

Seasonal variation in chaetognath and parasite species assemblages along the northeastern coast of the Yucatan Peninsula

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ABSTRACT: Chaetognaths are abundant carnivores with broad distributions that are intermediate hosts of trophically transmitted parasites. Monthly variations in chaetognath and parasite species distributions, abundance, prevalence, and intensity related to seasonal environmental changes were recorded in 2004 and 2005 in Laguna Nichupté, a coral reef, and the adjoining continental shelf of Quintana Roo, Mexico. Of 12 chaetognath species plus *Sagitta* spp., only 5 (*Ferosagitta hispida*, *Flaccisagitta enflata*, *Sagitta* spp., *Serratosagitta serratodentata*, and *Pterosagitta draco*) were parasitized. These species were parasitized with 33 types of flatworms and unidentified cysts (likely protozoan ciliates), having an overall mean prevalence of 6%. Digenean metacercaria larvae numerically dominated the parasite assemblages. Cluster analysis defined 2 chaetognath species assemblages. One included 7 species inside Laguna Nichupté, where *F. hispida* was numerically dominant (98.9%); the other contained 13 chaetognath species in the continental shelf–coral reef region, where *F. enflata* was abundant (53%). Canonical correspondence analysis showed that Laguna Nichupté had highly variable and hostile conditions (relatively low salinity and high temperature) for chaetognath species except for *F. hispida*. The higher density of *F. hispida* promoted greater parasite diversity (23 types), dominated by *Brachyphallus* sp. metacercariae. *F. enflata* prevailed in the continental shelf–coral reef area, which had stable high salinity and relatively low temperature. *Monilicaecum* and unidentified digenean ‘type g’ infected 5 chaetognath species on the continental shelf. Distinct primary hosts (mollusks and copepods) and contrasting environmental conditions (salinity, dissolved oxygen concentration, and temperature) between Laguna Nichupté and the continental shelf promoted distinct chaetognath species assemblages, resulting in distinct parasite diversity and prevalence patterns.

KEY WORDS: Endohelminths · Component community · Habitat partitioning · Time series · Caribbean Sea

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INTRODUCTION

Chaetognaths are a major component in zooplankton assemblages worldwide and are recognized as voracious zooplanktophagous predators in the pelagic food web (Reeve 1970). They have a density-dependent influence on their prey populations, such as copepods, that dominate abundance and biomass

in zooplankton assemblages (Feigenbaum & Maris 1984, Villate 1991). Among factors that contribute to explain why chaetognaths are frequent intermediate or paratenic hosts of trophically transmitted endoparasites are that chaetognaths are rapacious and generalist carnivores (even cannibals), they can feed frequently on the first intermediate hosts, and they have relatively high population densities with broad zoo-

geographic patterns (from epipelagic to bathypelagic habitats). Additionally, chaetognaths undertake vertical migrations, which facilitates contact with infected first intermediate mollusk hosts near the bottom in neritic areas, or with infected second intermediate hosts, such as copepods, during their daily vertical migrations (Ho & Perkins 1985, Daponte et al. 2008). Thus, chaetognaths represent a large population biomass for parasites that facilitates parasite transmission from zooplankton to intermediate and final hosts (Ho & Perkins 1985, Gómez del Prado-Rosas et al. 2005, Daponte et al. 2008).

Several helminth parasites affect their chaetognath hosts, causing gigantism and inducing them to swim near the surface, which results in higher vulnerability to planktophagous predators (Pearre 1976, 1979). Parasites also cause wounds in the chaetognath tegument (Nagasawa & Nemoto 1984). Santhakumari (1992) reported that fungal infections change the color of the host, causing dark spots on the tegument of *Flaccisagitta enflata* and *Zonosagitta bedoti*, loss of transparency in the tail of *F. enflata*, and bumps or deformations of the body tegument (tumor-like structures). Øresland & Bray (2005) reported several flatworm parasites infecting chaetognaths and suggested that the polychaetes *Typhloscolex muelleri* and *Travislopsis dubia* explained headless chaetognaths observed in the samples; they also observed the copepod *Microsetella norwegica* infecting the chaetognath head.

Chaetognaths interact with at least 13 taxonomic groups of pathogens, micropredators, and parasites using many trophic strategies; in chronological order of discovery, they are (1) Digenea, (2) Monogenea, (3) Apicomplexa, (4) Nematoda, (5) Amoebozoa, (6) Dinoflagellata, (7) Ciliata, (8) Cestoda, (9) Euglenozoa, (10) Copepoda, (11) Polychaeta, (12) Bacteria,

and (13) Acanthocephala (Lozano-Cobo et al. 2017). Because most chaetognath species have broad geographic patterns, their parasites have been reported in many habitats. However, most reports were serendipitous, non-systematic, or short-term studies (<30 d) consisting of catalogues of parasites found with a description of parasite morphology (Weinstein 1972, Jarling & Kapp 1985). Historical research efforts complicate an emerging ecological perspective about how chaetognath species assemblages influence their parasitic species assemblages. Poulin (2007) argued that integrative parasitological studies might help to reveal consistent patterns detectable across taxa or geographical areas. Systematic zooplankton time series provide a geographically explicit and time dynamic perspective about parasite–host interactions in pelagic habitats.

To our knowledge, all monthly time series of chaetognath and parasite abundance and prevalence have been recorded in temperate coastal ecosystems (Kulachkova 1972, Weinstein 1972, Øresland 1986, Ohtsuka et al. 2004, Daponte et al. 2008) (Table 1). Kulachkova (1972) reported the prevalence of 6 parasite species of *Sagitta elegans*, currently valid as *Parasagitta elegans*, in Chupa Bay in the White Sea (1966–1969): *Brachyphallus crenatus*, *Derogenes varicus*, *Hemiurus levinseni*, *Scolex pleuronectis*, *Pseudophyllidea* sp., and *Contraecum* sp. Weinstein (1972) did a comprehensive study southwest of the St. Lawrence Seaway (1965–1966, 1968) about the component community of parasites of the numerically dominant chaetognath *P. elegans*. The ciliate *Metaphrya sagittae*, the metacercariae of *H. levinseni*, and a hemiurid trematode were common parasites of *P. elegans*, while the metacercariae of the hemiurid *D. varicus* were less common and the larvae of a *Contraecum*-type nematode and the cestode larvae of

Table 1. Synthesis of parasites recorded infecting chaetognaths during previous systematic zooplankton time series in the world oceans. Current valid chaetognath species names are given in parentheses

Reference	Time series	Study area	Host species	Parasites recorded
Kulachkova (1972)	1966–1969	Chupa Bay, White Sea, Russia	<i>Sagitta elegans</i> (<i>Parasagitta elegans</i>)	Digenea, Cestoda, Nematoda
Weinstein (1972)	1965–1966, 1968	Gulf of Saint Lawrence, Canada	<i>Sagitta elegans</i> (<i>Parasagitta elegans</i>)	Ciliata, Digenea, Cestoda, Nematoda
Øresland (1986)	1982–1983	Plymouth, England	<i>Sagitta setosa</i> (<i>Parasagitta setosa</i>)	Protozoa, Digenea, Cestoda, Nematoda
Ohtsuka et al. (2004)	1999–2000	Seto Inland Sea, Japan	<i>Sagitta crassa</i> (<i>Aidanosagitta crassa</i>), <i>Sagitta enflata</i> (<i>Flaccisagitta enflata</i>), <i>Sagitta nagae</i> (<i>Zonosagitta nagae</i>)	Ciliata
Daponte et al. (2008)	2000–2001	Mar del Plata, Argentina	<i>Sagitta friderici</i> (<i>Parasagitta friderici</i>)	Digenea, Cestoda, Nematoda

Scolex pleuronectis were quite rare. Øresland (1986) sampled 2 or 3 times per month in 1982 and 1983 off Plymouth, England, discovering 8 parasite species of *Parasagitta setosa*: the nematode *Hysterothylacium aduncum* (56% of all parasites), 5 digeneans (the hemiurids *Derogenes varicus* and *Lecithochirium* sp., the fellodistomid *Monascus filiformis*, a didymozoid, and a trematode-like *Adolescaria progastrica*), 1 cestode, and a possible protozoan. Parasites did not affect chaetognath reproduction or cause morphological injuries. In a time series in 1999–2000 in Seto, Japan, Ohtsuka et al. (2004) investigated a histophagous parasitic ciliate of copepods, *Vampyrophrya pelagica*, that eats the copepod carcass after the ciliates excyst in the gut of their chaetognath predators. The most recent monthly time series of chaetognaths and their parasites was carried out in the southern hemisphere at a site on the coast of Argentina in 2000–2001, where only 1 species (*Parasagitta friderici*) was collected (Daponte et al. 2008). *P. friderici* was infected with 7 types of larval parasites (plus 1 unidentified species): *Derogenes* sp., *Ectenurus virgulus*, Lepocreadiidae, *Monascus filiformis*, *Parahe-miurus merus*, and tetraphyllidean plerocercoids, as well as the copepod *Corycaeus amazonicus* attached to the body of chaetognaths (Daponte et al. 2008). All parasites of these 5 time series had low prevalences (<6%), which is a common finding in the marine pelagic habitat, where the number of hosts is relatively small in relation to the water volume. The parasite diversity of temperate chaetognath species seems to be low (<9 species) (Kulachkova 1972, Weinstein 1972, Øresland 1986, Ohtsuka et al. 2004, Daponte et al. 2008) (Table 1). Because previous time series studies have been monospecific, it is currently unknown how parasite species assemblages change among host chaetognath species over time, particularly in contrasting habitats where distinct chaetognath species dominate in abundance. Currently, it is unknown how parasitic species diversity interacts with chaetognaths in tropical latitudes. In this study, we analyzed tropical chaetognaths and their parasite assemblages in a shallow lagoon and adjacent continental shelf in the Caribbean Sea in 2004–2005.

Parasitism in chaetognaths in Mexico has been studied along the east coast of the state of Quintana Roo (Yucatan Peninsula), reporting digenean larvae infections (in cercaria and metacercaria stages) (Gómez del Prado-Rosas et al. 1999a,b, 2000, 2002, 2005, 2007b). These taxonomic studies, mostly larval stage descriptions, were relevant for further ecological studies about spatial and seasonal variability of the chaetognath–parasite interaction, such as abun-

dance and prevalence associated with contrasting environmental conditions. In the western Caribbean Sea, changes in chaetognath abundance are closely related to the dry and rainy seasons (Álvarez-Cadena et al. 2007, 2009). We analyzed a systematic monthly time series at 12 stations to study spatial and seasonal variability of helminth parasite and host interactions and to test the hypothesis that chaetognath species assemblages, inhabiting different habitats, may also promote distinct parasite species assemblages, especially a density-dependent association. We tested this hypothesis by comparing abundance and diversity of chaetognaths and their parasite species assemblages in a low-salinity shallow lagoon and in adjacent continental shelf–coral reef habitats. Our main goals were to (1) describe variability of chaetognath and helminth parasite habitats and seasons in terms of diversity, abundance, prevalence, and mean intensity, comparing a shallow, tropical lagoon with the adjacent continental shelf and coral reef habitats, and (2) quantitatively analyze host and parasite species assemblages (component community) as a function of temperature, salinity, pH, concentration of dissolved oxygen, and seasonal and annual rainfall periods in 2004 and 2005. This analysis could indicate that environmental factors among different habitats and seasons enhance chaetognath host abundance and how host abundance drives diversity, prevalence, and abundance of their parasite species assemblages.

MATERIALS AND METHODS

Sampling and study area

Our study area was the northeastern coast of the Yucatan Peninsula, covering a 50 km shore zone from Puerto Morelos to Cancún (20° 55' to 21° 05' N, 86° 40' to 86° 50' W; Fig. 1). This area is part of the second largest coral reef system of the world. Monthly zooplankton collection was conducted in 2004 and 2005 at 12 sampling stations in 3 interconnected areas: the Laguna Nichupté (area 48×10^6 m², 2.2 m mean depth, 4 sites), the continental shelf, without coral reefs (2 sites), and coral reefs (6 sites); the latter 2 areas had a seafloor depth <30 m (Fig. 1). Laguna Nichupté has a low tidal range (3–20 cm). The lagoon system is connected to the open sea through 2 narrow and shallow inlets (Cancún: 4 m deep, 30–40 m wide; Nizuc 3 m deep, 20–30 m wide) that promote relatively long flushing times (1.3–1.9 yr), with a characteristic east–west gradient in low salinity caused by ground-

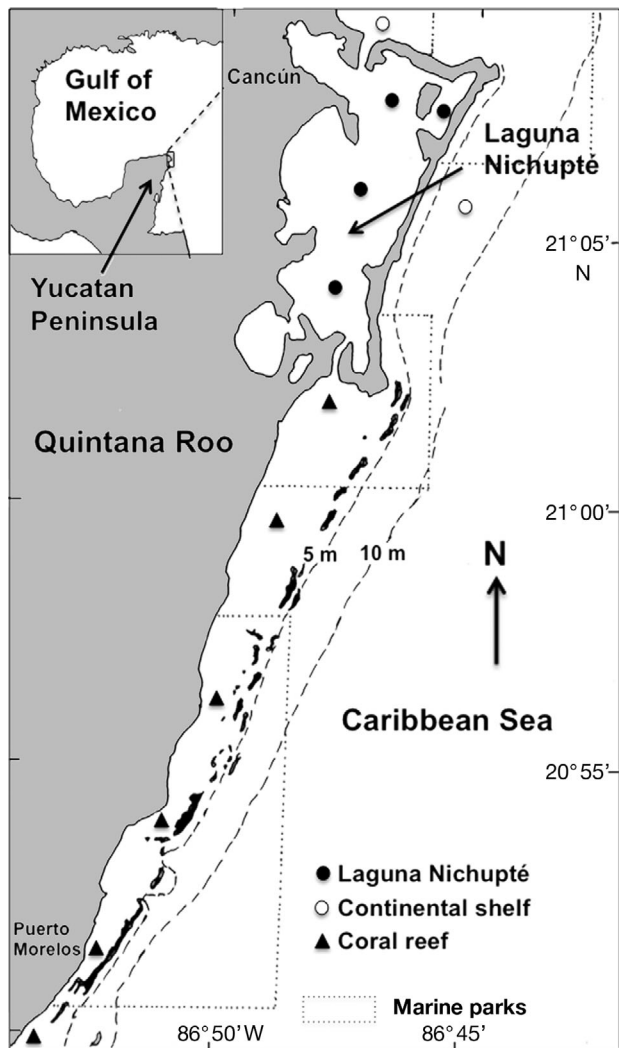


Fig. 1. Sampling stations in the Laguna Nichupté, continental shelf (without coral reefs), and coral reef areas where near-surface zooplankton were sampled every month from January 2004 through December 2005 in the State of Quintana Roo, Mexico

water discharge and rainfall, but with no significant vertical salinity gradient (Merino et al. 1990). In the Quintana Roo coastal area there is a prevailing northward current with a velocity of $>0.6 \text{ m s}^{-1}$ that eventually becomes part of the Yucatan Current, which enters the Gulf of Mexico (with transient, low-intensity countercurrents) (Merino 1986, Athie et al. 2011).

Zooplankton samples were collected in a conical zooplankton net (0.42 m mouth diameter, 1.2 m long, 330 μm mesh), towed near the surface (first 5 m) for 5 min in a circular path at a mean speed of 67 m min^{-1} . The filtered seawater volume (m^3) was estimated following standard methods (Smith & Richardson 1977). All samples were fixed in 4% formaldehyde solution

and then neutralized with saturated sodium borate to fix the chaetognaths and their parasites. Sea surface temperature (SST), salinity, pH, and dissolved oxygen (DO) concentration were measured with a calibrated multi-sensor. Mean and range of SST, salinity, and DO concentration were calculated per month for the entire time series to show seasonal and interannual environmental variability. Monthly mean and standard error of rainfall records from 2004 and 2005 were used to delimit the rainy season (Comisión Nacional del Agua, <http://sig.a.cna.gob.mx/basesdeDatos.aspx>).

Chaetognath and parasite identification and abundance

All chaetognaths were sorted from the entire zooplankton samples and identified to species level, using a standard taxonomic key (McLelland 1989). All chaetognaths were observed under an optical microscope to find parasites. These parasites were sorted for further taxonomic identification. Parasitized chaetognaths were dehydrated in a series of non-denatured ethanol solutions, from 30 to 100%. These chaetognath specimens were stained with Gömöri Trichrome and made transparent with methyl salicylate to observe the internal organs of the parasites. Each parasitized chaetognath was mounted with synthetic resin (xylene, 60%) for permanent slides (Salgado-Maldonado 1979) and photographed with a digital camera (Canon Power Shot A2500). Parasites were identified using taxonomic keys for each type of flatworm parasite (mostly focused on adult phases, rather than larval stages) (Yamaguti 1959, 1961, 1971, Anderson et al. 1974, Khalil et al. 1994, Gibson et al. 2002, Jones et al. 2005, Bray et al. 2008). Parasite and chaetognath total lengths were measured with a stereoscope (Carl Zeiss, SV11, 0.6–6 \times zoom magnification) equipped with a calibrated micrometer.

Total abundance of each chaetognath species and abundance of each parasitized chaetognath species (per type of parasite) was standardized to ind. m^{-3} . Both were averaged per month (12 stations) and year (2004 vs. 2005) for each sampling area to show their geographical and seasonal variability. We conceptually distinguish abundance of parasitized chaetognaths from abundance of parasites because the later requires an estimate of the standardized abundance of parasitized chaetognaths, multiplied per specific parasite intensity (or alternatively, the mean intensity per parasite type). Direct parasite abundance (without inclusion of intensity) is only valid when natural parasite intensity is 1 (i.e. nematodes, acanthocephalans).

Because several parasites have an intensity >1 (i.e. didymozoids and unidentified protozoan cysts), and it is not known if several parasites infect other types of hosts (beside chaetognaths), we analyzed only abundance of parasitized chaetognaths with each type of parasite. Parasite prevalence and mean intensity of infection were calculated according to Bush et al. (1997). Prevalence of all parasites of each chaetognath species was also averaged per month (12 stations) and per year to show seasonal variability in each area.

Data reduction and statistical methods

We estimated the average parasite/chaetognath size proportion (P/C_{sp}), using the parasite mean total length (TL, mm) from specimens analyzed and the maximum chaetognath TL (mm) per host species obtained from McLelland (1989). A simple linear regression model correlated the standardized parasitized chaetognath abundance (PCA) and the standardized total chaetognath abundance (TCA) per sampling station in the 3 areas. In both equations, abundance was expressed as ind. m^{-3} .

The association of TCA and PCA with environmental conditions was analyzed using non-parametric statistics. We prepared 2 matrices: (1) species matrix of abundance of chaetognaths parasitized with each type of parasite (123 sampling stations [rows] and 5 species of chaetognaths infected with 33 types of parasites [columns], including only sampling stations that yielded parasitized chaetognaths), (2) environmental matrix of the 123 sampling stations (rows) and 6 quantitative variables (columns): prevalence (%), temperature ($^{\circ}\text{C}$), salinity, DO concentration (mg l^{-1}), pH, and rainfall (mm mo^{-1}), plus 2 categorical variables: seasons (winter [Nov–Feb], dry [Mar–Jun], and rainy [Jul–Oct]) (Gasca et al. 1996, Álvarez-Cadena et al. 2007, 2008; <http://siga.cna.gob.mx/basesdeDatos.aspx>) and the habitat areas (Laguna Nichupté, continental shelf, and coral reef). Standardized abundance (ind. m^{-3}) of each chaetognath species and parasitized chaetognath species per parasite type were $\log(x + 1)$ transformed to decrease the variance of the data set (McCune et al. 2002).

We used the Sorensen distance measure and β -flexible linkage method ($\beta = 0.25$) for cluster analysis to segregate groups of chaetognath and parasite species, based on similarities of their relative abundance per sampling station (Field et al. 1982, McCune et al. 2002). A multi-response permutation procedure was applied to test for statistically significant differences between sampled groups defined with cluster analy-

sis, based on abundances of parasitized chaetognaths with each type of parasite. Because this is a non-parametric statistical test, it was not necessary to assume that abundances and environmental variables were normally distributed (McCune et al. 2002).

Canonical correspondence analysis (CCA) was carried out to compare environmental variables with distribution and abundance of parasitized chaetognaths and parasites per taxonomic entity. Analysis showed season bi-plot ordination of sampling units, based on parasitized chaetognath species abundance (per parasite type), where vectors of environmental variables represent the relative contribution of total observed variance. Species and sampling stations are the dominant multidimensional patterns in the distribution of species assemblages throughout environmental gradients in time and space (Ter Braak 1986). We were particularly interested in statistically comparing differences in the abundances of chaetognaths and their parasite species between Laguna Nichupté and the continental shelf–coral reef habitats. All statistical analyses were performed using PC-ORD 6 software (McCune et al. 2002).

RESULTS

Environmental conditions

The rainy season occurred from May through October in 2004 and 2005. Anomalously high rainfall occurred from 3 'category 5' hurricanes that caused anomalously low salinities (~ 16) from October through December in the lagoon (Fig. 2A,C). The lagoon had lower SST (except July 2004), was considerably less saline, and had lower DO concentration than the continental shelf–coral reef area (except in April and June 2004 and February and November 2005; Fig. 2B–D). Both years had similar seasonal environmental conditions except during October to December 2005, when the lagoon had anomalously low salinity (Fig. 2C).

Seasonal variability in diversity and abundance of chaetognaths and parasites

During this study, we identified 12 chaetognath species, as well as several *Sagitta* spp. that could only be identified to genus level because they were mostly damaged specimens (Table 2). All species occurred in both years, except *Flaccisagitta hexaptera*, which was found only in 2004, and *Eukrohnia hamata*, which was found only in 2005. The most abundant

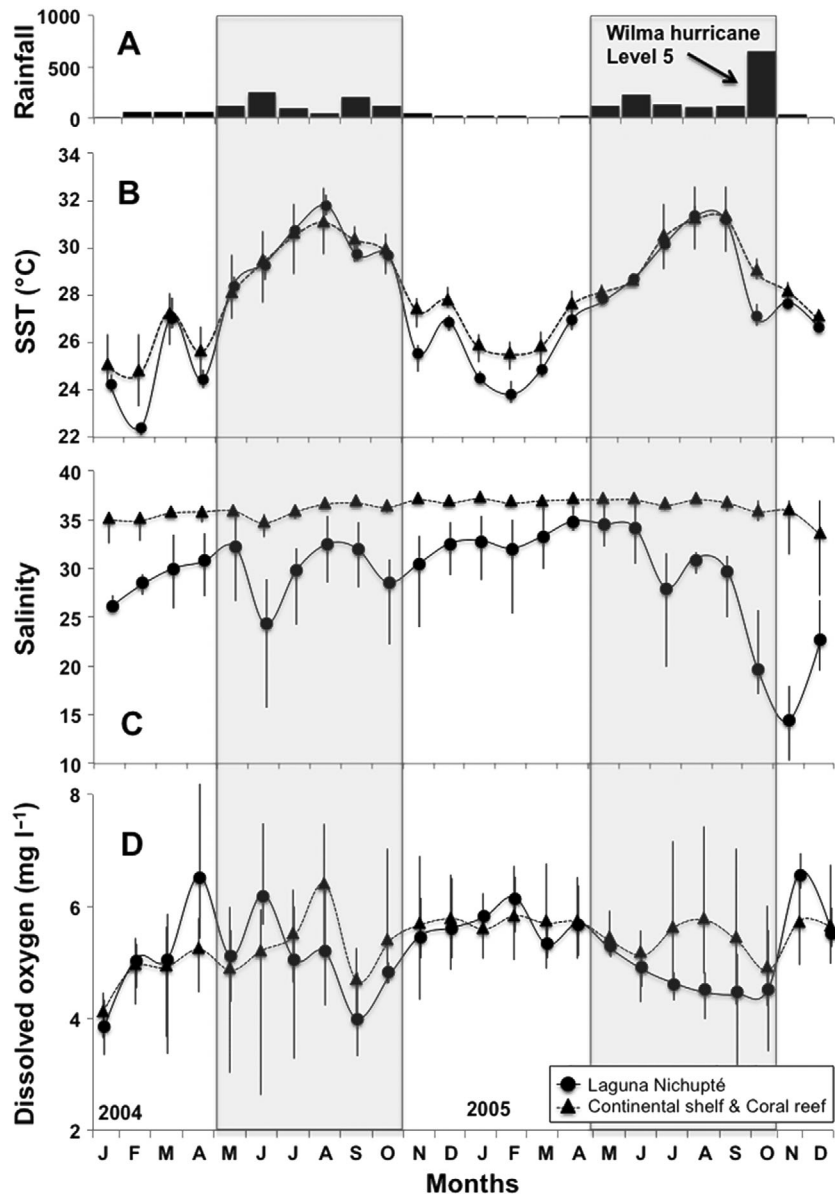


Fig. 2. Monthly time series of mean (symbols) and range (vertical bars) of environmental conditions recorded in Laguna Nichupté and the continental shelf and coral reef areas (Quintano Roo, Mexico) during 2004 and 2005. (A) Rainfall (mm mo^{-1}). The rainy season is shown in gray. On 19 October 2005, Hurricane Wilma (category 5) reached the Yucatan Peninsula. (B) Sea surface temperature (SST, $^{\circ}\text{C}$). (C) Salinity. (D) Dissolved oxygen concentration (mg l^{-1})

species, *Ferosagitta hispida* (87.6%), *Flaccisagitta enflata* (6.6%), and *Sagitta* spp. (2.4%), as well as the fifth (*Serratosagitta serratodentata*, 0.9%) and the seventh (*Pterosagitta draco*, 0.3%) most abundant species were the only species infected with parasites (Table 2, Fig. 3). Of 7 chaetognath species found in Laguna Nichupté, 5 were parasitized. *F. hispida* accounted for 98.9% of the chaetognath population in the lagoon (Fig. 3A,B). On the continental shelf

and in the coral reef, we found 13 chaetognath species; only 5 species were parasitized (*Sagitta* spp. data not shown because they were parasitized only in 2005; Fig. 3D,E).

Abundance of chaetognaths (with and without parasite infection) was generally lower during the rainy season than during the rest of the year (in both years; Fig. 3A,B,D,E). However, prevalence was typically higher during the rainy season than during the rest of the year (in both years; Fig. 3C,F). More parasitized *F. hispida* and *F. enflata* were recorded in 2005 than in 2004; however, overall parasite prevalence was higher in 2004 than 2005 (Fig. 3C,F). *F. hispida* had higher parasite prevalence (7.75%) than the other chaetognath species (*F. enflata* 5.01%, *P. draco* 4.76%, and *S. serratodentata* 0.24%) during 2004. *F. enflata* had higher parasite prevalence (8.99%) than the other chaetognath species (*S. serratodentata* 5.98%, *F. hispida* 5.85%, and *Sagitta* spp. 1.32%) during 2005.

We found highly diverse parasite assemblages (component community), composed of monogeneans, digeneans, cestodes, nematodes, and multiple unidentified protozoan cysts, including 33 distinct types of parasites identified to several taxonomic levels (Tables 3 & 4, Fig. 4). Most flatworm parasites were identified to genus level because helminth larvae have few structures of taxonomic value and there are few taxonomic keys for this life phase. Protozoan cysts and digenean trematodes were the most abundant and prevalent parasites infecting chaetognaths during both years, whereas the prevalence and abundance of cestodes, nematodes,

and monogeneans were lower. One monogenean larva was found at a station in 2004 on the continental shelf; it was an ectoparasite attached by 2 posterior hooks to the tegument of the middle part of the body of an *F. enflata* (Tables 3 & 4). Monogeneans and nematodes had an average intensity of 1 parasite host⁻¹, cestodes and digeneans had a mean intensity ranging between 1.0 and 1.9, and unidentified protozoan cysts had a mean intensity from 1.84 to 3.04 (Table 3).

Table 2. Total number and relative abundance (%) of specimens of each chaetognath species collected and evaluated for the presence of parasites in the northern region of Quintana Roo (Caribbean Sea, Mexico) in 2004 and 2005. Chaetognath species highlighted in **bold** were infected with at least 1 type of parasite

Chaetognath family and authority	Species and authority	2004	2005	Total	Relative abundance (%)
Eukrohniidae Tokioka, 1965	<i>Eukrohnia hamata</i> (Möbius, 1875)	0	3	3	0.0
Krohnittidae Tokioka, 1965	<i>Krohnitta pacifica</i> (Aida, 1897)	505	497	1002	1.5
Pterosagittidae Tokioka, 1965	<i>Pterosagitta draco</i> (Krohn, 1853)	126	44	170	0.3
Sagittidae Claus and Grobben, 1905	<i>Ferosagitta hispida</i> (Conant, 1895)	13 189	45 697	58 886	87.6
	<i>Flaccisagitta enflata</i> (Grassi, 1881)	2477	1935	4412	6.6
	<i>Flaccisagitta hexaptera</i> (d'Orbigny, 1843)	44	0	44	0.1
	<i>Mesosagitta minima</i> (Grassi, 1881)	2	86	88	0.1
	<i>Parasagitta helenae</i> Ritter-Zahony, 1910	7	28	35	0.1
	<i>Parasagitta friderici</i> Ritter-Zahony, 1911	7	16	23	0.0
	<i>Parasagitta tenuis</i> Conant, 1896	189	54	243	0.4
	<i>Sagitta bipunctata</i> Quoy & Gaimard, 1827	1	75	76	0.1
	<i>Sagitta</i> spp.	859	756	1615	2.4
	<i>Serratosagitta serratodentata</i> (Krohn, 1853)	419	184	603	0.9
Total chaetognath specimens analyzed (N)		17 825	49 375	67 200	
Total parasitized chaetognath specimens analyzed (np)		1153	2867	4020	
Prevalence % [(np/N) × 100]		6.47	5.81	5.98	

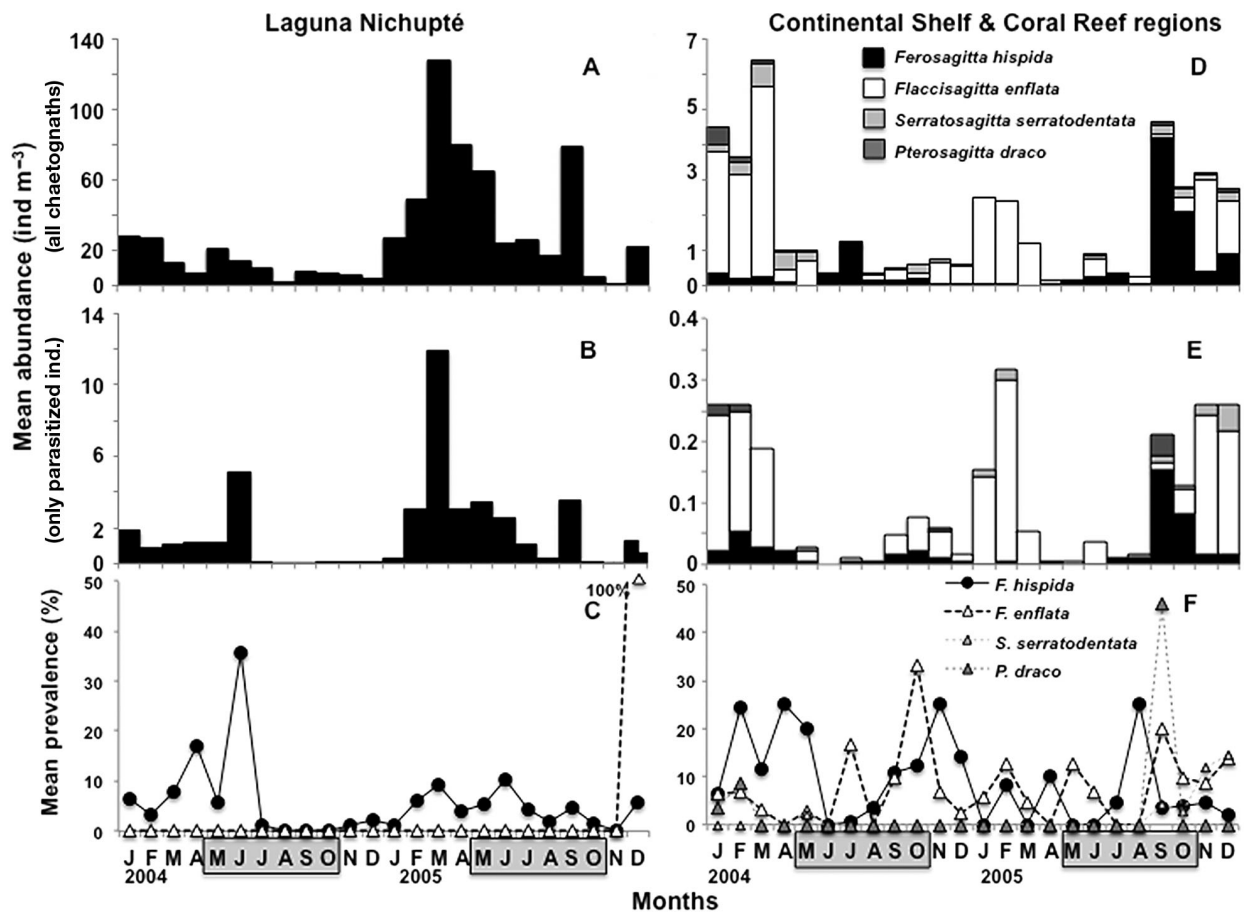


Fig. 3. Monthly mean abundance (ind. m⁻³) of 4 of 5 chaetognath species that were parasitized (*Sagitta* spp. infection is not shown) for (A,D) all individuals and (B,E) only parasitized individuals. (C,F) Prevalence rates per species recorded at Laguna Nichupté and continental shelf–coral reef regions during the 2004–2005 time series. Grey shading indicates rainy season

Table 3. Number of parasitized chaetognath hosts per type of parasite, prevalence (%), number of parasites observed, and mean intensity of each type of parasite that was found to infect chaetognaths in the Caribbean Sea, northern region of Quintana Roo, Mexico (17 825 chaetognaths analyzed in 2004; 49 375 chaetognaths analyzed in 2005). Values shown are results for 2004 / 2005

Parasite type	Total number of parasitized hosts	Prevalence (%)	Total number of parasites	Mean intensity
Monogenea	1 / 0	0.01 / 0	1 / 0	1 / 0
Digenea	343 / 438	1.92 / 0.89	648 / 491	1.89 / 1.12
Cestoda	4 / 7	0.02 / 0.01	6 / 7	1.5 / 1
Nematoda	2 / 1	0.01 / 0	2 / 1	1 / 1
Protozoan cysts	1146 / 2789	6.43 / 5.65	3480 / 5133	3.04 / 1.84

Monthly records showed that abundance of parasitized chaetognaths and richness of parasite species was considerably higher during the dry season than during the May to October rainy season (except in June 2004 when parasitized chaetognaths were also abundant), higher in 2004 than in 2005, and considerably higher in the lagoon than on the continental shelf and coral reef (Fig. 5). Unidentified protozoan cysts and Hemiuridae found favorable conditions to parasitize *F. hispida* and dominated the lagoon parasite assemblage (Fig. 5A,C). *Monilicaecum* (a digenean) and unidentified protozoan cysts were the dominant parasites infecting 5 chaetognath species on the continental shelf and coral reef (Fig. 5B,D). Thus, considerably different parasite assemblages were observed inside and outside the lagoon. Parasitized chaetognath abundance (PCA) had a significant negative density-dependent relationship with total chaetognath abundance (TCA) in the lagoon [PCA = 0.00071 (TCA) – 0.2325 ($r^2 = 0.71$)] and on the coastal shelf and coral reef [PCA = 0.079 Ln (TCA) – 0.0275 ($r^2 = 0.65$)]. This means that higher prevalence rates were mostly observed at sampling stations where chaetognaths had low abundance.

Parasite/host size proportion

The mean parasite-chaetognath host size proportion (P/Csp) of the 5 parasitized chaetognaths was small (0.052) (Table 5). *F. hispida*, with a maximum TL of 12 mm, had the highest mean P/Csp (0.243), while the larger *S. serratodentata* had a mean P/Csp of 0.008, based on the relatively small size of parasites. Although *F. enflata* had the largest maximum TL (25 mm), the mean P/Csp was 0.23 because *F. enflata* was infected with several relatively large parasites, i.e. nematodes and *Procamallanus* species (Table 5). The smallest P/Csp occurred among un-

identified protozoan cysts that were present in all parasitized chaetognath species (Table 5).

Abundance of chaetognaths and parasites associated with environmental conditions

Cluster analysis provided 2 groups of sampling stations at a cutoff at 12% of similarity, based on location and abundance of chaetognaths, parasitized chaetognaths, and composition of parasite species. Species in the first group were numerically dominated by *F. hispida*, which mostly inhabited the lagoon (Group 1: *F. hispida*). Species in the second group, numerically dominated by *F. enflata*, were mostly found on the continental shelf and coral reef (Group 2: *F. enflata*) (Fig. 6).

Group 1 was divided into 2 subgroups, of which one included only sampling stations from the lagoon (both years), where *F. hispida* was present in high abundance and *F. enflata* in low abundance (Subgroup 1A). Subgroup 1A included 45 sampling stations in the lagoon (40% of the samples were collected in 2004 [January–July] and 60% in 2005 [January–September, December]; Table 4). In this subgroup, *F. hispida* and *F. enflata* were infected with 24 types of parasites. *F. hispida* was numerically dominant, with a mean abundance of 0.54 ind. m^{-3} and present at all sampling stations. Unidentified protozoan cysts were the most prevalent parasites, with a mean abundance of 1.86 ind. m^{-3} and present at all sampling stations. The mean parasite prevalence inside Laguna Nichupté was particularly high (10.3%, range: 0.74–85.6%), and parasitized hosts were living in a habitat with the lowest mean salinity recorded, with relatively low mean temperature, rainfall, oxygen concentration, and high pH (Table 4).

The second subgroup, 1B, included 18 sampling stations at which most samples were collected during 2005 (72%, vs. 28% in 2004) from the 3 areas (mostly outside the inlets of the lagoon), where *F. hispida* had low abundance. Subgroup 1B included mostly samples collected from the stations inside the lagoon (55%), followed by the coral reef (39%) and continental shelf (1%) and included 5 parasitized chaetognath species. *F. hispida* was the dominant species, with a low mean abundance of 0.12 ind. m^{-3} and present at all continental shelf–coral reef sampling stations. There were 11 distinct types of parasites. Unidentified protozoan cysts (0.03 ind. m^{-3}) and the

Table 4. (A) Mean abundance (ind. m⁻³) and relative frequency (%) of the 5 parasitized chaetognath species and their parasites, and (B) mean environmental conditions per sampling group, resulting in 2 cluster analysis groups of stations with distinct chaetognath species assemblages: one group was numerically dominated by *Ferosagitta hispida* in Laguna Nichupté (LN) and the other was dominated by *Flaccisagitta enflata* on the continental shelf (CS). Each group was subdivided in 2 subgroups. The total number of zooplankton samples collected at the 12 sampling stations during 2004–2005 is shown in parentheses for each subgroup

(A) Abundance	Species abbrev.	Group 1: <i>Ferosagitta hispida</i>				Group 2: <i>Flaccisagitta enflata</i>			
		Subgroup 1A LN (n = 45)		Subgroup 1B LN-CS (n = 18)		Subgroup 2A CS 2004 (n = 19)		Subgroup 2B CS 2005 (n = 41)	
		Mean abund.	Relative frequency	Mean abund.	Relative frequency	Mean abund.	Relative frequency	Mean abund.	Relative frequency
Chaetognath hosts									
<i>Ferosagitta hispida</i>	Fh	54.07	100.0	10.69	100.0	0.15	84.2	0.49	85.4
<i>Flaccisagitta enflata</i>	Fe	0.01	8.9	0.07	44.4	0.80	68.4	4.27	100.0
<i>Sagitta</i> spp.	Sspp.			0.17	38.9	0.34	57.9	0.33	58.5
<i>Serratosagitta serratodentata</i>	Ss			0.17	38.9	0.34	57.9	0.33	58.5
<i>Pterosagitta draco</i>	Pd			0.03	16.7	0.03	31.6	0.16	41.5
Parasites									
Gyrodactylidae larva	Gl							0.02	2.4
<i>Cercaria owreae</i>	Co					0.11	10.5	0.10	4.9
<i>Monilicaecum</i> type	Mo	0.13	6.7	0.28	22.2	0.11	10.5	5.61	100.0
Hemiuridae	He	3.62	44.4	0.89	44.4			0.12	9.8
<i>Hemiurus</i> sp.	Hsp	0.31	15.6	0.11	5.6				
<i>Parahemiurus</i> sp.	Phsp	0.29	24.4						
<i>Lecithochirium</i> sp.	Lsp	0.27	15.6	0.56	16.7				
<i>Brachyaphallus</i> sp.	Bsp	0.67	24.4	1.44	33.3			0.02	2.4
<i>Paralecithochirium</i> sp.	Plsp							0.02	2.4
<i>Opisthadena</i> sp.	Osp	0.02	2.2			0.05	5.3		
<i>Dinosoma</i> sp.	Dsp	0.20	11.1	0.44	22.2			0.05	4.9
<i>Opechona pyriforme</i>	Op	0.02	2.2					0.27	17.1
<i>Tergestia</i> sp.	Tsp	0.02	2.2	0.44	11.1			0.07	2.4
Digenea a	da							0.02	2.4
Digenea b	db							0.02	2.4
Digenea c	dc	0.02	2.2						
Digenea d	dd	0.02	2.2						
Digenea e	de	0.02	2.2						
Digenea f	df	0.02	2.2					0.02	2.4
Digenea g	dg	10.47	33.3	0.39	16.7	0.42	21.1	1.27	31.7
Sporocyst	Spor	0.13	4.4						
Plerocercoid a	pa	0.02	2.2						
Plerocercoid b	pb	0.16	8.9						
Plerocercoid c	pc							0.02	2.4
Plerocercoid d	pd					0.05	5.3		
Plerocercoid e	pe							0.02	2.4
Plerocercoid f	pf							0.05	2.4
Nematode larva	Nl	0.02	2.2					0.02	2.4
<i>Procamallanus</i> (<i>Spirocamallanus</i>) sp.	Ps sp							0.02	2.4
Platyhelminth a	plaa	0.02	2.2						
Platyhelminth b	plab	0.22	15.6	0.06	5.6				
Platyhelminth c	plac	0.02	2.2						
Unidentified protozoan cysts	uPC	186.16	100.0	3.00	55.6	1.42	79.0	4.02	61.0
(B) Environmental conditions									
Abbrev.	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
Prevalence (%)	P	10.3	0.74–85.6	2.5	0.32–8.0	8.5	0.00001–33	10.9	1.61–33.3
Temperature (°C)	T	27.5	22.1–32.6	28.7	24.7–32.6	27.9	23.9–32.2	26.8	24.2–29.4
Salinity	S	31.11	20.8–36.75	33.05	19.4–37.3	35.16	27.2–37.4	36.08	27.3–37.65
Dissolved oxygen (mg l ⁻¹)	DO	5.02	3.25–7.0	5.45	3.98–7.04	5.34	3.03–7.49	5.19	3.64–6.74
pH	pH	8.12	7.58–8.51	7.90	7.21–8.28	8.01	7.27–8.37	8.11	7.39–8.32
Rainfall (mm yr ⁻¹)	R	79.8	8.6–249.9	217.6	16–649.2	75.3	8.6–208.2	81.4	8.6–649.2

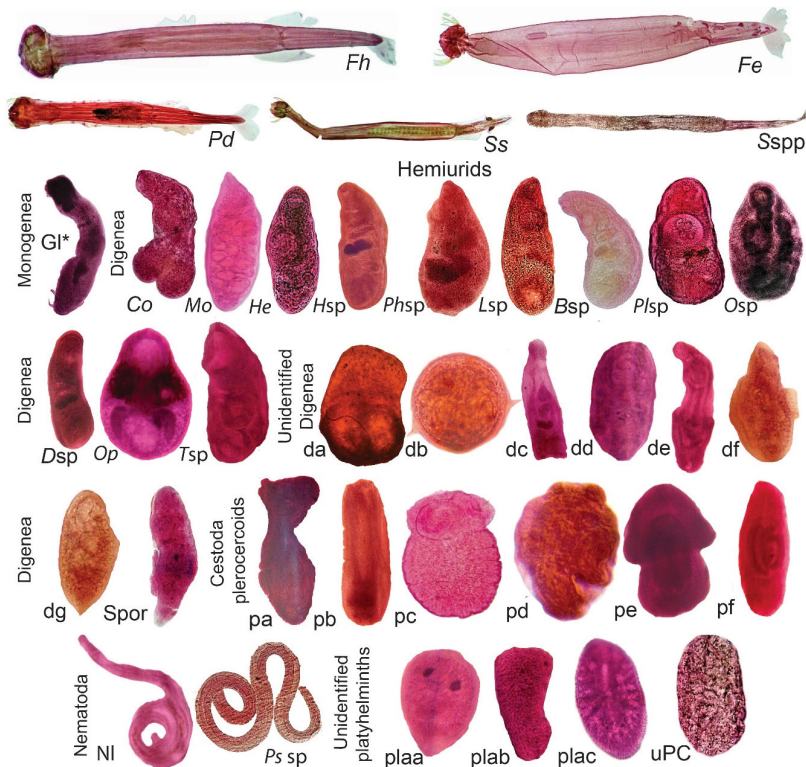


Fig. 4. Diversity of parasites that were found to infect chaetognaths in Quintana Roo, Mexico (2004–2005). Hosts are shown in the top 2 rows. All abbreviations are defined in Table 4

hemiuroid *Brachyphallus* sp. (0.01 ind. m⁻³) were the most abundant parasites. The mean prevalence was the lowest in the study area (2.5%, range: 0.3–8.0%). This mixed area had the highest mean temperature (28.7°C; range: 24.7–32.6°C) and annual rainfall (217.6 mm yr⁻¹; range: 16–649.2 mm yr⁻¹) of the coastal area and relatively low salinity caused by the mix of lagoon and the continental shelf waters (Table 4).

Group 2 had 2 subgroups of sampling stations from the continental shelf and coral reef. Subgroup 2A was dominated by *F. enflata* and included a larger number of zooplankton samples collected in 2004 (68%). Subgroup 2B included more zooplankton collected during 2005 (61%). The shift in composition between 2004 and 2005 suggests a considerable interannual change in species and abundance of chaetognath parasites.

In Subgroup 2A, most of the sampling stations were in the coral reef (47%). Although *F. enflata* had relatively low abundance (0.008 ind. m⁻³) and a moderate frequency of appearance (68%), this was the species with the highest abundance of 5 parasitized chaetognath species in the subgroup. *F. hispida* was frequently sampled in this region (84%), but had very low abundance (0.002 ind. m⁻³). Unidentified

protozoan cyst parasites were most abundant (0.014 ind. m⁻³) and frequent (79%), followed by the unidentified digenean type g (0.004 ind. m⁻³ and 21%). The mean parasite prevalence of this subgroup was moderate (8.51%; range: 0.00001–33%). SST at stations in this subgroup was high (mean 27.9°C; range: 23.9–32.2°C). This area received the lowest annual rainfall, resulting in a highly saline habitat with high DO content (Table 4).

In Subgroup 2B, *F. enflata* was the most abundant (0.042 ind. m⁻³) and frequent (100%) chaetognath species (Table 4). There were 5 parasitized chaetognath species, with a diverse assemblage of 20 distinct types of parasites (Table 4). The *Monilicaecum* larval type (0.056 ind. m⁻³), unidentified protozoan cysts (0.040 ind. m⁻³), and digenean type g (0.013 ind. m⁻³) were the most abundant parasites in this subgroup of sampling stations. Mean prevalence of chaetognath parasites was the highest recorded in the study area (mean 11%; range: 1.61–

33.3%). Stations had the lowest mean surface temperature (26.8°C) and the highest mean surface salinity (36.08) in the study area (Table 4). The multi-response permutation procedure analysis showed significant differences among the 4 subgroups (*t*-statistic: -48.9098, *A* = 0.5061, *p* = 0.0001).

CCA

Three environmental ordination axes explained 10.1% of the variation among chaetognaths and abundance of parasitized chaetognaths in terms of habitat and seasons. The first axis showed a low gradient in salinity in the lagoon, with *F. hispida* being numerically dominant (upper part of the ordination) to a relatively high salinity across the continental shelf and coral reef and high diversity of chaetognaths and parasites (lower part of the ordination). Along axis 1, *F. hispida* was positively correlated with temperature, concentration of DO, and rainfall and negatively correlated with salinity and pH (Fig. 7; Table 5). Along axis 2, the gradient of diversity of parasites showed a high correlation with prevalence in the left part of the ordination

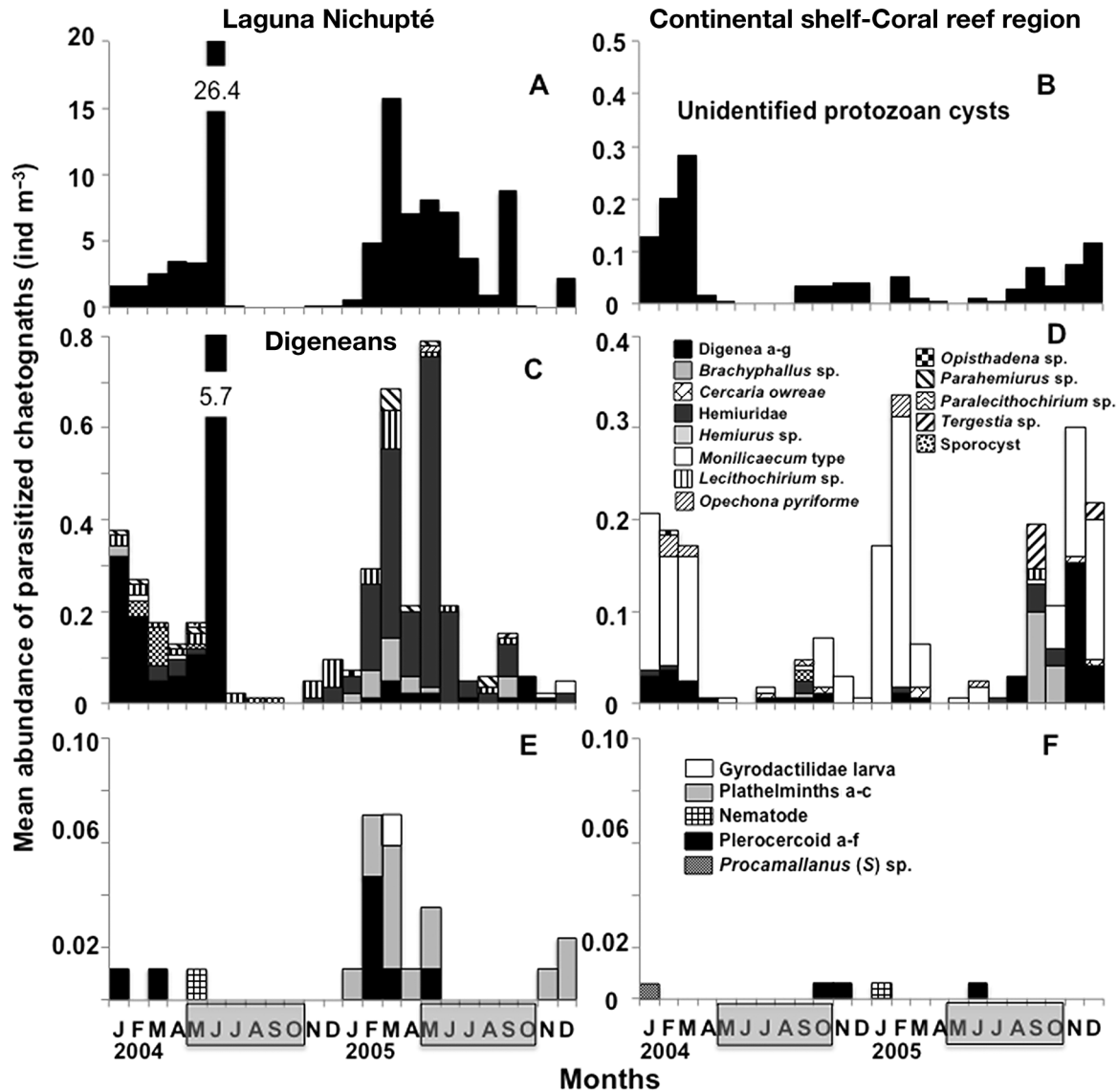


Fig. 5. Comparison of monthly mean abundance (ind. m^{-3}) of parasitized chaetognaths (per type of parasite) recorded at Laguna Nichupté and continental shelf–coral reef regions during the 2004–2005 time series: (A, B) unidentified protozoan cysts, (C, D) several digenean parasites, and (E, F) monogenean, platyhelminth, and nematode parasites obtained from each region

and pH and the less prevalent parasites in the right part of the ordination graph. Subgroups 1A and 1B were correlated with high temperatures and low salinity, environmental conditions typical of the lagoon. Sampling stations in Subgroups 2A and 2B had positive correlations with high salinities and relatively low temperatures. Group 2 and Subgroup 1A were correlated with the highest levels of parasite prevalence (Fig. 7). This analysis indicates that the distinct conditions in the lagoon and its composition of chaetognath and parasite species are more related than across the continental shelf and coral reef (Fig. 7).

DISCUSSION

Seasonal variability in chaetognath and parasite diversity and abundance

This is the first systematic time series to estimate monthly changes in abundance and prevalence of multiple chaetognath and parasite species associated with environmental variability in a neritic tropical coastal ecosystem. Previous time series investigated single chaetognath host species over time in coastal temperate ecosystems, viz. the St. Lawrence Seaway (Weinstein 1972), White Sea (Kulachkova

Table 5. Parasite/chaetognath size proportion (P/Csp) estimated using mean parasite total length (TL, mm) recorded in the northern region of Quintana Roo (Caribbean Sea, Mexico) in 2004 and 2005 and maximum TL (mm) (as reported by McLelland 1989) for 5 chaetognath hosts. –: Parasite not present in a chaetognath species; nm: parasite present, but TL was not measured

Parasite	Parasite mean TL	P/Csp				
		<i>Ferosagitta hispida</i> (TL = 12)	<i>Flaccisagitta enflata</i> (TL = 25)	<i>Serratosagitta serratodentata</i> (TL = 13)	<i>Pterosagitta draco</i> (TL = 13)	<i>Sagitta</i> spp. (TL = 19)
Gyrodactylidae larva	0.220	–	0.009	–	–	–
<i>Cercaria owrae</i>	0.031	–	0.001	–	–	–
<i>Monilicaecum</i> type	0.148	0.012	0.006	0.011	0.011	0.008
Hemiuridae	0.201	0.017	0.008	0.015	–	0.011
<i>Parahemiurus</i> sp.	0.358	0.030	–	–	–	–
<i>Lecithochirium</i> sp.	0.195	0.016	–	–	–	–
<i>Brachyaphallus</i> sp.	0.373	0.031	0.015	0.029	–	0.020
<i>Paralecithochirium</i> sp.	0.269	0.022	–	–	–	–
<i>Opisthadena</i> sp.	0.450	0.038	0.018	–	–	–
<i>Dinosoma</i> sp.	0.239	0.020	0.010	–	–	0.013
<i>Opechona pyriforme</i>	0.166	0.014	0.007	–	–	–
<i>Tergestia</i> sp.	0.143	0.012	0.006	–	–	0.008
Digenea a	0.093	–	0.004	–	–	–
Digenea b	0.064	–	0.003	–	–	–
Digenea c	0.623	0.052	–	–	–	–
Digenea d	0.092	0.008	–	–	–	–
Digenea e	0.365	0.030	–	–	–	–
Digenea f	0.112	0.009	–	–	–	–
Digenea g	0.160	0.013	0.006	–	0.012	–
Sporocyst	0.210	0.018	–	–	–	–
Plerocercoid a	0.282	0.024	–	–	–	–
Plerocercoid b	0.056	0.005	–	0.004	–	–
Plerocercoid c	0.150	–	0.006	–	–	–
Plerocercoid d	0.256	–	0.010	–	–	–
Plerocercoid e	0.369	0.031	–	0.028	–	–
Plerocercoid f	0.435	–	0.017	–	–	–
Nematode larva	0.310	0.026	0.012	–	–	–
<i>Procamallanus</i> (<i>Spirocamallanus</i>) sp.	0.960	0.080	–	–	–	–
Platyhelminth a	nm	–	–	–	–	–
Platyhelminth b	0.155	0.013	0.006	0.012	–	–
Platyhelminth c	nm	–	–	–	–	–
Unidentified protozoan cysts	0.010	0.008	0.004	0.008	0.008	0.005
Mean P/Csp		0.243	0.023	0.008	0.015	0.010

1972), northeastern Atlantic (Øresland 1986), southwestern Atlantic (Daponte et al. 2008), and the Seto Inland Sea (Ohtsuka et al. 2004) (Table 1). These investigations reported a relatively low diversity of parasite species assemblages. In our study, we found considerably larger numbers of parasite species (33 types of parasites) and in a larger number of chaetognath host species (5 species) than previous time series. Worldwide, parasite diversity is geographically biased. We know disproportionately less about parasites in the tropics than in higher latitudes (Kamiya et al. 2014, Poulin 2001, 2014). Investigations of parasite diversity, as a function of latitudinal zones, show no predictable pattern because different parasite species are not using the hosts to the same degree and because parasite taxonomy is still incomplete (Poulin 2007, Kamiya et al. 2014).

Thus, predicting how many species can exploit a particular host is impossible (Poulin 2007, 2014). The high diversity of parasites observed off the Yucatan Peninsula results from a systematic effort to identify chaetognath hosts and comparing parasite–chaetognath assemblages of 2 adjacent but environmentally distinct habitats with pronounced differences in salinity. The relatively high diversity of chaetognaths along the northeastern coast of Quintana Roo is likely a response to a narrow continental shelf (<6 km wide) that is affected by strong ocean currents (Merino 1986, Gasca et al. 1996, Athie et al. 2011). This explains why we collected oceanic species on the continental shelf and coral reef (*Eukrohnia hamata*, *Pterosagitta draco*, *Flaccisagitta enflata*, *F. hexaptera*, *Mesosagitta minima*, *Sagitta bipunctata*, and *Serratosagitta serratodentata*).

species (<12 mm TL), making it more difficult to detect parasites than in larger oceanic chaetognaths, such as *F. enflata* (<25 mm TL) (McLelland 1989); moreover, it has a relatively restricted neritic distribution on both sides of the tropical-equatorial Atlantic Ocean (Alvariño 1965).

Except for *F. hispida* and *F. enflata*, all oceanic species were collected at relatively low abundances, reducing the likelihood of being parasitized. One interesting finding is that of the 13 chaetognath species found in our study, only *F. hispida*, *F. enflata*, *S. serratodentata*, *P. draco*, and *Sagitta* spp. (including several unidentified species) were parasitized. The first 2 species and *Sagitta* spp. were numerically dominant, thus representing a large available intermediate host reservoir for endoparasites. One new finding is that *P. draco* is a new host of helminths in the Caribbean Sea, while another 3 chaetognath species were previously found parasitized with digeneans, cestodes, and nematodes in other regions of the world (Reimer et al. 1975, Shimazu 1978, Jarling & Kapp 1985, Øresland 1986, Mazzoni 1986, Pierrot-Bults 1990). Seven chaetognath species have been reported as intermediate or paratenic hosts off the Yucatan Peninsula. *F. enflata*, *F. hispida* (Gómez del Prado-Rosas et al. 1999b, 2002, 2005, 2007b), and *S. serratodentata* (Gómez del Prado-Rosas et al. 1999a,b, 2005, 2007b) are the most commonly found hosts in these reports. Less frequently parasitized species are *S. bipunctata*, *P. helenae*, and *P. friderici* (Gómez del Prado-Rosas et al. 1999b, 2005). It is not clear why the other 7 species were not infected; likely, it is associated with a density-dependent parasite–host process, feeding habits, or size of parasites and host (Poulin & Valtonen 2001). Relatively low abundance and frequency of the other chaetognath species and smaller body length may explain why they did not appear to be parasitized. Moravec et al. (1995), Lafferty (1999), and Poulin & Valtonen (2001) suggested that one of the most important factors influencing the presence of certain parasites is that the host species must have a high population density. This is true for *F. hispida*, a very abundant species and the only chaetognath found in the lagoon (Álvarez-Cadena et al. 1996a), and for *F. enflata*, the most abundant species along the continental shelf–coral reefs (Ramírez-Ávila & Álvarez-Cadena 1999).

We found 12 chaetognath species (plus *Sagitta* spp.), which represent 71% of the 17 chaetognath species previously recorded along the eastern Yucatan Peninsula coast (Suárez-Morales et al. 1990, Gasca et al. 1996, Álvarez-Cadena et al. 1996a,b, 2007, Ramírez-Ávila & Álvarez-Cadena 1999,

Hernández-Flores 2003). The Caribbean Sea and Gulf of Mexico host 24 chaetognath species (McLelland 1989). The most abundant chaetognaths in our study were *F. hispida*, *F. enflata*, *S. serratodentata*, *K. pacifica*, *P. draco*, and *F. hexaptera*, which were also reported by Michel & Foyo (1976). The prevalence and mean intensity of parasites in our study were considerably higher than those reported in other studies of chaetognaths along the coast of the Yucatan Peninsula (Tables 3 & 6). Our work was an extremely systematic effort to inspect every specimen collected in all zooplankton samples. Prevalence and abundance found in the Gulf of Mexico and Caribbean Sea was even higher than parasites infecting other zooplankton taxonomic groups, such as jellies, euphausiids, and fish larvae (Table 7). This suggests that chaetognaths are major biomass reservoirs for trophically transmitted parasites in this region (Table 7). Our extensive and systematic sampling and analyzing effort over 2 yr detected more diverse and higher rates of prevalence than any previous studies, which involved shorter, non-systematic sampling periods or serendipitous discoveries of parasites at tropical latitudes. However, these earlier studies provided valuable taxonomic knowledge for identifying helminth parasites in this region.

The most enigmatic and non-helminth type of parasite found in our study were the unidentified protozoan cysts. Weinstein (1972) reported chaetognaths with abnormally flaccid and swollen body when they were infected with *Metaphrya sagittae* ciliate cysts. Ciliates were dispersed throughout the hemocoel of *Parasagitta* (low prevalence of 1–2.6% and low intensity, but considerable increase as chaetognath size increases). *M. sagittae* parasitizes chaetognath species in 7 other regions (Weinstein 1972, Jarling & Kapp 1985, Øresland 1986). Ohtsuka et al. (2004) found *Vampyrophrya pelagica* ciliates swimming in the digestive track of 3 species of chaetognaths. Based on the diversity of cell size and shape along the Yucatan Peninsula, we suspect that multiple unidentified protozoan species infect chaetognaths, but the identification of these protozoans awaits future studies.

Although chaetognaths display extensive daily vertical migrations (up to hundreds of meters), our near-surface sampling method collected chaetognaths in the first 5 m. However, chaetognaths in our area of study should move shorter distances in the water column because the bottom of the lagoon is <5 m and that of the continental shelf is <40 m. Higher densities near the sea floor may increase interaction with benthic and demersal prey and predators.

Table 6. Canonical correspondence analysis and Pearson and Kendall correlations with ordination axes (123 sampling stations) of chaetognath and parasite species abundance and environmental conditions observed in the Caribbean Sea, Mexico (2004–2005)

Variables	Axis 1			Axis 2			Axis 3		
	r	r ²	tau	r	r ²	tau	r	r ²	tau
Chaetognaths									
<i>Ferosagitta hispida</i>	0.228	0.052	0.346	-0.251	0.063	-0.360	-0.155	0.024	-0.111
<i>Flaccisagitta enflata</i>	-0.246	0.061	-0.379	0.267	0.071	0.403	-0.131	0.017	-0.062
<i>Pterosagitta draco</i>	-0.177	0.031	-0.217	0.218	0.047	0.244	-0.179	0.032	-0.122
<i>Serratosagitta serratodentata</i>	-0.212	0.045	-0.274	0.161	0.026	0.193	0.043	0.002	0.018
<i>Sagitta</i> spp.	-0.212	0.045	-0.274	0.161	0.026	0.193	0.043	0.002	0.018
Parasites									
Prevalence	0.218	0.047	0.086	0.266	0.071	0.218	-0.082	0.007	-0.106
Parasites (total)	0.371	0.138	0.305	-0.054	0.003	-0.127	-0.078	0.006	-0.230
Gyrodactylidae larva	-0.023	0.001	0.010	0.134	0.018	0.123	-0.160	0.026	-0.119
<i>Cercaria owreae</i>	-0.017	0.000	0.037	0.046	0.002	0.008	-0.044	0.002	-0.045
<i>Monilicaecum</i> type	-0.233	0.054	-0.265	0.352	0.124	0.378	-0.149	0.022	-0.095
Hemiuridae	0.018	0.000	0.107	-0.102	0.010	-0.141	0.034	0.001	0.034
<i>Parahemiurus</i> sp.	0.219	0.048	0.202	-0.055	0.003	-0.063	-0.209	0.044	-0.189
<i>Lecithochirium</i> sp.	0.208	0.043	0.232	-0.204	0.042	-0.118	-0.013	0.000	-0.025
<i>Brachyaphallus</i> sp.	0.026	0.001	0.061	-0.063	0.004	-0.151	0.187	0.035	0.051
<i>Paralecithochirium</i> sp.	-0.009	0.000	0.023	-0.092	0.009	-0.090	0.069	0.005	0.086
<i>Opisthadena</i> sp.	-0.087	0.008	-0.067	0.039	0.002	0.034	0.011	0.000	0.031
<i>Dinosoma</i> sp.	-0.119	0.014	-0.088	0.015	0.000	0.015	0.218	0.047	0.092
<i>Opechona pyriforme</i>	-0.143	0.020	-0.140	0.194	0.038	0.188	-0.058	0.003	0.014
<i>Tergestia</i> sp.	-0.070	0.005	-0.032	0.007	0.000	-0.027	0.060	0.004	0.103
Digenea a	-0.076	0.006	-0.075	0.111	0.012	0.115	-0.047	0.002	-0.067
Digenea b	-0.091	0.008	-0.113	0.094	0.009	0.102	-0.018	0.000	-0.015
Digenea c	0.014	0.000	0.042	-0.008	0.000	-0.015	-0.039	0.002	-0.059
Digenea d	-0.041	0.002	-0.013	-0.001	0.000	-0.010	0.056	0.003	0.073
Digenea e	0.014	0.000	0.042	-0.008	0.000	-0.015	-0.039	0.002	-0.059
Digenea f	0.041	0.002	0.071	0.020	0.000	0.001	-0.025	0.001	-0.024
Digenea g	0.287	0.082	0.080	0.035	0.001	0.085	-0.017	0.000	-0.115
Sporocyst	0.307	0.094	0.170	0.020	0.000	-0.029	-0.007	0.000	-0.036
Plerocercoid a	0.134	0.018	0.105	-0.023	0.001	-0.029	-0.229	0.053	-0.128
Plerocercoid b	-0.013	0.000	0.064	-0.012	0.000	-0.078	-0.018	0.000	-0.022
Plerocercoid c	0.013	0.000	0.040	0.049	0.002	0.029	-0.024	0.001	-0.027
Plerocercoid d	-0.070	0.005	-0.063	-0.025	0.001	-0.038	0.069	0.005	0.084
Plerocercoid e	-0.085	0.007	-0.092	0.026	0.001	0.010	0.116	0.013	0.109
Plerocercoid f	-0.067	0.004	-0.056	0.073	0.005	0.061	-0.049	0.002	-0.071
Nematode larva	-0.066	0.004	-0.053	0.095	0.009	0.082	0.015	0.000	0.033
<i>Procamallanus</i> (<i>Spirocamallanus</i>) sp.	-0.032	0.001	-0.004	0.085	0.007	0.088	-0.166	0.028	-0.123
Platyhelminth a	0.077	0.006	0.079	-0.070	0.005	-0.077	-0.080	0.006	-0.086
Platyhelminth b	0.173	0.030	0.131	-0.226	0.051	-0.182	-0.023	0.001	-0.017
Platyhelminth c	0.014	0.000	0.042	-0.008	0.000	-0.015	-0.039	0.002	-0.059
Unidentified protozoan cysts	0.383	0.146	0.376	-0.072	0.005	-0.178	-0.083	0.007	-0.268
Environmental conditions									
Temperature	0.039	0.002	-0.011	-0.226	0.051	-0.161	0.516	0.266	0.390
Salinity	-0.936	0.876	-0.704	0.684	0.468	0.421	0.380	0.145	0.308
Oxygen concentration	-0.113	0.013	-0.149	-0.018	0.000	0.002	0.573	0.329	0.357
Potential hydrogen	-0.057	0.003	-0.101	0.538	0.289	0.362	-0.251	-0.063	-0.210
Rainfall	-0.085	0.007	-0.020	0.026	0.001	-0.022	0.603	0.364	0.369

Under the greatly contrasting conditions in the lagoon and continental shelf, where different chaetognath host species numerically dominate, there is likely to be distinct host diversity, including primary (mollusks), intermediate (copepods, fishes), and final hosts (fish,

sea birds, and marine mammals), that promotes distinct differences in parasite prevalence and species composition as they transit from the intermediate chaetognath hosts. Distinct parasites seem to find suitable primary, intermediate, and definitive hosts

Table 7. Summary of parasites reported to infect zooplankton in the Gulf of Mexico and Caribbean Sea

Host	Parasite	Total organisms analyzed	No. of parasitized organisms	Prevalence (%)	Mean intensity	Study area	Reference
Endoparasites							
Chaetognaths	<i>Torticaecum</i> type (Digenea, Didymozoidae)	22508	1	0.004	1	Quintana Roo, Caribbean Sea	Gómez del Prado-Rosas et al. (1999a)
Chaetognaths	<i>Cercaria owreae</i> (Digenea)	19524	22	0.11	1	Quintana Roo, Caribbean Sea	Gómez del Prado-Rosas et al. (1999b)
Hydrodromedusa	<i>Opechona pyriforme</i> (Digenea, Lepocreadiidae)	2548	10	0.39	1.5	Quintana Roo, Caribbean Sea	Gómez del Prado-Rosas et al. (2000)
Chaetognaths	Accacoeliidae (Digenea)	14583	2	0.14	1	Mexican Caribbean Sea	Gómez del Prado-Rosas et al. (2002)
Chaetognaths	<i>Brachyphallus</i> sp. (Digenea, Hemiuriidae)	22508	19	0.084	1	Mexican Caribbean Sea	Gómez del Prado-Rosas et al. (2005)
Fish larvae	<i>Ectenurus</i> sp. (Digenea, Hemiuriidae)	396	20	5	1–16	Puerto Morelos, Quintana Roo	Gómez del Prado-Rosas et al. (2007a)
	<i>Lecithochirium</i> sp. (Digenea, Hemiuriidae)	1235	13	5.53	1	Quintana Roo, Caribbean Sea	Gómez del Prado-Rosas et al. (2007b)
Chaetognaths	<i>Monilicaecum</i> type (Digenea Didymozoidae)	22508	8	0.037	1	Quintana Roo, México	Morales-Hernández (2009)
Hydrodromedusa	<i>Linton</i> sp. 1 (Fellodistomidae, Lintoniinae)	396	20	2.89	1–3	Quintana Roo, Caribbean Sea	
	<i>Linton</i> sp. 2 (Fellodistomidae, Lintoniinae)	1235	13	5.53	1	Quintana Roo, Caribbean Sea	
	<i>Bacciger</i> sp. (Fellodistomidae, Baccigerinae)	22508	8	0.037	1–2	Quintana Roo, Caribbean Sea	
	<i>Lepocreadium</i> sp. (Lepocreadiidae, Lepocreadiinae)	396	20	0.05	1	Quintana Roo, México	
	<i>Opechona</i> sp. 1 (Lepocreadiidae, Lepocreadiinae)	1235	13	0.05	1	Quintana Roo, México	
	<i>Opechona</i> sp. 2 (Digenea, Lepocreadiidae, Lepocreadiinae)	22508	8	0.08	1	Quintana Roo, México	
Fish larvae	<i>Brachyphallus</i> sp. (Digenea, Hemiuriidae)	1125	1	0.08	1	Laguna Bojórquez, Cancún, Mexico	Gutiérrez-Heredia (2008)
Euphausiids	Heterophyidae (Digenea)	1125	1	0.08	1	Banco Chinchorro, Caribbean Sea	González-Solis et al. (2013)
Euphausiids	Trypanorhyncha (Cestoda, Eutetrarhynchidae gen. sp.)	1125	1	0.08	1	Banco Chinchorro, Caribbean Sea	González-Solis et al. (2013)
Ectoparasites							
Euphausiids	<i>Oculophryxys bicaulis</i> (Crustacea, Isopoda, Dajidae)	2	2	100	1 (female), 1–2 males attached to marsupium	Gulf of Mexico 25°33.5'N, 88°27.5'W	Shields & Gómez-Gutiérrez (1996)
Euphausiids	<i>Heterophryxus appendiculatus</i> (Crustacea, Isopoda, Dajidae)	Not estimated, free-swimming specimens	2	Not estimated	1 (female), 1 male attached to marsupium of the female	Cozumel, Western Caribbean Sea, Mexico	Gómez-Gutiérrez & Castellanos Osorio (2010)

in this shallow lagoon. The Gulf of Mexico and Caribbean Sea contain >50% of Mexico's coastal wetlands, nearly 6000 km² of lagoons, and the most extensive areas of coral reefs in Mesoamerica. These habitats sustain more than 8500 species of marine invertebrates and fishes, 328 species of birds, 29 species of marine mammals, and 5 species of marine turtles (Benitez et al. 2014). High species diversity should also promote a proportionately highly diverse parasitic species assemblage, as observed in the area of study, compared with temperate ecosystems (Table 1). A diverse assemblage of cestode and trematode generalist species parasitizes mollusks (first intermediate hosts) and fish (second intermediate hosts) in the Caribbean Sea (Cake 1976, Argáez-García 2003, Jensen 2009). For example, at least 93 species of cestodes have been reported in the Gulf of Mexico, parasitizing 244 host species (Jensen 2009). Larval cestodes infect invertebrates (Cnidaria, Mollusca, decapod crustaceans), and adult cestodes infect actinopterygians, elasmobranchs, and marine mammals (Mignucci-Giannoni et al. 1998, Jensen 2009). Copepods interact with an assemblage of diverse parasitic species, including bacteria (on the body surface and in the gut), ectoparasites (fungi, diatoms, ellobiopsids, apostomes and suctorian ciliates, and larvae of epicaridean isopods), and endoparasites (dinoflagellates, gregarines, haplosporidians, digeneans, cestodes, nematodes, and acanthocephalans) (Ho & Perkins 1985, Huys & Bodin 1997). Most helminth species have complex life cycles that involve intermediate invertebrate hosts that, after being preyed on by predators, complete their life cycle by infecting top predators. Shimazu (1978) reported that chaetognaths are infected with helminth larvae after they prey on copepods, which are frequently the second intermediate host. Ho & Perkins (1985) argued that almost all metacercariae found in the hemocoel of marine copepods belong to a single family, Hemiuridae, a large family of parasites that invade the esophagus and stomach of fish. Hemiuridae were the most diverse and frequent parasites of chaetognaths in our study area.

In a monthly time series (December 1990–November 1991) carried out at 3 stations in Laguna Nichupté and the adjacent continental shelf, decapod larvae (39%) and copepods (29%) were the most abundant and diverse zooplankton taxonomic groups (Álvarez-Cadena & Segura-Puertas 1997). Those authors reported a total of 47 copepod species, with 14 species in Laguna Nichupté dominated by *Acartia tonsa* (35–94% of total copepod abundance in the lagoon) and 42 species on the continental shelf, numerically

dominated by *Paracalaus quasimodo* (21–40%). These copepods may be frequent prey of chaetognaths in this region, particularly because *A. tonsa* has been reported as an intermediate host of nematodes in other regions (Balbuena et al. 1998). Thus, chaetognaths act as intermediate or paratenic hosts for helminth larvae before they reach the nektonic intermediate or final host, as known for parasites in the family Didymozoidae that infect several fish species (Shimazu 1978, Pierrot-Bults 1990, Gómez del Prado-Rosas et al. 2007b). Although helminths and other parasites of zooplankton have been studied in the Gulf of Mexico and Caribbean Sea (Table 7), published information describing parasite life cycles is still fragmented. Gómez del Prado-Rosas et al. (2011) recorded metacercariae of the family Hemiuridae, *Brachyphallus* spp., and *Parahemiurus* spp., infecting the calanoid copepod *Acartia (Odontacartia) lilljeborjii* that are frequent prey of chaetognaths. Almeida et al. (2009) observed that some chaetognaths in Brazil were highly infected with *Parahemiurus merus* that released eggs and hatched inside the coelom of the chaetognath. This was also observed in *Parahemiurus* spp. of chaetognaths collected in the upper Gulf of California (Lozano-Cobo et al. 2012).

Parasites infecting the chaetognath's head, coelom, gut, and ovaries are similar to those described by Nagasawa (1991). The caudal septa should also be listed as a frequent microsite of infection. We did not find epibionts on chaetognaths. However, we found only 2 types of ectoparasites infesting chaetognaths (monogenean Gyrodactylidae larvae and the unidentified platyhelminth type c). This is the second record of a monogenean infesting a chaetognath since the first monogenean was discovered in 1858 infesting *Sagitta germanica* (currently known as *Parasagitta setosa*) (Leuckart & Pagenstecher 1858). Because we observed a monogenean Gyrodactylidae larval ectoparasite on only one occasion, and these monogeneans supposedly infest fish gills and skin, we propose that this was an accidental infestation. Chaetognaths have a soft skin with epidermal cells that produce mucus (Shinn 1997, Perez et al. 1999). Mucus and soft epidermis seems to be an unfavorable substrate for epibiont organisms, in contrast to infested zooplanktonic crustaceans that possess a hard exoskeleton (Chivelli et al. 1993, Ohtsuka et al. 2004, 2011, Walkusz & Rolbiecki 2007, Gómez-Gutiérrez et al. 2010). Thus, we propose the hypothesis that such morphological features may explain why chaetognaths do not have epibionts and have a comparatively lower incidence of ectoparasites than endoparasites.

Parasite–host size proportion

Chaetognaths have lower carbon content (mean 34.3% of dry body weight) than zooplanktonic crustaceans (copepods, euphausiids, mysids), polychaetes, fish larvae (means ranging between 41.7 and 47.6%), but higher carbon content than siphonophores and Hydromedusae (means ranging between 10.4 and 16%) (Beers 1966). This pattern among taxonomic groups is also true for nitrogen and phosphorus contents (Beers 1966). We propose the hypothesis that parasites of chaetognaths are typically small (overall mean P/Csp = 0.052), perhaps as a parasite adaptation to infect hosts with a relatively small carbon content and with a high proportion of water (Table 5). Even the largest observed parasites (nematode and *Procamallanus* [*Spirocamallanus*] sp. larvae) have small P/Csp in comparison with parasites observed on other zooplanktonic organisms. The small P/Csp contrasts with the proportionally large helminth parasites that infect zooplanktonic crustaceans that usually have relatively high carbon content (Huys & Bodin 1997, Gómez-Gutiérrez et al. 2010, Gregori et al. 2012, 2013). Alves & Luque (2001) mentioned that helminth larvae typically cause negligible damage to their hosts, unless they are present in large intensities, increasing the P/Csp (or biomass proportion).

Environmental conditions related to chaetognath–parasite associations

We found highly diverse chaetognath species along the continental shelf and a virtually monospecific dominance by *F. hispida* in the lagoon. The lagoon had a distinctive assemblage of host and parasite species that differed from the assemblages found on coral reefs and the continental shelf. The 2 habitats experience seasonal changes in environmental conditions; chaetognath abundance declines during the rainy season, particularly in the lagoon, where the shallow bottom (<3 m) causes highly variable temperature, salinity, and oxygen concentration. During the rainy season, particularly during hurricane events, salinity decreases and creates harsh conditions for all chaetognath species, except *F. hispida*. The shallow lagoon has a characteristic low salinity (caused by rainfall and groundwater discharge) and slow flushing time (1.3–1.9 yr) because mixing with the water over the continental shelf requires flowing through 2 shallow (<4 m) and narrow mouths (<30 m wide) (Merino 1986, Merino et al. 1990, Athie et al. 2011) that favor numerical dominance of the

euryhaline *F. hispida* over other chaetognath species that cannot reproduce and maintain stable populations inside the lagoon. Because *F. hispida* and *F. enflata* were the most abundant species, they defined the associations of chaetognath and parasite species into 2 distinct habitats. The transitional conditions with numerical dominance of *F. hispida* over *F. enflata* were previously reported on Yucatan coral reefs (Ramírez-Ávila & Álvarez-Cadena 1999). The location where *F. enflata* had high abundance and high parasite species richness prevailed in the low temperatures and high salinities typical of the continental shelf (McLelland 1989, Crelier & Daponte 2004). Suárez-Caabro (1955) reported that *F. enflata* is a eurythermic species inhabiting areas with temperatures ranging from 16 to 32°C.

As in other reports, our CCA showed that salinity was significantly and positively correlated with high abundance of *F. enflata*, *S. serratodentata*, and *P. draco*, typically where oligotrophic conditions, as well as relatively low primary and secondary production, prevail (Álvarez-Cadena et al. 1996b, Ramírez-Ávila & Álvarez-Cadena 1999). Álvarez-Cadena et al. (2007) reported that low abundance of chaetognaths is associated with locations and periods with low DO. The northern coast of Quintana Roo has less coral reef habitat, but the sea floor is mostly white coral sand, where strong currents and wave dynamics are present. At shallow depths, this habitat favors seagrass and macroalgae meadows that decrease seawater DO. The presence of extensive seagrass beds creates a habitat where only *F. hispida* attain high population densities, decreasing rapidly on the continental shelf and coral reef areas. The lagoon is generally unsuitable for chaetognath species that inhabit the continental shelf.

In summary, we discovered that the most abundant chaetognath species (*F. hispida*, *F. enflata*, and *Sagitta* spp.) and moderately abundant species (*S. serratodentata* and *P. draco*) are prey with a highly diverse parasitic species assemblage at tropical latitudes. Low chaetognath abundance is likely the most parsimonious explanation why the other 8 species did not show parasitism (relative abundance 0.1–1.5%), including *K. pacifica* and *P. tenuis*, which are the fourth (1.5%) and sixth (0.4%) most abundant chaetognath species in the study area (Table 2). We conclude that parasites have a close association with abundance and species composition of chaetognaths based on seasonal variations and lagoon–coastal habitats, with distinct parasite relative abundances among host species in each habitat. Environmental conditions in Laguna Nichupté are favorable for *F.*

hispida, but are inhospitable to other oceanic chaetognath species. In this shallow lagoon, with mangroves and seagrass, there may be enhanced benthic interaction of chaetognaths with mollusks (and other primary hosts), which favors higher prevalence of digeneans and cestodes. We conclude that, since infected chaetognaths respond differently to saline environmental conditions, numerically dominant chaetognath species in the contrasting lagoon and continental shelf habitats and their prey also promote distinct parasite species assemblages. Future ecological studies should compare parasitic diversity among distinct chaetognath species from different biogeographic regions (Poulin 2007, 2014, Kamiya et al. 2014), with emphasis on seasonal variability to explore seasonal dynamics of parasites among prey and predators of chaetognaths.

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