens of both taxa, identified by their general morphology, were isolated and kept alive until use. Additional gastrotrich specimens were collected for species level identification, while others were preserved in absolute ethanol for future molecular analyses. The identification to species of the copepod was carried out on the specimens used in the predation trials.

2.3. Species Identification

Gastrotrichs were individually picked using a hand-made glass micropipette and transferred on a microscope slide, in a drop of 1% $MgCl_2$ solution. Morphological analysis and photographic vouchering were conducted on living, relaxed animals using a Nikon Eclipse Ni-U microscope equipped with differential interference contrast Nomarski optics (DIC) and a Nikon Digital Sight 10 digital camera, controlled through the Nikon NIS-Elements D software (v.4.6).

Copepod specimens were identified based on morphological characters, including appendage segmentation and chaetotaxy, following Einsle (1993) [20] and Mirabdullayev & Defaye (2022) [21]. Specimens were dissected, mounted in lactic acid medium, and examined under a light microscope.

2.4. Predation Experiments

The predation chamber (Figure 3) was assembled using a pre-cleaned, single-well concavity glass microscope slide (BRAND®). The well was filled with a small aliquot of the original water, previously filtered through a 0.2 μm Minisart® membrane. In each independent trial, a single gastrotrich specimen was introduced into the chamber and allowed to acclimate for approximately 2 minutes before a single cyclopoid copepod was added. The copepods used differed in sex and developmental stage, including an adult male, an adult female, a gravid female, and a late copepodite. Shortly after introducing the copepod, the chamber was loosely sealed with a 20 × 20 mm coverslip, supported at the corners by small sticky clay feet to ensure stability. The prepared slide was then placed under the microscope, and the gastrotrich specimen was monitored and video-recorded for any potential predation events. Afterward, the predator was retrieved from the cavity slide, fixed in 70% ethanol, and sent out for identification (see above).

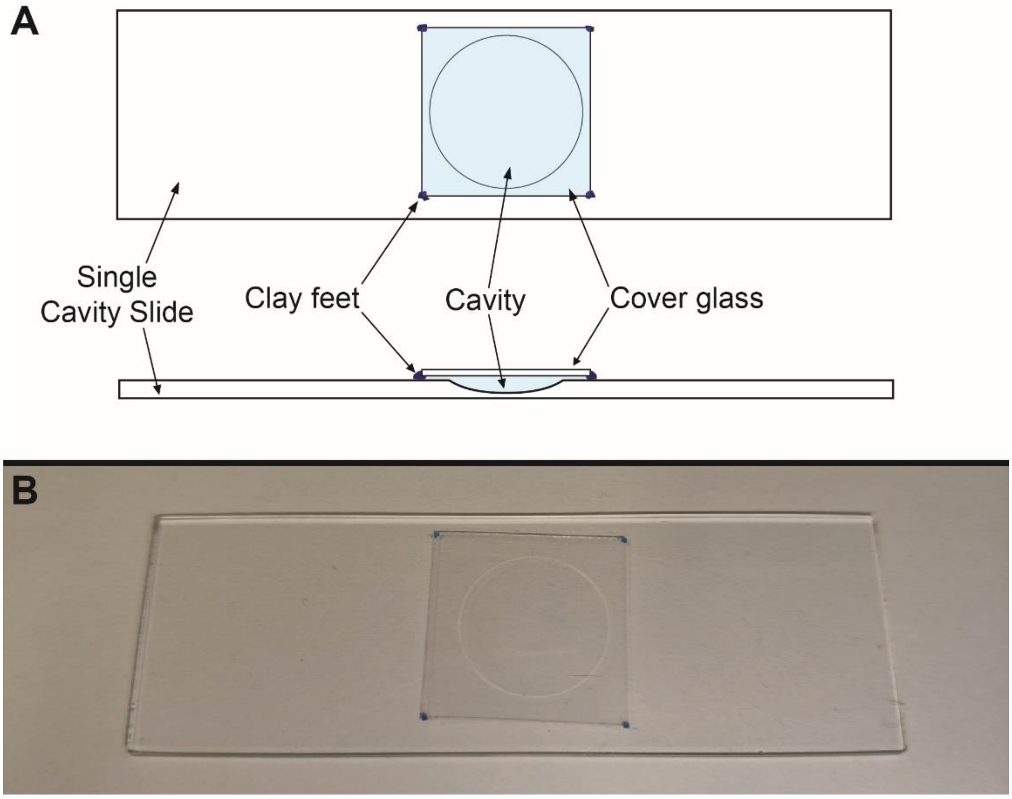

Figure 3. Predation chamber. (A) Schematic representation of the setup: the cover glass is set in place over the cavity by the clay feet at the corners. (B) Actual chamber with prey and predator inside.

3. Results

3.1. Species Identification

Gastrotricha: Slender body, with a total length measuring 380-417 μm, of which approximately 115 μm correspond to the iconic, bamboo-like segmented furca; each segment bears short, symmetrically arranged setae along the posterior margin. Body width at head/neck/trunk/furcal base, measured at U5/U16/U40/U70, is 42-44 μm /28-38 μm /51-60 μm/24-31 μm, respectively. The head is pentalobate and carries a distinct cephalion, epipleurae, hypopleurae, and a lamelliform hypostomion. The dorsolateral cuticular covering consists of polygonal scales, varying in size according to body region; each scale bears a short, simple, and slender spine. A group of longer spines occurs dorsally in the caudal region (U65), and six pairs of ventral spines protrude within the intrafurcal space. The ventral interciliary field is entirely covered by small scales, morphologically similar to the dorsal ones and each provided with a distinct spine, followed posteriorly by a pair of

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large oval, keeled perianal scales, each bearing a pronounced posterior spine. The mouth is large, 10-12 μm in diameter; the pharynx is robust, cylindrical, 63-72 μm long and 25-28 μm wide. The pharyngo-intestinal junction is located at U19. The intestine, broader anteriorly, gradually tapers toward the caudal end; the anus opens ventrally at U69.

The morphometric data reported above match the diagnostic features of Polymerurus nodicaudus (Voigt, 1901), a widely distributed species repeatedly recorded in Italy, including the Emilia-Romagna region where the present sampling was conducted [2,22,23].

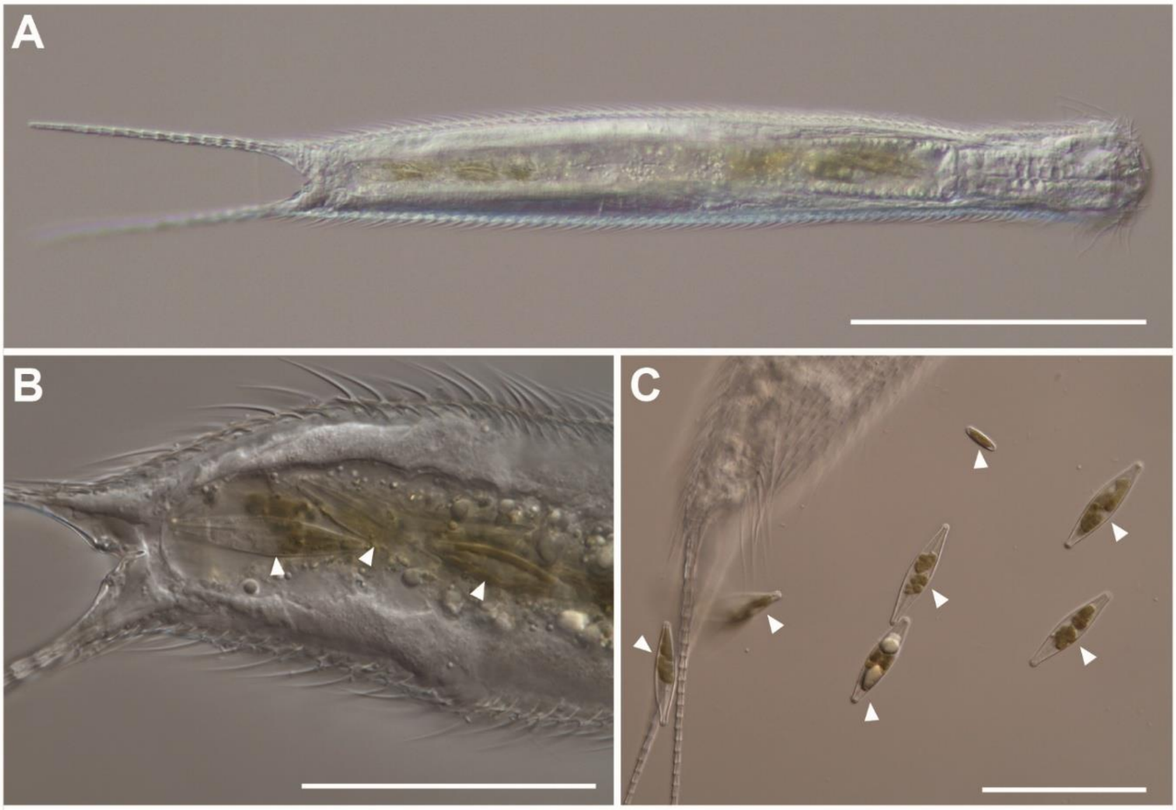

Figure 4. One of the gastrotrich specimens identified as *Polymerurus nodicaudus*. (A) Habitus; the gut appears green due to the presence of ingested diatoms, shown in detail in (B) and (C). (B) Close-up of the posterior region of the body, with diatoms clearly visible within the gut (arrow-heads). (C) Diatoms expelled from the body as a result of compression by the coverslip (arrow-heads). Differential interference contrast (DIC, Nomarski) microscopy. Scale bars = 50 μm.

Copepoda: The morphometric characteristics of the examined cyclopoid specimens match the diagnostic characters reported for Microcyclops varicans (Sars, 1863) in the recent redescription provided by Mirabdullayev & Defaye (2022) [21]. M. varicans is a widely distributed freshwater cyclopoid [20]. In Italy, M. varicans is considered a relatively common component of freshwater zooplankton and has been documented across multiple regions, from northern to southern areas, occurring in both permanent and temporary waters Within the Emilia-Romagna region, the species has been recorded in small ponds, floodplain water bodies, and artificial basins, often associated with vegetated margins and detritus-rich substrates [21]. It is an opportunistic feeder, exhibiting omnivorous to predatory habits and preying on a wide range of microinvertebrates [24,25]. Its broad ecological tolerance and wide distribution make it a typical representative of cyclopoid communities in shallow freshwater systems.

3.2. Predation Experiments

Predation was consistently observed in all four experimental trials, occurring irrespective of the predator's age or sex (Figure 5). At the beginning of each trial, gastrotrichs were actively crawling on the substrate by means of their locomotory ciliation. After approximately 6-11 minutes from the introduction of the predator into the experimental chamber, the copepod approached the prey and initiated contact using its oral appendages (Figure 5A, D, G, J). This interaction was immediately followed by a sudden cessation of movement in the gastrotrich, indicating rapid immobilization.

The copepod then secured the prey beneath its anterior region, firmly grasping and restraining it with its mouth appendages. During this phase, the predator manipulated the gastrotrich with its appendages (Figure 5B, E, H, K), likely facilitating feeding. After the feeding phase, the copepod moved away, leaving behind only small remains of the prey. In most cases, these consisted of the head region and, more frequently, the posterior end bearing the furca, indicating that consumption was substantial but incomplete (Figure 5C, F, I, L).

In a single instance, the adult cyclopoid male deviated from this pattern by capturing the prey and carrying it away rather than consuming it in situ (Figure 5J–L).

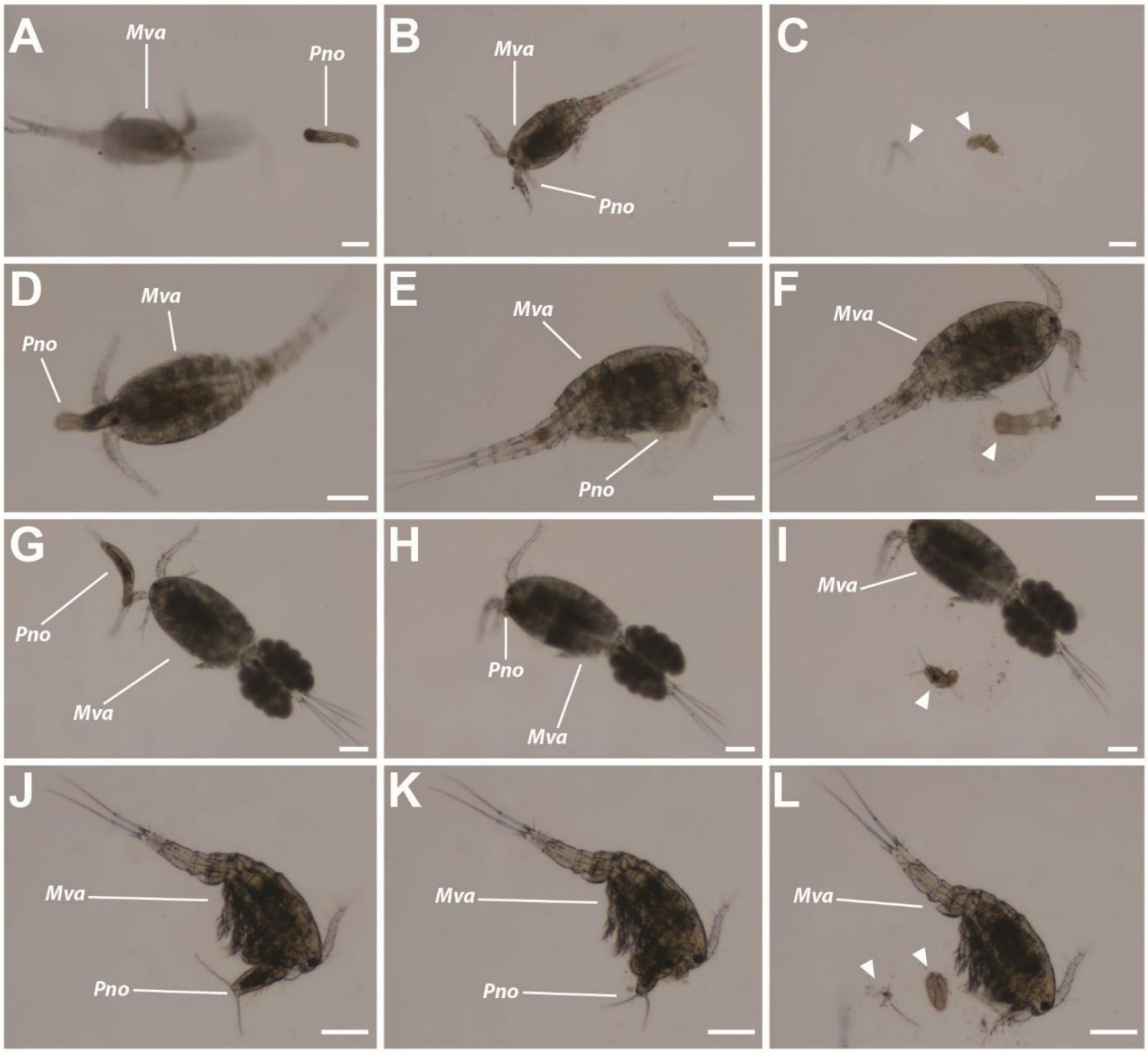

Figure 5. Sequential frames from video recordings illustrating predation on *Polymerurus nodicaudus* (Pno) by *Microcyclops varicans* (Mva). The sequences represent different sex and developmental stages of the predator: adult male (A–C), adult female (D–F), gravid female (G–I), and late copepodite (J–L). In each sequence, the first frame (A, D, G, J) shows the attack phase, the second (B, E, H, K) the grasping and manipulation of the prey with the oral appendages, during which the gastrotrich is immobilized and positioned beneath the anterior region of the predator, and the third (C, F, I, L) the remains following partial consumption, typically consisting of the head and/or the posterior furcal region (arrowheads). Scale bars = 100 μm.

4. Discussion

The initial examination of freshwater samples was conducted without narcotization or manipulation of the fauna; thus, the observed predator–prey interactions likely approximate natural conditions. Subsequent repeated observations under controlled conditions confirmed that the interaction between the copepod and the gastrotrich was not incidental, but occurred consistently and followed a similar behavioural sequence.

The predation events observed indicate that *Macrocyclops varicans* feeding on *Polymerurus nodicaudus* results in partial (approximately 30–75% of the prey, excluding furca) rather than complete consumption. Most events, from initial contact to disengagement, lasted between 5 and 15 seconds, whereas a single event, associated with a higher degree of prey consumption, extended to approximately 80 seconds (Table 1). Neither handling time nor consumption level appeared to be related to the predator's sex or developmental stage. However, these observations should be considered preliminary, as the limited number of replicates does not allow for robust statistical inference.

Table 1. Summary of predation event characteristics for *M. varicans* feeding on *P. nodicaudus*, including predator developmental stage and sex, time before the first contact, handling time, and consumption degree.

Predator's sex and age	Time before first contact	Manipulation time	Consumption degree
Adult male	~ 6 minutes	13 seconds	Approximately 50%
Adult female	~ 11 minutes	15 seconds	Approximately 30%
Adult gravid female	~ 7 minutes	5 seconds	Approximately 40%
Late Copepodite	~ 9 minutes	80 seconds	Approximately 75%

This pattern raises questions about the mechanisms shaping the interaction between predator and prey. One possible explanation lies in the spined cuticular armature of *Polymerurus nodicaudus*, which may reduce palatability or impose mechanical constraints on ingestion. Similar defensive effects have been documented in copepod–rotifer systems, where spines and rigid projections hinder capture and handling [26].

Alternatively, the copepod may selectively exploit the most accessible or nutritionally rewarding portions of the prey, in accordance with optimal foraging theory [27–32]. In all observed cases, consumption primarily involved the trunk region, which contains the bulk of soft tissues as well as the reproductive structures and developing eggs (e.g., [33–35]). Gastrotrich eggs are rich in energetic reserves [11], making this region particularly profitable compared to terminal structures such as the furca, which are non-fleshy and consistently left behind.

Partial consumption may also reflect constraints related to prey handling and digestion. Handling time is a critical component of predation, and prey requiring prolonged manipulation may be abandoned before complete ingestion, especially when prey density is high. In the present study, *P. nodicaudus*, one of the largest freshwater gastrotrichs, occurred at relatively high numbers, potentially favouring selective feeding. Moreover, physiological limitations such as gut capacity or digestion rate may restrict the amount of tissue that can be processed within a given time frame [36,37].

Finally, we cannot exclude the possibility that incomplete consumption reflects aspects of copepod foraging behaviour, such as surplus killing. Under conditions of high prey availability, predators may damage or partially consume multiple prey items without fully exploiting each of them, thereby maximizing energy intake rates [38,39]. Although this phenomenon is better documented in larger predators, similar dynamics may operate at microscopic scales.

Overall, these observations suggest that partial consumption of *P. nodicaudus* arises from a combination of prey morphology, energetic profitability, and predator handling constraints.

5. Conclusion

Cyclopoid copepods have a highly variable diet, comprising both algal and animal food sources [24,25]. The animal preys documented so far encompass a wide variety of taxonomic groups, including oligochaetes, rotifers, insects, other crustaceans, etc. [24,25,40,41]. Despite the numerous studies focusing on the cyclopoids feeding, the present study provides the first documented evidence of a predation event on a gastrotrich (e.g., [24,42–54]).

Our observations show that *Polymerurus nodicaudus* can be actively preyed upon by cyclopoid copepods, but is consistently only partially consumed, with the trunk region preferentially exploited and more rigid structures such as the furca left behind. This pattern is consistent with predictions from optimal foraging theory, suggesting that the exploitation of gastrotrichs is shaped by a trade-off between energetic gain and handling constraints.

Overall, these findings highlight that gastrotrichs are not only primary consumers but also a previously overlooked prey resource in freshwater systems, thereby reinforcing their role as a trophic link between the microbial loop and higher trophic levels. Future research should assess how widespread such interactions are across habitats and taxa, and whether cyclopoid copepods exhibit prey selectivity toward different gastrotrich species, potentially based on body size, morphology, or defensive structures.

More broadly, the experimental approach adopted here offers a promising framework for investigating predator–prey interactions at the microscale. The use of a simple predation chamber allows for controlled, repeatable observations of behavioural dynamics, and could be effectively applied to test hypotheses on prey choice, handling strategies, and the role of morphological traits in mediating trophic interactions among meiofaunal organisms.

Author Contributions: Conceptualization, F.S and M.A.T.; methodology and data acquisition, all authors; resources, F.S. and M.A.T.; writing—original draft preparation, F.S. and M.A.T.; writing—review and editing, all authors. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data supporting this study are available within the article. Supplementary video materials cannot be provided through the journal platform; however, they are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflicts of interest.

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