



Article The Infection of Paracalanid Copepods by the Alveolate Parasite Ellobiopsis chattoni Caullery, 1910 in a Subtropical Coastal Area

José E. Martinelli Filho¹, Felipe Gusmão², Flavio A. Alves-Júnior^{3,4} and Rubens M. Lopes^{5,*}

- ¹ Biological Oceanography Laboratory, Geosciences Institute, Centre for Advanced Studies of Biodiversity, Federal University of Pará (UFPA), Campus Universitário do Guamá, Belém 66075-110, Brazil
- ² Instituto do Mar, Federal University of São Paulo (UNIFESP), Santos 11060-001, Brazil
- ³ Centro Universitário Brasileiro-UNIBRA, Rua Padre Inglês, 257, Boa Vista, Recife 50050-230, Brazil
- ⁴ Carcinology Laboratory (Labcrust) Prof. Dra. Kátia Cristina de Araújo Silva, Federal Rural University of Amazonia (UFRA), Avenida Tancredo Neves, 2501, Terra Firme, Belém 66077-830, Brazil
- ⁵ Department of Biological Oceanography, Oceanographic Institute, University of São Paulo (USP), São Paulo 05508-120, Brazil
- * Correspondence: rubens@usp.br

Abstract: Paracalanid copepods, common in tropical zooplankton communities, are known hosts for a variety of parasites. Nevertheless, relatively little is known about the prevalence and consequences of parasitism in these copepods. In this study, we analyzed the relationship between two paracalanid copepods, *Parvocalanus crassirostris* and *Paracalanus* spp., with a common parasite, the alveolate protist *Ellobiopsis chattoni*, in a subtropical environment on the south-east Brazilian coast. We assessed the frequency and abundance of parasites in juveniles and adult male and female copepods. We observed that 22 out of 4014 *Paracalanus* spp. (0.55%) and 98 out of 3920 *P. crassirostris* were infected (2.5%). *E. chattoni* were rarely found in other taxa (about 0.05% for *Oithona* spp. and *Acartia lilljeborgii*). The parasites were most frequently attached to cephalosome appendages (73.6%), with up to four cells per copepod. The parasites were more prevalent in adults than juveniles, and adult females were more frequently infected than males. *E. chattoni* had a likely negative impact on copepod growth because the infected females were smaller than the non-infected females (p < 0.001). Females are usually bigger and live longer than males, which could account for their high frequency of infection.

Keywords: parasitism; marine zooplankton; *Parvocalanus crassirostris; Paracalanus;* Ellobiopsidae; South Atlantic

1. Introduction

Copepods are the dominant metazoans in the marine pelagic environment, playing fundamental roles in biogeochemical cycles and energy transfer to higher trophic levels. Ecological investigations in recent decades have shifted the focus on copepods from simply being major phytoplankton consumers [1] to important components of microbial food webs [2] and as hosts for gut-specific bacteria [3] and eukaryotic parasites [4]. A wide range of symbiotic relationships between marine pelagic copepods and other organisms such as *Vibrio cholerae* [5], parasitic dinoflagellates [6], and epicarid isopods [7] has been documented, several of which may cause severe injuries to copepod hosts, as reported for certain parasitic protists [4,8]. However, very little is known about the ecological aspects and consequences of parasitic protists such as ellobiopsids on copepods [9–11].

It has been suggested that juvenile copepods encounter *Ellobiopsis* spores during feeding activity, when the infection process takes place [10,12–14]. Copepod life cycles can be influenced by parasitic protists, which may induce castration, the mutation of sexual characteristics, or even sex changes during the later copepodid stages [15,16]. The parasites may also influence the metabolic and reproductive rates of the copepod hosts [17], as



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). observed in *Undinula vulgaris* [10] and *Calanus helgolandicus* [11]. However, the effect of *Ellobiopsis* on copepod host biology and reproduction is poorly investigated [10,11], despite the many reports on the occurrence of *Ellobiopsis* spp. attached to copepods (e.g., [18]).

Ellobiopsis has a multinucleate, alveolate parasite body divided into two sections, a trophomere and a gonomere. The trophomere is the cell vegetative phase, bearing a root-like structure that penetrates the tissue of the host, and the gonomere is distally located and responsible for the sporulation process; both grow outside the host body [19]. A single *Ellobiopsis* may reach a biovolume as large as 1/15 of its host [10]. *Ellobiopsis* probably has a low infection specificity as more than 25 pelagic copepod species, and a few decapod zoea such as *Portunus*, have been documented as hosts [12,17,19,20].

Ellobiopsis hosts are virtually unknown in the South Atlantic, except for a single publication [9]; most records come from the North Atlantic, the North Sea, and the Mediterranean [11,21–25]. Here, we aimed to describe the copepod hosts for *E. chattoni* Caullery 1910, the abundance and frequency of infestation of this parasite in a subtropical coastal region in the South-West Atlantic, and the potential effects of the parasite on the host species.

2. Materials and Methods

Zooplankton was sampled off Ubatuba, São Paulo state, on the south-east Brazilian coast, at two coastal stations located at $23^{\circ}30'59''$ S; $45^{\circ}06'10''$ W (station A) and $23^{\circ}31'27''$ S and $45^{\circ}04'54''$ W (station B), using a small motorboat. Sampling took place mostly in the morning on alternate days during the austral summer and winter of 2009 and 2010 as well as the summer of 2011 for a total of 23 sampling periods (Table S1). Station B (10 m depth) was sampled on two occasions (26 January 2009 and 18 July 2009) when high waves, winds, and associated risks prevented sampling at the regular station, A (~30 m depth). The stations were ~2 km apart and under the influence of the same water mass. Plankton was sampled for 2 to 3 min by subsurface horizontal tows with a 100 μ m mesh-size plankton net equipped with a calibrated flowmeter to estimate the filtered volume. All samples were preserved in a 4% formaldehyde–seawater buffered solution.

The copepods were identified following the taxonomic literature for the South and Central Atlantic [26–30] and counted to estimate the abundance (ind m⁻³) and frequency (%) of infected specimens by developmental stages and sex. These were determined according to the usual morphological characteristics [26,27,31,32] and split into juvenile copepodids (CI-V), adult females (F), and adult males (M). A minimum of 30 individuals of each dominant copepod taxon were counted in sample aliquots to estimate the copepod abundances [28]. The infected copepods were enumerated in larger subsamples (from 1/10 to whole samples) because of their low prevalence in the samples (Table S1). Naupliar abundances were not estimated as the 100 μ m plankton net failed to quantitatively capture the larval stages of most copepod species in the region [33].

The prosome length and width of the copepods and the parasite size (major length and width, excluding the stalk) were measured under a stereomicroscope equipped with a digital camera with the aid of Image J software after staining the samples with Bengal rose. The *Paracalanus* specimens were grouped as *Paracalanus* spp. because the identification accuracy was limited by the image resolution and the small body size of these copepods. A microscope analysis of selected individuals suggested that *P. quasimodo* was the dominant *Paracalanus* species in the samples, followed by *P. indicus* and occasional occurrences of *P. aculeatus* and an unidentified *Paracalanus* spp. [33].

Ellobiopsis chattoni parasites were identified based on their tube-like structure in the distal part of the forming gonomere and the occurrence of a single gonomere, an exclusive characteristic of the species (Figure 1) [21,22,24,25]. The gonomeres were assigned to three categories according to [14,21]: absent; immature (visible cell constriction, but at different developmental stages); and mature (fully developed). The initial developmental stages of parasites may have been underestimated in our samples due to the image resolution and parasite size (<15 µm length without the stalk). The frequency of occurrence of the



parasites by attachment location on the copepods (antenna, mouth appendages, prosome, etc.) was analyzed for paracalanid copepods.

Figure 1. Paracalanid copepods infected by *Ellobiopsis chattoni*: (**A**) *Paracalanus indicus* with two adhered parasites; (**B**) *P. indicus* showing *E. chattoni* adhering to a mouth appendage; (**C**,**D**) *Parvocalanus crassirostris* with parasites attached to the antenna. (**A**,**B**) Scale = 200 μ m; (**C**) scale = 80 μ m; (**D**) scale = 60 μ m.

Comparisons between the sexes and developmental stages were performed on the paracalanid copepods to verify a possible differential occurrence of *E. chattoni* with these categories. The data were tested for normality and an equal variance by the Shapiro–Wilk and Lilliefors tests, respectively. The abundance data were not fit for parametric tests, so non-parametric statistical tests were used instead. A comparison of the multiple groups was made using a Kruskal–Wallis test, followed by a Student–Newman–Keuls test when the differences were significant; Mann–Whitney tests were used for pairwise comparisons. All statistical analyses were considered with a 5% significance level [34].

The effect of the hosts on the copepod size was tested by comparing the prosome length of parasitized adult copepods with the same number of random non-parasitized copepods from the same sex and sample. The host and parasite biovolumes (μ m³) were estimated by $V = 4/3 \ a \ b^2$, where *a* was the copepod or protist length and *b* was their width, assuming that both the copepods and *E. chattoni* had a spherical ellipsoid format. The Spearman test was used to assess the correlation between the copepod and parasite body volumes.

3. Results

A total of 7934 paracalanids (4014 *Paracalanus* spp. and 3920 *Parvocalanus crassirostris*), 19,219 *Oithona* spp., and 8302 *Acartia lilljeborgii* were inspected. An infection was observed in 98 *Parvocalanus crassirostris* (2.5% of the total), 22 *Paracalanus* spp. (0.5% of the total), 8 oithonids (3 *Dioithona oculata*, 3 *Oithona hebes*, and 2 *O. plumifera*), and 4 specimens of *Acartia lilljeborgii* (~0.05%). The most frequently infected developmental stages were adult

females in *Parvocalanus crassirostris* and copepodids in *Paracalanus* spp. (Table 1). *Acartia lilljeborgii*, *Dioithona oculata*, *Oithona hebes*, and *O. plumifera* are herein reported for the first time as hosts for *E. chattoni*.

Table 1. The total amount of examined and infected copepods for each sex and developmental stage for *Parvocalanus crassirostris* and *Paracalanus* spp. and the respective frequency of infection (F.I.). M: adult male; F: adult female; C: juvenile copepodid, stages I to V.

N	Parvocalanus crassirostris				Paracalanus spp.			
	Total	Μ	F	С	Total	Μ	F	С
Observed	3920	597	1211	2014	4014	260	302	3430
Infected	98	14	61	23	22	7	1	14
F.I. (%)	2.5	2.4	5	1.1	0.6	2.7	0.3	0.4

A total of 61 copepod taxa were identified (Table S2). *Paracalanus* spp. was the most abundant copepod taxon, varying from 59 ind m⁻³ on 21 July 2010 to 3982 ind m⁻³ on 26 January 2009. The estimated abundance of infected *Paracalanus* spp. was 2 ± 3 ind m⁻³ for juveniles, 11 ± 11 ind m⁻³ for males, and 2 ± 2 ind m⁻³ for females (Table 2). *Parvocalanus crassirostris* was the third most abundant copepod species during this study, with a large abundance range between 41 ind m⁻³ on 22 January 2010 and 3282 ind m⁻³ on 26 January 2009. The estimated abundance of infected *P. crassirostris* was 6 ± 11 ind m⁻³ for juveniles, 4 ± 6 ind m⁻³ for males, and 16 ± 28 ind m⁻³ for females (Table 2).

Table 2. Abundance estimates of infected *Parvocalanus crassirostris* and *Paracalanus* spp. (ind. m^{-3}) for each sampling occasion. C: juvenile copepodid, stages I to V; F: adult females; M: adult males; F + M: all adults.

Season	Period	Species	С	F	М	M + F
Summer	01/26	P. crassirostris	9	84	19	103
2009	01/26	Paracalanus spp.	8	4	25	29
	07/18	P. crassirostris	2	13	6	19
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M	07/22	P. crassirostris	32	7	4	11
Winter 2009	07/22	Paracalanus spp.	2	3	20	23
	07/26	P. crassirostris	1	7	1	8
	07/26	Paracalanus spp.	0	1	3	4
	07/21	P. crassirostris	0	2	0	2
	07/21	Paracalanus spp.	0	0	$\begin{tabular}{ c c c c c } \hline M & M + F \\ \hline 19 & 103 \\ 25 & 29 \\ \hline 6 & 19 \\ 1 & 1 \\ 4 & 11 \\ 20 & 23 \\ 1 & 8 \\ 3 & 4 \\ \hline 0 & 2 \\ 1 & 1 \\ 1 & 2 \\ 2 & 2 \\ 1 & 1 \\ 1 & 2 \\ 2 & 2 \\ 0 & 9 \\ 26 & 30 \\ \hline 0 & 2 \\ 6 & 7 \\ \hline \end{tabular}$	
117 1 2010	07/26	P. crassirostris	0	1	1	2
Winter 2010	07/26	Paracalanus spp.	0	0	2	2
	07/30	P. crassirostris	2	9	0	9
	07/30	Paracalanus spp.	4	4	26	30
Summer	01/24	P. crassirostris	0	2	0	2
2011	01/24	Paracalanus spp.	1	1	6	7

Parasitized copepods were observed during all winter and summer seasons sampled (Table S1). The seasonal and interannual differences could not be reliably estimated because of the low number of observations during the summer of both years. The females of *Parvocalanus crassirostris* were more frequently infected than males (p = 0.04), representing 61 of the 98 infected specimens, and the adults were more frequently infected than the immature copepodid stages (p = 0.04). The differences between the sex and developmental stages were not significant for *Paracalanus* spp. and were not tested for *Acartia lilljeborgii* and *Oithona* spp. due to the low number of infected copepods. The prosome length between the uninfected and infected females of *P. crassirostris* was significantly different (Table 3). The *Parvocalanus crassirostris* and *E. chattoni* biovolume showed a significant but weakly

positive correlation ($r^2 = 0.21$), indicating that larger parasites were often associated with larger copepods. However, this was not observed for *Paracalanus* spp. (Figure 2).

Table 3. Results of the Mann–Whitney test comparing the prosome length (μm) between uninfected and infected copepods for adult males and females of *Parvocalanus crassirostris* and *Paracalanus* spp. F: adult females; M: adult males.

Species	Species Category		$\begin{array}{l} \textbf{Mean} \pm \textbf{S.D.} \\ \textbf{Infected} \end{array}$	Sample Number (N)	<i>p</i> -Value
Parvocalanus	М	322.2 ± 17.6	307.7 ± 29.2	14	0.383
crassirostris	F	398.8 ± 24.5	381.7 ± 22.9	60	< 0.001
Davacalanus	Μ	434.4 ± 66.7	376.9 ± 26.9	7	0.128
Furuculunus spp.	F	-	-	1	-



Figure 2. Relationship between the biovolume (μ m³, log scale) of infected paracalanid copepods (*Paracalanus* spp. and *Parvocalanus crassirostris*) and the respective attached *Ellobiopsis chattoni* parasites.

In *P. crassirostris*, 77 specimens carried a single parasite cell and 18 carried 2 parasite cells. The occurrence of three or four *E. chattoni* cells on a single copepod was rare, occurring on three individuals only. For *Paracalanus* spp., 20 specimens had a single *E. chattoni* attached; more than one parasite cell occurred only on two copepod hosts. No difference was found in the size of *P. crassirostris*, whether the copepods were carrying one or more parasites.

Nearly 80% of the parasites were attached to cephalosome appendages, including maxillipeds, maxillae, and antennae (Figure 1). Other less frequent adhesion sites were the swimming legs and the urosome (Table 4). The preferential adhesion site did not differ between the sexes or developmental stages.

	Parvocalanus crassirostris				Paracalanus spp.			
	С	F	Μ	%	С	F	М	%
Mouth appendages	4	32	8	42.7	6	1	5	46.2
Antennae	4	30	3	35.9	5	1	1	26.9
Prosome	2	12	6	19.4	3	-	3	23.1
Others	-	1	1	1.9	-	-	1	3.8

Table 4. *Ellobiopsis chattoni* adhesion sites on the host copepod species (*Parvocalanus crassirostris* and *Paracalanus* spp.). C: juvenile copepodid, stages I to V; F: adult females; M: adult males; %: frequency of adhesion at each site.

The *Ellobiopsis chattoni* size varied widely, with a minimum and maximum length of 17 and 153 μ m, respectively. The average length and width were 75.7 \pm 30.2 μ m and 44.1 \pm 14 μ m, respectively, and the average biovolume was 804,117 \pm 714,671 μ m³. From a total of 143 detected parasites, the gonomere was absent in 38.5%, immature in 39.2%, and mature in 22.3% of the specimens.

4. Discussion

The description of *Ellobiopsis* dates from more than a century ago [21], but knowledge of the biology and taxonomy of this genus has slowly advanced in the last decades [14,35]. The literature on *Ellobiopsis* is mostly restricted to its occurrence and host prevalence. The parasite has been recorded in association with several species of calanoid copepods [18–20,36–38], occasionally on Harpacticoida [37], and on decapod larvae [19]. The incidence of *Ellobiopsis* on freshwater hosts is uncertain and probably related to yet-unidentified parasites [4,39].

Parvocalanus crassirostris, Paracalanus spp., and *Oithona* sp. have previously been reported as hosts [35,36]. This study is the first account for *Acartia lilljeborgii, Dioithona oculata, Oithona hebes,* and *O. plumifera* as hosts for *E. chattoni;* it is the second *Ellobiopsis* record for the South Atlantic to date [9].

Despite the growing list of hosts, geographical variations seem to exist regarding the association of *Ellobiopsis* with copepods. For instance, *Calanoides carinatus* was infected on the Namibian shelf [40], but an infection was absent for such species at the Bay of Biscay, Spain, where *Calanus helgolandicus* was the main host, followed by sporadic infections on *Ctenocalanus vanus, Temora longicornis,* and *Pseudocalanus elongatus* [11]. Here, the parasite was observed on six different taxa, but numerically important only for paracalanids. In [18] only the parasitism of *Ellobiopsis* for *Bestiolina similis* was described. The geographical distribution of *E. chattoni* is widespread, and has been observed in the Arabian Sea [18,41], on the coast of Tanzania [10], the North Sea [24], the Norwegian Sea [42], the Mediterranean [21], Indian coastal waters [43,44], and Alaska [45], indicating the possibility of a species complex [14].

The *E. chattoni* found in Ubatuba were generally smaller (~20–160 μ m) than the 250–750 μ m range reported in other studies [9,11–22,39]. Although the stalks were not considered in our length measurements, other investigations did the same [10,14,43]; hence, that alone should not explain the variability in the parasite size among the regions. Such size differences might result from our study reporting infections in host species smaller than those reported in the literature, particularly from the northern hemisphere, or parasite genotypic variability.

It cannot be ruled out that *E. chattoni* represents a species complex because of the high variation in host specificity between localities, the wide geographical distribution, and the substantial variation in the parasite size. Recent studies (e.g., [18]) lack a molecular identification of the parasite and have, therefore, relied on morphological characteristics. A molecular approach, in addition to diverse sampling locations and hosts, should be considered in future studies to determine whether *E. chattoni* is an independent species or a species complex [18].

Despite the apparently higher number of infected copepods during winter compared with summer, the seasonality could not be properly assessed in this study due to an unbalanced sampling frequency between the seasons. *Ellobiopsis* infections have been reported to temporally vary, but without a consistent seasonal pattern when different locations are considered. For instance, the infection rate was higher during the summer in the Clyde Sea [24], from late autumn through winter in the Mediterranean Sea [12], and during winter in the estuarine and coastal waters of Iraq [37].

The infection rates observed here for paracalanid copepods were within a lower range of those recorded elsewhere for copepods carrying *Ellobiopsis* [13,20,38,42]. *P. crassirostris* and *Paracalanus* spp. were the prevalent hosts off Ubatuba whilst other abundant copepods such as *A. lilljeborgii* or oithonids remained virtually devoid of parasites, with a few exceptions.

The positive relationship between the host and parasite size could be explained by the higher proportion of infected females in comparison with the males, which are smaller in paracalanids. Nevertheless, infected *P. crassirostris* females had smaller body sizes compared with the non-infected specimens. As copepods do not molt after reaching maturity, size differences are most likely related to a development impairment in the pre-adult stages. An ellobiopsid infection might negatively impact individual energy input and expenditure by affecting the copepod motility and feeding efficiency; thus, an early infected individual would reach maturity with a small body size. As observed in other studies [11,24,43], most parasites were found adhered to cephalosome appendages such as the mouth parts and antennae, which generate feeding currents for prey capture [46], suggesting that the adhesion and infection mechanisms are connected to copepod feeding behavior.

The maximum number of parasites registered here was four (in a few individual hosts), but up to 15 *Ellobiopsis* have been observed on a single copepod; a few of these parasites were smaller than 15 μ m [24]. The small size of immature parasites at early developmental stages could represent a potential explanation for our findings as we relied on a stereomicroscope to inspect nearly 8000 paracalanid copepods, preventing a more detailed microscopic analysis.

E. chattoni has been assigned as the causative agent of tumor-like anomalies (TLAs) in copepods [47]. However, from the 132 infected copepods analyzed in our samples, none displayed TLAs, which was in line with the results from a laboratory study showing a TLA absence in copepods during and after *Ellobiopsis* gonomere sporulation [43]. In addition, TLA protrusions have not been observed in marine copepods infected by *Ellobiopsis* [9,11,14,39]. An *Ellobiopsis* infection has been suggested to raise copepod mortality [47] but, instead of TLAs, a reduced feeding efficiency and an increased visibility to predators [48,49] are more plausible explanations.

5. Conclusions

This is the second report of *E. chattoni* as a copepod parasite in the South Atlantic, nearly one century after its first account in the region [9]. Four previously unreported host copepod species were found in this study, including acartiids and oithonids, but the parasites were mostly prevalent in paracalanids, particularly in *Parvocalanus crassirostris*. The size of females was impacted by *E. chattoni* infections, which suggested that copepod fitness in general is affected by the presence of parasites [48]. Further experimental studies are needed to verify the negative effects of the parasite on growth, egg production, and the fitness of paracalanid hosts as well as the selection and specificity of the hosts.

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/jmse10121816/s1, Table S1: Zooplankton sampling dates from 2009 to 2011. Aliquot sizes analyzed to estimate parasitized copepod abundances, date and time of sampling, tidal period, and copepod taxa infected by *Ellobiopsis chattoni* are provided. *: Sampling performed at the protected station (B); -: absence of infected copepods. Table S2: pelagic copepod species found off Ubatuba, south-east Brazil from 2009–2011. *: Host species for *Ellobiopsis chattoni*. **Author Contributions:** J.E.M.F. and R.M.L. were responsible for the conceptualization, methodology, investigation, funding acquisition, and resources; J.E.M.F. performed the fieldwork and was responsible for the data curation; all authors contributed equally to the formal analysis, writing, and visualization, and approved the publication. All authors have read and agreed to the published version of the manuscript.

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