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Monthly Occurrence of Endoparasites of Chaetognaths in a Coastal System of the Mexican Central Pacific

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Abstract: The prevalence of endoparasites associated with chaetognath abundance in the coastal waters of the Mexican Central Pacific was studied fortnightly from November 2010 to December 2011. A total of 35 (0.21%) out of 16,407 chaetognaths were found to be parasitized. Five out of twelve chaetognath species (*Flaccisagitta enflata*, *F. hexaptera*, *Parasagitta euneritica*, *Serratosagitta pacifica*, *Zonosagitta bedoti*) were found to be parasitized by nine endoparasitic taxa: Protists (two morphotypes), digenean metacercariae [Didymozoidae, Hemiuridae, *Parahemiurus* sp., Lepocreadiidae, *Prosorhynchus* sp. (Bucephalidae)], and cestodes (metacestodes) [Tetraphyllidea (two morphotypes)]. *Parasagitta. euneritica* and *Z. bedoti* were the most abundant chaetognath species, and *Protist* sp. 2 and *Tetraphyllidea* sp. 1 were the most abundant parasites. The highest prevalence for most of the endoparasite species occurred in June, and the values varied according to three hydroclimatic periods: stratified (S), semi-mixed (SM), and mixed (M). Eight non-infected chaetognath species, two parasitized chaetognaths (*F. enflata* and *S. pacifica*), and two parasites (*Protist* sp. 1 and *Tetraphyllidea* sp. 2) were associated with warm temperatures (S and SM periods); in contrast, *P. euneritica*, *Z. bedoti*, parasitized *F. hexaptera*, and the parasite *Tetraphyllidea* sp. 1 showed a strong local preference for cooler temperatures, high productivity, and high biomass conditions (M periods). We discovered the occurrence of the digenean *Prosorhynchus* sp. (Bucephalidae) parasitizing the chaetognath *P. euneritica*, and this is the first report of *Prosorhynchus* parasitizing chaetognaths worldwide. We also confirmed the presence of Lepocrediidae (metacercariae larval stage) infecting *F. hexaptera*, a parasite that had only been recorded infecting other chaetognaths of the Atlantic Ocean. The parasite diversity affecting the chaetognath populations of the Central Mexican Pacific coast likely differs between the offshore, outer slope areas, and the surveyed coastal system.

Keywords: chaetognatha; endoparasite; Pacific Ocean

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1. Introduction

Chaetognaths, also known as arrow worms, are small, highly abundant pelagic and demersal organisms found in marine zooplankton. They occupy an intermediate trophic level in marine ecosystems, acting as both predators and prey for a variety of marine organisms. Consequently, they play a crucial ecological and trophic function in maintaining the balance and health of these ecosystems [1,2]. Research on chaetognaths and their interactions with endoparasites has uncovered various insights into their ecological relationships and the impacts of parasitism on marine ecosystems. Research on parasites of chaetognaths has also significantly contributed to the understanding of their most common prey, like copepod parasites, including ecological interrelationships of zooplankton and diseases in chaetognaths, which have been particularly well studied in Tokyo Bay, the western English Channel, and the Indian Ocean [3–5]. Studies conducted by Pierrot-Bults [6] cover the population structure and feeding habits of chaetognaths, examining the distribution patterns and diseases of chaetognaths and contributing to the broader understanding of their ecological roles [6,7]. Most studies of chaetognath parasites focus on their taxonomy, emphasizing a single taxon or a few specific parasitic taxa, sometimes derived from isolated observations [8], while ecological interactions between the entire community of parasites of chaetognaths and their environmental variability remain poorly understood, only a few studies of parasites of chaetognaths have been published for the Eastern Tropical Pacific [9–12]. A nematode larvae *Hysterothylacium* sp. was reported as a parasite of the deep-living epibenthic chaetognath *Heterokrohnia involucrum* Dawson, 1968 in the Gulf of California [9], and unidentifiable larval acanthocephalans parasitized planktonic epipelagic chaetognaths [10]. Two additional studies were carried out on the shelf-break of the Central Mexican Pacific, where epibiont cysts (likely Protists), endoparasitic Protists (i.e., apicomplexans, dinoflagellates, and ciliates), endoparasitic platyhelminths (digeneans and cestodes), acanthocephalans, nematodes, and other unidentified endoparasites were found parasitizing seven of nine chaetognath species distributed in that area [10,11]. A recent study provided morphological and genetic data for the identification of Didymozoidae (Trematoda: Digenea) larval stages parasitizing both the heteropod mollusc *Firoloida desmaresti* Lesueur, 1817 (first host) and chaetognaths (second host) in the Gulf of California [12].

Understanding the relationship between chaetognaths and their endoparasites has broader implications for marine biodiversity and ecosystem health. It provides insights into the complexities of food web interactions and the potential impacts of environmental changes, such as climate change and pollution, on parasite–host dynamics. Therefore, in the present study, we analyzed all chaetognath species, together with their parasites, obtained fortnightly from the coastal waters of Navidad Bay, Jalisco, on the Mexican Central Pacific, for a year. We aimed to study the seasonal changes in the abundance of chaetognaths and the prevalence values of the parasites infecting the chaetognaths and to record whether there is a relationship, such as involving local seasonal hydrographical variability, which has previously been characterized [13–15] as three distinct periods: (1) cold or mixed (M), (2) warm stratified (S), and (3) semi-mixed transitional (SM).

2. Materials and Methods

2.1. Sampling and Data Collection

A total of 43 zooplankton samples and vertical hydrographic profiles of temperature, salinity, and dissolved oxygen concentrations were obtained approximately every two weeks from Nov 2010 to Dec 2011 in Navidad Bay, off Jalisco, Mexico (Mexican Central Pacific, 19°09′03″ N, −104°44′50″ W) (Figure S1, Supplemental Material). In addition to the biweekly samples, three to five extra zooplankton samples (a total of 15 replicates) were collected per month during February–April and August–October 2011.

The methodology used for environmental and zooplankton sampling of the present study was described in detail in two previous studies [14,15].

2.2. Chaetognath and Parasite Morphological Identification

All of the chaetognaths were sorted out from all zooplankton samples, counted, and identified to the species level using standard taxonomic keys [16–18]. Chaetognaths are transparent (alive and preserved in formaldehyde) and typically have few parasites inside their body. Therefore, parasites can be accurately counted per host individual. Thus, intensity was measured as the number of parasite individuals of the same taxa infecting a single chaetognath host. Each chaetognath specimen was parasitologically examined using a stereo microscope (Stemi Zeiss DV4, Carl Zeiss Ltd., Cambridge, UK) following standard methods [10–12,19]. The parasitized chaetognaths were dehydrated in a series of 30–100% nondenatured ethanol solutions to eliminate the 4% formalin of the original sample and stained with Gömöri Trichrome stain. Host and parasite specimens were then prepared with clove oil and mounted in synthetic resin (60% xylene) on permanent slides to observe and draw the external and internal diagnostic morphological characteristics of each parasite morphospecies [10–12,19] under an optical microscope (Leica DMLB, Leica Microsystems, Weztlar, Germany). The parasite larval stages were identified based on diagnostic morphological criteria of previous regional studies [3,9–12,19], specialized taxonomic keys for adult digeneans [20–22], and other records of larval cestodes parasitizing marine invertebrates and vertebrates [12,23,24]. The parasite specimens were photographed using a digital camera (Canon Power Shot A2500, Canon, Melville, NY, USA), and each taxon was drawn to show the taxonomically relevant characters. Because the samples were preserved in formaldehyde and are over 10 years old, molecular identification of the parasites was not attempted.

2.3. Data Analysis

2.3.1. Abundance and Prevalence

The standardized abundance of the chaetognaths with and without parasites was expressed as the number of individuals per cubic meter (ind. m^{-3}). We used Quantitative Parasitology V3.0 software and calculated descriptive statistics and confidence intervals (95%) for unbiased prevalence using Sterne's method (http://www.zoologia.hu/qp/qp.html, accessed on 11 May 2024) [25,26] to compare the prevalence of each chaetognaths species, including uninfected specimens (Table S3).

2.3.2. Ecological Ordination

We conducted a direct gradient analysis with a canonical correspondence analysis (CCA) to infer the potential relationships among the environmental gradients and biological data [27,28]. Two matrices were used for multivariate analyses: (1) chaetognath abundance (not parasitized), parasitized chaetognaths, endoparasitic taxa (columns) and sampling dates (rows), and (2) eight measured environmental variables (columns), including temperature at 10 m (°C), salinity at 10 m (PSU), depth of the mixing layer (m), daily coastal upwelling index (m^3 s^{-1} 100 m coastline), coastal upwelling index 15 days before sampling day, zooplankton displacement biovolume (mL 1000 m^{-3}), depth of the upper boundary of the oxygen minimum layer (m), 10 m chlorophyll-*a* concentration (mg Chl-*a* m^{-3}), and the same sampling dates (rows) used in the species matrix. We also analyzed a categorical variable of the three main hydro-climatic periods prevailing around the study area [13–15]. All standardized abundances were transformed to Log_{10} (x + 1) to decrease the variance of chaetognath and parasite abundance [28]. Each environmental variable was transformed using generalized relativization to give the same comparable weight independently of the respective range scales of each environmental variable. The statistical significance of the first three canonical axes was calculated by applying Monte Carlo permutation tests (n = 999 random permutations). We used centered and normalized scores for the CCA ecological ordination (PC-ORD Multivariate of Ecological Data v.6.0 software [28].

3. Results

3.1. Hydrographic Seasonal Variability

During Nov 2010 and Dec 2011, minimum temperatures (21.8–23.0 °C) and maximum salinities (34.5–34.6 PSU) were recorded at a 10 m depth during the mixed period (Feb–May) (Figure 1a). Maximum temperatures (26.8–29.7 °C) and minimum salinities (32.7–34 PSU) were observed during the stratified period (July–November). The dissolved oxygen concentrations ranged between 3.5 and 6.0 mL O_2 L^{-1}, with peaks during the Semi-mixed (Jun and December–January) (8 mL O_2 L^{-1}) and mixed (6.0 mL O_2 L^{-1}) periods (Figure 1a). Mean monthly 10 m chlorophyll-*a* concentration showed typically >2 mg Chl-*a* m^{-3} during the mixed period (with a peak of 4.2 mg Chl-*a* m^{-3} in March 2010) and <2 mg Chl-*a* m^{-3} during both the semi-mixed and stratified periods (Figure 1b).

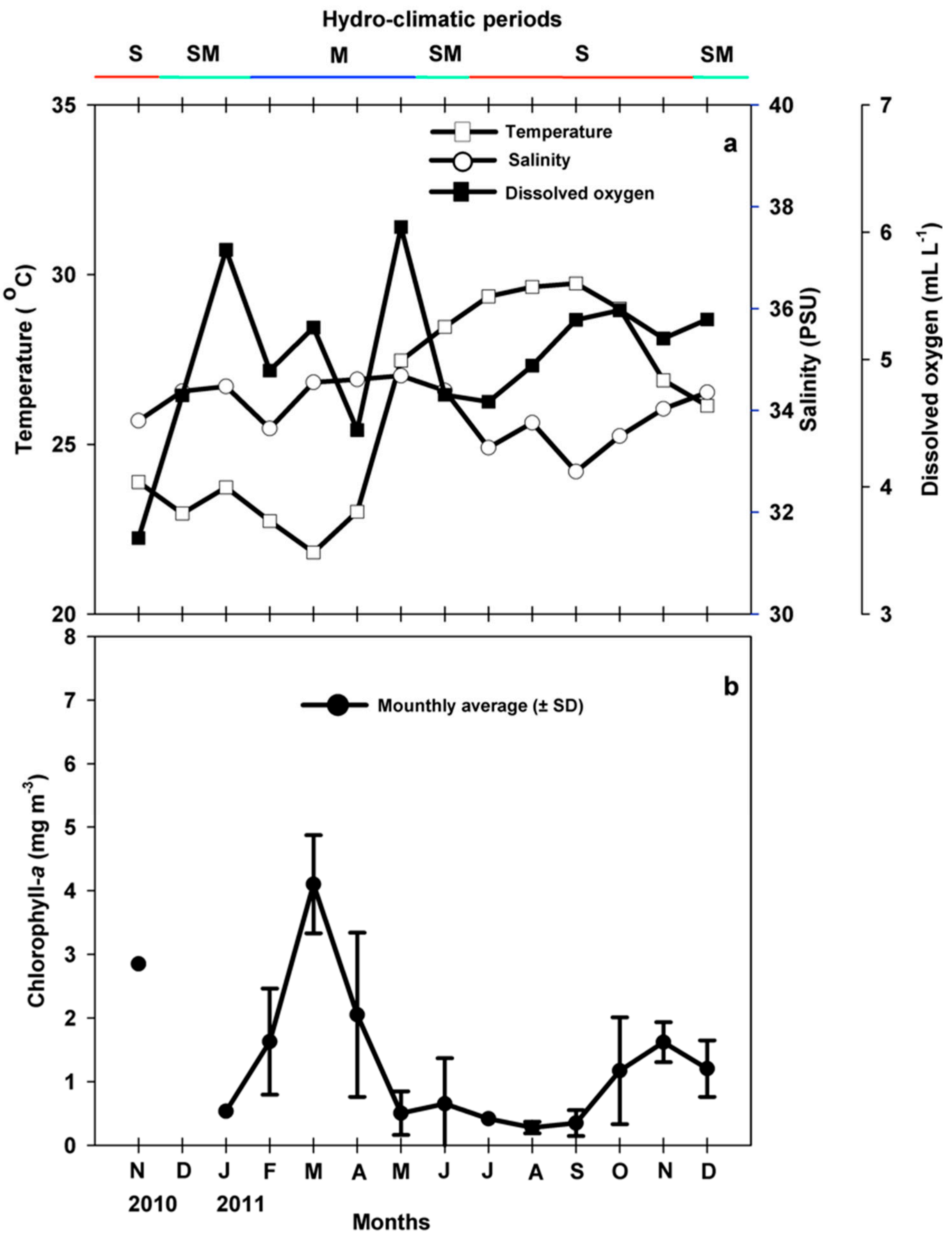

Figure 1. Monthly time series of mean (**a**) 10 m seawater temperature (°C), salinity (PSU), and dissolved oxygen concentration (mL O_2 L^{-1}) and (**b**) 10 m chlorophyll-*a* concentration (mg Chl-*a* m^{-3}; ±SD) recorded at 10 m depth during November 2010–December 2011 in the nearshore region of Navidad Bay, Jalisco, Mexico. Hydroclimatic periods: cold mixing (M, February–May) (blue line), warm stratified (S, July–November) (red line), and semi-mixed transition (SM, January, June and December) (green line).

3.2. Community Structure of Chaetognaths and Their Parasites

A total of 16,407 chaetognaths were collected during the study period. Of the twelve chaetognath species recorded, only five species were found to be parasitized (35 specimens). *Flaccisagitta hexaptera* had the highest prevalence (4.08%) recorded in this study. The overall infection prevalence was 0.21% (16,407 total chaetognaths/35 infected chaetognaths) (Table 1). Nine taxa of endoparasites were observed parasitizing five species of chaetognaths (Figure 2a–i and Figure S2a–i). *F. enflata* was infected by four taxa of parasites: Protist sp. 1, Hemiuridae, Tetraphyllidea sp. 1 y Tetraphyllidea sp. 2. *S. pacifica* was infected by two taxa of parasites: Protist sp. 1 y Protist sp. 2. *Parasagitta euneritica* was the species with the highest parasite richness, with five different taxa of parasites recorded: Protist sp. 1, Didymozoide sp., *Parahemiurus* sp., Hemiuridae sp., and *Prosorhynchus* sp. The chaetognath

Z. bedoti was infected with three taxa of parasites: Didymozoide sp., Hemiuridae sp., and Tetraphyllidea sp., while *F. hexaptera* was infected by three taxa of parasites: Didymozoide sp., Lepocreadiidae sp., and Tetraphyllidea sp. (Table 2).

Table 1. Total number of chaetognaths collected at Navidad Bay (November 2010–December 2011). Parasitized chaetognath species are shown in bold.

Species and Authority	Number of Analyzed Chaetognaths	Number of Parasitized Chaetognaths (Hosts)	Prevalence of Parasites (%)
Aidanosagitta neglecta (Aida, 1897)	17	0	0
Aidanosagitta regularis (Aida, 1897)	135	0	0
Aidanosagitta septata (Doncaster, 1903)	444	0	0
Ferosagitta robusta (Doncaster, 1903)	46	0	0
***Flaccisagitta enflata* (Grassi, 1881)**	**1015**	**8**	**0.79**
***Flaccisagitta hexaptera* (d'Orbigny, 1843)**	**147**	**6**	**4.08**
***Parasagitta euneritica* (Alvariño, 1962)**	**7317**	**16**	**0.22**
Serratosagitta bierii (Alvariño, 1961)	34	0	0
***Serratosagitta pacifica* (Tokioka, 1940)**	**397**	**3**	**0.76**
***Zonosagitta bedoti* (Beraneck, 1895)**	**6542**	**2**	**0.03**
Krohnitta pacifica (Aida, 1897)	19	0	0
Pterosagitta draco (Krohn, 1853)	294	0	0
Total number of chaetognaths analyzed (N)	16,407		
Total number of parasitized chaetognaths analyzed (np)		**35**	
Total prevalence % [(np/N) × 100]			**0.21**

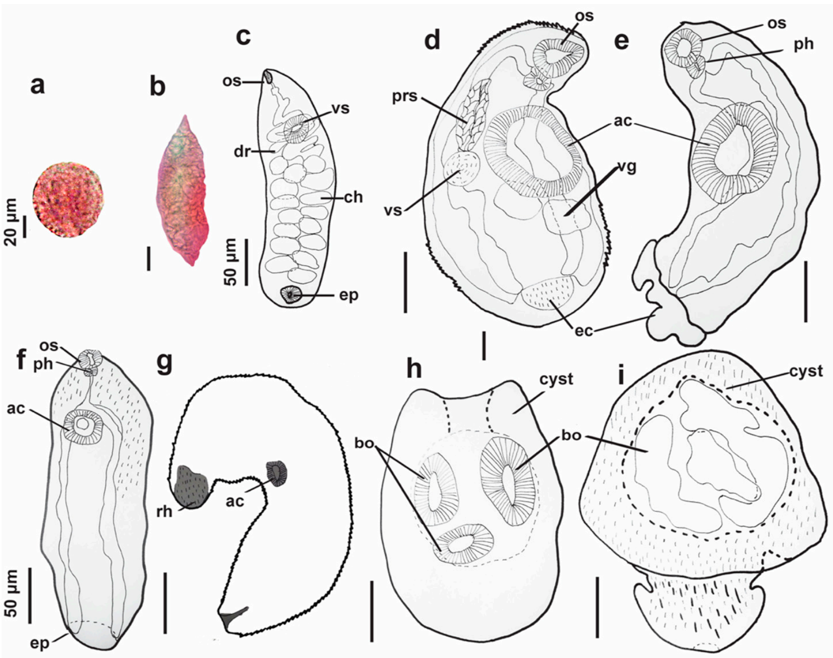

Figure 2. Diagram of the nine taxa of endoparasites that were found infecting five species of chaetognaths collected November 2010–December 2011 at Navidad Bay, Jalisco, Mexico. (**a**) unidentified Protist sp. 1, (**b**) unidentified Protist sp. 2; (**c**) Didymozoidae gen. sp. metacercariae, (**d**) *Parahemiurus* sp. metacercariae, (**e**) Hemiuridae gen. sp. metacercariae, (**f**) Lepocreadiidae gen. sp. metacercariae, (**g**) *Prosorhynchus* sp. metacercariae, (**h**) Tetraphyllidea sp. 1 metacestode, (**i**) Tetraphyllidea sp. 2 metacestode. Scale bar = 20 µm (**a**,**b**) and 50 µm (**c**–**i**). Abbreviations: ac = acetabulum; bo = bothrid muscular; ch = chamber caecum; dr = "Drusenmagen"; ec = ecsoma; os = oral sucker; ep = excretory pore; ph = pharynx; prs = prostatic cells; rh = rynchus; vg = vitellogenic glands; vs. = seminal vesicle.

Table 2. Taxa of parasites, total number of parasitized chaetognaths, prevalence of chaetognaths (%), and intensity of parasites found in five out twelve chaetognaths species collected during November 2010–December 2011 in the Bahía de Navidad, Jalisco, Mexico.

Parasite Taxa	Chaetognath Host Species	Prevalence of Infection (%)	Intensity (No. Parasites per Host)
Protist sp. 1 (Ciliata)	*Flaccisagitta enflata*	0.10	1
	Serratosagitta pacifica	3.02	12
	Parasagitta euneritica	0.04	3
Protist sp. 2	*Serratosagitta pacifica*	1.01	4
Didymozoide sp. (metacercariae)	*Parasagitta euneritica*	0.10	7
	Zonosagitta bedoti	0.03	2
	Flaccisagitta hexaptera	0.69	1
Parahemiurus sp. (metacercariae)	*Parasagitta euneritica*	0.07	5
Hemiuridae sp. (metacercariae)	*Zonosagitta bedoti*	0.02	1
	Flaccisagitta enflata	0.10	1
	Flaccisagitta hexaptera	2.07	3
	Parasagitta euneritica	0.08	6
Lepocreadiidae sp. (metacercariae)	*Flaccisagitta hexaptera*	0.69	1
Prosorhynchus sp. (metacercariae)	*Parasagitta euneritica*	0.01	1
Tetraphyllidea sp. 1 (metacestode)	*Flaccisagitta enflata*	0.49	5
	Flaccisagitta hexaptera	2.76	4
	Zonosagitta bedoti	0.02	1
Tetraphyllidea sp. 2 (metacestode)	*Flaccisagitta enflata*	0.10	1

3.3. Seasonal Variability of Chaetognath and Parasite Abundances

Monthly prevalences were higher during June (2.5%, semi-mixed period), August and September (1%, stratified period), and April 2011 (1%, mixed period) than during the rest of the time series (Figure 3a). Of the five parasitized chaetognaths species, *P. euneritica* (0.111 ind. m^{-3}), and *F. enflata* (0.024 ind. m^{-3}) were considerably more abundant than *F. hexaptera* (0.024 ind. m^{-3}), *S. pacifica* (0.027 ind. m^{-3}), and *Z. bedoti* (0.10 ind. m^{-3}) (Figure 3a). The abundance and species composition of the parasites and their hosts changed during the winter semi-mixed transitional hydroclimatic period (SM, December). In December, the chaetognath species *S. pacifica*, *F. enflata*, and *P. euneritica* were found to be parasitized by two to three species of Protist spp., Didymozoidae sp., and/or Tetraphyllidea sp.1), with Protist sp.1 being the numerically dominant parasite taxon in terms of abundance, whereas no parasites were found in January (Figure 3a,b). In the cold mixing (M, February–May) and warm stratified (S, July–November) periods, the number of chaetognath species in which parasites were found was minimal, with one to two species (Figure 3a). In contrast, the number of parasite species was one to two in the cold mixing vs. one to four in the warm stratified periods (Figure 3b).

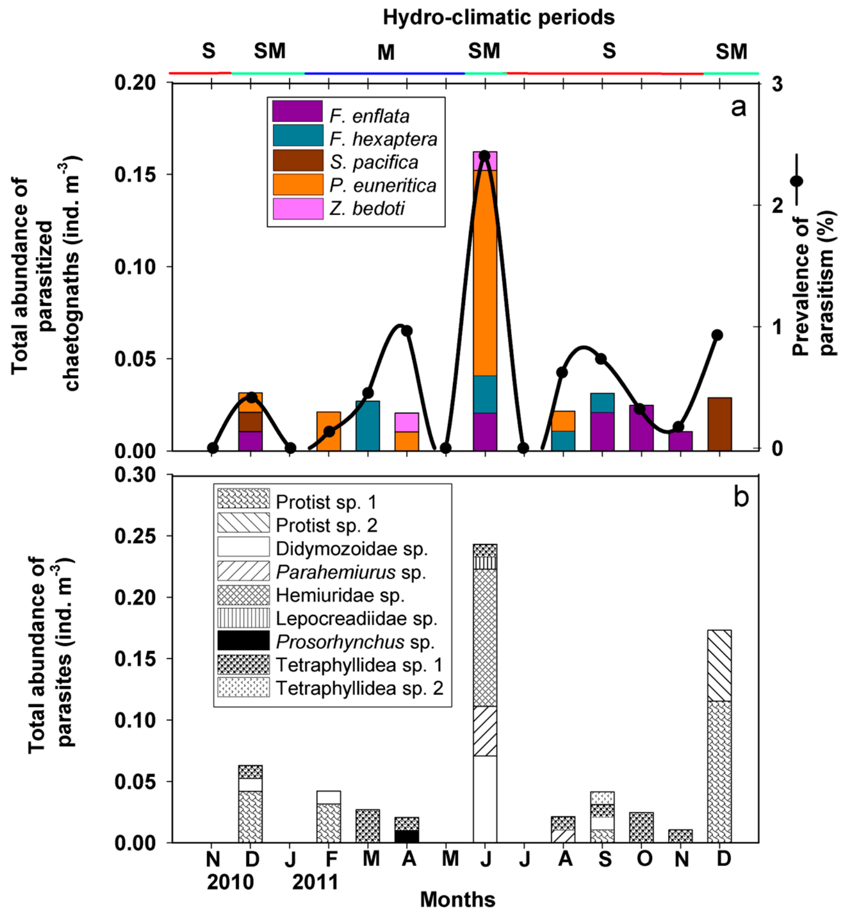

Figure 3. Seasonal variability of the (**a**) total abundance of parasitized chaetognaths and (**b**) total abundance of parasites collected monthly during November 2010–December 2011 in the nearshore region of Navidad Bay, Jalisco, Mexico. Hydroclimatic periods: cold mixing (M, February–May), warm stratified (S, July–November), and semi-mixed transition (SM, January, June, and December).

3.4. Seasonality of Parasitized Chaetognaths

The CCA triplot segregated the zooplankton samples into clusters according to the three hydroclimatic periods (stratified, semi-mixed, and mixed; Figure 4). A Monte Carlo test indicated that species–environment correlations for only the first axis were statistically significant (p = 0.063) and explained a low portion of the total variance (11.2%) for chaetognath abundance and parasitized chaetognaths vs. parasites as a function of the seasonal environmental temporal gradients that prevailed during the zooplankton time series (Figure 4, Table 3). The axis was strongly correlated with 10 m-Temp and deep mixed layer (MLD) but negatively correlated with 10 m-Chl-*a*, upwelling index 15 before sampling day (15-CUI), and zooplankton displaced biovolume (ZDB).

Eight chaetognath species (Serratosagitta pacifica, Ferosagitta robusta, Pterosagitta draco, Serratosagitta bierii, Aidanosagitta septata, Flaccisagita enflata, Aidanosagitta neglecta, and Flaccisagitta hexaptera), two parasitized chaetognath species (Flaccisagitta enflata, and Serratosagitta pacifica), and two taxa of parasites (Tetraphyllidea sp. 2 and Protist sp. 1) were associated with warm temperatures and low zooplankton displaced biovolume conditions, typical of the conditions that prevailed during the stratified and semi-mixed periods. In contrast, *Parasagitta euneritica* and *Zonosagitta bedoti* parasitized *Flaccisagitta hexaptera*, and the parasite Tetraphyllidea sp. 1 correlated with this first axis, which is associated with the cooler temperatures and high zooplankton displaced biovolume that occurred mostly during the mixed period. Three parasitized chaetognaths species (*Serratosagitta pacifica*, *P. euneritica*, and *Z. bedoti*) and several parasites (i.e., Tetraphyllidea sp. 1, Prosorhynchus sp., Didymozoidae sp., Lepocreadiidae sp., Hemiuridae sp., Parahemiurus sp., Protist sp. 2) were primarily found in samples from the mixed period (Figure 4, Table 3).

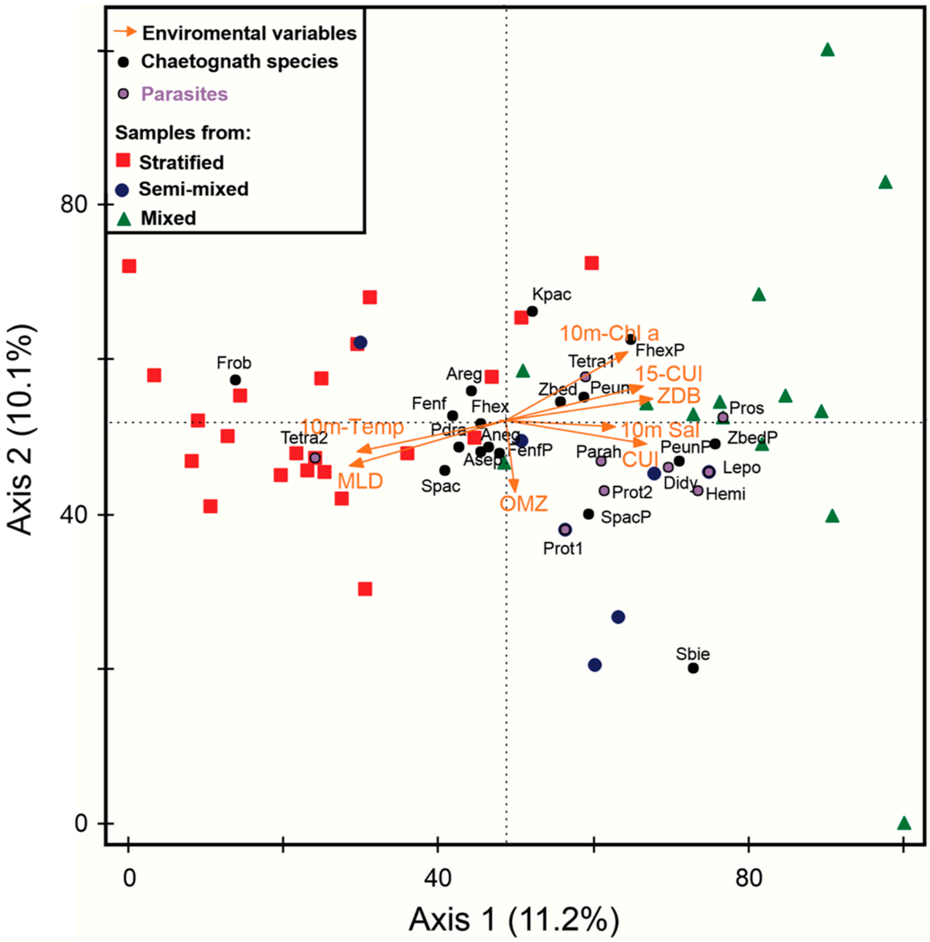

Figure 4. Canonical correspondence analysis using eight environmental variables and abundances of 26 taxa (chaetognaths, parasitized chaetognaths, and parasites) collected from 43 zooplankton samples during November 2010–December 2011 bi-weekly time series located in the nearshore region of Navidad Bay, Jalisco, Mexico. Environmental variables (orange arrow): temperature at 10 m (10 m-Temp), salinity at 10 m (10 m-Sal), depth of mixing layer (MLD), daily coastal upwelling index (CUI) ($m^3\ s^{-1}$ per 100 m of coastline), coastal upwelling index 15 days before the sampling day (15-CUI) ($m^3\ s^{-1}$ per 100 m of coastline), zooplankton displacement biovolume (ZDB), oxygen minimum zone (OMZ), and 10 m chlorophyll-*a* concentration (10 m-Chl-*a*). Chaetognath species (black circle): *Ferosagitta robusta* (Frob), *Aidanosagitta regularis* (Areg), *A. neglecta* (Aneg), *A. septata* (Asep), *Flaccisagitta enflata* (Fenf), *F. hexaptera* (Fhex), *Pterosagitta draco* (Pdra), *Serratosagitta pacifica* (Spac), *S. bierii* (Sbie), *Krohnitta pacifica* (Kpac), *Zonosagitta bedoti* (Zbed) and *Parasagitta euneritica* (Peun). Chaetognath parasitized species (spP black circle): *F. enflata* (FenfP), *F. hexaptera* (FhexP), *S. pacifica* (SpacP), *P. euneritica* (PeunP) and *Z. bedoti* (ZbedP). Parasites taxa (purple circle): Protist sp. 1 (Prot1), Protist sp. 2 (Prot2), Didymozoidae gen sp. (Didy), *Parahemiurus* sp. (Parah) Hemiuridae gen sp. (Hemi) Lepocreadiidae gen sp. (Lepo) *Prosorhynchus* sp. (Pros) Tetraphyllidea sp. 1 (Tetra1), and Tetraphyllidea sp. 2 (Tetra2).

Table 3. Canonical correspondence analysis using eight environmental variables and the abundances of 26 taxa (chaetognaths, parasitized chaetognaths, and parasites) collected from 43 zooplankton samples during November 2010–December 2011 bi-weekly time series located in the nearshore region of Navidad Bay, Jalisco, Mexico. Species–environment correlations were only significant for the first axis ($p = 0.063$; Monte Carlo randomization test). The Pearson correlation ≥0.40 with each ordination axis is shown in bold.

Environmental variables/Ordination axes	1	2	3
Eigenvalues	0.115	0.105	0.052
Cumulative variance % explained	11.2	21.3	26.3
Species–environment Pearson correlations	0.741	0.762	0.634
Species–environment Kendall correlations	0.584	0.497	0.373
Intra-set correlations of environmental variables with species axes			
10 m Temperature (10 m-Temp)	**0.816**	−0.185	−0.079
10 m Salinity (10 m-Sal)	−0.370	0.367	**−0.431**
Mixed layer depth (MLD)	**0.706**	−0.258	**−0.490**
Upper boundary of the OMZ (OMZ)	0.352	**0.490**	−0.365
CUI in the zooplankton sampling day (CUI)	−0.394	**0.579**	0.273
CUI-15 days before zooplankton sampling (15-CUI)	**−0.661**	0.299	−0.363
10 m Chlorophyll-*a* concentration (10 m-Chl-*a*)	**−0.828**	−0.083	0.145
Zooplankton displaced biovolume (ZDB)	**−0.691**	0.192	0.105

The second axis explained 10.5% of the total cumulative variance and, although there were no significant correlations with environmental variables, the axis was positively associated with the upwelling index 15 before sampling day (CUI) and the upper boundary of the OMZ (shallower depth) recorded in the study area.

4. Discussion

4.1. Component Community of Parasites

The parasitized chaetognaths (*F. enflata*, *F. hexaptera*, *P. euneritica*, *S. pacifica*, and *Z. bedoti*) recorded in the present study time series exhibited a three-fold lower parasite diversity (nine taxa) than that previously reported offshore at the shelf-break of the Central Mexican Pacific (twenty-eight taxa) [11,12].

Despite the lower diversity recorded, we discovered the occurrence of the digenean *Prosorhynchus* sp. (Bucephalidae) parasitizing the chaetognath *P. euneritica*. This is the first report of *Prosorhynchus* parasitizing chaetognaths worldwide [10,11,19]. However, it is likely that this infection was accidental because only a single specimen was found among the 16,407 chaetognath specimens analyzed, and it is known that Bucephalidae larvae typically parasitize benthic molluscs as their first intermediate host, followed by marine fish as secondary intermediate and definitive hosts [29,30].

We also confirmed the presence of Lepocrediidae (metacercariae larval stage) parasitizing chaetognaths in the Pacific Ocean. Lozano-Cobo et al. [11] reported *Lepocreadiidae*, metacercariae from the chaetognath *F. enflata* in the Mexican Central Pacific; however, in the present study, we found it infecting the chaetognath *F. hexaptera*. With the exception of these two records, metacercariae of Lepocreadiidae have been known only as parasites of Atlantic Ocean chaetognaths: *viz*., *Parasagitta setosa* and *P. elegans* from the English Channel, United Kingdom [31], *Sagitta* sp. and *P. elegans* in the North Sea [29,32,33], *Sagitta* sp., off the coasts of Denmark [34], *F. enflata* from the Indian Ocean [35], *P. friderici* in Mar de Plata, Argentina [35,36], and parasitizing *Ferosagitta hispida* and *F. enflata* from the Yucatan Peninsula, Mexico [11].

The rest of the platyhelminth parasites found in the present study (Digeneans: Didymozoidae sp., *Parahemiurus* sp., Hemiuridae sp., and Cestodes: Tetraphyllidea sp. 1, Tetraphyllidea sp. 2) have been previously reported from the self-break of the studied area in the Eastern Tropical Pacific [11,12], and also from the Yucatan Peninsula [10,19,37,38]. All of these reports suggest that infection by Lepocreadiidae metacercariae stages in chaetognaths is widespread worldwide. Our record of *Prosorhynchus* sp. increases our knowledge of the parasite community infecting pelagic chaetognaths in the Eastern Tropical Pacific, where instances of acanthocephalans parasitizing chaetognaths were recently discovered [10].

Jarlin and Kapp [39] found a low prevalence (0.21%, n = 8600 chaetognath individuals) of metacercaria *Cercaria owreae*, *Ectenurus lepidus* in the larval stage, and other ciliates from chaetognaths collected at Great Meteor Bank on the Atlantic Ocean. This low prevalence is comparable to the prevalence of parasite value estimated in the present study (35 out of 16,407 chaetognaths, 0.21% infected), indicating the typically low prevalence found in zooplankton organisms.

4.2. Parasite–Host Abundance and Prevalence Relationship

We demonstrated that, except for *Flaccisagitta hexaptera*, the prevalence of parasitized chaetognaths was extremely low (0.0001–0.8%) in the nearshore area of the Central Mexican Pacific. In contrast, Lozano-Cobo et al. [11] reported a density-dependent relationship between parasites and their chaetognath hosts in shelf-break waters of the study area, harboring a pelagic community with higher host and parasite diversity, prevalence, and abundance. The trophically transmitted parasites of chaetognaths observed in the coastal system (present study) (0.21%) and in the shelf-break area (2.3%) of the Jalisco coast were within the expected low prevalence values (<3%) for zooplanktonic carnivores of low trophic levels [10,11,19,39]. The prevalence of parasites typically increases substantially in final hosts, up to >80% in populations of blue whales and fin whales in the Gulf of California [40].

This richness and prevalence patterns observed in the shelf-break [11] and nearshore Jalisco coast (present study) agree with the cross-shelf gradients of chaetognath species assemblages observed in the Caribbean Sea, with higher species diversity and, therefore, potentially higher parasite diversity in shelf-break waters than in nearshore waters [10,11,19]. Other parasitological studies with short sampling periods (<four months) in the western Caribbean Sea also show a considerably lower prevalence of endoparasites in chaetognaths (0.004–0.084%) [38,39,41,42]. This seems to be a problem relating to small zooplankton sampling sizes because a two-year monthly survey in the Caribbean Sea recorded 33 taxa parasitizing five chaetognath species with a moderately high prevalence rate (6%) [10,19]. It is interesting to note that we can indirectly infer an interspecific density-dependent relationship, as numerically dominant chaetognath species, such as *P. euneritica* (44%), *Z. bedoti* (40%), and *F. enflata* (6%), were parasitized, while low abundance chaetognaths (<2.9%) were not found parasitized. This is probably a result of the low likelihood that a parasite will find an individual of a rare chaetognath species and that an infection will occur, adding to the low likelihood of collecting such a sample.

Host population density is one of the main factors influencing population control in terms of the density and prevalence of trophic-transmitted endoparasites [11,43]. However, it is relevant to note that, in the present study, only five of the twelve chaetognath species were parasitized (42%), but these five species were the most abundant overall. However, in shelf-break waters, from the nine chaetognaths collected, seven of them were parasitized (78%), indicating that endoparasites in both regions may be parasitizing the most abundant chaetognath species populations. Thus, it can be predicted that in an isolated monospecific chaetognath community like that of *F. hispida* located in a lagoonal system on the Mexican Caribbean coast [44], parasite diversity will be low. Based on our results, we infer that there is a more complex food web at the shelf-break [11] than in the surveyed coastal system in the central Mexican Pacific. Therefore, although the diversity of the species of chaetognaths recorded in the present study was high (12 species), representing 75% of the 16 species of chaetognaths previously recorded in the Central Mexican Pacific [11] and 34% of the chaetognath species richness recorded in the Eastern Tropical Pacific [11–19,45–47], the parasite diversity was three-fold lower than that reported in previous studies in the shelf-break waters of Jalisco [10,11,19]. Thus, this study is likely an adequate representation of the chaetognath species known for the northern boundary of the Eastern Tropical Pacific.

Finally, all of the parasite species showed considerably low prevalences, which is a common finding in marine zooplankton, where the number of hosts is reduced in relation to the habitat size.

5. Conclusions

Prevalence and parasite abundance (ind. m^{-3}) showed a density-independent relationship with their chaetognath host species throughout the year, with high chaetognath abundance and low parasite prevalence in the nearshore region of the Mexican Central Pacific. This implies that parasites have large available populations, but for ecological (mismatch in time or space) or biological (immune system or behavior) reasons yet to be studied, parasites infect these large host populations in low proportion. This study provides unprecedented records of parasites taken from chaetognaths both at worldwide and regional scales. However, factors such as the total study time (only 13 months) and the low prevalence of endoparasites 0.21% (35/16,407) demonstrate that a longer study time accompanied by physical–chemical analyses and greater sampling effort is necessary to sustain this approach. It is still unclear how environmental variables can influence parasite species and their hosts. There are global approaches used to study responses to climate change, but at the regional or mesoscale level, the response of parasites to physical factors is practically unknown. In a pelagic environment, microorganisms are exposed to a multitude of dynamic factors. Investigating the life cycle of any kind of parasite is complex, time consuming, and conceptually challenging. Molecular methods can only help identify the larval stages of parasites infecting zooplankton if adult parasites infecting hosts of higher trophic levels are also studied, matching the gene sequences between larvae and adults.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/parasitologia4030021/s1, Figure S1: Sampling and data collection location of the biweekly zooplankton (November 2010–December 2011) at the NAVI Station at Navidad Bay (BN), coast of Jalisco, Mexico. Figure S2: Diagram of the nine taxa of Endoparasites that infect five species of chaetognaths collected November 2010–December 2011 of Navidad Bay, Jalisco, Mexico; Table S1: Diagnostic taxonomical characteristics and mean body size (TL = total length; W = width) used to identify each type of endoparasite (9 taxa) showing the site infection of chaetognath species collected from November 2010 to December 2011 in Bahía de Navidad, Jalisco, Mexico. Table S2: Relative size relationship between chaetognaths (hosts) and their parasites collected in Navidad Bay during November 2010–December 2011. Gonad development stage was assigned using the 0–V stages classification proposed by Colman [13] and simplified to I–III (immature) and IV (mature) stages by Alvariño [14]. Table S3: Prevalence values and 95% confidence intervals of the infection in five chaetognaths species of the nearshore region of Navidad Bay, Jalisco, Mexico. References [48–55] are cited in Supplementary Materials.

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