Zootaxa 2095: 60–68 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Diversity of Siphonophora (Cnidaria: Hydrozoa) in the Western Caribbean Sea: new records from deep-water trawls

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Abstract

Siphonophores are one of the least known gelatinous zooplankters in the tropical waters of the Northwestern Atlantic. Most of the regional knowledge about their diversity and distribution is based on surface samples (0–200 m). Siphonophores were collected from oceanic waters off the Mexican Caribbean across an expanded sampling range (0–940 m) during two cruises and were taxonomically examined. A total of 47 siphonophore species were recorded, of these, 14 had not been found in this sector of the Caribbean Sea and 10 represent new records for the Caribbean Basin. The number of species currently known from the western Caribbean is increased from 42 to 56. Some of these species also represent new records for the Northwestern Tropical Atlantic region. The greatest relative increase was observed among species of *Lensia*, five of which are exclusively deep-living forms dwelling below 300 m. A revised, expanded checklist of the siphonophores of the Western Caribbean is also provided. These results confirm the need of further deep sampling to increase our understanding of Caribbean siphonophore diversity.

Key words: siphonophores, gelatinous zooplankton, marine biodiversity

Introduction

Siphonophores are a widespread and abundant group of colonial gelatinous cnidarians that play important roles in the trophic web of the pelagic realm (Mackie *et al.* 1987; Pugh 1996). Currently, there are about 175 known species grouped into three orders: Cystonectae, Physonectae, and Calycophorae, each with a distinctive morphological organization (Pugh 1999). While evidence suggests that Cystonectae and Calycophorae are monophyletic, the physonects likely represent a grade that gave rise to Calycophorae (Dunn *et al.* 2005; Pugh 2006).

Most siphonophore species collected by standard plankton nets belong to the highly diverse order Calycophorae, which comprises nearly 65% of all known siphonophore species. The other two orders, Physonectae and Cystonectae, are typically viewed as less diverse and abundant. However, when other sampling gear and techniques (e.g. diving, submarines) are used, nearly 60% of species and 75% of individuals collected are representatives of Physonectae (Pugh 1999). Across broad oceanic regions, particularly within the tropics, our knowledge of the diversity and distribution of these cnidarians is based mainly on collections from the upper layers of the ocean. Relatively little is known about the deep-living siphonophore fauna of tropical areas.

In Mexican waters knowledge concerning the group is limited mainly to epipelagic layers. There are 89 species of Siphonophora recorded from Mexican waters of the Pacific and the Atlantic (Suárez-Morales and Gasca 1991; Gasca 2002; Pugh and Gasca 2009), and most of these are epipelagic. According to Margulis (1984), epipelagic siphonophores (0–200 m) are distributed only in this layer, while most other species occur in deeper strata or have wider depth distributions. While this pattern may be generally true, the extent of

 Accepted by A. Collins: 11 Apr. 2009; published: 8 May 2009

exceptions is unknown. Further, siphonophore distribution in the upper 200m and at depth can also be influenced by characteristics of different water masses (see Mackie *et al.* 1987). Hence, in order to appreciate the real diversity of these cnidarians, deeper sampling from different regions is needed.

In the Caribbean Basin the most important previous work is that by Stepanjants (1975), who studied epi- and mesopelagic siphonophores at selected sites in the central and eastern sectors of the Caribbean, but not in the westernmost sector. Other surveys in the Caribbean (Owre and Foyo 1972; Michel and Foyo 1976) focused on the distribution and ecology of a few selected species. Gasca (2002) pointed out that despite the increase in the number of publications concerning western Caribbean siphonophores, the accumulated number of species recorded has grown little during the last five decades and that a significant increase in recorded richness could be expected if the fauna dwelling below 400 m were sampled.

A series of zooplankton samples collected off the Mexican coast of the Caribbean at an expanded depth range (0–940 m), reveal new data about the diversity of siphonophores. A revised list of species and new local and regional records are provided, together with a comparative analysis of siphonophore diversity of the western Caribbean with that of adjacent tropical areas. Comments on selected species or new records are also given.

Materials and methods

Zooplankton samples obtained during two oceanographic surveys of oceanic waters of the Mexican Caribbean, western sector of the Caribbean Basin were examined. The first cruise (CARIBE-2002B) took place June 1–27, 2002 on board the R/V "Antares", a vessel of the Mexican Ministry of the Navy. Twenty zooplankton samples were obtained by oblique tows at different depths between the surface and 600 m. The sampling gear was a standard CalCOFI net (0.33 mm filtering mesh, mouth diameter: 0.74 m) provided with a digital flowmeter. Samples were fixed and preserved in a buffered formalin solution. The second cruise was carried out between March 14 and April 4, 2006, on board the R/V "Gordon Gunter", operated by NOAA-ECOSUR. During this cruise only six zooplankton samples were collected at three oceanic sites by using a MOCNESS net (square-mouthed, 1m per side, 0.3 mm filtering mesh); it was towed at different depths between the surface and 941 m. Sampling locations are shown in Fig. 1. Samples were fixed in 4% formalin and preserved in a solution of sea water (95%), propylene-glycol (4.5%), and propylene-phenoxytol (0.5%). Siphonophores were sorted from the original samples and identified. The works by Totton (1965) and Bouillon *et al.* (1992, 2006) were followed for the basic taxonomic arrangement of families and higher taxa. Based on morphological and molecular data, Dunn *et al.* (2005) proposed the creation of a new group, Codonophora to contain the Calycophorae and Physonectae. However, no suggestion about the rank of the new group or its subordinate taxa were given so it is unclear how best to include this phylogenetic information in a ranked classification. In addition, the inclusion of genera and species within Agalmatidae took into account the work by Pugh (2006). The identification of siphonophore species followed Totton (1965) and Pugh (1996, 1999). Some species mentioned in the literature under a different name were included in this account with the new, accepted nomen.

Results and discussion

A revised list of siphonophores recorded from the western Caribbean is presented in Table 1. It includes all previous records together with those resulting from the two cruises reported in this paper. The names used in this table are those currently recognized as valid.

Of the 47 siphonophore species recorded during both cruises, 39 (83%) are members of Calycophorae, 7 (15%) of Physonectae, and 1 (2%) of Cystonectae. Up to 14 taxa have not been hitherto recorded in the western Caribbean (marked with an asterisk in Table 1); out of these, 10 are calycophorans, 3 physonects, and

1 is a cystonect.

The order Cystonectae is represented in the western Caribbean by three species belonging to the two known genera (*Physalia* and *Rhizophysa*). The finding of *R. eysenhardti* represents the first record in the Caribbean (see Stepanjants 1975; Gasca 2002) and the second in the Northwestern Tropical Atlantic (NWTA) (Pugh & Gasca 2009). In the Eastern Pacific it can be common in surface layers (Purcell 1981).

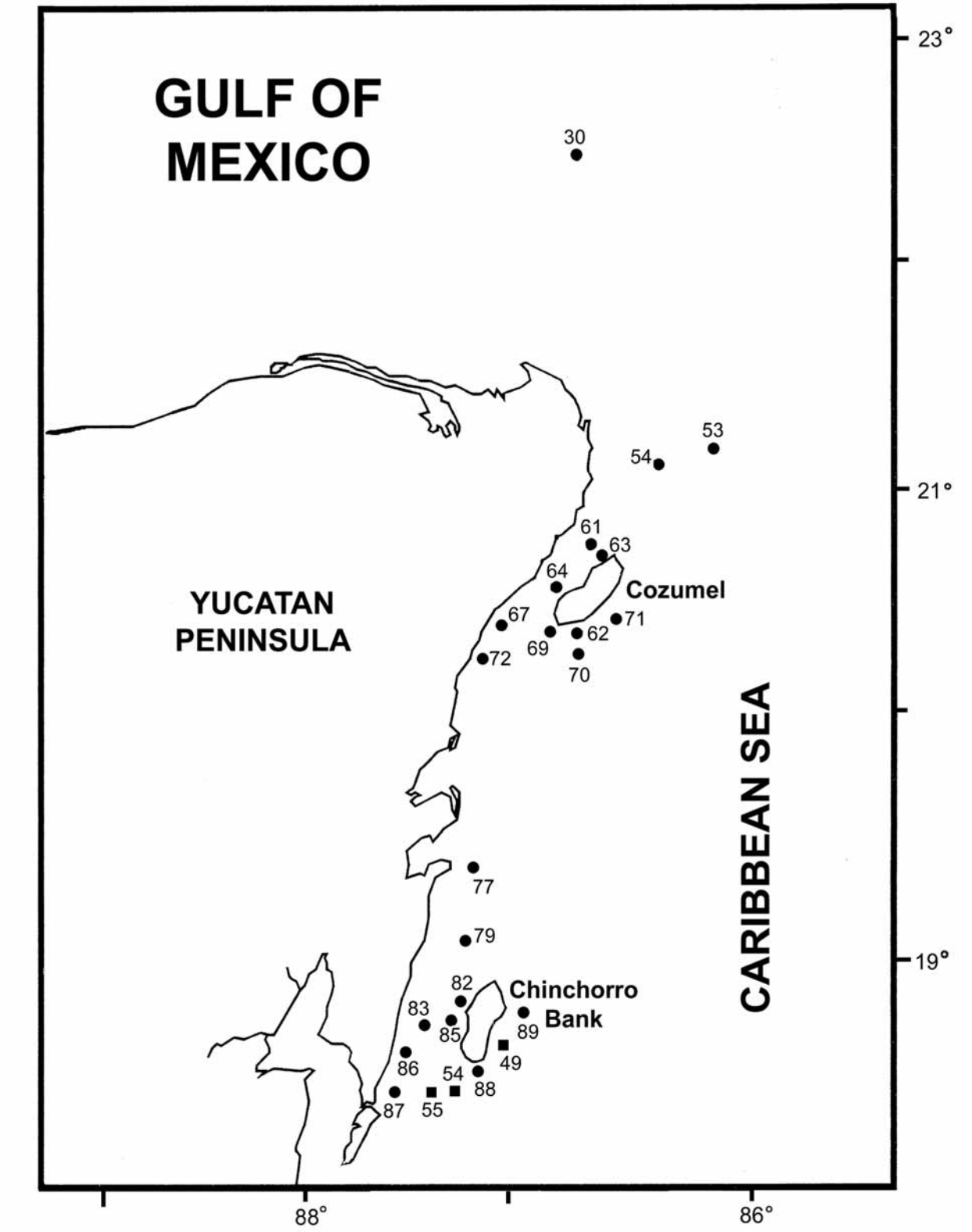

FIGURE 1. Surveyed area in the western Caribbean; solid circles indicate stations visited during the Caribe 2002b cruise and squares denote those from GG 2006.

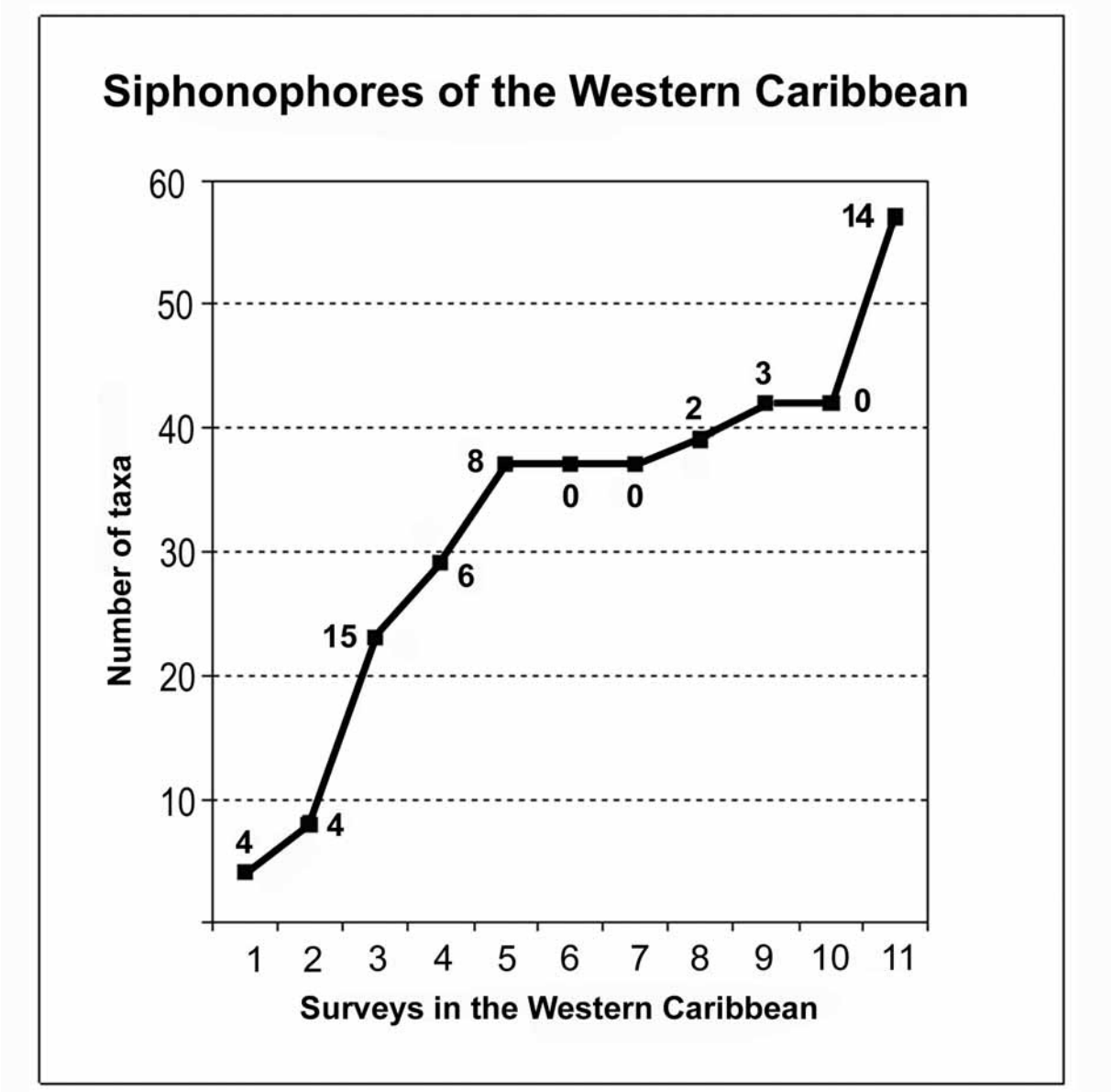

FIGURE 2. Historical records of siphonophores from the western Caribbean since 1972 including the new information yielded by the recent collections in 2002 and 2006 from this survey at an expanded vertical sampling range. The figures on the graphic line indicate the number of new records from each survey to complete the total of 56 taxa. 1. Owre & Foyo (1972); 2. Michel & Foyo (1976); 3. Gasca & Suárez-Morales (1989a); 4. Gasca & Suárez-Morales (1989b); 5. Gasca (1990a); 6. Gasca (1990b); 7. Gasca & Suárez-Morales (1991); 8. Gasca (1997a); 9. Gasca (1997b); 10. Gasca (1999); 11. This survey.

Within the order Physonectae, *Cordagalma ordinata* (Haeckel, 1888) has been hitherto found only from the Gulf of Mexico (Gasca 1993, 2002; Pugh & Gasca 2009), but not in the Caribbean itself (Stepanjants 1975; Gasca 2002). This species, found in the two cruises studied, is known to be epipelagic (0–200 m) (Pugh 1999); it is frequently encountered but not abundant in tropical waters. The genus *Forskalia* contains seven species (Pugh 2003), of which only two, *F. edwardsi* and *F. contorta* were collected during this survey; the latter has been recorded also as its synonym *F. leuckarti*. Both are distributed vertically within the 0–200 and 0–500 m ranges, respectively (Pugh 1999). Records for these species in the Atlantic Ocean are restricted to the Southeastern region and the Mediterranean and they had not been found in the Caribbean Basin or in the NWTA.

TABLE 1. Siphonophores (Cnidaria: Hydrozoa: Siphonophora) recorded in the western Caribbean during each of the two cruises studied. Taxa included as "non-Agalmatidae" follows Pugh (2006).

Species	GG2006	Caribe2002b
Order Cystonectae Haeckel, 1887		
Family Rhizophysidae Brandt, 1835		
Rhizophysa eysenhardti Gegenbaur, 1859 *+	X	X
Order Physonectae Haeckel, 1888		
Family Agalmatidae Brandt, 1835		
Agalma elegans (Sars, 1846)	X	
A. okeni Eschscholtz, 1825	X	X
Nanomia bijuga (Chiaje, 1841)		X
"non-Agalmatidae"		
Cordagalma ordinata (Haeckel, 1888) *+	X	X
Frillagalma vityazi Daniel, 1966	X	
Family Forskaliidae Haeckel, 1888		
Forskalia edwardsi Kölliker, 1853 *+		X
F. contorta (Milne Edwards, 1841) *+		X
Order Calycophorae Leuckart, 1854		
Family Prayidae Kölliker, 1853		
Amphicaryon acaule Chun, 1888	X	X
A. ernesti Totton, 1954		X
Desmophyes annectens Haeckel, 1888		X
Family Hippopodiidae Kölliker, 1853		
Hippopodius hippopus (Forskål, 1776)	X	X
Vogtia glabra Bigelow, 1918 *	X	X
Family Diphyidae Quoy & Gaimard, 1827		
Chelophyes appendiculata (Eschscholtz, 1829)	X	X
Diphyes bojani (Eschscholtz, 1829)	X	X
D. dispar Chamisso & Eysenhardt, 1821	X	X
Eudoxoides mitra (Huxley, 1859)	X	X
E. spiralis (Bigelow, 1911)	X	X
Lensia achilles Totton, 1941 *+		X
L. ajax Totton, 1941 *+	X	
L. campanella (Moser, 1925)	X	X
L. campanella petrovski Alekseev, 1984 *+	X	
L. conoidea (Keferstein & Ehlers, 1860)*		X
L. conoidea pacifica Stepanjants, 1967 *+	X	
L. cossack Totton, 1941	X	X
L. exeter Totton, 1941 *	X	X
L. fowleri (Bigelow, 1911)		X
L. hostile Totton, 1941 *	X	
L. hotspur Totton, 1941	X	X
L. leloupi (Totton, 1954) *+		X

to be continued.

TABLE 1. (continued)

Species	GG2006	Caribe2002b
L. lelouveteau Totton, 1941*	X	X
L. meteori (Leloup, 1934*)*	X	X
L. multicristata (Moser, 1925)	X	X
L. subtilis (Chun, 1886)		X
L. subtilis var. *chuni* (Totton, 1954)		X
Muggiaea kochi (Will, 1844)	X	X
Sulculeolaria chuni (Lens & van Riemsdijk, 1908)	X	X
S. monoica (Chun, 1888)	X	X
S. turgida (Gegenbaur, 1853)		X
S. quadrivalvis Blainville, 1834	X	
Family Abylidae L. Agassiz, 1862		
Abyla haeckeli Lens & van Riemsdijk, 1908	X	X
A. trigona Quoy & Gaimard, 1827	X	X
Abylopsis eschscholtzi (Huxley, 1859)	X	X
A. tetragona (Otto, 1823)	X	X
Bassia bassensis (Quoy & Gaimard, 1833)	X	X
Ceratocymba leuckarti (Huxley, 1859)	X	X
Enneagonum hyalinum Quoy & Gaimard, 1827	X	X

* Not hitherto recorded in the Western Caribbean.
+ Not hitherto recorded from the Caribbean Basin.

The order Calycophorae is the most diverse group of Siphonophora. It contains the most abundant species of the Caribbean epiplankton (Gasca & Suárez-Morales 1991; Gasca 1997b, 1999, Table 1). *Lensia* is the most diverse calycophoran genus and some species have a complex taxonomy (Pugh and Pagès 1997). It includes both epipelagic and deep-living species. Among the former, *Lensia leloupi* is recorded here for the first time in the entire NWTA. According to Pugh (1999) this species closely resembles and can be confused with its congener *L. subtiloides* (Lens and van Riemsdijk, 1908), an Indo-Pacific form. The Caribbean specimens (nectophores) have the distinctive characters described by Pugh (1999) for *L. leloupi*, including five ridges, of which the two lateral ones do not reach the ostial margin. There is only one previous regional record of *Lensia conoidea*, from the Gulf of Mexico (Vasiliev 1974); it is here reported for the first time from western Caribbean waters after its record from the eastern Caribbean at a depth range of 200–500 m (Stepanjants 1975). It has been reported as a mesopelagic form also in the Eastern Pacific (Alvariño 1985) and across a broad latitudinal range in the Atlantic Ocean (Margulis 1971). An anterior nectophore collected in the samples examined resembles that depicted under the name *L. conoidea pacifica* by Stepanjants (1967) and Margulis and Alekseev (1985); this subspecies was tentatively included as such in Table 1. *Lensia campanella petrovskyi*, a member of the *L. campanella* species complex (Margulis & Alekseev 1985) was also obtained during both cruises. It was distinguished by the number of ridges and the length of the oral plate, and by the length and shape of the somatocyst (see Margulis & Alekseev 1985). The presumed distributional patterns of this subspecies included the Caribbean but no actual records have been hitherto published from this basin. Furthermore, earlier records of *L. campanella* from the central and eastern sectors of the Caribbean (Stepanjants 1975) could represent one or more of the subspecies of this complex; these specimens should be taxonomically examined in order to define their subspecific identity.

Five deep-living species of *Lensia* were captured in this survey (Table 1). These forms have different vertical distributional ranges, from 200 to 2000 m (Margulis 1971; Stepanjants 1975; Pugh 1999). The known

ranges of these true mesopelagic forms overlap: *L. ajax*: 200–1000 m, *L. lelouveteau*: 500–2000 m, *L. hostile*: 500–2000 m, *L. achilles*: 500–900 m, *L. exeter*: 400–2000 m (Margulis 1971; Stepanjants 1975; Alvariño 1985; Pugh 1999). Stepanjants (1975) recorded *Lensia exeter, L. hostile,* and *L. lelouveteau* from the central and eastern Caribbean; the records of *L. achilles* and *L. ajax* are the first in the Caribbean Basin and the NWTA. Prior to this report, 15 species of the genus *Lensia* had been recorded from the Caribbean Basin (Stepanjants 1975) but only seven were known from the western Caribbean (Gasca 2002).

The 14 new records of Siphonophora found during this survey increased the number of taxa recorded from the western Caribbean area by roughly a third, from 42 to 56 (Fig. 2). Ten species recorded in this survey represent first records for the entire Caribbean Basin, only five species previously recorded in the area did not occur in this survey; these are *Physalia physalis* Linneaus, 1754, *Rhizophysa filiformis* (Forskål, 1775), *Athoribia rosacea* (Forskål, 1775), *Physophora hydrostatica* Forskål, 1775, and *Ceratocymba sagittata* (Quoy & Gaimard, 1827) (Gasca, 2002). The results of this survey are the most relevant progress in the knowledge of the diversity of the western Caribbean siphonophore fauna in terms of new records even though the accumulated number of previous zooplankton samples (more than 300) was much higher than that examined in this work (26).

The order Calycophorae is represented in the western Caribbean by 41 species, whereas both the order Cystonectae and the Physonectae are represented by 13 species only. This difference is attributed both to the historical emphasis given to sampling the upper layers in the region (Gasca 2002) and the known diversity of these groups.

Currently, deep-living forms are represented by only 7 species in the western Caribbean; in Stepanjants' (1975) survey, the deep-living species (14) represented 23% of the records from the central and eastern Caribbean. Hence, these forms may still be underrepresented in the western Caribbean sector despite the new records described here. Meso- or bathypelagic genera such as *Chuniphyes* and *Crystallophyes* plus several other species of *Lensia* are probably present in the western sector of the Caribbean Basin but have not yet been collected.

The number of new records reported herein (14) was not equally distributed when comparing the two sample gears used. The CalCOFI net captured 41 species of which ten are new records. Of these, five are deep-living forms. The sampling effort was greater (20 samples) than in the second cruise (2006), during which only 6 samples were obtained, and the number of species was lower (37) but the number of new records was slightly higher (11), including only 3 deep-living forms. Both nets were equally efficient in sampling epipelagic siphonophores but the CalCOFI net collected more deep-living species than the MOCNESS, mostly small forms of *Lensia*.

The new records for Mexican waters (Table 1) raises the national (Atlantic + Pacific coasts) total account of siphonophore species from 89 (Gasca 2002) to 96. At a regional scale, the known species richness of siphonophores from this part of the Caribbean is still low when compared with that from other adjacent tropical areas, including the remaining sectors of the Caribbean (Stepanjants 1975: 60 species), the Gulf of Mexico (Gasca 2002; Pugh & Gasca 2009: 80 species), and the Mexican Pacific (Gasca 2002: 73). Further study of the deep-living siphonophore fauna of these large, poorly known areas of the NWTA is likely to yield additional information on the regional diversity of these cnidarians, particularly if submarines are used (e.g. Pugh & Youngbluth 1988).

Acknowledgments

We thank the captains and crews of the research vessels "Gordon Gunter" (NOAA-SEFSC) and "Antares" (Mexican Ministry of Navy) for collection of samples in the western Caribbean. Lourdes Vásquez-Yeomans and John Lamkin kindly allowed me to participate in the project "Larval Fish and Physical Oceanography Survey of the Mesoamerican Reef System", supported by the NOAA-Southeast Fisheries Science Center. The author received a grant from CONACYT, Mexico. The comments and suggestions of three referees

significantly improved an earlier version of this contribution. Also, the editorial work and support by Allen Collins is deeply appreciated.

References

Alvariño, A. (1985) Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California (Diphyinae, Siphonophora, Coelenterata). *Investigaciones Marinas,* Centro Interdisciplinario de Ciencias Marinas, 6 (No. Esp.2), 1–37.

Bouillon, J., Boero, F., Cicogna, F., Gili, J.M. & Hughes, R.H. (1992) Non-Siphonophoran Hydrozoa: what are we talking about? *Scientia Marina*, 56, 279–284.

Bouillon, J., Gravili, C., Pagès, F., Gili, J.M. & Boero, F. (2006) An Introduction to Hydrozoa. *Mémoires Museum National d' Histoire Naturelle*, 194, 7–591.

Dunn, C.W., Pugh, P.R. & Haddock, S.H.D. (2005) Molecular phylogenetics of the Siphonophora (Cnidaria), with implications for the evolution of functional specialisation. *Systematic Biology*, 54, 916–935.

Gasca, R. (1990a) Composición, distribución y abundancia de los sifonóforos (Coelenterata: Hydrozoa) de las costas de Yucatán y Quintana Roo, México. Master of Science Thesis. Facultad de Ciencias, Universidad Nacional Autónoma de México. Mexico.

Gasca, R. (1990b) Sifonóforos (Coelenterata: Siphonophora) de las costas de Quintana Roo. *In:* Navarro, D. & Robinson, J.G. (eds.). *Diversidad Biológica en la Reserva de la Biósfera de Sian Ka'an, Quintana Roo, México*. Centro de Investigaciones de Quintana Roo/Program of Studies in Tropical Conservation, University of Florida. Mexico City. pp. 109–125.

Gasca, R. (1993) Especies y abundancia de sifonóforos (Cnidaria: Hydrozoa) en la región sur del Golfo de México. *Caribbean Journal of Science*, 29, 220–225.

Gasca, R. (1997a) Nuevos registros y ampliación de ámbito de especies de Siphonophora (Cnidaria) en aguas del Atlántico Mexicano. *Revista de Biología Tropical*, 45, 933–934.

Gasca, R. (1997b) Sifonóforos (Cnidaria: Hydrozoa) del Mar Caribe Mexicano (agosto, 1986). *Hidrobiológica*, 7, 51–57.

Gasca, R. (1999) Sifonóforos de aguas superficiales del Mar Caribe Mexicano. *Revista de Biología Tropical*, 47(Supl. 1), 113–122.

Gasca, R. (2002) Lista faunística y bibliografía comentadas de los sifonóforos (Cnidaria) de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 73, 123–143.

Gasca, R. & Suárez-Morales, E. (1989a) Nota acerca de los sifonóforos (Cnidaria: Siphonophora) del Canal de Yucatán. *Caribbean Journal of Science*, 25, 66–70.

Gasca, R. & Suárez-Morales, E. (1989b) Sifonóforos (Cnidaria) de las costas de Quintana Roo y Yucatán durante el verano de 1984. *Boletín de Instituto Oceanográfico de la Universidad de Oriente*, 28, 9–14.

Gasca, R. & Suárez-Morales, E. (1991) Siphonophores (Cnidaria) of upwelling areas of the Campeche Bank and the Mexican Caribbean Sea. *Hydrobiologia*, 216/217, 497–502.

Mackie, G.O., Pugh, P.R. & Purcell, J.E. (1987) Siphonophore Biology. *Advances in Marine Biology*, 24, 97–262.

Margulis, R.Y. (1971) On the distribution of siphonophores of the genus *Lensia* in the Atlantic Ocean. *Oceanology, Moskow*, 11, 99–104.

Margulis, R.Y. (1984) The dependence of vertical distribution of the Siphonophora of the World Ocean of the boundaries of water layers. *Zhurnal Obshchei Biologii*, 45, 472–479.

Margulis, R.Y. & Alekseev, D.O. (1985) On the genus *Lensia* (Siphonophora, Calycophora). *Zoologicheskii Zhurnal*, 64, 5–15.

Michel, H.B. & Foyo, M. (1976) *Caribbean Zooplankton. Part. I. Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae*. Washington, D.C., Office of Naval Research. Department of Navy.

Owre, H.B. & Foyo, M. (1972) Studies on Caribbean zooplankton: description of the program and results of the first cruise. *Bulletin of Marine Science*, 22, 483–521.

Pagès, F. (2002) The status of three rare siphonophores (Cnidaria, Hydrozoa) described by Tamiji Kawamura: *Bathyphysa japonica, Athorybia longifolia* and *Forskalia misakiensis*. *Scientia Marina*, 66, 375–382.

Pugh, P.R. (1996) Siphonophora. *In:* Gasca, R & Suárez-Morales, E. (eds.). *Introducción al Estudio del Zooplancton Marino*. ECOSUR/CONACYT. Mexico City. pp. 71–100.

Pugh, P.R. (1999) Siphonophorae. *In:* Boltovskoy, D. (ed.). *South Atlantic Zooplankton*. Backhuys Publishers. Leiden. pp 467–511.

Pugh, P.R. (2003) A revision of the family Forskaliidae (Siphonophorae: Physonectae). *Journal of Natural History*, 37, 1281–1327.

Pugh, P.R. (2006) The taxonomic status of the genus *Moseria* (Siphonophora, Physonectae). *Zootaxa*, 1343, 1–42.

Pugh, P.R. & Gasca, R. (2009) Siphonophora (Cnidaria Hydrozoa) of the Gulf of Mexico. *In:* Felder, D. L. & Camp,

D.K. (eds.). *Gulf of Mexico–Origins, Waters, and Biota. Biodiversity.* Texas A&M University Press. College Station. pp. 720–736.
Pugh, P.R. & Pagès F. (1997) A re-description of *Lensia asymmetrica* Stepanjants, 1970 (Siphonophorae: Diphyidae). *Scientia Marina*, 61, 153–161.
Pugh, P.R. & Youngbluth, M.J. (1988) Two new species of prayine siphonophore (Calycophorae, Prayidae) collected by the submersible Johnson-Sea-Link I and II. *Journal of Plankton Research*, 10, 637–657.
Purcell, J.E. (1981) Feeding ecology of *Rhizophysa eysenhardti* siphonophore predator of fish larvae. *Limnology and Oceanography*, 26, 424–432.
Stepanjants, S. (1967) Siphonophores of the seas of the USSR and the north western part of the Pacific Ocean. *Opredeliteli po Faune SSSR*. (Classification key of the Fauna of Russia), 96, 1–216.
Stepanjants, S. S. (1975) Species composition and distributional patterns of Siphonophora of the Caribbean, Gulf of Mexico and adjacent waters of the Atlantic. *Transactions of the P.P. Shirshov Institute of Oceanology*, 100, 96–126.
Suárez-Morales, E. & Gasca, R. (1991) *Sifonóforos de México. Biología y Ecología*. Centro de Investigaciones de Quintana Roo (CIQRO). Mexico City.
Totton, A. K. (1965) *A Synopsis of the Siphonophora*. Trustees of the British Museum (Natural History). London.
Vasiliev, V. (1974) Distribución de los sifonóforos en el Golfo de México durante el periodo de primavera-verano en el año 1969. *Ciencias* La Habana, Serie 8(12), 1–51.