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NOTA CIENTÍFICA

Ctenophores and siphonophores are alternative hosts in the life cycle of didymozoids in the Gulf of California

Los ctenóforos y los sifonóforos son hospederos alternativos en el ciclo de vida de los didimozoides en el Golfo de California

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ABSTRACT

Background. Few studies exist of parasites of zooplanktonic organisms. This situation increases the odds to discover new species of parasites, new types of parasitic interactions, and reports that increase the geographic distribution ranges worldwide. Ctenophores and siphonophores are relevant intermediary or paratenic host of numerous marine endoparasites due their carnivorous habits. **Goals.** We report the parasitic interaction between the metacercariae of didymozoids (Digenea) with a ctenophore and a siphonophore species based on observations of alive gelatinous zooplankton in the Gulf of California. **Methods.** Zooplankton was collected from 27 oceanographic stations during day and night using a standard Bongo net in an oceanographic cruise carried out during June-July 2016 in the Gulf of California. Zooplankton was observed alive immediately after collection. **Results.** We observed four ctenophore specimens of *Pleurobrachia bachei* (intensity of parasitism = 2-3 parasites per host) and a siphonophore specimen of *Muggiaea atlantica* (intensity = 1) parasitized with a total of nine metacercariae Didymozoidae morphologically identified as larval type Monilicaecum. Didymozoids were found in two different sampling stations, and in three different microhabitats (pharynx, meridional canal below of the ctene rows, and pharyngeal canal) in the *P. bachei* and in the subumbrellar cavity of *M. atlantica*. **Conclusions.** We proposed that ctenophores and siphonophores act as alternative host in the life cycle of didymozoids. Didymozoids infecting ctenophores and siphonophores are only know from the Atlantic Ocean. We do the first record of didymozoid parasitizing ctenophores and siphonophores in the Gulf of California, extending its distribution range from the Atlantic Ocean to the Pacific Ocean.

Keywords: Didymozoidae, metacercariae, Ctenophora, Siphonophora, Gulf of California.

RESUMEN

Antecedentes. Existen pocos estudios de parásitos en organismos zooplanctónicos, por lo tanto, esto incrementa la posibilidad de descubrir nuevas especies de parásitos, nuevos tipos de interacciones parasitarias y la adición de nuevos registros que amplíen su rango de distribución geográfica. Los ctenóforos y sifonóforos son relevantes hospederos intermediarios y paraténicos de endoparásitos marinos debido a sus hábitos carnívoros. **Objetivos.** Se registra una nueva interacción parasitaria entre las metacercarias de didimozoides (Digenea) con una especie de ctenóforo y una especie de sifonóforo observando zooplancton gelatinoso vivo en el Golfo de California. **Métodos.** El zooplancton fue recolectado en 27 estaciones oceanográficas durante el día y la noche utilizando una red Bongo estándar en un crucero oceanográfico realizado en junio-julio de 2016 en el Golfo de California. El zooplancton fue observado vivo inmediatamente después de su recolección. **Resultados.** Se observaron cuatro especímenes del ctenóforo *Pleurobrachia bachei* (con intensidad de 2-3 parásitos por hospedero) y un espécimen del sifonóforo *Muggiaea atlantica* parasitados con un total de nueve metacercarias didimozoides identificadas morfológicamente como larvas tipo Monilicaecum. Los didimozoides fueron encontrados en dos diferentes estaciones y en tres diferentes microhábitats (faringe, canal meridional debajo de la hilera de peine y canal faríngeo) en *P. bachei* y en la cavidad subumbrelar de *M. atlantica*. **Conclusión.** Se propone que los ctenóforos y sifonóforos actúan como hospederos alternativos en el ciclo de vida de los didimozoides. Los didimozides que infectan ctenóforos y sifonóforos han sido reportados únicamente del Océano Atlántico. Se reporta el primer registro de didimozoides parasitando ctenóforos y sifonóforos en el Golfo de California, extendiendo su rango de distribución del Océano Atlántico al Océano Pacífico.

Palabras clave: Didymozoidae, metacercaria, Ctenophora, Siphonophora, Golfo de California.

INTRODUCTION

The life cycle of parasitic digeneans, cestodes, and nematodes is complex because they develop different larval stages in two or three invertebrate hosts (including holoplanktonic and sessile gastropod, cnidarians, ctenophores and chaetognaths), and use small fishes as intermediate or paratenic hosts, and before parasitizing as adult the definitive vertebrate host (Marcogliese, 1995; Diaz Briz *et al.,* 2012; Louvard *et al.,* 2022a, b; Lozano-Cobo *et al.,* 2022). Heteropods and chaetognaths serve as significant intermediate hosts for digenean larvae (Lozano-Cobo *et al.,* 2022) and parasitic copepods, such as the harpacticoid *Microstella norvegica* that infect ctenophores (Morales-Ávila *et al.,* 2023). Despite the few records of parasites in ctenophores and siphonophores, this zooplanktonic groups are considered among the most relevant intermediary or paratenic hosts, due to their carnivorous feeding strategy preying mostly on free-living copepods, which can act as second intermediate host, and being prey of numerous larger predators that act as definitive hosts (Marcogliese, 1995).

Metacercariae of the families Lepocreadiidae, Faustulidae, and Hemiuridae are the most frequently reported digenean larvae infecting ctenophores and siphonophores as intermediate hosts (Lauckner, 1980; Stunkard, 1980; Yip, 1984; Martorelli 1996, 2001; Morandini *et al.,* 2005; Martell-Hernández *et al*., 2011; Cribb *et al.,* 2024). However, metacercariae of family Didymozoidae parasitizing ctenophores and siphonophores are rarely reported only from the Atlantic Ocean (Table 1) (Reimer *et al.,* 1971, 1975; Yip, 1984), particularly in Mexico, where no records have been reported to date.

Table 1. Historic records of metacercariae larval stage of Didymozoidae parasitizing ctenophores (A) and siphonophores (B) species worldwide.

Host species		Parasite/larvae stage	Microhabitat	Locality	Reference
A) Phylum Ctenophora					
Class Tentaculata					
Order Cyddipida					
Family Pleurobrachiidae					
	Hormiphora sp.	Didymozoidae		Atlantic Ocean	Reimer *et al.* (1975)
	Pleurobrachia sp.	Didymozoidae		North Sea	Reimer *et al.* (1971)
	Pleurobrachia sp.	Didymozoid larvae	External wall of the posterior pharynx and on the wall of the tentacular sheath	Galway Bay, western Ireland	Yip (1984)
	***Pleurobrachia bachei* A. Agassiz, 1860**	**Type Monilicaecum**	**Ctenes, tentacle base and pharynx**	**Gulf of California**	**Present study**
Class Nuda					
Order Beroida					
Family Beroidae					
	Beroe cucumis Fabricius, 1780	Didymozoid larvae	embedded in the body tissue		Yip (1981)
B) Phylum Cnidaria					
Class Hydrozoa					
Order Siphonophorae					
Family Agalmatidae					
	Halistemma sp.	Didymozoidae		North Sea	Reimer *et al.* (1971)
Family Diphyidae					
	Dimophyes arctica (Chun, 1987)	Didymozoidae		North Sea	Reimer *et al.* (1971)
	Sulculeolaria sp. (Syn= *Galetta* sp.)	Didymozoidae		Atlantic Ocean	Reimer *et al.* (1975)
	Muggiaea atlantica Cunningham, 1892	Didymozoidae		Atlantic Ocean	Reimer *et al.* (1975)
	Muggiaea atlantica	**Type Monilicaecum**	**Subumbrellar cavity (nectosac)**	**Gulf of California**	**Present study**

Adults didymozoid species are found frequently as endoparasites (mesentery, intestine, and kidney) of carnivorous marine fishes as Scombridae (Bárcenas de los Santos *et al*., 2021; Freire *et al*., 2024), or as ectoparasites in Serranidae fishes (Mele *et al*., 2022; Rodríguez *et al*., 2024), and the larvae stage has been recorded in at least six taxonomic groups of marine invertebrates (Reimer *et al.,* 1971, 1975; Gómez del Prado-Rosas *et al*., 2007; Louvard *et al*., 2022a, b, 2024) and fish larvae (Felizardo *et al*., 2011). However, Didymozoidae is a parasitic taxonomic group with broad taxonomic problem. Therefore, it is necessary to continue with morphological, molecular and diversity studies of host species to discover new patterns of their parasitic infections.

The goal of present paper is to document the observation *in vivo* of didymozoid metacercariae infecting gelatinous zooplankton (ctenophores and siphonophores) during summer 2016 in the Gulf of California. This represents an increase in knowledge of the larval stages of Platyhelminthes in the marine gelatinous zooplankton.

MATERIALS AND METHODS

Zooplankton samples were collected from 27 oceanographic stations during an oceanographic cruise (R/V El Puma; ICMyL-UNAM) carried out between 22 June and 17 July 2016 in the central and southern region of the Gulf of California (Fig. 1). Zooplankton was collected during day and night using a standard Bongo net, 0.6-m mouth diameter provided with a cylindrical–conical 505 µm mesh net, following standard methods (Smith & Richardson, 1977). Zooplankton samples were observed alive immediately after collection under a stereomicroscope (Carl Zeiss, SV11 model, 0.6–6.6X magnification) to search of parasites of gelatinous zooplankton. Each parasitized host and its parasite were photographed alive with a Canon G11 digital camera fixed to the optical stereoscope (Carl Zeiss SV11) and measured with a calibrated micrometer. Digital images were edited with Adobe Photoshop (Adobe Systems Incorporated). The samples were fixed in 70% ethanol after *in vivo* observation. The ctenophores and the siphonophore hosts were

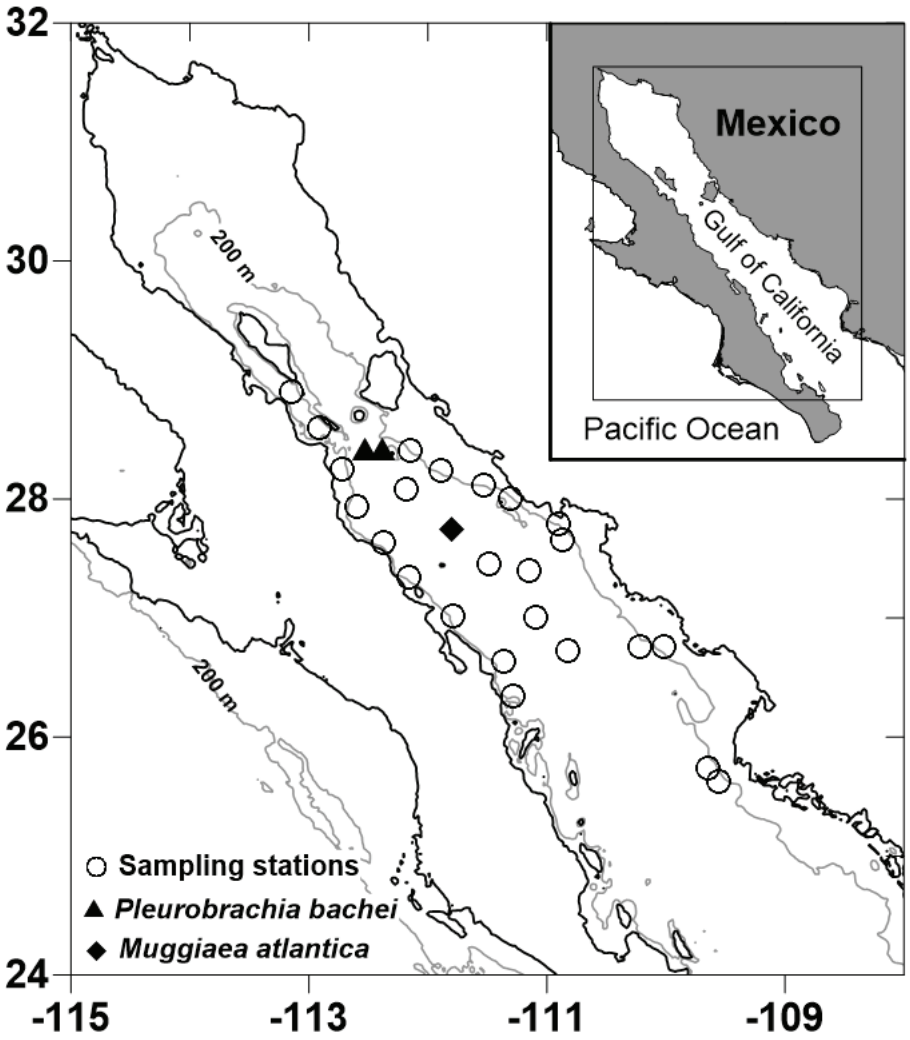

Figure 1. Map of area of study showing the zooplankton samples collected (○) and sample stations with parasitic infection in *Pleurobrachia bachei* (▲) and *Muggiaea atlantica* (♦) during June-July 2016 in the central region of the Gulf of California.

identified according to taxonomic criteria of Mills & Haddock (2007), Alvariño (1981), and Bouillon *et al.* (2004). Digenean metacercariae were identified according to morphological criteria of Pozdnyakov & Gibson (2008), and previous records of morphological and molecular didymozoid metacercariae reported infecting chaetognaths of the Mexican Pacific (Lozano-Cobo *et al.,* 2018, 2022). Intensity of parasitism was estimated according to Bush *et al.* (1997). Map of area of study showing the zooplankton samples collected and sample stations with parasitic infection was plotted using the Surfer 10v software.

RESULTS

Because present study focused only on parasitized ctenophores and siphonophores observed alive, the abundance and prevalence of parasitism was not estimated here. However, parasites of gelatinous zooplankton were observed only in three out the 27 zooplankton samples collected and analyzed during the entire oceanographic cruise (Fig. 1). A total of nine metacercariae of Didymozoidae were observed in four specimens of the ctenophore *Pleurobrachia bachei* A. Agassiz, in L. Agassiz, 1860 (intensity of parasitism was 2-3 parasites per host) (Fig. 2A-C; Table 2), and one metacercariae in one specimen of the siphonophore *Muggiaea atlantica* Cunningham, 1892 (Fig. 2D-E; Table 2).

Metacercariae of ctenophores and siphonophores were morphologically identified as type Monilicaecum because they had an oval-to-cylindrical elongate body with rounded extremities, thick cuticle without spines, and body transversely striated (Fig. 2A-E). Oral sucker slightly ellipsoidal in the anterior portion of body. Ventral sucker round, muscular, situated near level of anterior third portion of body. Mouth subterminal, pharynx not seen and esophagus not clearly visible. 'Drusenmagen' (or stomach) present, round located at intestinal bifurcation, dorsal and lateral to the ventral sucker. Intestinal caecum at each side occupies lateral regions of the body, moniliform type, sinuous and each one composed with 4-8 inflated chambers oriented towards the posterior end of the body and near the posterior third of the hind-body. Excretory vesicle saccular, small, or contracted, located posterior to intestinal caecum. Excretory pore terminal. No reproductive structures were observed (Fig. 2C, E). Didymozoids were found in three different microhabitats in the *P. bachei* specimens (pharynx, meridional canal below of the ctene rows, and pharyngeal canal) and only was found one didymozoid in the subumbrellar cavity (nectosac) of *M. atlantica* (Table 2). The size of the individual hosts and their parasites are shown in the Table 2.

DISCUSSION

Records of didymozoids in ctenophores and siphonophores are scarce worldwide. We report the first record of metacercariae type Monilicaecum (Didymozoidae) parasitizing ctenophores and siphonophores in the Gulf of California. In fact, this record extends its distribution range to the entire Pacific Ocean because all previous records have been done in the Atlantic Ocean (Table 1). Only exist four publications reporting metacercariae didymozoids parasitizing ctenophores from North Sea, western Ireland, and the Atlantic Ocean (Reimer *et al.,* 1971, 1975; Yip, 1981, 1984) and two records parasitizing siphonophores from the North Sea and Atlantic Ocean (Reimer *et al.,* 1971, 1975). Ctenophore and siphonophore in these previous records are the same host species that those reported in the present study (*Pleurobrachia bachei* and *Muggiaea atlantica*). *P. bachei* is infected with the copepod *Microsetella norvegica* (Harpacticoida, Ectinosomatidae) in the eastern Gulf of California (Morales-Ávila *et al.,* 2023). This is the only previous record of the interactions of ctenophores with their parasites in the Gulf of California. However, didymozoids have been most frequently recorded parasite infecting chaetognaths in the Mexican Pacific, including the Gulf of California

Table 2. Body size (TL = Total length, W = width), intensity of infection, and the microhabitat of metacercariae parasites infecting each gelatinous zooplankton host.

Sampling station	Date (dd:mm:yy)	Time (h)	Bongo maximum sampling depth (m)	Host species	TL (mm)	W (mm)	Intensity of infection		TL (mm)	W (mm)	Microhabitat
E74	29/06/2016	21:43	201	*Pleurobrachia bachei* A. Agassiz, 1860	7.9	8.2	2	a	0.24	0.09	Pharynx
								b	0.47	0.06	Meridional canal below of the ctene rows
E74	29/06/2016			*P. bachei*	7.7	7.1	3	a	0.17	0.06	Pharynx
								b	-	-	Pharyngeal canal
								c	-	-	Meridional canal below of ctene rows
E74	29/06/2016			*P. bachei*	17.5	17.0	2	a	0.14	0.06	Pharynx
								b	0.51	0.05	Pharyngeal canal
E93	02/07/2016	14:47	218	*P. bachei*			2	a	0.30	0.08	Pharynx
					11.1	9.0		b	-	-	Pharyngeal canal
E94	02/07/2016	22:37	199	*Muggiaea atlantica* Cunningham, 1892	1.6	1.3	1	a	0.21	0.06	Subumbrellar cavity (nectosac)

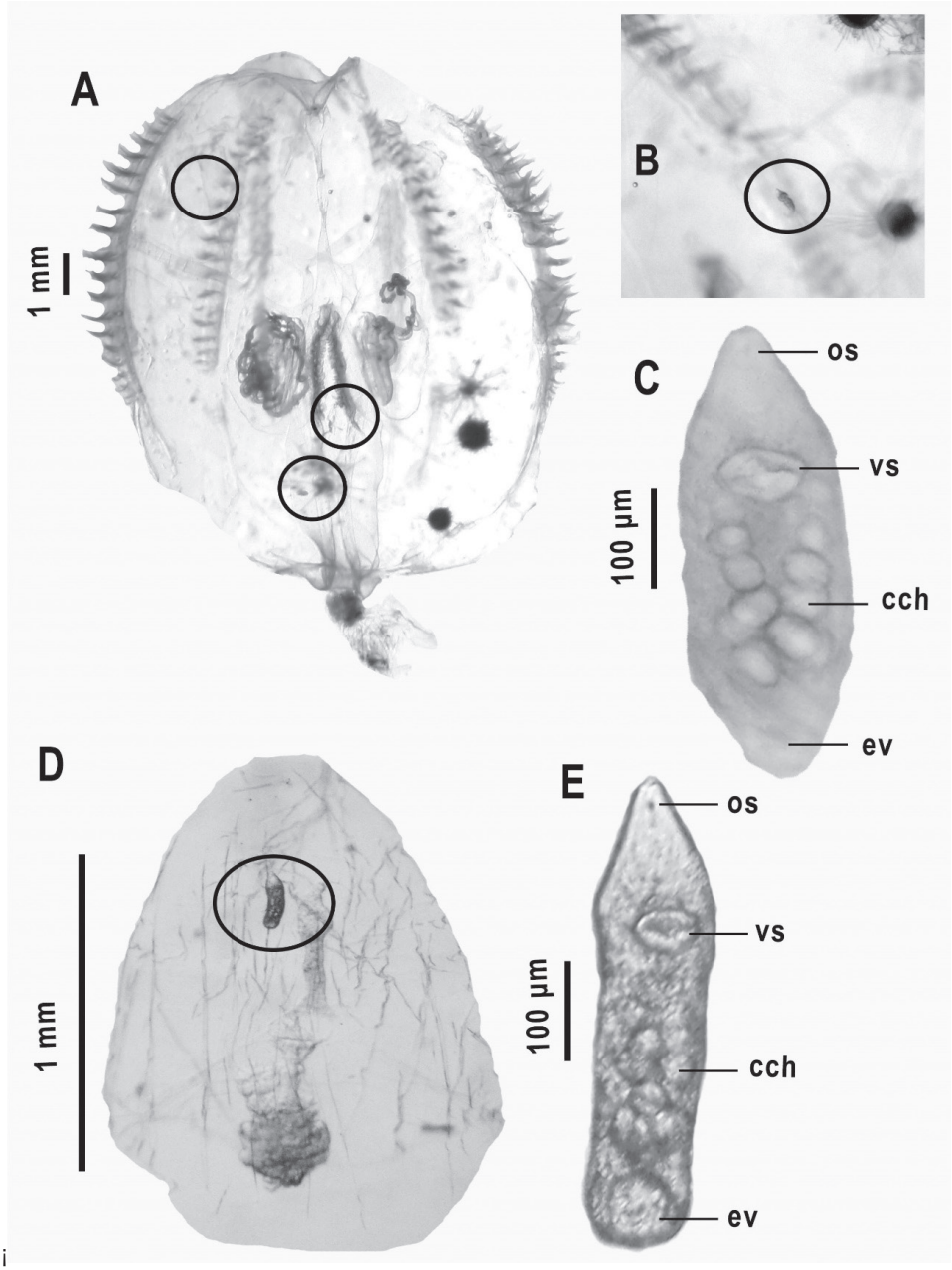

Figure 2. Morphological observations of metacercariae Didymozoidae parasitizing the ctenophore *Pleurobrachia bachei* (A-C) and the siphonophore *Muggiaea atlantica* (D-E) in the Gulf of California. Distribution of metacercariae in the hosts are shown in the circle (A-B, D) and morphology of metacercariae didymozoid in ventral view are shown in figure C, D. cch = caecal chambers; ev = excretor vesicle; os= oral sucker; vs = ventral sucker. Scale bars= 1 mm (A, D) and 100 µm (C-D).

(Lozano-Cobo *et al.,* 2018, 2022; Plascencia-Palomera *et al.,* 2024), and the Caribbean Sea (Gómez del Prado-Rosas *et al.,* 1999, 2007; Lozano-Cobo *et al.,* 2017). The ctenophore and siphonophore host species have circumtropical-subtropical biogeographic distribution. *Pleurobrachia bachei* distributes from Northeastern Pacific Ocean (Alaska) to Acapulco, Guerrero, Mexico (Ruiz-Escobar *et al.,* 2015; Puente-Tapia *et al.,* 2021) and *Muggiaea atlantica* distributes in the temperate eastern and northwestern Pacific Ocean (Alvariño, 1971) including the Gulf of California where is the most frequent and abundant species in the siphonophore assemblage (Brinton *et al.,* 1986; Esquivel-Herrera, 2000; Silveyra-Bustamante *et al.,* 2020). In general, studies about the diversity, abundance, and spatial and temporal distribution of ctenophores in the Mexican Pacific and Gulf of California are scarce (Ruiz-Escobar *et al.,* 2015; Puente-Tapia *et al.,* 2021), and *P. bachei* was reported as abundant in a study of the composition of zooplankton of three estuaries from Mazatlán, Sinaloa (Álvarez-León, 1980). Siphonophores are a zooplanktonic group difficult to study because they are frequently damaged during zooplankton sampling tows. The characterization of the epipela-

gic siphonophore communities of the Gulf of California was investigated in four oceanographic cruises (Mar-Apr, Jul-Aug, Nov-Dec 1984, and June 1986) where *M. atlantica* was the species that contributed more to the variability of siphonophore communities as indicator of neritic waters with high plankton abundance (Esquivel-Herrera, 2000). However, *M. atlantica* was recorded with low frequency (in August-September 1977) in the Gulf of California (Gasca & Suárez, 1991), but the most abundant species of siphonophore in Cabo Pulmo National Park, located southwest of the Gulf of California (Silveyra-Bustamante *et al*., 2020). So, the low prevalence of didymozoid parasites may be due to the natural low abundance of ctenophores and siphonophores, that are just smaller prevalence than those recorded in chaetognaths that seem to be more frequent intermediate hosts (Gómez del Prado-Rosas *et al.,* 1999, 2007; Lozano-Cobo *et al.,* 2017, 2018, 2022; Plascencia-Palomera *et al.,* 2024). Therefore, there still many parasites to be discovered in the ctenophores and siphonophores that are distributed in the Pacific Ocean and the Gulf of California. Metacercariae didymozoids are also frequently reported infecting cephalopods collected from central and eastern North Pacific and Gulf of California (Overstreet & Hochberg, 1975), and from Brazil (Vidal & Haimovici, 1999).

Although the ctenophores and siphonophores and their parasites were fixed in non-denatured ethanol, it was not possible to perform a molecular identification of the parasites. Lozano-Cobo *et al*. (2022) identified using molecular analysis (mitochondrial cytochrome c oxidase subunit I gene, *cox1*) three morphotypes of metacercariae Didymozoidae of type Monilicaecum: didymozoid sp. 1, didymozoid sp. 2, and didymozoid sp. 3 parasitizing two species of chaetognaths *Flaccisagitta enflata* (Grassi, 1881) and *Flaccisagitta hexaptera* (d'Orbigny, 1836) and the holoplanktonic mollusks *Firoloida desmarestia* Lesueur, 1817 in the Gulf of California. Therefore, it is likely that several of the nine metacercariae of didymozoids found in the present study infecting ctenophores and siphonophores correspond to at least one of these three morphotypes previously mentioned in chaetognaths. Metacercariae found in the present study match with the morphological description of the specimens identified as Monilicaecum in Lozano-Cobo *et al.* (2022). Although the metacercariae infecting ctenophores and siphonophores in the present study were slightly larger (0.14 – 0.51 mm LT and 0.5 – 0.9 mm W) (Table 2) than those previously recorded in chaetognaths from the Gulf of California (0.15 – 0.25 mm LT and 0.04 – 0.10 mm W) (Lozano-Cobo *et al*., 2022). Considering this observational evidence of larval didymozoids reported in these three distinct host species, life cycle could be as follows: the first intermediate hosts are planktonic gastropods (like *Firoloida desmarestia*), second intermediate are small crustaceans (i.e. copepods) and chaetognaths, the third intermediate or paratenic hosts are zooplanktonic invertebrates (including gelatinous carnivorous zooplankton) and small fishes, and the definitive hosts are large predatory fishes, mostly fish species of the family Scombridae (Bárcenas de los Santos *et al.,* 2021; Louvard *et al.,* 2022a, b; Lozano-Cobo *et al.,* 2022). We proposed that ctenophores and siphonophores act as alternative hosts in the life cycle of didymozoids, particularly when intermediate hosts are scarce or when free-living larval stages of didymozoids are highly abundant. They are likely paratenic host in epipelagic zones, because the zooplankton samples were collected with a bongo net from 300 m depth to sea surface. We additionally speculate there are the same didymozoid species that those found in chaetognaths (Lozano-Cobo *et al.,* 2022) because ctenophores and siphonophores share similar vertical habitat that chaetognaths in the Gulf of California (Alvariño, 1967; Gasca & Suárez, 1991; Esquivel-Herrera, 2000; Silveyra-Bustamante *et al.,* 2020). An additional study is necessary to increase the number of records of ctenophores and siphonophores to infer the ecological parameters of parasitism that can be used as evidence of their function as hosts in the life cycle of didymozoids. The present study represents a new geographic record for these parasites in the Gulf of California, Mexico extending its distribution range from the Atlantic Ocean to the Pacific Ocean.

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