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Predation by *Coleps* sp. (Ciliophora, Prostomatea) on polyps of *Hydra* (Cnidaria, Hydrozoa)

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ABSTRACT

Predation by *Coleps* sp. (Ciliophora, Prostomatea) on polyps of *Hydra* (Cnidaria, Hydrozoa).

The present study reveals a novel predator-prey interaction in freshwater ecosystems: that of a free-living protozoan, *Coleps* sp., and polyps of the genus *Hydra*. Despite the common perception that larger body size confers competitive advantages, this finding shows that a large number of small-sized phagotrophic organisms, *Coleps* sp., attack *Hydra* polyps in groups, first attack their tentacles, and then gradually consuming the entire polyps. This finding was observed in Hydra vulgaris and Hydra sinensis specimens collected in freshwater bodies in São Paulo, Brazil. This discovery challenges traditional notions of size-based competitiveness and demonstrates that *Coleps* sp. can overcome the defensive barrier of hydra's cnidocytes. The study highlights the adaptability of *Coleps* sp. in its ability to prey not only on other protozoans, but also on multicellular organisms such as hydras. This suggests an even more complex predation dynamic that could have significant implications for the structure of freshwater zooplankton communities. This work provides a basis for future research into the ecological importance of “minor” predators such as *Coleps* sp. in regulating aquatic communities and underscores the need for more detailed studies to better understand the interactions between *Hydra* and *Coleps* sp., and how these relationships affect zooplankton populations and the overall dynamics of aquatic ecosystems.

KEY WORDS: predator-prey interactions, protozoa, freshwater cnidarians.

RESUMEN

Predación por* Coleps *sp. (Ciliophora, Prostomatea) sobre pólipos de* Hydra *(Cnidaria, Hydrozoa).

El presente estudio revela una nueva interacción predador-presa en ecosistemas de agua dulce: el de un protozoo de vida libre, Coleps *sp. y pólipos del género* Hydra*. A pesar de la percepción común de que un mayor tamaño corporal confiere ventajas competitivas, este hallazgo muestra que un gran número de* Coleps *sp., organismo fagotrófico de pequeño tamaño, ataca en conjunto a pólipos de hidra, ataca en primera instancia sus tentáculos, y, de manera progresiva, consume los pólipos en su totalidad. Este hallazgo se observó en ejemplares de* Hydra vulgaris *e* Hydra sinensis *recolectadas en diversos cuerpos de agua en São Paulo, Brasil. Es otro hecho que pone en duda las nociones tradicionales sobre la competitividad basada en el tamaño y que evidencia que* Coleps *sp. logra superar la barrera defensiva de los cnidocistos de hidra. El estudio resalta la adaptabilidad de* Coleps *sp. en su capacidad para predar no solo a otros protozoos, sino también a organismos* *multicelulares como las hidras. Esto sugiere una dinámica de predación aún más compleja que podría tener implicancias significativas en la estructura de las comunidades zooplanctónicas dulceacuícolas. Este trabajo proporciona una base para futuras investigaciones sobre la importancia ecológica de predadores "menores" como* Coleps *sp. en la regulación de las comunidades acuáticas y subraya la necesidad de estudios más detallados para comprender mejor las interacciones entre* Hydra *y* Coleps *sp., y cómo estas relaciones afectan a las poblaciones de zooplancton y a la dinámica general de los ecosistemas acuático.*

PALABRAS CLAVES: *interacciones predador-presa; protozoos; cnidarios dulceacuícolas.*

INTRODUCTION

The impact of animal competition, demographic changes and species diversity has been extensively examined through both theoretical approaches and empirical research in ecology (Slobodkin, 1962, 1966; Chesson, 2000; Tilman, 1987; Adler et al., 2007; Kaliszewicz, 2012). Interactions between species are part of the framework that forms the complexity of ecological communities and are extremely important in shaping community dynamics (Agrawal et al., 2007)

When analyzing the competitive interactions between species or individuals, larger animals appear to be competitively superior according to a generalization arising from many studies (Persson, 1985; Sebens, 1986; Ramsay et al., 1997; Westerberg et al., 2004; Zeng & Lu, 2009; Nakayama & Fuiman, 2010; Nascimento et al., 2011). In such cases, the competition for food concerns not only unrelated individuals but also clone-mates. If these animals are predators, then competition will be more likely to occur (Kneib, 1984).

In general, competition for food can take two forms: (1) exploitative competition, when food is consumed directly, thereby depriving other individuals of that food (Schoener, 1983) and (2) interference competition, through direct physical contact (Broadie & Bradshaw, 1991; Dye, 1984), chemical inhibition by toxins (Ikeshoji & Mulla, 1970; Dye, 1984) or cannibalism (Mogi, 1978).

The most common cnidarian in freshwater bodies is *Hydra*, a small hydrozoan with a solitary polyp that reaches sizes of l-20 mm in body length (Slobodkin & Bossert, 1991). The genus *Hydra* has a wide geographical distribution and occurs on all continents except in Antarctica (Jankowski et al., 2008). Living in a variety of freshwater habitats, both ectodermal and endodermal epithelial surfaces of *Hydra* are continuously exposed to environments in which a liter of these waters includes members of all domains of life, like viruses, bacteria, archaea, and eukarya (Augustin et al., 2010).

Hydras have a lot of interactions with other organisms of the zooplankton community: epizoic with ciliates (Trembley, 1744; Rösel von Rosenhof, 1755; Ehrenberg, 1838; Stein, 1854, 1859), phoretic relationships with odonates (Stoks & De Bruin, 1996; Grabow & Martens, 2000; Shull et al., 2012; Brochard & van der Ploeg, 2014; Wildermuth & Martens, 2019; Maynou & Martín, 2021), parasitosis with amoebas and microsporidia (Entz, 1912; Spanenberg & Claybrook, 1961; Stiven, 1962, 1964; Maxwell, 1969; Page & Robson, 1983; Deserti et al., 2023a) and the association par excellence, the endosymbiosis with algae of the genus *Chlorella* (Trembley, 1744; Huss et al., 1993, 1994; Kawaida et al., 2013).

Hydras are considered to be extremely efficient predators (Slobodkin & Bossert, 2001; Deserti et al., 2017). Massaro et al. (2013) concluded that *Hydra viridissima* and *Hydra salmacidis* from Brazil are likely top predators in their own habitats, as they are protected from predators by toxins released by the nematocysts as well as their low mobility. Few predators attack cnidarians because of their cnidocysts, which make them unpalatable. Turtles, fish, crabs, echinoderms and flatworms are known to be some of the known predators of marine cnidarians (Slobodkin & Bossert, 1991). Dodson and Cooper (1983) observed that crayfish feed on the freshwater medusa *Craspedacusta sowerbii*, while Hyman (1940) and Kanaev (1969) reported that *Hydra* polyps are preyed upon by certain platyhelminthes, although it has been observed that those smaller platyhelminthes avoid contact with these cnidarians (Slobodkin & Bossert, 2001). Even, the freshwater platyhelminth, *Microstomum lineare*, preys on *H. oligactis* and kidnaps its cnidocysts (Krohne, 2019). Cuker and Mozley (1981) tested whether the gastropods *Valvata* sp. and *Lymnea* sp. preyed on hydras, demonstrating that *Lymnea* consumed hydras only when they had no other food available, covering the polyps with mucus to protect themselves from their cnidocysts. However, predation on freshwater cnidarians remains poorly researched.

The plankton community is heterogeneous. The zooplankton assemblage inhibiting freshwater mostly comprises Protozoa, Coelenterate, Rotifera, Gastrotricha, Bryozoa and Arthropoda (Battish, 1992). Most zooplankton occupy the second or third trophic level of the aquatic food web as such these herbivores, carnivores and omnivores play a significant role in aquatic food webs (Kumar & Jawahar, 2012).

Of particular significance among these zooplankton constituents are the Protozoa, ubiquitous microorganisms that wield considerable ecological importance across freshwater habitats (Sherr & Sherr, 2002). Among them, phagotrophic protists, comprising heterotrophic and mixotrophic flagellates, ciliates, and dinoflagellates. Characterized by their unicellular nature and heterotrophic feeding habits, these organisms play pivotal roles in nutrient cycling, shaping microbial communities and influencing higher trophic levels (Sherr & Sherr, 2002; Medeiros et al., 2013). Their dietary versatility, encompassing bacteria, algae, and even fellow zooplankton, underscores their ecological significance (Sherr & Sherr, 2002).

In this intricate web of interactions, *Coleps* sp., a free-living protozoan, emerges as a formidable predator within the zooplankton community. Equipped with toxicysts to aid in carnivorous feeding, *Coleps* sp. utilizes offensive extrusomes, often abundant in the oral region, to capture and consume its prey (Foissner, 1984; Foissner et al., 1999). These extrusomes, synthesized within Golgi or Endoplasmic Reticulum vesicles, are triggered by suitable stimuli, leading to the discharge of their contents outside the cell (Buonanno et al., 2014). *Coleps* sp. feeds on bacteria, algae, flagellates, living and dead ciliates, and dead individuals of its own species, but it is also histophagous, that is, it feeds on living plants and animal tissue (Foissner et al., 1999; Buonanno et al., 2014).
In this context of biological interactions, hydras, being organisms preyed upon by *Coleps* sp., play a crucial role in trophic dynamics. It has been observed that this ciliate can also feed on multicellular organisms (Foissner et al., 1999), as evidenced in this study. Although hydras, despite their apparent simplicity, are complex creatures with a variety of defenses against predators, the ability of *Coleps* sp. to overcome these defenses and consume live hydras suggests an intriguing predation dynamic.

Based on the findings presented, we hypothesize that predation by *Coleps* sp. on Hydra polyps not only compromises the stability and survival of both populations involved but also profoundly affects trophic dynamics within freshwater ecosystems, with significant implications for their structure and functionality. Understanding these predation dynamics is essential for unraveling the complexity of trophic interactions in these environments. The insights gained from this research expand our comprehension of predator-prey relationships and their implications for ecosystem health and stability, highlighting the role of "minor" predators in regulating aquatic communities and maintaining ecological balance.

MATERIALS AND METHODS

Study sites and Animal collection

During August 2021 and April, May and June 2023 a sampling campaign was carried out in freshwater bodies of São Paulo state, Brazil (Fig. 1). The macrophytes *Enidra sessilis*, *Eichhornia crassipes* and *Egeria* sp. (Carvalho et al., 2005a, b) were collected and transported to the laboratory where they were conditioned in standard aquariums with aerators and a natural photoperiod. The macrophytes were observed under stereomicroscope looking for *Hydra* polyps.

Observations of predator - prey interaction

Hydras collected were examined and identified species of the *vulgaris* and *viridissima* group respectively (Deserti et al., 2023b; Wang et al., 2009); more specifically: *Hydra vulgaris* and *H. sinensis* from Lago Ness (22° 20' 19.3"S, 48° 58' 59.8"W) and Prainha de Arealva (22° 1' 19.4"S, 48° 53' 21.4"W), and *H. vulgaris* from Rio Tietê (22° 19' 18.6"S, 48° 44' 4.1"W), São Paulo state, Brazil (Fig. 1).

Each polyp was placed in a Petri dish with water from its environment and observed daily for one week.

The taxonomic identification of *Coleps* sp. involved a review of specific literature (Khal, 1930; Foissner et al., 1994; Foissner et al., 1999; Lynn, 2010). These references contained taxonomic keys and morphological descriptions, providing information concerning the distinguishing characteristics and diagnostic features of the *Coleps* genus.

The polyps that showed anatomical lacerations were observed under a stereomicroscope and subsequently with a microscope, photographed and filmed using the Opticam Microscopia OPT HD 3.7 and Motic Images Plus 3.1 software, respectively.

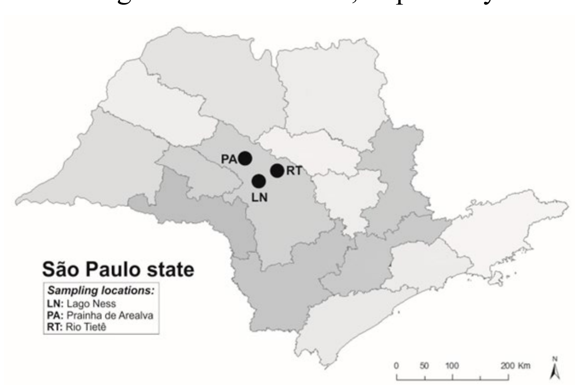

Figure 1. Collection locations in the state of São Paulo, Brazil. *Sitios de muestreos en São Paulo, Brasil.*

RESULTS

During the maintenance of the polyps in the laboratory, some were observed being attacked by a large number of smaller organisms (Video 1, supplementary information, available at https://hdl.handle.net/11336/247753). As a result, these polyps exhibited various anatomical lacerations. In specimens visibly under attack, the first observed lesion was the shortening of the tentacles. In Figure 2A, only a small portion of the tentacles remains, retracted close to the hypostome, approximately less than 10 percent of the total length of the tentacles when they are in a normal, relaxed, and healthy state (see average sizes in Table 1).

The organisms that preyed on hydra were identified as *Coleps* sp. (Fig. 2, Table 1) (Khal, 1930; Foissner et al., 1994; Foissner et al., 1999; Lynn, 2010). It is characterized by its barrel shape and a body covered with calcified plates arranged in longitudinal rows, forming a protective armor. The cilia are organized in 15-16 longitudinal rows, with three or four spines visible at the posterior end, along with an elongated caudal cilium. The oral opening is located at the anterior end of the cell (Kahl, 1930; Foissner, 1984).

Just one or two hours after the initial observation of polyps being attacked by *Coleps* sp., the tentacles were completely consumed, leaving only the polyp column (Fig. 2C). These polyps lay detached, no longer anchored to the substrate by their pedal disc. Even under these conditions, the hydras remained alive, while large numbers of *Coleps* sp. continued attacking the column, feeding on its cells.The effect of the toxicysts' content highlights a strategic advantage for *Coleps* in environments with multiple prey options. Notably, it has been observed that the effect of the

Table 1. Width and length measurements (mm) of *Coleps* sp., *Hydra vulgaris* and *Hydra sinensis* collected from Lago Ness, Rio Tietê and Prainha de Arealva, São Paulo state, Brazil. *Medidas de ancho y largo (mm) de* Coleps *sp.,* Hydra vulgaris *y* Hydra sinensis *colectadas del Lago Ness, Rio Tietê y Prainha de Arealva, Estado de São Paulo, Brasil.*

		Coleps sp.	*Hydra vulgaris*	*Hydra sinensis*
Width (mm)	minimum	0.26	0.10	0.04
	maximum	0.34	0.48	0.55
	media	0.29	0.22	0.10
Length (mm)	minimum	0.19	1.80	1.35
	maximum	0.29	11.61	7.65
	media	0.23	3.99	3.13

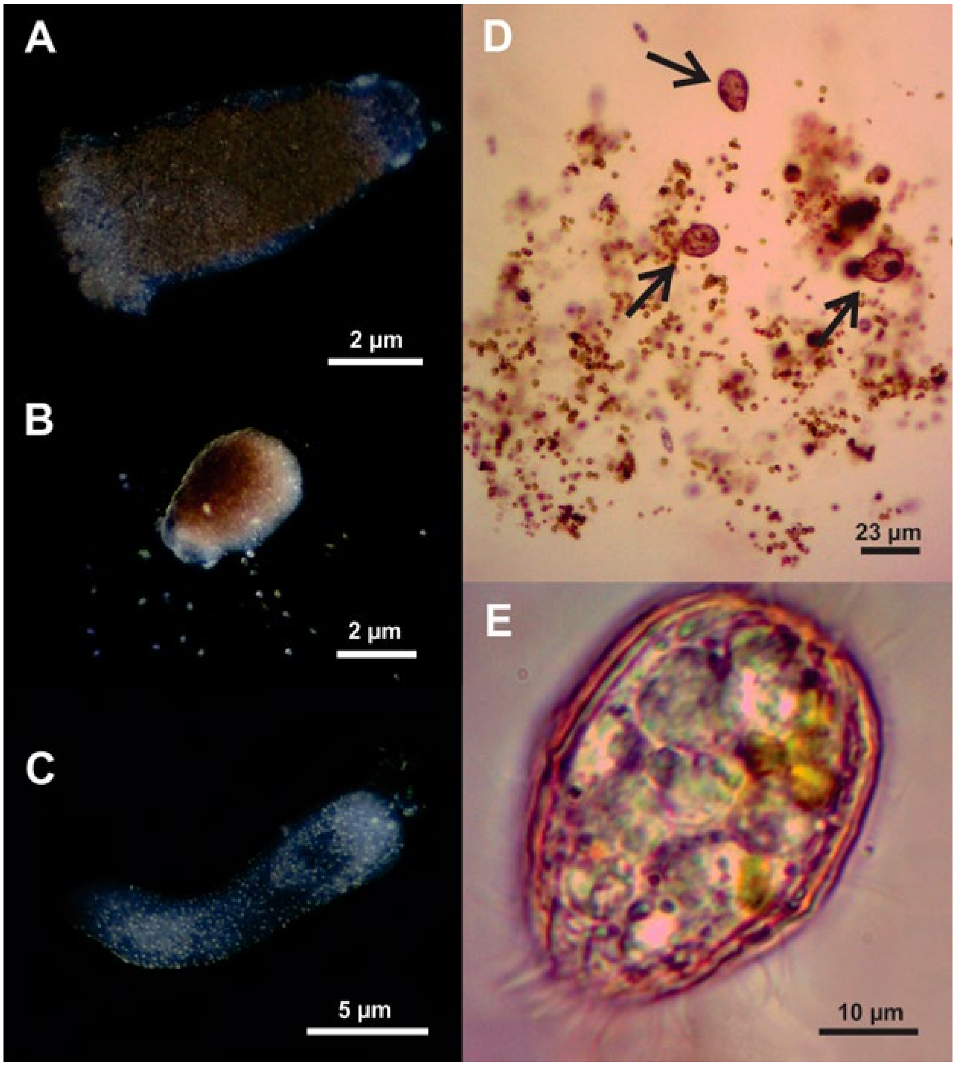

Figure 2: A, B, C. Different morphological lacerations in *Hydra vulgaris* predated by *Coleps* sp., **D**: *Coleps* sp (arrows) preying on disintegrated tissue of *Hydra sinensis* and **E**: specimen of *Coleps* sp. *Diversas laceraciones morfológicas en* Hydra vulgaris *predada por* Coleps *sp.,* ***D****:* Coleps *sp. (flechas) predando sobre tejido desintegrado de* Hydra sinensis *y* ***E****: Ejemplar de* Coleps *sp.*

toxicysts' toxins typically takes between 5 and 10 minutes to immobilize the prey (Buonanno et al., 2014). This period allows *Coleps* to detach momentarily, potentially as a strategy to evade any defensive mechanisms, such as the cnidocysts of *Hydra*, minimizing the risk of prolonged contact and counterattacks. The toxicysts of *Coleps*, which inject toxins into prey through tube-like structures, ensure optimal effectiveness in immobilizing the prey (Buonanno et al., 2014)

Moreover, the coordinated behavior observed among *Coleps* individuals is another notable aspect of their predation strategy. While some adhere to the prey until the toxins become effective, others wait to take advantage of the immobilized polyp, showcasing a form of cooperative hunting that significantly enhances predation success.

In an advanced stage of predation, only a small propagule of cells remained (Fig. 2B), which, within a few hours, was entirely disintegrated (Fig. 2D). Depending on the polyp's size, this small propagule was fully disintegrated between 12 to 24 hours after the attack began. Once the polyp fully disintegrated, *Coleps* sp. continued to feed on the remaining tissue.

To confirm that the anatomical lacerations were indeed caused by predation from *Coleps* sp., several polyps in the propagule stage (Fig. 2B) were transferred to new Petri dishes. The polyps were washed three times with Culture Solution M (Lenhoff, 1983) to remove as many *Coleps* sp. individuals as possible. After washing, the polyps were placed in a new Petri dish with the same culture solution and observed daily under a stereomicroscope.

Within 24 hours of the final transfer, some improvement in the polyps was observed, as they initially returned to a relaxed state. Approximately 48 hours after the transfer, the tentacles had grown to about 30 percent of their normal size. By 72 to 96 hours post-transfer, the tentacles had reached at least 80 percent of their normal size, the polyps were attached by their pedal discs to the base of the capsule, standing in a fully upright position. All polyps were feeding efficiently, appearing to return to a normal state of health.

DISCUSSION

The relationship described here between *Hydra* polyps and *Coleps* sp. individuals is a typical predator-prey interaction, with notable results observed in the predator's hunting efficiency and adaptability.

Species interactions form the basis for many ecosystem properties and processes and the nature of these interactions can vary depending on the evolutionary context and environmental conditions in which they occur (Lang & Benbow, 2013). Feeding is one of an organism's most basic interactions with the environment and is a function of many physiological parameters (Lasker et al., 1982).

Contrary to a generalization arising from many studies, a larger body size is not always the key to competitive superiority amongst animals (Kaliszewicz, 2013). Massaro et al. (2013) performed a few experiments to determine nymphs of Odonata Anisoptera (Insecta), the phantom midge larvae of *Chaoborus* sp. (Insecta), adults of Copepoda Cyclopoida (Crustacea) and the small fish *Poecilia reticulata*, like possible predators of the hydras. After 24 hours, the exposed polyps had not been consumed or showed signs of attack, so the authors concluded that none of these major organisms were predators of *Hydra*. *Hydra* also play a role like predators and have been shown to ingest cladocerans, copepods, rotifers, larval fish and other prey of sizes much larger than polyps (Schwartz & Hebert, 1989; Link & Keen, 1995; Walsh, 1995; Elliott et al., 1997; Deserti et al., 2017.). Even, this genus is considered like efficient predators in pond communities (Schwartz et al., 1983). However, hydras are sessile cnidarians and not exempt from predatory pressure, facing threats from constituents of the zooplankton.

Kalisewicz's (2013) concept in relation to body size and competitive superiority is also exemplified in the adaptability and versatility of feeding methods of *Coleps* sp. that are pivotal in survival and dominance within its ecological niche (Auer et al., 2004). *Coleps* sp., as a voracious phagotrophic protozoan, constitutes a significant predator within this zooplanktonic community. They can rely on different strategies that allow them to survive in a variety of habitats and to avoid unfavorable conditions (Auer et al., 2004). The non-selective nature of its feeding habits categorizes *Coleps* sp. as a general consumer, feeding on bacteria, algae, and other organisms (Foissner et al., 1999). The nutritional strategy of histophagy likely arises from *Coleps*'s possession of toxicysts, which the ciliate utilizes to aid in its carnivorous feeding. Additionally, its oral structure enables the ingestion of live organisms through suction (Buonanno et al., 2014). Thus, the relationship between body size and competitive superiority may be more intricate than previously surmised, with environmental factors and species-specific interactions potentially playing a pivotal role in determining competition outcomes.

In this sense, the key to the success of *Coleps* sp. predation on *Hydra* may be due to a combination of factors. Some of these factors may be mainly associated with: (1) a detriment to the health of the polyps with the consequent impossibility of facing certain predators, (2) biotic or abiotic factors that favor a massive proliferation of *Coleps* sp., (increased food supply, predator avoidance, etc.) (Auer et al., 2004), and (3) the ingestion of *Hydra* as a feeding strategy of *Coleps* sp. in response to changes in the composition and structure of zooplankton in relation to new limnological parameters.

Particularly, *Coleps* sp. demonstrates a great ability to evade and tolerate the stinging, agglutinating, and penetrating effects of *Hydra* cnidocysts. A notable strategy for achieving this evasion is the temporary detachment following the release of toxicysts, a defensive mechanism that allows it to avoid the prey's counter-defenses (Buonanno et al., 2014). Other organisms with sizes and swimming abilities similar to or even greater than those of *Coleps* sp. are not immune to stenoteles and desmonemes which in most cases paralyze and subsequently ingest their prey (Burnett, 1973; Deserti et al., 2017). In contrast, organisms that do not trigger a feeding response and are detected by the polyps as potential threats are kept away from the polyps' surface by the defensive properties of the holotrichous isorhiza, thereby avoiding damage (Burnett, 1973). The described behavior of temporary detachment after the release of toxins by *Coleps* sp. may be hypothesized as a defensive strategy against prey with potent counter-defenses, such as *Hydra*'s cnidocysts. This adaptive behavior, combined with the morphological advantages of toxicysts and coordinated group hunting, emphasizes the complexity and adaptability of *Coleps* sp. in its ecological niche, strategically positioning itself in the aquatic environment (Buonanno et al., 2014). This study, however, expands current knowledge by demonstrating the ability of *Coleps* sp. to attack larger and well-defended prey, suggesting that predation pressure in freshwater ecosystems is more diverse than previously thought.

Even though *Hydra* occupies one of the lower trophic levels within freshwater food webs, changes in their population could have an indirect but significant effect on the rest of the freshwater community (Quinn et al., 2012). Ecologically, this genus plays the role of both predators and prey (Slobodkin & Bossert, 2001), hence occupies an important role in structuring the planktonic in aquatic ecosystems (Schwartz et al., 1983). The effect of *Coleps* sp. predation on *Hydra* polyps may be one of the many causes of the disappearance of *Hydra* populations. Distinguishing those factors that could alter the predator-prey relationship between *Hydra* and *Coleps* requires much more specific studies. However, this first approach with this new interspecific relationship reveals certain features regarding the superiority and competitive abilities between one genus and the other. It also allows us to theorize about possible consequences on population dynamics, the intricate web of relationships between organisms in freshwater communities and the pressure of natural selection to which populations of organisms are exposed.

This initial research may lead to a better understanding of both the ecology of *Hydra* and the role of “minor” predator groups in structuring zooplanktonic communities.

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AUTHOR CONTRIBUTIONS

MID: Conceptualization; Funding acquisition; Formal analysis; Data curation; Writing - review and editing; Investigation; Resources; Writing - original draft; Supervision; Validation; Visualization. FMMA: Formal analysis; Data curation; Writing - review and editing; Investigation; Visualization. FHA: Data curation; Writing - review and editing; Investigation; Visualization. SNS: Funding acquisition; Formal analysis; Data curation; Writing - review and editing; Investigation; Resources; Supervision; Validation.

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