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# Evidence does not support the conclusion that *Hexarthra intermedia* (Rotifera, Monogononta, Flosculariaceae) causes mortality in *Bosmina longirostris* (Cladocera, Diplostraca, Branchiopoda)

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## ABSTRACT

**Evidence does not support the conclusion that *Hexarthra intermedia* (Rotifera, Monogononta, Flosculariaceae) causes mortality in *Bosmina longirostris* (Cladocera, Diplostraca, Branchiopoda)**

Based on observations of preserved samples, Jaramillo-Londoño & Pinto-Coelho (2010) describe a putative ecological relationship between the rotifer *Hexarthra intermedia* and the cladoceran *Bosmina longirostris* as a fusion of parasitism and interference competition. They argue that *H. intermedia* enter the filtering chamber of *B. longirostris* allowing the rotifer to exploit food collected by *Bosmina*, while simultaneously receiving protection from predators. In addition, they surmise that the result of this interaction can lead to death of *Bosmina*. We posit two simpler explanations for their observations. (1) Presence of *H. intermedia* in the cladoceran's filtering chamber is an artifact of the collection methods. (2) Statistical correlations between the population levels of these two species simply means that the environment was suitable for their growth. Thus until additional evidence corroborates their findings, the simpler explanations should prevail.

**Key words**: freshwater, inference competition, María Rosa Miracle, parasitism, zooplankton

## *RESUMEN*

***La evidencia no soporta la conclusión de que* Hexarthra intermedia *(Rotifera, Monogononta, Flosculariaceae) es la causa de la mortalidad de* Bosmina longirostris *(Cladocera, Diplostraca, Branchiopoda)***

*Jaramillo-Londoño y Pinto-Coelho (2010) describen una relación ecológica putativa entre el rotífero* Hexarthra intermedia *y el cladócero* Bosmina longirostris *como una fusión de parasitismo y competencia por interferencia con base en observaciones hechas en muestras preservadas. Se argumenta que* H. intermedia *ingresa a la cámara de filtración de* B. longirostris *permitiendo al rotífero aprovechar los alimentos recolectados por* Bosmina*, y al mismo tiempo recibir protección de los depredadores. El resultado de esta interacción puede llevar a la muerte de* Bosmina*. Postulamos explicaciones más simples para sus observaciones. (1) La presencia de* H. intermedia *en la cámara de filtrado del cladócero es un resultado del método de recolección del mismo. (2) Las correlaciones estadísticas entre los niveles de población de estas dos especies simplemente significan que el ambiente era adecuado para su crecimiento. Por lo tanto, hasta que la evidencia adicional corrobore sus hallazgos, las explicaciones más simples deben prevalecer.*

**Palabras clave**: *agua dulce, competencia por interferencia, María Rosa Miracle, parasitismo, zooplancton*

## Preface

This paper, along with the others appearing in this volume, lauds the meticulous research of Prof. Dr. María Rosa Miracle. During her distinguished career spanning five decades she greatly expanded our understanding of the ecological niche of rotifers (Miracle, 1974; Carmona *et al.*, 1989; Esparcia *et al.*, 1989; Vicente & Miracle, 1992; Miracle *et al.*, 1995; Armengol & Miracle, 1999; Miracle *et al.*, 2007; Miracle *et al.*, 2014; Onandia *et al.*, 2015). Her thorough work should serve as a guide to other investigations. Here we emphasize the care that must be taken in studies that explore interactions of rotifers with other zooplankton species and in drawing inferences that expand the rotiferan niche.

## INTRODUCTION

Understanding community structure and population dynamics of zooplankton, as well as the details of their biotic interactions, requires studies across several scales, both spatial and temporal. At large spatial scales studies have examined zooplankton in many freshwaters systems. These kinds of studies inform us about how edaphic conditions influence zooplankton community composition and development (Balayla *et al.*, 2010; Obertegger *et al.*, 2010; Pinel-Alloul & Mimouni, 2013; Hiltunen *et al.*, 2015; Gozdziejewska *et al.*, 2016). Study at small spatial scales revealed the patchiness of the plankton (Lehman & Scavia 1982; Schuler *et al.*, 2017), as well microhabitat preferences among species (Walsh, 1995; Van de Meutter *et al.*, 2004; Kuczynska-Kippen & Nagengast, 2006). Research across long-term temporal scales (years to decades) has uncovered information about the dynamics of populations yielding information about when species appear and disappear seasonally, yearly, or longer (Herzig, 1987; Hampton *et al.*, 2006; Hampton & Schindler, 2006; Muirhead *et al.*, 2006; Smith *et al.*, 2009; Obertegger *et al.*, 2011; Francis *et al.*, 2014). At intermediate timescales (weeks to months) investigations have provided details about individual species or a suite of similar species (Ruttner-Kolisko, 1977; Fey *et al.*, 2010; Sastri *et al.*, 2014; McMeans *et al.*, 2015). At the smallest timescales (minutes to days) we have learned some of the details of how individual species interact with each other and their abiotic environment (Burns & Gilbert, 1986; Kirk & Gilbert, 1988; Kirk & Gilbert 1990; Hampton & Gilbert, 2001; Diéguez & Gilbert 2011; Sarma *et al.*, 2011). Thus, from the collective research across these scales several influential techniques and concepts have been established including, for example, the egg ratio technique, the microbial loop, community hysteresis and compensatory dynamics in zooplankton communities, feeding specializations, and other unique behaviors. Of course, the weight of these concepts has been amplified by careful observation and critical analysis. More importantly, these concepts have been confirmed by repeated observations and experimentation.

Edmondson's egg ratio technique has been used to analyze the population dynamics of a variety of zooplankton populations (Edmondson, 1960; Edmondson *et al.*, 1962; Edmondson, 1968; Balayla & Moss, 2003). Other researchers subsequently modified the technique; the collective outcome was an important tool for study of *in situ* population dynamics (Caswell, 1972; Paloheimo, 1974). Elucidation of the microbial loop gave new insight into energy flow and nutrients cycling in aquatic systems (Azam *et al.*, 1983; Stockner & Porter, 1988; Arndt, 1993; Jürgens & Jeppesen, 2000; Azémar *et al.*, 2006; Kissman *et al.*, 2017). Careful examination of zooplankton community structure during perturbations has led to a better understanding of both hysteresis and compensatory dynamics (e.g., Fischer *et al.*, 2001; Frost *et al.*, 2006; Pace *et al.*, 2013). Several accounts have documented the concept of feeding specialization in zooplankton. Actually understanding feeding specialization in these taxa has been an important area of research for many years (Wallace *et al.*, 2006 and references therein). Undeniably, the field is replete with studies that have explored this subject, either in field or laboratory settings (e.g., Edmondson, 1965; Bodgan & Gilbert, 1984; Stemberger & Gilbert, 1987; Williamson & Vanderploeg, 1988; Brett & Müller-Navarra, 1997; Jackson & Thomas Kiørboe, 2004; Noyon & Froneman, 2014; Onandia *et al.*, 2015; Benedetti *et al.*, 2016).

Research also has documented the occurrence of interesting trophic interactions among protists and micrometazoans (i.e., cladocerans, fungi, and rotifers). Here we note four examples. (1) Ciliates and heliozoans engulf whole rotifers (Wallace *et al.*, 2015). (2) Soil and aquatic fungi feed as saprophytic parasites on rotifers and nematodes (Barron, 1980; Robb & Barron, 1982; Barron & Szijarto, 1984; Fialkowska & Pajdak-Stós, 2018). (3) Rotifer species of *Dicranophorus* and *Proales* are carrion feeders, cleaning out the carapaces of dead cladocerans and copepods, as well as the bodies of freshwater oligochaetes (Nogrady *et al.*, 1993; Wallace *et al.*, 2006). (4) Rotifers also are predatory on cladocerans. The rotifer *Dicranophorus isothes* Harring & Myers, 1928 is a predator, feeding strictly on cladocerans such as *Alona*, *Chydorus*, and small *Moina*. Harring & Myers (1928) provide a brief description of this rotifer's

**Table 1.** An analysis of the argument presented by Jaramillo-Londoño and Pinto-Coelho (2010) regarding interactions between *Hexarthra intermedia* and *Bosmina longirostris*. *Un análisis del argumento presentado por Jaramillo-Londoño y Pinto-Coelho (2010) sobre las interacciones entre* Hexarthra intermedia *y* Bosmina longirostris.

| Our comment number (Original Pagination) | Synopsis of the authors' points | Our remarks |
|---|---|---|
| 1 (962) | Samples were preserved in 4% formalin and transported back to the laboratory for analysis. | No chemical agents were added to reduce potential for osmotic shock. No anesthetization was attempted. Preserved animals can become agitated during transportation. |
| 2 (963) | ≤4 well-preserved *Hexarthra* were present inside empty carapaces of *Bosmina*; see Fig. 3B. | Distortion is common during preservation of cladocerans (e.g., the body pulls away from the carapace). *Hexarthra* may then enter an empty carapace. |
| 3 (963) | *Hexarthra* density was positively correlated with both density of *Bosmina* and with their exuviae, suggesting existence of a recurrent association and also the possible impact of *Hexarthra* on *Bosmina* death rates. | Statistical correlation does not necessarily mean causation. An alternative explanation that could be proposed is that both species are responding to favorable conditions (e.g., availability of food, temperature, and few predators). |
| 4 (964) | *Hexarthra* has malleoramate trophi, prefers food sizes of <6 µm. It moves with darting a motion that results in *Bosmina* becoming prey. | These two sentences comprise a 3-part syllogism. The logical fallacy that this argument presents is discussed in the body of our text. |
| 5 (964) | *Hexarthra* in the filtering chamber of *Bosmina* suggests a fusion of parasitism with interference competition. | No evidence has been provided to document live *Hexarthra* entering the thoracic region of *Bosmina* where suspension feeding takes place. |
| 6 (964) | *Hexarthra* causes noticeable damage to the "hosts", this relationship also approaches some form of parasitism (Fig. 5). | No evidence has been provided that qualifies as noticeable damage having been inflicted on the *Bosmina*. |

predatory activities. NB: A permanent slide deposited in The Academy of Natural Sciences of Philadelphia [ANSP] (now The Academy of Natural Sciences of Drexel University) and pictured in Jersabek *et al.* (2003) depicts a putative predatory event between *D. isothes* and *Alona* sp. (F.J. Myers is credited with the preparation of this slide [Specimen Preparation ANSP 912]). Also the rotifer *Asplanchnopus multiceps* (Schrank, 1793) is known to feed on cladocerans and rotifers (Nandini & Sarma, 2005). Other unusual feeding habits exhibited by rotifers are reviewed in Wallace *et al.* (2006).

However, another novel trophic pathway has been reported that requires additional analysis. Jaramillo-Londoño & Pinto-Coelho (2010) report that the rotifer *Hexarthra intermedia* (Wiszniewski, 1929) [hereafter *Hexarthra*] interact with the limnetic cladoceran *Bosmina longirostris* (O.F. Muller, 1785) [hereafter *Bosmina*], ultimately resulting in mortal damage being inflicted on the cladoceran. As of this writing we are aware of > 12 papers that have cited this paper, but most only reference it without commenting on its findings (e.g., Santos-Wisniewski *et al.*, 2011; Jaramillo-Londoño & Aguirre-Ramírez, 2012; Pauwels *et al.*, 2014; Kotov & Fuentes-Reines, 2015; Ergönül *et al.*, 2016; Gürbüzer *et al.*, 2017). Because observation regarding *Hexarthra* impacting *Bosmina* influences our understanding of the freshwater food web, in general, and specifically the niche and trophic dynamics of rotifers, we believe that the methods and conclusions of this paper need to be re-examined carefully. In the spirit of Miracle's careful attention to detail, we review the methodology, results, and conclusions of Jaramillo-Londoño & Pinto-Coelho (2010) and offer alternative explanations to their observations.

## EVIDENCE AND A REINTERPRETATION

The research of Jaramillo-Londoño & Pinto-Coelho (2010) was based on preserved zooplankton samples taken from the Vargem das Flores Reservoir, located ca. 20 km southwest of Belo Horizonte, Minas Gerais, Brazil. The unusual conclusion proposed in this paper is that *Hexarthra* exploit a new trophic-ecological niche axis (page 964) representing "… a fusion of parasitism with interference competition." The implied logic is that the food for *Hexarthra* in this reservoir is composed mainly of small coccoid shaped cells, which provide only some of the dietary needs for this rotifer. These authors hypothesized that *Hexarthra* is able to find additional nutritional resources by intruding into the filtering chamber of *Bosmina*, thereby exploiting resources (algal particles filtered by *Bosmina* and residing in its filtering chamber). In addition, while in the filtering chamber *Hexarthra* also receives shelter from predators. We highlight six instances where the evidence provided is insufficient to support the authors' conclusions (Table 1). In presenting our analysis (below) we quote the authors.

**Point 1** (Page 962). "All samples were preserved in 4 % formalin for further laboratory processing." The statement gives no indication whether their preservation methods followed the standard protocol for preserving plankton samples as described by Downing & Rigler (1984). As these researchers point out, unless care is taken cladocerans can become distorted (ballooning). Ballooning often results in a forward flexure of the abdomen, which exposes the brood chamber and permits loss of developing young (see Haney & Hall, 1973). Thus poor preservation may be the cause of the animal's flexing seen in Fig. 1B. The result of distortion of the *Bosmina* specimens during fixation may be, in part, responsible for *Hexarthra* ending up in the filtering chamber of *Bosmina* in the preserved samples.

**Point 2** (Page 963). "It was common to detect up to four well-preserved individuals of *H. intermedia* inside empty bodies of *B. longirostris*." It is well known by researchers who study *Hexarthra* that they frequently adhere to one another and to other materials in preserved samples – sometimes even the arms adhere to the bodies of other rotifers (S. Nandini, S.S.S. Sarma, & R. Shiel, pers. comm.; EJW, pers. obs.). This fact can account for the connection of *Hexarthra* to live *Bosmina* that were killed during preservation, as well as to their exuviae. With sufficient agitation during transport to the laboratory the spine-bearing arms of *Hexarthra* could easily become entangled with *Bosmina*.

**Point 3** (Page 963). "The density of *H. intermedia* was positively correlated with the density of *B. longirostris* containing *H. intermedia* … , and with the occurrence of carapaces of *B. longirostris* containing *H. intermedia* … (Fig. 4)." If the carapaces are exuviae, then the occurrence of *Hexarthra* within them may well be simply circumstantial. "These results and correlations suggest not only the existence of a recurrent association between these two species, but also the possible impact of *H. intermedia* intrusions on death rates of *B. longirostris*." A positive correlation between two factors does not mean cause and effect. Given that both species are suspension feeders, a correlation of population sizes probably indicates that they are responding to favorable conditions in the habitat. That is, there is adequate food and probably also favorable temperature and few predators. This association does not confirm cause and effect of an "… impact of *H. intermedia* intrusions on death rates of *B. longirostris*."

**Point 4** (Page 964). One paragraph, comprising two sentences, essentially constitutes a three-part categorical syllogism, which may be presented as follows.

1. "*Hexarthra intermedia* has a mastax with malleoramate trophi … , and prefers [to consume] particles smaller than 6 µm … ."
2. "Its darting movements [of *Hexarthra*] offer some protection against predation … , and"
3. "so [due to the darting movements of *Hexarthra*] *B. longirostris* becomes an easy prey to capture … ."

Unfortunately, the elements in this syllogism are not logically connected. The fact that *Hexarthra* has malleoramate trophi has nothing to do with the fact that this rotifer can move by darting movements (jumps). While frequent jumps by *Hexarthra* may increase encounters with other large planktonic organisms, they do not make *Bosmina* an easy prey. Indeed the darting movements or jumps of *Hexarthra* (and other rotifers such as *Polyarthra*) are escape movements that move the animals away from disturbances in the water, not toward them (Kirk & Gilbert, 1988; Kak & Rao, 1998; Hochberg & Ablak Gurbuz, 2008; Hochberg *et al.*, 2017). Thus, the rapid evasive movements of *Hexarthra* appear to protect it from being swept into the branchial chambers of cladocerans.

The statement that "… *B. longirostris* becomes an easy prey to capture … ." [by *Hexarthra*] is puzzling. The typical diet of *Hexarthra* is known to comprise particles in the size range of bacteria and algae (≤ 6 µm) (Bouvy *et al.*, 1994; Pagano *et al.*, 1998). These limits in food size are a function of morphology of its malleoramate trophi, which are used to process food by a grinding action (Fontaneto & De Smet, 2015). Additionally, the mastax (with trophi) lies deep enough inside *Hexarthra*'s body to prevent the animal from protruding its trophi through the mouth to grasp individual prey items. That sort of predatory behavior is seen in raptorial, predatory rotifers such as *Asplanchna* and *Asplanchnopus* (Wallace *et al.*, 2015; H. Segers, pers. comm.). Thus, *Hexarthra* is simply not mechanically suited to feed on large cladoceran prey. To do so would require extruding its trophi from its mouth, cutting thorough the exoskeleton, and then rending tissues for ingestion.

**Point 5** (Page 964). The authors note that "… intrusion of individuals of *H. intermedia* in the filtering chamber of *Bosmina* is not a trivial feature, … ." The photomicrographs of *Hexarthra* and *Bosmina* (Figs. 1B-D) do not support this assertion. They show the following: Fig. 1B – one *Hexarthra* near the exit of the brood chamber and another attached to the legs; Fig. 1C – one *Hexarthra* in an empty carapace of *Bosmina*; and Fig. 1D – a small *Bosmina* in juxtaposition with a carapace from a larger animal, with one, perhaps two, *Hexarthra* also adhering to the carapace. The positioning could be a result of preservation artifacts as discussed above.

Heeg & Rayner (1988) also have described close associations among zooplankton in preserved samples. They reported *Hexarthra mira* (Hudson, 1871) forming short, conspecific chains of between two and seven individuals. In some chains *Trichocerca chattoni* (Beauchamp, 1907) were also present. They also reported that both *H. mira* and *T. chattoni* attached to *B. longirostris*. These observations are similar to those made by Jaramillo-Londoño and Pinto-Chelho (2010), and thus we conclude that their observations also are misinterpretations of preservation artifacts.

**Point 6** (Page 964). The authors state "… intrusion of individuals of *H. intermedia* in the filtering chamber of *Bosmina* is not a trivial feature, since it reveals signs of a new ecological relationship that could be seen as a fusion of parasitism with interference competition. … … Nevertheless, since it causes noticeable damage to the "hosts", this relationship also approaches some form of parasitism (Fig. 5)." The authors offer no documentation of *Hexarthra* inflicting damage to *Bosmina*. Actually, studies of rotifer-cladoceran interactions have documented the reverse; rotifers that have been swept into the branchial chamber of large cladocerans are often damaged (sometimes lethally) (Fradkin, 1995). We conclude that the relationship conceptualized in Fig. 5 is not warranted.

## DISCUSSION

The possibility for the novel feeding dynamic of *Hexarthra* outlined by Jaramillo-Londoño & Pinto-Coelho (2010) is intriguing, but premature. Indeed simpler interpretations of their observations are warranted. The observation that the population size of *Hexarthra* was correlated to that of *Bosmina* is a misinterpretation of statistical correlation; it does not support an argument for cause and effect. Photomicrographs of *Hexarthra* in contact with *Bosmina* and even inside empty carapaces could be artifacts of the collection methods and the fact that *Hexarthra* adheres to materials in preserving fluids. Of course, we know that cladocerans and rotifers do interact by exploitative and/or interference competition with cladocerans possessing the competitive advantage (Gilbert, 1985; 1989), and that anostracans can consume *Hexarthra* sp. (Starkweather, 2005). However, the evidence provided by Jaramillo-Londoño & Pinto-Coelho (2010) reports no competitive advantage of *Bosmina* over *Hexarthra*. We suggest that additional research should be undertaken to explore the potential for competition between these taxa.

We agree with the author's final conclusion: "The final question regarding the effects of *H. intermedia* on *B. longirostris* is the potential impact of this interaction on *Bosmina* populations. Resolving this question will require a more exhaustive study." We suggest that such an exhaustive study requires the systematic application of the criteria outlined by Platt (1964) for scientific problems. This means formulating multiple working hypotheses that are testable, refutable, and repeatable. In this case, the study must include meticulous observations of live *Hexarthra* in close association with live *Bosmina*. Thus, until further evidence is obtained the answer to the question as to whether a new trophic interaction occurs between these two species is no.

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