



## An updated checklist of ctenophores (Ctenophora: Nuda and Tentaculata) of Mexican seas

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### ABSTRACT

Ctenophores are one of the most conspicuous and frequent groups of the gelatinous zooplankton community, but their regional diversity in tropical and subtropical latitudes remains largely unknown. We provide an overview and update of the current knowledge of the diversity in Mexican seas, including ocean and coastal-neritic environments of the Gulf of Mexico, the Mexican Caribbean Sea, and the Mexican Pacific Ocean. Ctenophore records were reviewed based on the available scientific and gray literature, the Naturalista network ([www.naturalista.mx](http://www.naturalista.mx)), and the ctenophore species collected in the Gulf of California by the Monterey Bay Aquarium Research Institute. A total of 33 taxa (Class Nuda and Tentaculata) were found to occur in Mexican seas, of which 12 of the 33 taxa (36.4 % of the total) were recorded in the Gulf of Mexico, 7 (21.2 %) in the Mexican Caribbean Sea, 25 (75.8 %) in the Gulf of California, 11 (33.3 %) in the Eastern Tropical Pacific, and only 1 (3.0 %) are known in the Northeastern Pacific. Up to nine taxa included in our account represent first records for Mexico (i.e., *Bathocyroe fosteri*, *Kiyohimea usagi*, *Lampocteis cruentiventer*, *Leucothea* sp., *Aulacoctena* sp., *Haekelia beehleri*, *Charistephane fugiens*, *Bathycytena chuni*, and *Hormiphora californensis*). Due to the lack of data on benthic ctenophores and the sparse studies on oceanic and deep-living species, it is expected that the list will grow as new surveys are performed in the deep sea. The lack of long-term studies on Mexican ctenophores have limited our capacity to draw valid conclusions on their abundance, total diversity, endemism, and trophic ecology in Mexico.

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### 1. Introduction

Ctenophores (pronounced “teen-o-fours”) have been described as the most beautiful, delicate, seemingly innocent yet most voracious predators in the plankton community (Mianzan et al., 2009). They are exclusively marine organisms, dwelling in all oceans at all depths, from polar to tropical waters, inshore to offshore, and from the surface to the deep sea (Mianzan et al., 2009; Mills, 2010).

Ctenophores have attracted attention the last decade, mainly as a result of the enigma around their potentially increased abundances around the world. Despite the increased attention, they remain either understudied or disregarded in most food web investigations and monitoring programs, and are defined as one of the most difficult groups of pelagic animals to study (Majaneva,

2014). Consequently, their diversity and ecological roles are often grossly oversimplified and misunderstood, leading to biased views of ecosystem functioning (Majaneva, 2014). In addition, ctenophores share traits such as efficient predation behavior, the ability to starve and shrink during periods of low food availability and to tolerate increased temperatures, as well as high reproductive capacity, making them likely to take advantage of changing environmental conditions (Majaneva, 2014).

The phylum Ctenophora, also known as comb jellies, is a small and well-defined group of planktonic and benthic gelatinous predators (Mianzan, 1999). The total number of species varies considerably depending on the source and whether potential synonymies have been taken into consideration. For example, according to Mills and Haddock (2007) and Mills (2010) there are between 100 to 150 species of ctenophores worldwide; a recent classification by Mills (1998-present), accounts for a total of 188 species belonging to two classes, nine orders, 30 families, and 55 genera, whereas Appeltans et al. (2012) recognized 190 species worldwide. Also, it has been proposed that the number of ctenophore species has been underestimated globally, stating

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that at least 25–50 species have not yet been formally described (unsampled and undiscovered) (Appeltans et al., 2012; Mianzan et al., 2009; Mills, 1998–present; Mills and Haddock, 2007); moreover, the number of undescribed ctenophore species in the deep-sea regions has not yet been estimated (Mills and Haddock, 2007; Podar et al., 2001). According to Appeltans et al. (2012), the total estimated number of species in ctenophoran fauna (expert-based) is between 315 and 500; and the estimated percent of all existing species that are currently described is between 38 and 60%.

Ctenophora is one of the least known invertebrate phyla in Mexico (Martínez-Meyer et al., 2014). The study of this gelatinous group in Mexican waters is incomplete and infrequent, lacking essential information like the true number of species, their spatial and temporal distribution and dynamics, abundance, and ecological roles (e.g. natural diet, feeding–growth–reproductive rates, biological associations, among others). The diversity of Mexican ctenophore fauna has been accounted for in several works (see Bigelow, 1912; Cruz González et al., 2018; Moss, 2009; Ruíz-Escobar et al., 2015); however, data are not comprehensive: some of them focused on particular regions and none included all Mexican seas. Particularly, Bigelow (1912) and Ruíz-Escobar et al. (2015) included only species from the Pacific; Moss (2009) from the Gulf of Mexico, while Cruz González et al. (2018) excluded the Mexican Caribbean Sea, because this region has not been studied. The main objective of the present work is to provide a complete, updated check-list of the ctenophore species reported from Mexican seas as a baseline for further studies aiming to describe the ecological role of this species in marine ecosystems of Mexico.

## 2. Material and methods

In order to prepare the checklist of the Ctenophora from Mexican seas (including jurisdictional Mexican waters of the Gulf of Mexico, Mexican Caribbean Sea, and Mexican Pacific Ocean) we searched for records and occurrence data of this gelatinous group following a review and analysis of published scientific articles, gray literature, as well as a Mexican biodiversity web site [www.naturalista.mx](http://www.naturalista.mx) (Naturalista, CONABIO, 2020; Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico), linked via [www.inaturalist.org](http://www.inaturalist.org) to the global iNaturalist community. On this site, users (mainly professionals in the area of the biological sciences) identify the species to create a species inventory. For ctenophores, many of the photographed species have been identified or corroborated by specialists in this group. Only those records that were identified/corroborated by at least one specialist were included in our list.

We also added unpublished ctenophore records collected or observed by the Monterey Bay Aquarium Research Institute (MBARI, California, USA) in the Gulf of California in February 2012 and March 2015 at different depths during cruises of the R/V Western Flyer and ROV Doc Ricketts. Blue-water SCUBA diving was used to sample the upper 5–25 m of the water column in different regions of the Gulf (including Farallon, Alarcón, La Paz, Mazatlán, Cerralvo, and Pescadero Basins, as well as off La Paz, Baja California Sur) (Fig. 1). Other species were observed in the same gulf zones by ROV dives (here referred to as Dive Dnumber) performed at a depth range of ~100–3600 m to obtain epi-, meso- and bathypelagic samples/observations, thus adding to our knowledge of some of the deeper species distributed in this region of the Mexican Pacific Ocean.

We included each taxon found in the source, i.e. identified species or still as yet undetermined species referred to as “sp”. or genus rank in the literature. Using the taxa records, we prepared a faunal checklist for Mexican waters (Table 1), indicating the

presence/absence of the ctenophore species in each of the main marine regions of Mexico: (1) Mexican waters of Gulf of Mexico, (2) Mexican Caribbean Sea, (3) Gulf of California, (4) Northeastern Pacific, and (5) Eastern Tropical Pacific.

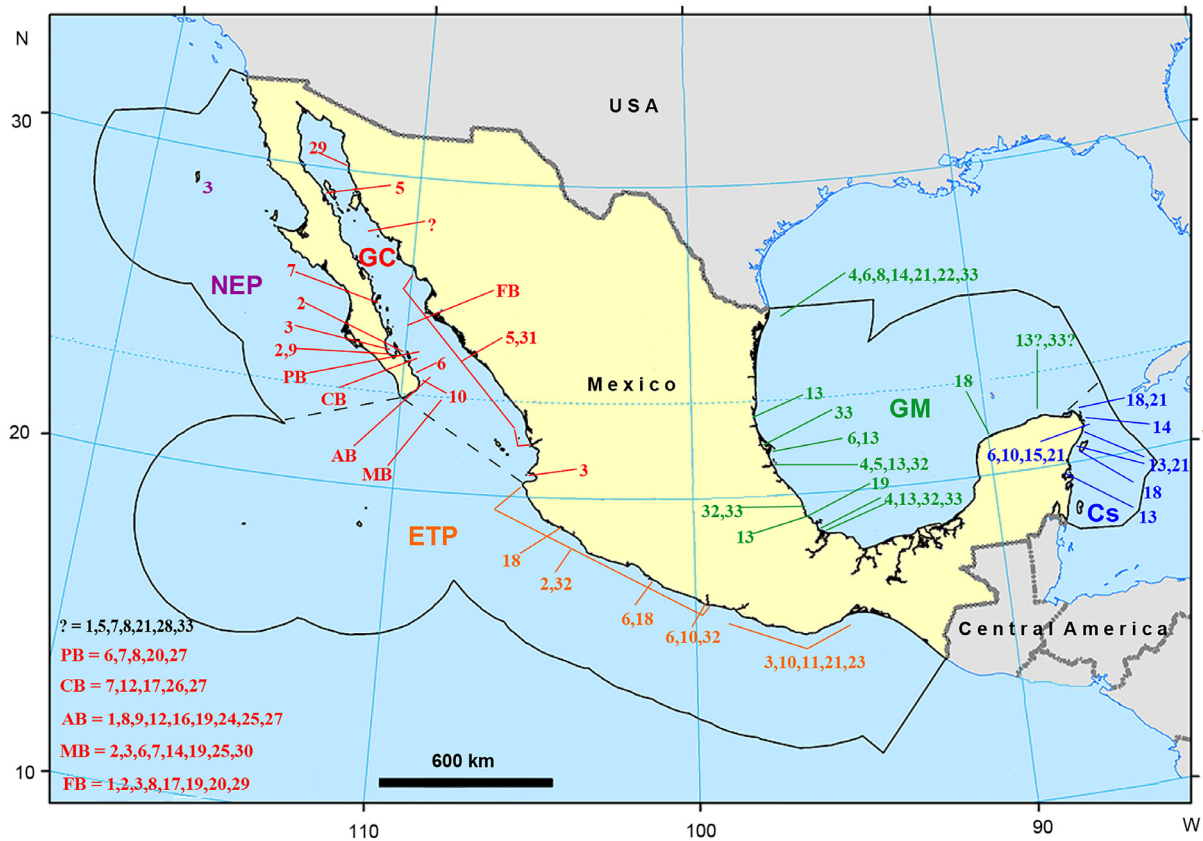
The Mexican jurisdictional waters of the Gulf of Mexico includes a northern limit of the Rio Bravo mouth (border limit with USA), the shelves and oceanic waters of the Tamaulipas, Veracruz, Tabasco, Campeche, and Yucatan state, while the limit with the Caribbean Sea was considered Cabo Catoche (northern Quintana Roo state, ~21°36'N, 87°06'W) (Niño-Torres et al., 2015). The Mexican Caribbean Sea spans from Cabo Catoche, Quintana Roo to the border with Belize (Niño-Torres et al., 2015). The Mexican Pacific Ocean was divided in three different regions: (1) Northeastern Pacific (from the border limit with the eastern coasts of the USA to Cabo San Lucas, Baja California Sur, 32°30'N, 118°24'W to 22°48'N, 110°00'W) (De la Lanza Espino, 1991); (2) Gulf of California (inland sea off the eastern side of the Baja California Peninsula with a southern limit from Cabo San Lucas to Cabo Corrientes, Jalisco) (Cano, 1991) and (3) Eastern Tropical Pacific (from Cabo Corrientes, Jalisco to border limit with Guatemala) (Flamand, 1991) (see Fig. 1).

For each ctenophore taxon we include data on: (1) distribution in Mexico, including locations. For each locality, in square brackets [name] we indicate the Mexican state where the taxon was observed, e.g. [Baja California Sur], [Veracruz], [Quintana Roo]; (2) global distribution, i.e. records in other geographic regions; (3) remarks, only for the “dubious records” we include some observations on each case, while for those ctenophores that were identified as new records, in this section we indicate the region of the new record. For specimens collected/observed by MBARI we include data on the material examined: number of specimens collected/observed; sampling date; sampling site; sampling method; depth of collection; species identifier. The taxonomical list follows the most recent nomenclatural data available (July 2020) at the WoRMS Network (World Register of Marine Species) (Mills, 1998–present) ([www.marinespecies.org](http://www.marinespecies.org)). We also provide photographs of some of the specimens observed during MBARI surveys, as well as some of the records identified by specialists at [naturalista.mx](http://naturalista.mx).

## 3. Results

We report here a total of 33 taxa, of which 26 (78.8%) have been identified at the species level and 7 (21.2%) at genus rank (Table 1). Of the 33 taxa, 5 (15.2%) belong to the Class Nuda and the remaining 28 taxa (84.8%) to the Class Tentaculata. A total of 9 taxa represent the first records for Mexico: *B. fosteri* Madin and Harbison, 1978, *K. usagi* Matsumoto and Robison, 1992, *L. cruentiventer* Harbison, Matsumoto and Robison, 2001, *Leucothea* sp., *Aulacoctena* sp., *H. beehleri* (Mayer, 1912), *C. fugiens* Chun, 1879, *Bathycytena chuni* (Moser, 1909), and *H. californensis* (Torrey, 1904). The records from [naturalista.mx](http://naturalista.mx) and those provided in the present study as personal observations, allowed us to include 7 taxa for the Mexican Caribbean Sea, which was a region that had no previous records (*C. veneris* Lesueur, 1813, *B. vitrea* (L. Agassiz, 1860), *Mnemiopsis leidyi* A. Agassiz, 1865, *E. vexilligera* Gegenbaur, 1856b, *Eurhamphaea* sp., *Leucothea* sp., and *O. maculata* (Rang, 1828)); (see Table 1).

In the Gulf of Mexico, up to 12 of the 33 identified taxa (36.4% of the total) have been recorded, 7 (21.2% of the total) in the Mexican Caribbean Sea, 25 (75.8% of the total) in the Gulf of California, 11 taxa (33.3% of the total) from the Eastern Tropical Pacific, and only 1 (3.0%) in the Northeastern Pacific. Two taxa (6.1% of the total) have been recorded exclusively in the Gulf of Mexico, from the Gulf of California included 14 taxa (42.4%) unique to that region, in the Caribbean Sea and Eastern Tropical



**Fig. 1.** Spatial distribution of ctenophore records in Mexican seas. GM (Gulf of Mexico), Cs (Caribbean Sea), GC (Gulf of California), NEP (Northeastern Pacific), ETP (Eastern Tropical Pacific); PB (Pescadero Basin), CB (Cerralvo Basin), FB (Farallon Basin), AB (Alarcón Basin), MB (Mazatlán Basin), ? (location not indicated); Numbers in red color indicate records from Gulf of California, Purple = Northeastern Pacific, Orange = Eastern Tropical Pacific, Green = Gulf of Mexico, Blue = Caribbean Sea; 1 (*Beroe abyssicola*), 2 (*Beroe cucumis*), 3 (*Beroe forskalii*), 4 (*Beroe ovata*), 5 (*Beroe* sp.), 6 (*Cestum veneris*), 7 (*Velamen parallelum*), 8 (*Thalassocalyce inconstans*), 9 (*Bathocyroe fosteri*), 10 (*Bolinopsis vitrea*), 11 (*Bolinopsis infundibulum*), 12 (*Bolinopsis* sp.), 13 (*Mnemiopsis leidyi*), 14 (*Eurhamphaea vexilligera*), 15 (*Eurhamphaea* sp.), 16 (*Kiyohimea usagi*), 17 (*Lampocteis cruentiventer*), 18 (*Leucothea* sp.), 19 (*Ocyropsis crystallina*), 20 (*Ocyropsis crystallina crystallina*), 21 (*Ocyropsis maculata*), 22 (*Ocyropsis maculata maculata*), 23 (*Ocyropsis maculata immaculata*), 24 (*Aulacocetna* sp.), 25 (*Haeckelia beehleri*), 26 (*Charistephane fugiens*), 27 (*Bathycytena cluni*), 28 (*Hormiphora palmata*), 29 (*Hormiphora californensis*), 30 (*Hormiphora* sp.), 31 (*Pleurobrachia bachei*), 32 (*Pleurobrachia pileus*), 33 (*Pleurobrachia* sp.).

Pacific we recorded only one taxon each one (3.0%), while the Northeastern Pacific has no exclusive ctenophore taxa.

These 5 maritime regions in general did not have taxa in common. The 3 regions of the Pacific Ocean have only one taxon in common, i.e. *B. forskalii* Milne-Edwards, 1841. The Gulf of California and the Eastern Tropical Pacific, as well as the Gulf of Mexico and Gulf of California were the regions with the greatest number of common taxa with 7 each one (21.2% of the total). The remaining pairwise comparisons are presented in Table 1. Fig. 1 shows the spatial distribution of ctenophore records from Mexican Seas.

On a per-site basis, *B. forskalii* was the most frequently recorded ctenophore, from 13 localities, followed by *Beroe* sp. (10), *O. maculata* and *C. veneris* (9), *M. leidyi* and *P. pileus* F. Müller, 1776 each with 8 localities, while the remaining taxa occurred in 7 or less localities.

The most speciose family was Pleurobrachiidae (6 taxa), followed by Beroidae and Ocyropsidae with 5 taxa each, Bolinopsidae (4), Eurhamphaeidae (3), Cestidae (2), while the remaining families were represented by a single taxon. The genera *Ocyropsis* and *Beroe* were represented with a total of 5 taxa each, followed by *Pleurobrachia* (3), *Hormiphora* (3), *Bolinopsis* (3), *Eurhamphaea* (2); each remaining genus was represented by one taxon.

Most of the specimens reported from the available literature and in [naturalista.mx](http://naturalista.mx) were collected in estuarine-lagoon systems and shallow coastal waters. The fewest individuals were sampled in oceanic waters or outside the continental shelf. This is

likely more indicative of the extent of human excursions, rather than reflecting the species themselves. In most of the records of coastal-neritic areas, ctenophores were collected at depths between 1 m and 30 m, while a few others were collected between 30 and 160 m. *T. inconstans* Madin and Harbison, 1978 represents the only species previously reported from depths greater than 200 m. The organisms reported during MBARI's surveys were observed in a range from 15 m to 2442 m depth. Therefore, these specimens represent the second records in mesopelagic waters and first from Mexican bathyal depths.

### 3.1. List of species with detailed spatial distribution in Mexican waters and worldwide

#### Phylum Ctenophora Eschscholtz, 1829

##### Class Nuda Chun, 1879

##### Order Beroida Eschscholtz, 1825

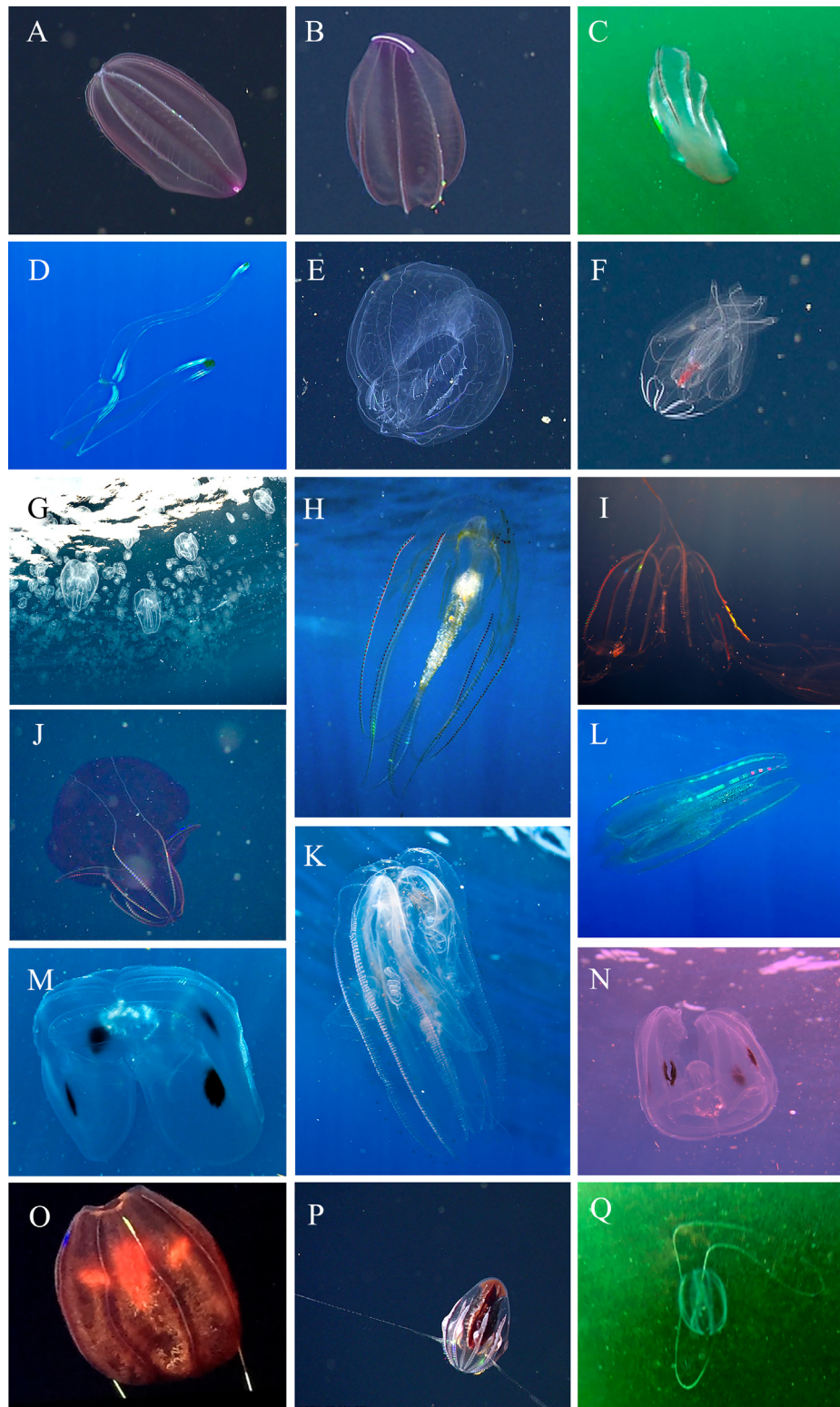
##### Family Beroidae Eschscholtz, 1825

##### Genus *Beroe* Muller, 1776

##### (1) *B. abyssicola* Mortensen, 1927

##### (Fig. 2A–B)

**Material examined.** 1 specimen collected, March 8th 2015, Farallon Basin (25°27'N, 109°51'W), Dive D722, 1584 m, id. SHD



**Fig. 2.** *In situ* photographs of ctenophores from Mexican waters. (A) *B. abyssicola* (Farallon Basin, Gulf of California, depth = 2094 m) (photo SHD Haddock); (B) *B. abyssicola* (Alarcón Basin, Gulf of California, depth = 2442 m) (photo SHD Haddock); (C) *B. forskalii* (Yelapa, Jalisco, Eastern Tropical Pacific) (photo Alejandra Castelo Corona); (D) *C. veneris* (Zihuatanejo, Guerrero, Eastern Tropical Pacific) (photo Raúl Ramírez Barragán); (E) *T. inconstans* (Farallon Basin, Gulf of California, depth = 252 m) (photo SHD Haddock); (F) *B. fosteri* (Alarcón Basin, Gulf of California, depth = 2226 m) (photo SHD Haddock); (G) *B. vitrea* (Cabo Pulmo, Baja California Sur, Gulf of California) (photo Patrick Webster); (H) *E. vexilligera* (Isla Blanca, Quintana Roo, Caribbean Sea) (photo Matteo Cassella); (I) *Eurhamphaea* sp. (Cancún Reefs, Quintana Roo, Caribbean Sea) (photo Christian Amador Da Silva); (J) *L. cruentiventer* (Cerralvo Basin, Gulf of California, depth = 1952 m) (photo SHD Haddock); (K) *Leucothea* sp. (Contoy Island, Caribbean Sea) (photo Jerónimo Avilés); (L) *Leucothea* sp. (Zihuatanejo, Guerrero, Eastern Tropical Pacific) (photo Raúl Ramírez Barragán); (M) *O. maculata* (Isla Blanca, Quintana Roo, Caribbean Sea) (photo Matteo Cassella); (N) *O. maculata* (Cancún Reefs, Quintana Roo, Caribbean Sea) (photo Christian Amador Da Silva); (O) *Aulacoctena* sp. (Alarcón Basin) (photo SHD Haddock); (P) *B. chuni* (Alarcón Basin, Gulf of California, depth = 841 m) (photo SHD Haddock); (Q) *H. californensis* (Puerto Libertad, Sonora, Gulf of California) (photo Raziel Hernández Pimienta). No scale bars for size are available for these photos.

**Table 1**

Checklist of ctenophores reported from Mexican waters. GM (Gulf of Mexico); Cs (Caribbean Sea); NEP (Northeastern Pacific); GC (Gulf of California); ETP (Eastern Tropical Pacific).

Ctenophore species	GM	Cs	Mexican Pacific Ocean			References
			GC	NEP	ETP	
Phylum Ctenophora						
Class Nuda						
Order Beroida						
Family Beroidae						
<b><i>Beroe abyssicola</i></b>			x			11,32
<b><i>Beroe cucumis</i></b>			x		x	13,14,32
<b><i>Beroe forskalii</i></b>			x	x	x	3,7,24,26,31,32
<b><i>Beroe ovata</i></b>	x					5,8,21
<b><i>Beroe sp.</i></b>	x		x		x	6,19,31
Class Tentaculata						
Order Cestida						
Family Cestidae						
<b><i>Cestum veneris</i></b>	x	x	x		x	4,5,9,14,31,32
<b><i>Velamen parallelum</i></b>			x			6,28,32
Order Thalassocalycida						
Family Thalassocalycidae						
<b><i>Thalassocalyce inconstans</i></b>	x		x			5,9,32
Order Lobata						
Family Bathocyroidae						
<b><i>Bathocyroe fosteri</i></b>			x			32
Family Bolinopsidae						
<b><i>Bolinopsis vitrea</i></b>		x			x	4,24,31
<b><i>Bolinopsis infundibulum</i></b>			x		x	3,7
<b><i>Bolinopsis sp.</i></b>			x			32
<b><i>Mnemiopsis leidyi</i></b>	x	x				8,9,21,23,30,31,32
Family Eurhamphaeidae						
<b><i>Eurhamphaea vexilligera</i></b>	x	x	x			5,20,31,32
<b><i>Eurhamphaea sp.</i></b>		x				31
<b><i>Kiyohimea usagi</i></b>			x			32
Family Lampoctenidae						
<b><i>Lampocteis cruentiventer</i></b>			x			32
Family Leucotheidae						
<b><i>Leucothea sp.</i></b>	x	x			x	31
Family Ocyropsidae						
<b><i>Ocyropsis crystallina</i></b>	x		x			21,32
<b><i>Ocyropsis crystallina crystallina</i></b>			x			15
<b><i>Ocyropsis maculata</i></b>	x	x	x		x	5,12,24,31
<b><i>Ocyropsis maculata maculata</i></b>	x					5
<b><i>Ocyropsis maculata immaculata</i></b>					x	3,7
Order Cydippida						
Family Aulacoctenidae						
<b><i>Aulacoctena sp.</i></b>			x			32
Family Haeckeliidae						
<b><i>Haeckelia beehleri</i></b>			x			32
Family Mertensiidae						
<b><i>Charistephane fugiens</i></b>			x			32
Family Bathyctenidae						
<b><i>Bathyctena chuni</i></b>			x			32
Family Pleurobrachiidae						
<b><i>Hormiphora palmata</i></b>			x			4,6
<b><i>Hormiphora californensis</i></b>			x			31
<b><i>Hormiphora sp.</i></b>			x			10,32
<b><i>Pleurobrachia bachei</i></b>			x		x	1,2,18,19,27
<b><i>Pleurobrachia pileus</i></b>	x				x	4,13,22,32
<b><i>Pleurobrachia sp.</i></b>	x		x			5,6,16,17,21,23,25

(continued on next page)

Table 1 (continued).

Ctenophore species	GM	Cs	Mexican Pacific Ocean			References
			GC	NEP	ETP	
Total taxa by region	12	7	25	1	11	
Common taxa all regions	0					
Common GM-GC	7					
Common GC-ETP	7					
Common GM-Cs	5					
Common GM-ETP	5					
Common Cs-ETP	4					
Common Cs-GC	3					
Common GC-NEP	1					
Common ETP-NEP	1					
Common GM-NEP	0					
Common Cs-NEP	0					

(1) Álvarez-León (1980); (2) Álvarez-León and Wedler (1982); (3) Bell Enríquez-García et al. (2013); (4) Bigelow (1912); (5) Biggs et al. (1984); (6) Brusca and Trautwein (2005); (7) Cruz González et al. (2018); (8) Esquivel et al. (1980); (9) Flores-Galicia and De la Cruz-Francisco (2018); (10) Francis et al. (2013); (11) Francis et al. (2016); (12) Francis et al. (2015); (13) Gamero-Mora et al. (2015); (14) Gasca and Browne (2017); (15) Gasca and Haddock (2004); (16) Gómez-Aguirre (1976); (17) Gómez-Aguirre (1977); (18) Gómez-Aguirre (1981); (19) Gómez-Aguirre (1991); (20) Moss (2009); (21) Ocaña-Luna et al. (2015); (22) Ocaña-Luna et al. (2017); (23) Ordóñez-López et al. (2010); (24) Ruíz-Escobar et al. (2015); (25) Ruíz-Guerrero and López Portillo-Guzmán (2006); (26) SEMARNAT (2013); (27) Signoret de Brailovsky (1975); (28) Stretch (1982); (29) Swift et al. (2009); (30) Vargas et al. (2006); (31) [naturalista.mx](http://naturalista.mx); (32) Present study.

Haddock; 1 specimen collected, March 9th 2015, Farallon Basin (25°26'56.112"N, 109°50'42.309"W), Dive D723, 2094 m, id. SHD Haddock; 1 specimen collected, March 14th 2015, Alarcón Basin (23°41'31.798"N, 108°49'0.166"W), Dive D728, 2442 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: locality unknown (Francis et al., 2016); Farallon and Alarcón Basins (present study).

**Global distribution.** Arctic Ocean: White Sea (Russia) (Seravin, 1996); Northeastern Pacific Ocean: from Vancouver Island (Canada) to California (USA) (Arai, 1988; Haddock and Case, 1999; Francis et al., 2015; Mills and McLean, 1991), Strait of Georgia (Berkeley, 1931); Northwestern Pacific Ocean: Japan (Lindsay and Hunt, 2005).

### (2) *B. cucumis* Fabricius, 1780

**Material examined.** 1 specimen collected, March 8th 2015, Farallon Basin (25°27'N, 109°51'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 1 specimen collected, March 7th 2015, off La Paz, Dive D731, 304 m, id. SHD Haddock; 1 specimen collected, March 7th 2015, La Paz Basin (24°30'3.092"N, 109°59'29.011"W), Dive D720, 381 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Farallon and La Paz Basin, off La Paz [Baja California Sur] (present study), Mazatlán Basin (22°55'N, 108°6.95'W) (Gasca and Browne, 2017); Eastern Tropical Pacific: [Jalisco, Colima, Michoacán, and Guerrero] (Gamero-Mora et al., 2015).

**Global distribution.** Northwestern Atlantic Ocean: Gulf of Maine (Bigelow, 1926; Haddock and Case, 1999), northeastern Gulf of Mexico (Moss, 2009), and Caribbean Sea (close to Venezuela) (Harbison et al., 1977); Southwestern Atlantic Ocean: from Brazil to Argentina (between 30°S and 59°S) (Mianzan, 1999; Oliveira et al., 2007); Northeastern Atlantic Ocean: southern Baltic Sea (northern Europe) (Hansson, 2006), Canary Islands (Hernández, 2003; Lozano Soldevilla et al., 2006), and Mediterranean basin (Haddock and Case, 1999; Shiganova and Malej, 2009); Northwestern Pacific Ocean: Japan (Lindsay and Hunt, 2005; Uchida, 1940); Northeastern Pacific Ocean: Santa Barbara Channel, off California (USA) (Haddock and Case, 1999; Podar et al., 2001); Southeastern Pacific Ocean: from Peru to Chile (between 3°S to 55°S) (Oliveira et al., 2016) and references therein; (Yáñez et al.,

2009); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010, 2014); Arctic Ocean (Moss, 2009).

### (3) *B. forskalii* Milne-Edwards, 1841

(Fig. 2C)

**Material examined.** 2 specimens collected, March 2015, Farallon Basin (25°27'N-109°51'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 1 specimen collected, March 2015, Mazatlán Basin (22°55'N, 108°07'W), SCUBA diving, ~15–25 m, id. SHD Haddock.

**Distribution in Mexico.** Northeastern Pacific: Guadalupe Island (~241 km off western Baja California Peninsula) [Baja California Norte] (SEMARNAT, 2013); Gulf of California: Farallon and Mazatlán Basins (present study), El Quelele, La Paz [Baja California Sur] ([naturalista.mx](http://naturalista.mx)), Yelapa (close to Puerto Vallarta) [Jalisco] ([naturalista.mx](http://naturalista.mx)); Eastern Tropical Pacific: Carrizalillo, Estacahuite, La Boquilla, La Mina, Mazunte, Panteón, Puerto Ángel, and Zipolite [Oaxaca] (Bell Enríquez-García et al., 2013; Cruz González et al., 2018; Ruíz-Escobar et al., 2015).

**Global distribution.** Northwestern Atlantic Ocean: Gulf Stream, Florida (USA) (Podar et al., 2001), Gulf of Mexico (northeastern and eastern area) (Moss, 2009); Southwestern Atlantic Ocean: southern Brazil (Oliveira and Migotto, 2014); Northeastern Atlantic Ocean: Canary Islands (Chun, 1889, 1898), Mediterranean basin (including the Gulf of Naples, Alboran Sea, northern Adriatic, and Black Sea) (Chun, 1880; Haddock and Case, 1999; Mills et al., 1996; Seravin et al., 2002; Shiganova and Malej, 2009); Northeastern Pacific Ocean: Santa Barbara Channel, off California (USA) (Haddock and Case, 1999; Podar et al., 2001), Monterey Bay, California (USA) (Francis et al., 2015); Southeastern Pacific Ocean: Peru (Oliveira et al., 2016); Northwestern Pacific Ocean: Japan (Lindsay and Hunt, 2005); Southwestern Pacific Ocean: Australia (Gershwin et al., 2014).

**Remarks.** First record for Gulf of California ([naturalista.mx](http://naturalista.mx); present study).

### (4) *B. ovata* Chamisso and Eysenhardt, 1821

**Distribution in Mexico.** Gulf of Mexico: Tamaulipas coasts [Tamaulipas] (Biggs et al., 1984), Tampamachoco lagoon [Veracruz] (Esquivel et al., 1980), Mandinga Lagoon System and Alvarado Lagoon System [Veracruz] (Ocaña-Luna et al., 2015).

**Global distribution.** Western Atlantic Ocean: from the USA to Argentina (Haddock and Case, 1999; Mianzan, 1999; Oliveira

et al., 2016; Purcell et al., 2001; Schiariti et al., 2020 and references therein); Northeastern Atlantic Ocean: Canary Islands (Chun, 1889, 1898), Mediterranean basin (including Gulf of Naples, Adriatic Sea, Black Sea, Caspian Sea) (Chun, 1880; Mills et al., 1996; Shiganova and Malej, 2009; Shiganova et al., 2001, 2014b, 2019; Volovik and Korpakova, 2004), Denmark (northern Europe) (Shiganova et al., 2014b); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010).

##### (5) *Beroe* sp.

**Distribution in Mexico.** Gulf of Mexico: Tampamachoco lagoon [Veracruz] ([naturalista.mx](http://naturalista.mx)); Gulf of California: adjacent area of the northern zone of de los Angeles Bay [Baja California Norte] ([naturalista.mx](http://naturalista.mx)), Río Mayo (estuaries and freshwater marshes of Etchoropo and Moroncarit) [Sonora], Yavaros lagoon [Sonora], Agiabampo lagoon [Sonora], Topolobampo lagoon [Sinaloa], Presidio and Baluarte Rivers System (Bocas de Barrón, Chamela, El Ostial and Agua Dulce estuaries, freshwater marsh of Huizache, and Caimanero lagoon) [Sinaloa], Cañas and Acaponeta Rivers System [Nayarit], Santiago Tuxpan and San Pedro Rivers Systems (del Pozo, bocas de Azadero, Camichín, and Talega estuaries) [Nayarit] (Gómez-Aguirre, 1991), and localities not indicated within the Gulf of California (Brusca and Trautwein, 2005).

**Remarks.** Distributional data of *Beroe* sp. resemble that of other congeners identified in Mexico. However, it is possible that the records from Tuxpan [Veracruz] in the Gulf of Mexico correspond to *B. ovata*, whereas those from the Pacific could be assignable to either *B. cucumis* and/or *B. forskalii* because both species are known from this region of the Pacific. *B. abyssicola* has been reported from this region, but at greater depth (Berkeley, 1931).

#### Class Tentaculata Eschscholtz, 1825

##### Order Cestida Gegenbaur, 1856b

##### Family Gegenbaur, 1856b

##### Genus *Cestum* Lesueur, 1813

##### (6) *C. veneris* Lesueur, 1813

(Fig. 2D)

**Material examined.** 1 specimen collected, March 2015, Mazatlán basin (22°55'N, 108°07'W), SCUBA diving, ~15–25 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of Mexico: Tamaulipas coast [Tamaulipas] (Biggs et al., 1984), Lobos Reef [Veracruz] (Flores-Galicia and De la Cruz-Francisco, 2018); Mexican Caribbean Sea: Cancún coasts [Quintana Roo] ([naturalista.mx](http://naturalista.mx)); Gulf of California: Pescadero Basin (24°19'N, 109°12'W) (Gasca and Browne, 2017), Mazatlán Basin (present study), Los Barriles [Baja California Sur] ([naturalista.mx](http://naturalista.mx)); Eastern Tropical Pacific: close to Zihuatanejo coasts [Guerrero] ([naturalista.mx](http://naturalista.mx)), Acapulco [Guerrero] (Bigelow, 1912).

**Global distribution.** Northwestern Atlantic Ocean: Georges Bank (southern Gulf of Maine) (Bigelow, 1926), Bahamas (Haddock and Case, 1999), northwestern and northeastern Gulf of Mexico (Moss, 2009); Central and Southwestern Atlantic Ocean: from Colombia to Brazil (Harbison et al., 1978; Mianzan, 1999; Mianzan and Guerrero, 2000; Oliveira, 2007; Oliveira et al., 2007); Northeastern Atlantic Ocean: Canary Islands (Fol, 1869), Mediterranean basin (Chun, 1880; Mills et al., 1996; Shiganova and Malej, 2009 and references therein); Northeastern Pacific Ocean: Santa Barbara Channel, off California (USA) (Haddock and Case, 1999; Podar et al., 2001); Southeastern Atlantic Ocean: Chile (near Valparaiso coast) (Oliveira et al., 2016); Northwestern Pacific Ocean: Hatoma

Knoll Hydrothermal Vent (Philippine Sea) (Lindsay et al., 2015), Japan (Lindsay and Hunt, 2005); Southwestern Pacific Ocean: New Zealand (Mianzan et al., 2009), Australia (Gershwin et al., 2014).

**Remarks.** First record for Caribbean Sea ([naturalista.mx](http://naturalista.mx)).

##### Genus *Velamen* Krumbach, 1925

##### (7) *V. parallelum* (Fol, 1869)

**Material examined.** 1 specimen collected, March 2015, Cerralvo Basin (24°11'N, 109°38'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 1 specimen collected, March 10th 2015, Pescadero Basin (24°19'N, 109°12'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 3 specimens collected, March 2015, Mazatlán Basin (22°55'N, 108°07'W), SCUBA diving, ~15–25 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: ~2–3 km east of Puerto Escondido [Baja California Sur] (Stretch, 1982), Cerralvo, Pescadero, and Mazatlán Basins (present study), and localities not indicated within the Gulf (Brusca and Trautwein, 2005).

**General distribution.** Southwestern Atlantic Ocean: from Venezuela to Brazil (between 10°N and 2°S) (Harbison et al., 1978; Mianzan, 1999; Nogueira et al., 2015; Oliveira et al., 2007); Northeastern Atlantic Ocean: Canary Islands (Fol, 1869), Mediterranean basin (Mayer, 1912; Mills et al., 1996); Northeastern Pacific Ocean: Monterey Bay, California (USA) (Francis et al., 2015), California (USA) (Haddock and Case, 1999; Luo et al., 2014; Mills and Haddock, 2007; Podar et al., 2001); Southeastern Atlantic Ocean: Peru and Chile (Oliveira et al., 2016 and references therein; Palma and Apablaza, 2004); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010, 2014); Indian Ocean (Harbison et al., 1978).

##### Order Thalassocalycida Madin and Harbison, 1978

##### Family Thalassocalycidae Madin and Harbison, 1978

##### Genus *Thalassocalyce* Madin and Harbison, 1978

##### (8) *T. inconstans* Madin and Harbison, 1978

(Fig. 2E)

**Material examined.** 2 specimens collected, March 2015, Farallon Basin (25°27'N, 109°51'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 10 specimens collected, March 2015, Pescadero Basin (24°19'N, 109°12'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 1 specimen collected, March 2015, Alarcón Basin (23°41.5'N, 108°49'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 1 specimen collected, Farallon Basin, March 10th 2015, Dive D723, 252 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of Mexico: Tamaulipas coasts [Tamaulipas] (Biggs et al., 1984); Gulf of California: locality unknown (Swift et al., 2009), Farallon, Pescadero and Alarcón Basins (present study).

**Global distribution.** Northwestern Atlantic Ocean: Bahamas (Haddock and Case, 1999); Northeastern Atlantic Ocean: Mediterranean basin (Laval et al., 1989; Mills et al., 1996); Northeastern Pacific Ocean: Monterey Bay, California (USA) (Francis et al., 2015), off California (USA) (Haddock and Case, 1999; Luo et al., 2014; Podar et al., 2001; Wrobel and Mills, 1998, 2003); Eastern Tropical Pacific: Isla del Coco National Park (Costa Rica) (Corrales-Ugalde et al., 2017); Southeastern Pacific Ocean: Chile

(from 23°S to 37°S) (Oliveira et al., 2016 and references therein); Northwestern Pacific Ocean: Japan (Lindsay and Hunt, 2005).

#### Order Lobata Eschscholtz, 1825

#### Family Bathocyroidae Harbison and Madin, 1982

#### Genus *Bathocyroe* Madin and Harbison, 1978

#### (9) *B. fosteri* Madin and Harbison, 1978

(Fig. 2F)

**Material examined.** 1 specimen collected, March 20th 2012, Alarcón Basin (23°33'29.246"N, 108°46'58.249"W), Dive D337, 2226 m, id. SHD Haddock; 3 specimens collected, March 7th 2015, off La Paz, Dive D721, 300 m/307 m/346 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Off La Paz [Baja California Sur], Alarcón Basin (present study).

**Global distribution.** Northwestern Atlantic Ocean: Cape Code, Massachusetts (USA), Cape Hatteras, Carolina (USA), Tortugas, Florida (USA) (Miller et al., 2000); Gulf of Mexico (northeastern region, USA) (Moss, 2009); Bahamas (Haddock and Case, 1999; Youngbluth et al., 1988); Northeastern Atlantic Ocean: western Mediterranean basin (Alboran Sea) (Mills et al., 1996); Northwestern Pacific Ocean: Japan (Toyokawa et al., 1998); Northeastern Pacific Ocean: Monterey Bay, California (USA) (Francis et al., 2015; Zeidler and Browne, 2015), Santa Barbara, California (USA) (Miller et al., 2000).

**Remarks.** First record for Mexico (present study).

#### Family Bolinopsidae Bigelow, 1912 Genus *Bolinopsis* L. Agassiz, 1860

#### (10) *B. vitrea* (L. Agassiz, 1860)

(Fig. 2G)

**Distribution in Mexico.** Mexican Caribbean Sea: Eastern Cancún coasts [Quintana Roo] (naturalista.mx); Gulf of California: Cabo Pulmo [Baja California Sur] (naturalista.mx); Tropical Pacific: Acapulco harbor [Guerrero] (Bigelow, 1912), Corralero Lagoon, Puerto Ángel, Zipolite, and Punta Cometa [Oaxaca] (Ruíz-Escobar et al., 2015).

**Global distribution.** Arctic Ocean: White Sea (Russia) and Barentz Sea (Kamshilov, 1960; Seravin, 1998), Norway (fjords of the northern region) (Falkenhaus, 1996); Northwestern Atlantic Ocean: Gulf of Mexico (localities not indicated) (Sears, 1954), Florida–Bahamas region (West Indies) (Haddock and Case, 1999; Mayer, 1912); Southwestern Atlantic Ocean: from Suriname to Brazil (between 11°N and 24°S) (Harbison et al., 1978; Oliveira and Migotto, 2006; Oliveira et al., 2007); Northeastern Atlantic Ocean: Mediterranean basin (e.g. Lucic et al., 2011; Mills et al., 1996; Öztürk et al., 2011; Shiganova and Malej, 2009); Northeastern Pacific Ocean: Southern California Bight (USA) (Luo et al., 2014); Central Pacific Ocean: Galápagos Islands, Ecuador (Alvarino and Leira, 1986; Bigelow, 1912); Tropical Indian Ocean (Harbison et al., 1978).

**Remarks.** First record for Caribbean Sea and Gulf of California (naturalista.mx).

#### (11) *B. infundibulum* (OF Müller, 1776).

**Distribution in Mexico.** Eastern Tropical Pacific: Panteón, Zipolite, Mazunte, Estacahuite, La Mina, La Boquilla [Oaxaca] (Bell Enríquez-García et al., 2013; Cruz González et al., 2018).

**Global distribution.** Boreal–Arctic Ocean: Canadian Arctic Sea (Raskoff et al., 2005, 2010); Northwestern Atlantic Ocean: from

Gulf of Maine (New England, USA) to Labrador Sea (Bigelow, 1926; Haddock and Case, 1999), Caribbean Sea (Honduras) (Almeida et al., 2016); Northeastern Atlantic Ocean: along the northern Europe, southern Baltic Sea (Hansson, 2006; Lenz, 1973), Norwegian waters (Båmstedt and Martinussen, 2015; Falkenhaus, 1996), Scotland coasts (North Sea) (Gamble, 1977), and Barents Sea (Zelickman, 1972); Northeastern Atlantic Ocean: western Mediterranean basin (Alboran Sea) (Haddock and Case, 1999; Mills et al., 1996); Northeastern Pacific Ocean: from the Bering Sea to California (USA) (Burton et al., 2017; Francis et al., 2015; Haddock and Case, 1999; Luo et al., 2014; Mills and Haddock, 2007).

#### (12) *Bolinopsis* sp.

**Material examined.** 1 specimen observed, March 18th 2012, Cerralvo Basin (24°12'42.066"N, 109°38'20.151"W), Dive D335, 172 m, id. SHD Haddock; 1 specimen observed, March 18th 2012, Cerralvo Basin (24°12'42.199"N, 109°38'20.111"W), Dive D335, 180 m, id. SHD Haddock; 1 specimen observed, March 18th 2012, Cerralvo Basin (24°12'40.95"N, 109°38'23.13"W), Dive D335, 260 m, id. SHD Haddock; 1 specimen observed, March 19th 2012, Alarcón Basin (23°37'0.574"N, 109°45'1.112"W), Dive D336, 93 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Cerralvo and Alarcón Basin (present study).

#### Genus *Mnemiopsis* L. Agassiz, 1860

#### (13) *M. leidyi* A. Agassiz, 1865

**Distribution in Mexico.** Gulf of Mexico: del Carpintero lagoon [Tamaulipas] (naturalista.mx), Alvarado Lagoon System [Veracruz], Tampamachoco lagoon [Veracruz] (Esquivel et al., 1980), Tuxpan, Enmedio, Tanhuijo, and Lobos Reefs (Lobos-Tuxpan Reefs System) [Veracruz] (Flores-Galicia and De la Cruz-Francisco, 2018), Veracruz Reefs System (Southern Vergara Bay) [Veracruz] (Ocaña-Luna et al., 2015; naturalista.mx), Mandinga Lagoon System [Veracruz] (Ocaña-Luna et al., 2015; Vargas et al., 2006; naturalista.mx; FA Puente-Tapia personal observation), Yucatan litoral (localities not indicated) (= as *M. mccradyi*) [Yucatan] (Ordóñez-López et al., 2010); Mexican Caribbean Sea: western Cozumel Island [Quintana Roo] (naturalista.mx; FA Puente-Tapia personal observation), Ascención Bay (R Gasca personal observation), and Puerto Morelos Reef National Park [Quintana Roo] (FA Puente-Tapia personal observation).

**Global distribution.** Western Atlantic Ocean: estuaries and bays along temperate and subtropical North (including Gulf of Mexico), Central (Caribbean Sea), and South Atlantic waters of America (Almeida et al., 2016; Bayha et al., 2014; Costello et al., 2012; Harbison et al., 1978; Kremer, 1994; Mianzan, 1999; Moss, 2009; Oliveira et al., 2016; Purcell et al., 2001); Northeastern Atlantic Ocean: Mediterranean basin (including Black, Azov, and Caspian Seas) (Bayha et al., 2014; Dumont et al., 2004; Ivanoc et al., 2000; Purcell et al., 2001; Studenikina et al., 1991; Shiganova and Malej, 2009), North Europe: western and central Baltic Sea (Bayha et al., 2014; Hansson, 2006; Javidpour et al., 2006), North Sea (Danish and Netherlands waters) (Bayha et al., 2014; Shiganova et al., 2014a).

**Remarks.** First record for Caribbean Sea (naturalista.mx; present study).



**Family Eurhamphaeidae Krumbach, 1925****Genus Eurhamphaea Gegenbaur, 1856****(14) *E. vexilligera* Gegenbaur, 1856b**

(Fig. 2H)

**Material examined.** 3 specimens collected, March 12th 2015, Mazatlán Basin (22°55'N, 108°07'W), SCUBA diving, ~15–25 m, id. SHD Haddock.

**Distribution in Mexico.** Tamaulipas coasts [Tamaulipas] (Biggs et al., 1984; Moss, 2009); Mexican Caribbean Sea: Eastern Blanca Island and northeastern Cancún [Quintana Roo] ([naturalista.mx](http://naturalista.mx)); Gulf of California: Mazatlán Basin (present study).

**Global distribution.** Northwestern Atlantic Ocean: Bahamas region (Haddock and Case, 1999), northeastern Gulf of Mexico (Moss, 2009), Honduras (Caribbean Sea) (Almeida et al., 2016); Central and Southwestern Atlantic Ocean: America: from Venezuela (12°N) (Caribbean Sea) to Brazil (1°S) (Harbison et al., 1978; Mianzan, 1999; Mills, 1998–present; Oliveira et al., 2007); Northeastern Atlantic Ocean: Canary Islands (Fol, 1869), Mediterranean basin (Chun, 1880; Haddock and Case, 1999; Mills, 1998–present; Mills et al., 1996); Northeastern Pacific Ocean: Santa Barbara Channel, off California (USA) (Haddock and Case, 1999); Western Pacific Ocean: Hatoma Knoll Hydrothermal Vent (Phillipine Sea) (Lindsay et al., 2015).

**Remarks.** First record for Caribbean Sea ([naturalista.mx](http://naturalista.mx)) and Gulf of California (present study).

**(15) *Eurhamphaea* sp.**

(Fig. 2I)

**Distribution in Mexico.** Mexican Caribbean Sea: northeastern Cancún [Quintana Roo] ([naturalista.mx](http://naturalista.mx)).

**Remarks.** The record of this taxon was present in the same locality of *E. vexilligera*, therefore, is probable that *Eurhamphaea* sp. is *E. vexilligera*.

**Genus Kiyohimea Komai and Tokioka, 1940****(16) *K. usagi* Matsumoto and Robison, 1992**

**Material examined.** 1 specimen collected, March 16th 2015, Alarcón Basin (23°37'1.92"N, 108°45'1.44"W), Dive D725, 168 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Alarcón Basin (present study).

**Global distribution.** Northeastern Atlantic Ocean: Northeast African coasts (Hoving et al., 2018); Northwestern Pacific Ocean: Japan (Toyokawa et al., 1998); Northeastern Pacific Ocean: Monterey Submarine Canyon, California (USA) (Burton et al., 2017; Matsumoto and Robison, 1992).

**Remarks.** First record for Mexico (present study).

**Family Lampoctenidae Harbison, Matsumoto and Robison, 2001****Genus Lampocteis Harbison, Matsumoto and Robison, 2001****(17) *L. cruentiventer* Harbison, Matsumoto and Robison, 2001**

(Fig. 2J)

**Material examined.** 1 specimen collected, March 18th 2012, Cerralvo Basin (24°11'2.767"N, 109°38'1.986"W), Dive D334, 1592

m, id. SHD Haddock; 1 specimen collected, March 9th 2015, Farallon Basin (25°27'N, 109°51'W), Dive D723, 1651 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Cerralvo and Farallon Basins (present study).

**Global distribution.** Northeastern Pacific Ocean: Monterey Submarine Canyon, San Diego, California (USA) (Burton et al., 2017; Francis et al., 2015; Harbison et al., 2001), between Clarion and Clipperton Islands (12°49'45"N, 116°37'47"W) (=as *L.cf. cruentiventer*) (Amon et al., 2017); Northwestern Pacific Ocean: Japan (Lindsay and Hunt, 2005).

**Remarks.** First record for Mexico (present study).

**Family Leucotheidae Krumbach, 1825****Genus Leucothea Mertens, 1833****(18) *Leucothea* sp.**

(Fig. 2K-L)

**Distribution in Mexico.** Gulf of Mexico: off Puerto Progreso [Yucatan]; Mexican Caribbean Sea: Contoy Island and western Cozumel Island [Quintana Roo] ([naturalista.mx](http://naturalista.mx)); Eastern Tropical Pacific: off Manzanillo [Colima]; close to Zihuatanejo coast [Guerrero] ([naturalista.mx](http://naturalista.mx)).

**Remarks.** First record for Mexico ([naturalista.mx](http://naturalista.mx)). According to Almeida et al. (2016), *L. multicornis* has been identified from Roatán Island, Honduras (Caribbean Sea). The fact that *Leucothea* sp. was observed in the south–southeastern Gulf of Mexico (Yucatan, close to Caribbean Sea) ([naturalista.mx](http://naturalista.mx)), as well as the northern Mexican Caribbean (Quintana Roo), suggests that these records could be assignable to *L. multicornis*. The record of *Leucothea* sp. in Colima and Guerrero could be assignable *L. pulcha* since part of the known distribution of this species includes the coasts of California (USA) (Matsumoto, 1988); therefore, more studies are necessary to identify the species of this genus distributed in Mexican Seas.

**Family Ocyropsidae Harbison and Madin, 1982****Genus Ocyropsis Mayer, 1912****(19) *O. crystallina* (Rang, 1828)**

**Material examined.** 22 specimens collected, March 2015, Farallon Basin (25°27'N, 109°51'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 13 specimens collected, March 2015, Alarcón Basin (23°37'N, 108°45'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 2 specimens collected, March 2015, Mazatlán Basin (22°55'N, 108°07'W), SCUBA diving, ~15–25 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of Mexico: La Blanquilla Reef (Veracruz Reef System) [Veracruz] (Ocaña-Luna et al., 2015); Gulf of California: Farallon, Alarcón, and Mazatlán Basins (present study).

**Global distribution.** Northwestern Atlantic Ocean: Gulf of Maine (Harbison et al., 1978), Honduras (Almeida et al., 2016), Tortugas, Florida (Mayer, 1912), Commonwealth of Dominica and the Republic of Trinidad and Tobago (Caribbean Sea) ([naturalista.mx](http://naturalista.mx)); Northeastern Atlantic Ocean: Canary Islands (Moro et al., 2013); Southwestern Pacific Ocean: New Zealand (coastal and oceanic areas) (Mills, 1998–present); Indian Ocean: Singapore ([naturalista.mx](http://naturalista.mx)).

**Remarks.** First record for Gulf of California (present study). *Ocyropsis* is a genus composed by five valid species: (1) *O. crystallina*, (2) *O. fusca* (Rang, 1827), (3) *O. maculata*, (4) *O. pteroessa* Bigelow,

1904, and (5) *O. vance* Gershwin, Zeidler and Davie, 2010, of which, *O. crystallina* and *O. maculata* have two subspecies each, i.e. *O. crystallina crystallina* and *O. crystallina guttata* Harbison and Miller, 1986, and *O. maculata immaculata* and *O. maculata maculata*, respectively (see Mills, 1998–present). Species are distinguished by the shape of the stomodeum, while subspecies are evaluated on the presence of pigment spots. Taking into account the available literature, we recognize in Mexican waters to *O. crystallina* and the subspecies *O. crystallina crystallina*, as well as *O. maculata* and the two subspecies (*O. maculata maculata*, and *O. maculata immaculata*).

#### (20) *O. crystallina crystallina* (Rang, 1828)

**Distribution in Mexico.** Gulf of California: Pescadero and Farallon Basins (Gasca and Haddock, 2004).

**Global distribution.** Northwestern Atlantic Ocean: northeastern and eastern of the Gulf of Mexico (Mills, 1998–present; Moss, 2009; Podar et al., 2001), Southern Sargasso (Harbison and Miller, 1986); Southwestern Atlantic Ocean: from Venezuela to Brazil (12°N to 24°S) (Harbison et al., 1978; Mianzan, 1999; Oliveira and Migotto, 2006; Oliveira et al., 2007); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010; Harbison and Miller, 1986).

#### (21) *O. maculata* (Rang, 1828)

(Fig. 2M–N)

**Distribution in Mexico.** Gulf of Mexico: Tamaulipas coasts [Tamaulipas] (Biggs et al., 1984); Mexican Caribbean Sea: Puerto Morelos [Quintana Roo], southwestern Cozumel Island, northeastern Cancún [Quintana Roo], eastern Isla Blanca [Quintana Roo], northwestern Contoy Island [Quintana Roo] (naturalista.mx); Gulf of California: within the Gulf (locality not indicated) (Francis et al., 2015); Eastern Tropical Pacific: Puerto Ángel and Zipolite [Oaxaca] (Ruíz-Escobar et al., 2015).

**Global distribution.** Northwestern and Central Atlantic Ocean: Sargasso Sea (Harbison et al., 1978), Gulf of Mexico (Mills, 1998–present), Honduras (Caribbean Sea) (Almeida et al., 2016); Southwestern Atlantic Ocean: from Venezuela to Brazil (between 12°N and 1°S) (Harbison et al., 1978; Harbison and Miller, 1986; Mianzan, 1999; Oliveira et al., 2007); Northeastern Pacific Ocean: Southern California Bright (Luo et al., 2014; Mills and Haddock, 2007), Mexico (Ruíz-Escobar et al., 2015), Panama (Gemmell et al., 2019); Indian Ocean: Pakistani coast (Shahnawaz and Oliveira, 2015).

**Remarks.** First record for Caribbean Sea (naturalista.mx); The name of *O. maculata* recalls the pair of large, dark, diffuse spots on the lobes, while other species of *Ocyropsis* do not have these spots or differ in size (see Gershwin et al., 2010; Harbison and Miller, 1986). Ruíz-Escobar et al. (2015) identified *O. maculata* from Oaxacan coasts, which were described as organisms with a body translucent, without dark spots in the inner side of the lobes. According to these authors, the specimens studied were similar to those described by Wrobel and Mills (2003), except for the absence of large dark spots in the oral lobes; therefore, following to Harbison and Miller (1986), this species can be regarded as *O. maculata immaculata*. However, Ruíz-Escobar et al. (2015) do not distinguish between the two subspecies of *O. maculata*, since they think that morphological variations are inherent to species and because the species level allows the inclusion of intermediary morphotypes. We tentatively consider the organisms reported by these authors as *O. maculata*, but for future reports on the diversity of ctenophores in Oaxacan coasts, this aspect should be considered and analyzed cautiously. The observations made by Ruíz-Escobar et al. (2015) represented the first record in this

region, but if this ctenophore were to be considered as the subspecies *O. maculata immaculata*, it would represent an additional record to those reported by Bell Enríquez-García et al. (2013) and Cruz González et al. (2018). Hence, this genus needs a formal taxonomic review, as well as genetic analysis in order to define the species that compose this group of ctenophores.

#### (22) *O. maculata maculata* (Rang, 1828)

**Distribution in Mexico.** Gulf of Mexico: Tamaulipas coasts [Tamaulipas] (Biggs et al., 1984).

**Global distribution.** Northwestern Pacific Ocean: Gulf of Maine (Harbison et al., 1978; Harbison and Miller, 1986); Southwestern Atlantic Ocean: from Venezuela to Northern of Brazil (Harbison et al., 1978; Harbison and Miller, 1986; Mianzan, 1999; Oliveira et al., 2007); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010; Harbison and Miller, 1986).

#### (23) *O. maculata immaculata* (Rang, 1828)

**Distribution in Mexico.** Eastern Tropical Pacific: Panteón beach, Zipolite, Mazunte, Estacahuite, La Mina, and La Boquilla [Oaxaca] (Bell Enríquez-García et al., 2013; Cruz González et al., 2018).

**Global distribution.** Northwestern Atlantic Ocean: Gulf of Maine, Southern Sargasso Sea (Harbison and Miller, 1986), Bahamas (Haddock and Case, 1999), Gulf of Mexico (northeastern and eastern region close to Cuba) (Almeida et al., 2016; Mills, 1998–present; Moss, 2009) Southwestern Atlantic Ocean: from Venezuela to Brazil (Harbison and Miller, 1986); Northeastern Atlantic Ocean: western Mediterranean basin (Alboran Sea) (Haddock and Case, 1999; Mills et al., 1996); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010; Harbison and Miller, 1986).

### Order Cydippida Gegenbaur, 1856

#### Family Aulacoctenidae Lindsay and Miyake, 2007

##### Genus *Aulacoctena* Mortenses, 1932

#### (24) *Aulacoctena* sp.

(Fig. 2O)

**Material examined.** 1 specimen observed, March 14th 2015, Alarcón Basin (23°41.5'N, 108°49'W), Dive D728, 1403 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Alarcón Basin (present study).

**Remarks.** First record for Mexico (present study).

#### Family Haeckeliidae Krumbach, 1925

##### Genus *Haeckelia* Carus, 1863

#### (25) *H. beehleri* (Mayer, 1912)

**Material examined.** 3 specimens examined, March 11th 2015, Alarcón Basin (23°37'N, 108°45'W), SCUBA diving, ~15–25 m, id. SHD Haddock; 2 specimens examined, March 13th 2015, Mazatlán Basin (22°55'N, 108°07'W), SCUBA diving, ~15–25 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Alarcón and Mazatlán Basins (present study).

**Global distribution.** Northeastern Pacific Ocean: Monterey Bay (Francis et al., 2016) and Santa Barbara, California (USA) (Podar et al., 2001).

**Remarks.** First record for Mexico (present study).

**Family Mertensiidae L. Agassiz, 1860****Genus *Charistephane* Chun, 1879****(26) *C. fugiens* Chun, 1879**

**Material examined.** 1 specimen collected, March 15th 2015, Cerralvo Basin (24° 11' 2.767" N, 109° 38' 1.986" W), Dive D730, 842 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Cerralvo Basin (present study).

**Global distribution.** Northwestern Atlantic Ocean: Gulf of Mexico (northeastern region) (Moss, 2009); Northeastern Atlantic Ocean: Canary Islands (Chun, 1889, 1898), Mediterranean basin (including Gulf of Naples, Adriatic Sea) (Batistić et al., 2014; Chun, 1880); Northeastern Pacific Ocean: Monterey Bay (Francis et al., 2015; Wrobel and Mills, 1998, 2003) and Point Conception, California (USA) (Haddock and Case, 1999); Central Pacific Ocean: Hawaii (Wrobel and Mills, 1998, 2003); Eastern Indo-Pacific Ocean (Wrobel and Mills, 1998, 2003).

**Remarks.** First record for Mexico (present study).

**Family Bathyctenidae Mortensen, 1932 (emend. Lindsay and Miyake, 2007)****Genus *Bathyctena* Mortensen, 1932****(27) *B. chuni* (Moser, 1909)**

(Fig. 2P)

**Material examined.** 1 specimen collected, March 14th 2015, Alarcón Basin (23° 41' N, 108° 49' W), Dive D728, 841 m, id. SHD Haddock; 1 specimen collected, March 16th 2015, Cerralvo Basin, Dive D730, 1063 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: Cerralvo and Alarcón Basins (present study).

**Global distribution.** Northeastern Pacific Ocean: Point Conception, California (USA) (Haddock and Case, 1999), Monterey Bay, California (USA) (Francis et al., 2015); Central Pacific Ocean: Hawaii (Haddock and Case, 1999).

**Remarks.** First record for Mexico (present study).

**Family Pleurobrachiidae Chun, 1880****Genus *Hormiphora* L. Agassiz, 1860****(28) *H. palmata* Chun, 1828**

**Distribution in Mexico.** Gulf of California: localities not indicated (Bigelow, 1912; Brusca and Trautwein, 2005).

**Global distribution.** Northeastern Atlantic Ocean: Canary Islands (Chun, 1889, 1898); Central Pacific Ocean: Hawaii Islands (Matthews, 1954); Northwestern Pacific Ocean: Japan (Inaba et al., 2020; Uchida, 1940; Yamazi, 1958).

**(29) *H. californensis* (Torrey, 1904)**

(Fig. 2Q)

**Distribution in Mexico.** Gulf of California: Puerto Libertad [Sonora] (naturalista.mx).

**Global distribution.** Northeastern Pacific Ocean: at least from off San Diego and Santa Barbara (California) and in Friday Harbor (Washington) (Gasca et al., 2014; Luo et al., 2014; Mills, 1987; Mills and Haddock, 2007; Smith-Beasley, 1992).

**Remarks.** First record for Mexico (naturalista.mx).

**(30) *Hormiphora* sp.**

**Material examined.** 1 specimen collected, March 12th 2015, Mazatlán Basin (22° 55' N, 108° 07' W), SCUBA diving, 25 m, id. SHD Haddock.

**Distribution in Mexico.** Gulf of California: 25° 26' 60" N, 109° 50' 69.9" W (Francis et al., 2013) and Mazatlán Basin (present study).

**Genus *Pleurobrachia* Fleming, 1822****(31) *P. bachei* A. Agassiz, 1860**

**Distribution in Mexico.** Gulf of California: from Río Mayo (estuaries and freshwater marshes of Etchoropo and Moroncarit) [Sonora], Yavaros lagoon [Sonora] (Gómez-Aguirre, 1981, 1991), Agiabampo lagoon [Sonora] (Gómez-Aguirre, 1981, 1991; Signoret de Brailovsky, 1975), Topolobampo lagoon [Sinaloa], Presidio and Baluarte Rivers System (Bocas de Barrón, Chamela, estuaries El Ostial and Agua Dulce, freshwater marsh of Huizache, and Caimanero lagoon) [Sinaloa] (Gómez-Aguirre, 1991), La Sirena, Urias and del Astillero estuaries [Sinaloa] (Álvarez-León, 1980), La Sirena, Urias, Astilleros, and Astillero estuaries [Sinaloa] (Álvarez-León and Wedler, 1982), Teacapán lagoon [Sinaloa] (Gómez-Aguirre, 1981), Cañas and Acaponeta Rivers estuarine system [Nayarit], Santiago Tuxpan and San Pedro Rivers estuarine systems (del Pozo, bocas de Azadero, Camichín, and Talega estuaries [Nayarit] (Gómez-Aguirre, 1991).

**Global distribution.** Northeastern Atlantic Ocean: Ireland coasts (Mills, 1998-present); Northeastern Pacific Ocean: From Kenai Fjords National Park, Alaska (USA) to San Diego, California (USA), including eastern Canada and USA coasts (see Flores and Brusca, 1975; Hirota, 1974; Podar et al., 2001, inaturalist.org); Southeastern Pacific Ocean: from Peru to Chile (3° S to 47° S) (Oliveira et al., 2016 and references therein; Yáñez et al., 2009).

**(32) *P. pileus* F. Müller, 1776**

**Distribution in Mexico.** Gulf of Mexico: La Mancha lagoon [Veracruz] (Ocaña-Luna et al., 2017), Tampamachoco lagoon [Veracruz] (FA Puente-Tapia personal observation), Mandinga Lagoon System [Veracruz] (FA Puente-Tapia personal observation); Eastern Tropical Pacific: Acapulco [Guerrero] (= as *P. pileus* var. *bachei*) (Bigelow, 1912), several localities [Jalisco, Colima, Michoacán, and Guerrero] (Gamero-Mora et al., 2015).

**Global distribution.** Northwestern Atlantic Ocean: from the Labrador Sea to Pamlico Sound, North Carolina (Bigelow, 1926; Nelson, 1925; Podar et al., 2001); Southwestern Atlantic Ocean: from south of Brazil to middle Argentine Sea (37° S to 47° S) (Mianzan, 1999; Mianzan and Guerrero, 2000; Schiariti et al., 2020); Northeastern Atlantic Ocean: Baltic Sea (Northern Europe) (see Hansson, 2006), Mediterranean basin (Mills et al., 1996; Shiganova and Malej, 2009 and references therein); Southeastern Atlantic Ocean: South Africa (southern Benguela ecosystem) (Gibbons et al., 2003); Northwestern Pacific Ocean: Japan waters (Yamazi, 1958); Southwestern Pacific Ocean: Australia (Gershwin et al., 2010).

**(33) *Pleurobrachia* sp.**

**Distribution in Mexico.** Gulf of Mexico: Tamaulipas coasts [Tamaulipas] (Biggs et al., 1984), Tamiagua lagoon and Alvarado Lagoon System [Veracruz] (Gómez-Aguirre, 1977), La Mancha lagoon [Veracruz] (Ruíz-Guerrero and López Portillo-Guzmán, 2006), Mandinga Lagoon System [Veracruz] (Ocaña-Luna et al., 2015), Yucatan coasts [Yucatan] (Ordóñez-López et al., 2010); Gulf of California: localities not indicated within the Gulf (Brusca and Trautwein, 2005; Gómez-Aguirre, 1976).

**Table 2**

List of taxa observed in adjacent regions of the Mexican seas. Number in superscript indicates: (1) species observed in some region of the Mexican seas but absent in some other; (2) species not recorded in any region of Mexico. NE and E (Northeast and Eastern of the Gulf of Mexico); GM (Gulf of Mexico), GC (Gulf of California); Northeastern Pacific (NEP); ETP (Eastern Tropical Pacific); Cs (Caribbean Sea).

Taxon	GM	Cs	NEP	References	Records in Mexico
<i>Beroe cucumis</i> <sup>1</sup>	NE		USA (California)	5,13,16	GC, ETP
<i>Beroe forskalii</i> <sup>1</sup>	NE	Honduras	USA (California)	1,4,13,16	GC, NEP, ETP
<i>Beroe mitrata</i> <sup>2</sup>	NE			13	–
<i>Beroe ovata</i> <sup>1</sup>	NE	Jamaica		13,15	GM
<i>Beroe sp.</i> <sup>1</sup>		Cuba		6,7,14	–
<i>Cestum veneris</i> <sup>1</sup>	NE		USA (California)	13,16	GM, Cs, GC, ETP
<i>Velamen parallelum</i> <sup>1</sup>	NE		USA (California)	4,8,11,13,16	GC, NEP, ETP
<i>Thalassocalyce inconstans</i> <sup>1</sup>	NE		Costa Rica	2	GM, GC
<i>Bathocyroe fosteri</i> <sup>1</sup>	NE			13	GC
<i>Bolinopsis infundibulum</i> <sup>1</sup>		Honduras	USA (California)	1,4,8,11	GC, ETP
<i>Eurhamphaea vexilligera</i> <sup>1</sup>	NE			13	GM, Cs, GC
<i>Kiyohimea aurita</i> <sup>2</sup>	NE			13	–
<i>Leucothea multicornis</i> <sup>2</sup>		Honduras		1	–
<i>Leucothea ochracea</i> <sup>2</sup>	NE			13	–
<i>Ocyropsis crystallina</i> <sup>1</sup>		Honduras, Jamaica		1,15	GM, GC
<i>Ocyropsis crystallina crystallina</i> <sup>1</sup>	NE, E			10,13,16	P
<i>Ocyropsis crystallina guttata</i> <sup>2</sup>	E			13	–
<i>Ocyropsis maculata</i> <sup>1</sup>			USA (California)	11	GM, Cs, GC, ETP
<i>Ocyropsis maculata maculata</i> <sup>1</sup>	NE			13	GM
<i>Ocyropsis maculata immaculata</i> <sup>1</sup>	NE, E	Cuba		1,13	ETP
<i>Charistephane fugiens</i> <sup>1</sup>	NE			13	GC
<i>Hormiphora californensis</i> <sup>1</sup>			USA (California)	3,8,9,11,17	GC
<i>Hormiphora palmata</i> <sup>1</sup>			Costa Rica	12	GC
<i>Pleurobrachia bachei</i> <sup>1</sup>			USA (California)	16	GC, ETP
<i>Pleurobrachia sp.</i> <sup>1</sup>		Cuba		6,7,14	–

(1) Almeida et al. (2016); (2) Corrales-Ugalde et al. (2017); (3) Gasca et al. (2014); (4) Haddock and Case (1999); (5) Harbison et al. (1977); (6) Hidalgo Rodríguez (2006); (7) Lalana et al. (2001); (8) Luo et al. (2014); (9) Mills (1987); (10) Mills (1998–present); (11) Mills and Haddock (2007); (12) Morales-Ramírez and Nowaczyk (2006); (13) Moss (2009); (14) Ortiz (2001); (15) Persad et al. (2003); (16) Podar et al. (2001); (17) Smith-Beasley (1992).

**Remarks.** The records of the distribution of *Pleurobrachia sp.* in the Gulf of Mexico resemble that of *P. pileus*, thus suggesting that Gulf of Mexico records of *Pleurobrachia sp.* refer to *P. pileus*, whereas records from the Gulf of California could be assignable *P. bachei*.

## 4. Discussion

### 4.1. Checklist of ctenophores species

We compiled a checklist of 33 ctenophore taxa, of which *Leucothea sp.* (naturalista.mx), *B. fosteri*, *K. usagi*, *L. cruentiventer*, *Aulacocotena sp.*, *H. beehleri*, *C. fugiens*, *B. chuni* (MBARI), and *H. californensis* (naturalista.mx) represent the first records for Mexican waters (see Table 1).

Consideration the lack of studies on both benthic ctenophores and meso- and bathypelagic communities in Mexico, as well as the records in areas adjacent to Mexican seas (e.g. Caribbean countries, American jurisdictional waters of the Gulf of Mexico, southwestern USA, and Central Pacific countries) it is presumed that there is a high number of undescribed and unrecorded species.

A way to predict more about the diversity of the deep-sea Ctenophora fauna in Mexican waters is based on the examination of records from neighboring, better known regions. The deep-living zooplankton of the North Pacific region (western Baja California Peninsula) have yielded many new records and undescribed deep-living species of different taxa (e.g. Burton et al., 2017; Gasca et al., 2014). The marine environment becomes more homogeneous across surrounding regions as depth increases (Vecchione et al., 2015), and looking at the deepest ctenophore records worldwide may provide a guideline for the diversity we may expect (Reimer et al., 2020). However, ctenophores still display an apparent lack of data. For instance, very little or no information has been published on meso- and bathypelagic species of the Gulf of Mexico, Caribbean Sea, and

Eastern Tropical Pacific. We only found some data from the American jurisdictional waters of the Gulf of Mexico (Moss, 2009), where *B. cucumis*, *B. forskalii*, and *T. inconstans* were reported in depths greater than 200 m.

In Table 2, we include a list of the records of ctenophore species distributed in adjacent areas of Mexico that have not been identified in Mexican waters or in at least one of the analyzed regions, e.g. *B. cucumis* has been recorded in Mexico in the Gulf of California and Eastern Tropical Pacific (Oaxaca), but according to Harbison et al. (1977) and Podar et al. (2001) it is possible to find it in the Californian coasts, while Moss (2009) reported it in the northeastern Gulf of Mexico.

Most of the species recorded in Mexican seas were collected in shallow waters of lagoon–estuarine systems and coastal–neritic areas (depth range between 1–160 m), while few species were observed from oceanic and deep-waters. This could be related to consistently stronger sampling efforts along Mexico's coastal and shelf areas, as well as the high costs and lack of adequate gear to sample the deep-sea. Only Swift et al. (2009) reported species collected at depths greater than 350 m. Although Gasca and Haddock (2004) and Gasca and Browne (2017) included the reports of gelatinous zooplankton in association with crustaceans in samples obtained at a depth range of 10–3000 m, the ctenophores reported in these works were observed between 10 and 15 m. In the present work, organisms collected by MBARI are reported from a depth range of 15–2442 m.

As for other gelatinous zooplankton groups such as the medusae, it is expected that new taxa and new records will occur from samples collected in deep waters (Segura-Puertas et al., 2003). Accordingly, the study of the plankton community performed by MBARI in the Gulf of California, allowed us to increase the number of ctenophore taxa in Mexican waters by a total of 7 new records, of which, 2 are epipelagic taxa and 5 were meso- and bathypelagic organisms. Considering the number of species recognized by Mills (1998–present) (n = 188), the number of taxa reported in the present checklist for Mexican waters represent almost 18% of the known ctenophore diversity.

**Table 3**

List of studies which include data on any aspect of the ctenophores from Mexican waters.

Authors	Taxon	Research goal	Locality
Gulf of Mexico Gómez-Aguirre (1977)	<i>Pleurobrachia</i> sp.	Description of the plankton of lagoon systems	Veracruz
Esquivel et al. (1980)	<i>Beroe ovata</i>	Description of the spatial–temporal variation of zooplankton community	Veracruz
Biggs et al. (1984)	<i>Mnemiopsis leidyi</i> <i>Beroe ovata</i>	Population density of gelatinous planktivores	Tamaulipas
	<i>Cestum veneris</i> <i>Thalassocalyce inconstans</i> <i>Eurhamphaea vexilligera</i> <i>Ocyropsis maculata</i> <i>Ocyropsis maculata maculata</i> <i>Pleurobrachia</i> sp.		
Ruíz-Guerrero and López Portillo-Guzmán (2006)	<i>Pleurobrachia</i> sp.	Description of invertebrate diversity	Veracruz
Vargas et al. (2006)	<i>Mnemiopsis leidyi</i>	Description of ichthyoplankton and coelenterates communities structure	Veracruz
Moss (2009)	Total species: 18	Census of Ctenophora of the Gulf of Mexico	Entire
Ordóñez-López et al. (2010)	<i>Mnemiopsis leidyi</i> (= as <i>M. mccradyi</i> )	Description of diversity of zooplankton groups	Yucatan
	<i>Pleurobrachia</i> sp. <i>Pleurobrachia</i> sp.		
Ocaña-Luna et al. (2015)		Macromedusae and ctenophores list species	Veracruz
	<i>Mnemiopsis leidyi</i> <i>Ocyropsis crystallina</i> <i>Beroe ovata</i>		
Ocaña-Luna et al. (2017)	<i>Pleurobrachia pileus</i>	Description of morphological analysis	Veracruz
Flores-Galicia and De la Cruz-Francisco (2018)	<i>Cestum veneris</i>	Records of medusae and ctenophores species	Veracruz
	<i>Mnemiopsis leidyi</i>		
Mexican Pacific Bigelow (1912)	<i>Cestum veneris</i> (= as <i>B. amphitrite</i> )	Description of faunal of ctenophores	Eastern Tropical Pacific
	<i>Bolinopsis vitrea</i> <i>Hormiphora palmata</i> <i>Pleurobrachia pileus</i> <i>Pleurobrachia bachei</i>		
Signoret de Brailovsky (1975)		Description of presence of ctenophores species	Sonora
Gómez-Aguirre (1976)	<i>Pleurobrachia</i> sp.	Notes on the biology and of <i>Pleurobrachia</i> sp.	Gulf of California
Álvarez-León (1980)	<i>Pleurobrachia bachei</i>	Description of the hydrology and zooplankton of three estuaries systems	Sinaloa
Gómez-Aguirre (1981)	<i>Pleurobrachia bachei</i>	Description of planktonic community of estuarine and lagoon systems	Nayarit, Sinaloa, Sonora
Álvarez-León and Wedler (1982)	<i>Pleurobrachia bachei</i>	Description of spatial distribution of hydroids and their associated fauna	Sinaloa
Stretch (1982)	<i>Velamen parallelum</i>	Abundances and feeding behavior	Gulf of California
Gómez-Aguirre (1991)	<i>Pleurobrachia bachei</i>	Faunal list and spatial distribution of Cnidaria and Ctenophora	Gulf of California
	<i>Beroe</i> sp. <i>Ocyropsis crystallina crystallina</i>		
Gasca and Haddock (2004)		Association between gelatinous zooplankton and hyperiid amphipods	Gulf of California
Brusca and Trautwein (2005)	<i>Beroe</i> sp.	Faunal list and spatial distribution of Cnidaria and Ctenophora	Gulf of California
	<i>Pleurobrachia</i> sp. <i>Thalassocalyce inconstans</i>		
Swift et al. (2009)		Feeding behavior, vertical distribution and anatomy description	Gulf of California
Bell Enríquez-García et al. (2013)	<i>Ocyropsis maculata immaculata</i>	Records of ctenophores species	Oaxaca

(continued on next page)

**Table 3** (continued).

Authors	Taxon	Research goal	Locality
Francis et al. (2013)	<i>Bolinopsis infundibulum</i> <i>Beroe forskalii</i> <i>Hormiphora</i> sp.	Study of transcriptome sequencing from six different phyla	Gulf of California and other regions of the world
SEMARNAT (2013)	<i>Beroe forskalii</i>	Biodiversity record	Reserva de la Biosfera Isla Guadalupe
Gamero-Mora et al. (2015)	<i>Pleurobrachia pileus</i>	Description of spatial distribution of GZ species (Hydrozoa, Ctenophores and Thaliacea)	Central Pacific Ocean
Ruíz-Escobar et al. (2015)	<i>Beroe cucumis</i> <i>Beroe forskalii</i> <i>Bolinopsis vitrea</i>	Records of ctenophores species	Oaxaca
Francis et al. (2015)	<i>Ocyropsis maculata</i> <i>Ocyropsis maculata</i>	Use of transcriptome data of 24 species of ctenophores to analyze the biosynthesis of the luciferin coelenerazine	Gulf of California and other regions of the world
Francis et al. (2016)	<i>Beroe abyssicola</i>	Analysis of transcriptome data from 30 species to identify an orthologs proteins similar to fluorescent protein	Gulf of California and other regions of the world
Gasca and Browne (2017)	<i>Cestum veneris</i>	Symbiotic association of gelatinous zooplankton with crustaceans and pycnogonid	Gulf of California
Cruz González et al. (2018)	<i>Beroe cucumis</i> <i>Bolinopsis infundibulum</i> <i>Ocyropsis maculata immaculata</i> <i>Beroe forskalii</i> <i>Hormiphora palmata</i>	Records of ctenophores species	Oaxaca

#### 4.2. General status of knowledge on ctenophores fauna in Mexico

The review carried out in the present study allowed us made a general analysis of the status of knowledge on ctenophores fauna from Mexican waters, which is characterized by a marked space–time discontinuity. Possibly, the earliest records of ctenophores in Mexico came from Bigelow (1912). After, there is an interval of more than 60 years without any reports of ctenophores in this region. The subsequent work was conducted by Signoret de Brailovsky (1975), therefore, the knowledge of ctenophores in Mexico is almost based on observations made within the last 45 years.

Most research has focused on restricted geographic areas and short time scales. So far, 30 studies dealing with ctenophores from Mexican seas have been published, of which 19 were for Pacific waters and 11 for the Gulf of Mexico, while in the Mexican Caribbean Sea there are no previous records from this region through scientific literature (see Table 3), being one of the lesser-known group in the Caribbean Sea (Miloslavich et al., 2010). Nonetheless, it is reasonable to assume that the species found between the Caribbean Islands and Panama are likely to occurs in the Mexican Caribbean as well.

Previous studies can be classified into 3 general items: (1) description of faunal composition or spatial distribution with some concentration data (abundances/biomass): 20 works; (2) ecological/biological aspects: 7 works, which describe biological interactions, feeding behavior and morphometry aspects; and (3) molecular-genomic items: 3 works, however, these works employed specimens from different regions of the world (including the Gulf of California), therefore, this information is not focused on Mexican Seas (Table 3).

In a general view, the ctenophores along the coasts of Mexico have received little attention, which is reflected by the few papers published on the topic (Table 3). With exception of a few surveys, most studies of zooplankton from Mexican waters do not focus on ctenophores, and gelatinous plankton are often

unlikely to be recovered by the most commonly used methodologies (e.g. net sampling). More specific sampling techniques and detailed observations will certainly provide more records in the future. According to Majaneva (2014), without proper monitoring and accurate species identification, it is impossible to assess changes in species composition, distribution, and the ecological impact of ctenophores.

The current knowledge available for Mexican waters (including the present checklist), provides a general overview of the diversity in this region, as well as certain aspects of its ecological role. However, the lack of works related to the benthic ctenophores species and the fauna in oceanic and deeper waters (except for Swift et al., 2009, and the present study), hinders ctenophore studies. Therefore, these communities remain poorly studied and largely underestimated or unevenly unknown. In addition to the space–time discontinuity previously mentioned, there have been few works that include abundance or biomass records of ctenophores from the primary regions of Mexican waters. Consequently, seasonal variation is of their occurrence and abundance cannot be described so far.

In general, ctenophores are present along the different seasons in Mexican coasts, varying only in relation to each species. For example, *P. bachei* has been identified at least from September to May (boreal autumn–spring) over a wide range of water temperature and salinities (between 23.6 and 30.6° C and 33.6 and 45.5 of salinity) in different regions of the Gulf of Mexico (see Álvarez-León, 1980; Gómez-Aguirre, 1981; Signoret de Brailovsky, 1975). This ctenophore and cladocerans have been considered as indicators of pollution, since they were identified with high abundances in regions affected by the domestic and industrial discharge (Álvarez-León, 1980). In addition, this author indicated that with the presence of high abundances of *P. bachei*, few individuals of chaetognaths were observed, indicating certain food competition between both types of predators. According to Gómez-Aguirre (1981), although several species of ctenophores have been observed in coastal lagoons of Sonora and Sinaloa

(Gulf of California), *P. bachei* is the most frequent and abundant species (dominant species), with both adult and larval stages being observed, indicating it is likely representing a permanent species in this region. Its larval stage has been located mainly in the mouth of coastal lagoons, while the adult stage was observed in the middle region of these lagoons or in more stable regions.

In other regions of Mexican Pacific waters, such as the central region (see Gamero-Mora et al., 2015) and the Gulf of California (see Gasca and Browne, 2017), *B. cucumis* has been observed during the spring; *B. forskalii* was observed from October to January in Oaxacan coasts (Bell Enríquez-García et al., 2013; Cruz González et al., 2018; Ruiz-Escobar et al., 2015), while *O. maculata immaculata* was observed from October to January in Oaxacan coasts (Bell Enríquez-García et al., 2013; Cruz González et al., 2018); on the other hand, the 65.6% of the individuals found of *T. inconstans* in the Gulf of California were above or in the oxygen minimum layer, in water with  $0.1 \text{ mL}^{-1}[\text{do}]$  or less and may were found in completely anoxic water (Swift et al., 2009).

In the Gulf of Mexico, *M. leidy* was identified over a wide temporal interval in different reef and lagoon systems of Veracruz, such as Tuxpan reef (from March to July and November) (Flores-Galicia and De la Cruz-Francisco, 2018), Veracruz reef system, Mandinga lagoon system, and Alvarado lagoon system (Veracruz) from February to September with surface temperatures that oscillated between 29 and 37 °C and salinity between 8 and 37 (Ocaña-Luna et al., 2015). According to Vargas et al. (2006), this ctenophore was identified as a dominant species in the zooplankton community during the early boreal autumn, while in Yucatán coasts was identified it associated with significant concentration of zooplankton, reaching high levels of individuals (Ordóñez-López et al., 2010); *B. ovata* from Mandinga and Alvarado lagoons showed affinity for salinities between 12 and 28 and temperatures between 29–30 °C (Ocaña-Luna et al., 2015), while *P. pileus* can be observed in some coastal lagoons of Veracruz from January to May with hydrological parameters of 20° to 30 °C of sea surface water temperature and a wide range of salinity (20–33) (Ocaña-Luna et al., 2017).

In contrast to commercial fish species and other zooplankton taxa, the abundance of ctenophores has not been monitored on a regular basis (e.g. Condon et al., 2012), and they have been completely excluded as a functional group from current ecological models (e.g. Tomczak et al., 2012). Long time series are essential for observing species distributions and abundances, and are therefore one of the core requirements for a wide variety of ecosystem studies. These systematic and continuous environmental records are also vital for detecting changes in marine ecosystems over seasonal, interannual, and even longer time frames (e.g. Condon et al., 2012). Although in the present study we provide a map (Fig. 1) with the spatial distribution of the different ctenophores records, we consider that due the paucity of data in several regions of Mexico, is not possible to make conclusions or hypotheses on distributional patterns of Ctenophora in Mexican waters.

Despite the fact that the importance of the gelatinous zooplankton (e.g. ctenophores and medusae) in marine food webs has been recognized, ecological knowledge of gelatinous zooplankton is strongly biased towards particular species, mainly scyphozoan medusae and the ctenophore *M. leidy* (Majaneva, 2014, and references therein). In Mexico, the ecological role of the ctenophores is still poorly studied, but they are known to have symbiotic association with other zooplankters. Gasca and Haddock (2004) documented the association between *O. crystallina* and the hyperiid amphipod *Oxycephalus clausi* Bovallius, 1887 in the Gulf of California, while Gasca and Browne (2017) reported the symbiotic association between *B. cucumis* and the hyperiid amphipod *Hyperoche mediterranea* Senna, 1908,

as well as between the ctenophore *C. veneris* and the hyperiid amphipod *Brachyscelus cruscolum* Spence Bate, 1861.

In both works, the role of the ctenophores as hosts in the life-cycle of this type of crustacean is reported. In general, hyperiid amphipods use the ctenophore as refuge for its progeny. For example, a female of *Oxycephalus clausi* (family Oxycephalidae) was observed taking care of juveniles demarsupiated into the ctenophore *O. crystallina*; the female was keeping the young individuals on the surface of the ctenophore and using her pereopods, and kept the ctenophore in constant motion, swimming about in different directions without losing contact with the host. This behavior represented the first report of maternal care within the family Oxycephalidae (Gasca and Haddock, 2004). Many planktonic crustaceans have been described as parasites of gelata species; however, it is often not clear what potential benefits are being gained from these putative host-symbiont associations and in many cases the nature of these associations remains vague or unknown (Gasca and Haddock, 2004 and references therein). Therefore, is necessary to carry out more studies to understand in detail the ecological role of ctenophores.

On the other hand, Álvarez-León and Wedler (1982) described the spatial distribution of 7 hydroids in different estuarine systems of the Gulf of California. Five of these habitats, reported the hydroids being associated with the ctenophore *P. bachei*. Although this possible association may be controversial due to the planktonic behavior of *P. bachei*, this work allows us to report the presence of this ctenophore in the region.

The role of ctenophores in marine food webs is more complex than previously thought. Ctenophores were long considered a trophic dead-end in marine food webs, but some studies indicate that they may be consumed by various groups (Mianzan et al., 2009), such as medusae, other ctenophores, sea turtles, fishes, and marine birds (e.g. penguin species) (see Eckert et al., 2012; Choy et al., 2017; Díaz Briz et al., 2017; Mianzan and Sabatini, 1985; Thiebot et al., 2017). In Mexican seas, no studies have been conducted that indicate the role of ctenophores as prey to any of the above-mentioned groups, while there are some investigations on the role of ctenophores as predators in Mexico, but the information available is insufficient to understand correctly the diversity of these relationships. Based on experimental observations, Stretch (1982) described the digestion rates and feeding strategy of *V. parallelum*, while Swift et al. (2009) reported the feeding behavior of *T. inconstans*. Ignoring spatial patterns can lead to erroneous conclusions concerning their predation impact (Majaneva, 2014). In addition, the relationship between predator size and prey size is of great importance when determining the outcome of interactions among species (Scharf et al., 2000). Thus, direct extrapolation from one species, or population, to another raises uncertainty when modeling basic ecological traits such as diet and foraging behavior, especially if individual size of the predators clearly differs between populations (Majaneva, 2014).

The work by Ocaña-Luna et al. (2017) is the only morphometry study between populations of the same species. These authors compared the height, tentacular and sagittal diameter of *P. pileus* in different localities of the coasts of Veracruz (Gulf of Mexico) in order to identify possible morphometric variations in each area analyzed. This type of study allows to identify morphological adaptations of a species to the diverse hydro-biological conditions observed in the distribution area. These data, together with molecular methods must be used to differentiate between morphologically similar ctenophore (morphotypes) and life stages (e.g. cydippid larvae stage) (Majaneva, 2014).

In Mexico, efforts to describe and understand other gelatinous groups in the five major marine regions are increasing, mainly in reference to the scyphomedusae (e.g. Gómez Daglio and Dawson, 2017; Segura-Puertas et al., 2003). The low number of specialists

presents an additional obstacle to improving our knowledge of the Mexican ctenophore community; currently, there is not a specialist in ctenophores in Mexico and in general view, the current number of specialists in the region devoted to gelatinous zooplankton (e.g. hydromedusae, scyphomedusae, stauromedusae, siphonophores, and pelagic tunicates) is too low to cover such a vast region and a variety of specialties. Even in surrounding regions, some taxa still display an apparent lack of data, such as the null information that has been published on the mesopelagic and abyssal ctenophore fauna of the Mexican Caribbean Sea and adjacent Caribbean zones, as well as the Eastern Tropical Pacific. In our view, Mexico is far behind other regions of the world in this aspect, so we consider the present effort to become a first step to motivate further studies on this remarkable group.

Ecological research usually requires rapid and accurate identification, but the researchers conducting the work may not have the taxonomic knowledge to do so with the necessary precision and consistency. While it may appear simple to count the species number of a sample, identifying specimens to species level is time consuming and requires special taxonomic expertise (Majaneva, 2014).

Several particular gaps must still be addressed in Mexico: studies of benthic species, deep-sea species, ecological roles, histories and lifecycles, and socio-economic importance. Knowledge about life histories of these species is strongly required to get an accurate understanding of their population dynamics and ecological roles. Without a proper description of biodiversity and its functioning over time, it is difficult to ensure appropriate ecosystem management (Schiariti et al., 2020). An appropriate methodology for collection (and observation) and sampling efforts focused on poorly known, or merely unexplored areas, and environments (oceanic and meso-bathypelagic), will continue improving our knowledge on the biodiversity of gelatinous zooplankton (including ctenophores) (Schiariti et al., 2020). For example, worldwide, there are known approximately 50 benthic ctenophore species (Mills, 1998-present), but in Mexico it is not on an overstatement to say that research on this type of ctenophores is completely lacking for the region. On the other hand, while several fish species feed almost exclusively on ctenophores (Díaz Briz et al., 2017), in Mexico there is no record of this type of trophic interaction.

Extensive *in situ* sampling, laboratory experiments, morphological and molecular identification analysis, traditional and molecular gut content analysis were combined to address system-specific questions and to better understand how important role the ctenophores might have in marine ecosystems (Majaneva, 2014).

A critical part of evaluating the impact of the ctenophores is an understanding of their population dynamics and the factors which control their abundances. Ideally, a discussion of population dynamics would include quantitative information on biogeographic and population data, somatic growth, reproduction, and mortality, as well as how these rates vary over time to produce the observed biomass. In the absence of information on relevant rates, ecologists often attempt to infer process from measurements of stocks and how they vary with time (Kremer, 1993). In summary, there are several critical questions which need to be evaluated regionally before the population dynamics of the different species understood well.

## 5. Conclusions

This work compiled all available data regarding Ctenophora along the Mexican waters (including meso- and bathypelagic species) and provided a database for future studies. Our results showed that ctenophore diversity in Mexico is far greater than

indicated by any of the previous studies due the records of deep sea species from the Gulf of California; therefore, we also indicate the need of precise bathypelagic studies, as well as studies to be focused in benthic ctenophores species that have not been adequately studies in Mexico yet. Due to the lack of benthic and deep sea data, it is far too premature to make conclusions on abundances, total diversity or ecology of the ctenophores in Mexican seas. The list of species compiled in the present study aims to foster and encourage further research on ctenophores in the region. Despite the challenges, there are many opportunities for progress available to the next generations of scientists studying the diverse waters of Mexico.

## CRedit authorship contribution statement

**F. Alejandro Puente-Tapia:** conceptualization, investigation, Writing - original draft. **Rebeca Gasca:** Field work, Writing - review & editing. **Agustín Schiariti:** Resources, conceptualization, Writing - review & editing. **Steven H.D. Haddock:** Resources, Field work, Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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