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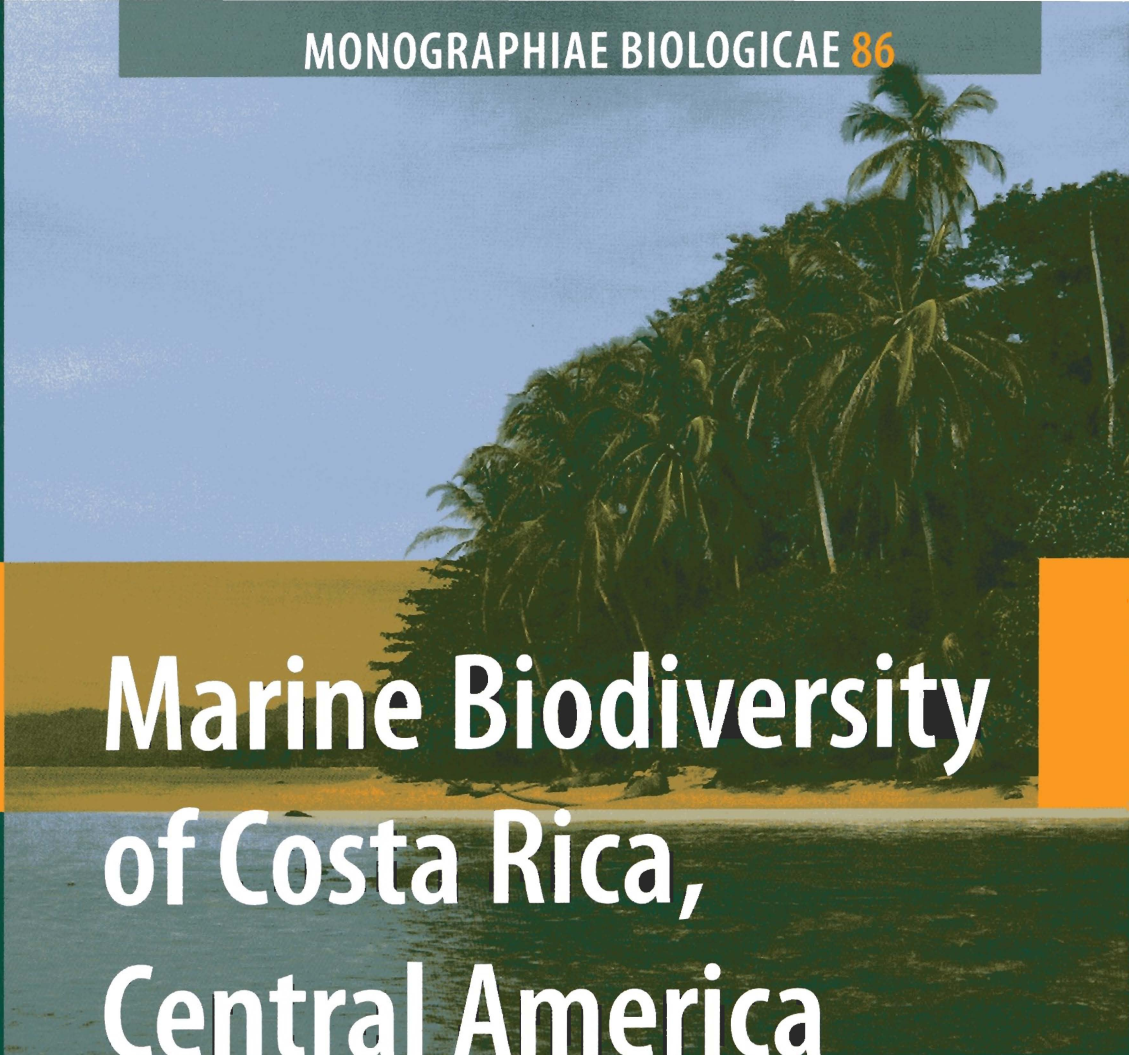

Marine Biodiversity of Costa Rica, Central America

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Editors

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Part 8
Siphonophores

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Physophora hydrostatica, a species from Pacific Costa Rica. (Photo: Steven H.D. Haddock)

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Abstract Thirty-seven species of siphonophores are listed for the Costa Rican coastal and oceanic waters. All species were recorded from the Pacific coast, seven of them have been also collected off the Caribbean coast. These figures represent 10% of the 70 species known from the Caribbean Sea, and 42% of the 87 species known from the eastern tropical Pacific. Overall, the species recorded in Costa Rican waters represent close to 37% of the nearly 100 species known to be distributed in the tropical-equatorial belt. The relatively low biodiversity of siphonophores in the Caribbean coast of Costa Rica is clearly a result of the scarcity of research in this region. All the species currently known from Costa Rica are epipelagic forms living between the surface and 200m, and have been recorded previously in the corresponding oceanographic regions of the Atlantic and Pacific oceans. Additional work in both oceanic and coastal waters is necessary, including coastal and estuarine ecosystems and also deep waters (>200m), which most probably harbor a diverse siphonophore fauna.

Introduction

The Subclass Siphonophora is a peculiar group of marine cnidarians (Class: Hydrozoa); it is part of the commonly known "gelatinous zooplankton," which includes hydromedusae, scyphomedusae, ctenophores, salps, and appendicularians among other taxa. Most of the species of siphonophores are fully planktonic forms. The Portuguese Man-of-War (*Physalia physalis*), floating at the surface of the water, and a small group of benthic forms (Family: Rhodaliidae) (Pugh 1999b) are two noteworthy exceptions.

The siphonophores are efficient predators distributed in the entire world ocean from the surface to thousands of meters deep. Most of them inhabit oceanic waters, but a few species can live in neritic areas, and are often present in high densities in both neritic and oceanic waters. They are all carnivorous forms, capturing their prey using poisonous nematocysts, and most species are assignable to a passive feeding behavior. The use of luminescent lures to attract preys has been discovered recently (Haddock *et al.* 2005a). Because of their predating efficiency, siphonophores can cause major impacts on the structure and dynamics of the zooplankton communities

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(Pagés *et al.* 1992). Recent studies have shown how pollution caused by human activities may have an impact on gelatinous zooplankton, including the population dynamics of siphonophores. These changes can eventually impact other components of the planktonic ecosystems (CIESM 2001).

We present a checklist of the siphonophores collected in coastal and oceanic environments of Costa Rica's Caribbean Sea and Pacific Ocean (Species Lists 8.1 and 8.2 are included on the CD-Rom). The lists include scientific results of international expeditions such as that of the "Albatross" in the eastern tropical Pacific during 1904 and 1905, and the "BONACCA" in the Western Caribbean Sea in 1963 (Alvariño 1972); they covered large areas of these regions, including a few stations in Costa Rican waters. Recent surveys of siphonophores in Costa Rican waters have been done and included basic aspects on the composition and distribution of this group (Ramírez 1988; Gasca & Suárez-Morales 1992; Nowaczyk 1998, Rodríguez 2001 unpublished data).

Taxonomic status/problems: The classic and best account on siphonophore taxonomy and morphology was written by Totton (1965); however, the systematics of the group has changed since then (Bouillon *et al.* 1992). Many species, mainly deepwater forms, have been described recently from different regions of the world (Pugh 1992a, b, c, 1995, 1999a, 2001, 2002, 2004; Pugh & Pagès 1995, 1997). Valuable publications on the biology and reproduction of the siphonophores are those by Mackie *et al.* (1987) and Carré & Carré (1993).

Siphonophores have been grouped into three orders, based on the presence of an apical pneumatophore (Cystonectae and Physonectae; absent in Calycophorae), and on the presence (Physonectae and Calycophorae) or absence (Cystonectae) of nectophores. The structure and life cycle of this group are complex. They have been designated as "colonies" formed by zooids, medusoids, and polypoids, each with different forms and functions. The complexity of siphonophores is not restricted to their morphological and physiological diversity; it extends also to the specific terminology used to define each of these variable structures. A recent revision of the morphological nomenclature in siphonophores is given in Haddock *et al.* (2005b). Nectophores and bracts are of particular importance for taxonomic identification.

Siphonophores are fragile, thus making it difficult to study them both taxonomically and ecologically. The use of traditional trawl nets may produce serious damages to the organisms and consequently complicate their identification and/or quantification. In recent years, blue water diving, submersibles, and remotely operated vehicles (ROVs) have solved most of this problem. It is now possible to obtain complete organisms and images of siphonophores, thus facilitating the identification of species and providing valuable information about their biology, ecology, and behavior. However, this kind of equipment is expensive (especially submersibles), and for developing countries it is almost impossible to acquire and maintain them. Due to this situation, most of the information on deepwater siphonophores is concentrated in a few sites around the world; hence, epipelagic trawls are, historically and currently, the most important source of the available information on the group. Moreover, the task of fixation-preservation of an intact organism is difficult. The slow addition of magnesium chloride to the seawater while the organism is swimming helps to create a condition for relaxation previous to the fixation and preservation in formalin.

Their phylogenetic relations are still obscure and under investigation. There are few specialists working in the field, and some of them are listed below.

Species richness. The number of nominal species of siphonophores known to date is about 170 (worldwide), with many others discovered but yet undescribed. There are surveys on the general diversity of siphonophores in different regions of the Atlantic Ocean, such as the works by Pugh (1999b) in the southwestern Atlantic (96 species), by Stepanjants (1975) and by Suárez & Gasca (1991) in the Caribbean Sea and Gulf of Mexico (62 species), and by Pugh & Gasca (in press) for the Gulf of Mexico (80 species). In the Central Pacific Ocean, between 10°N and 20°S, Stepanjants (1977) recorded 55 species. Suárez & Gasca (1991) recorded 48 species from Mexican Pacific waters.

Overall, the diversity of siphonophores known in Costa Rica represents close to 20% of the known diversity of the group worldwide. In regional terms, the number of species estimated to inhabit the Pacific Ocean adjacent to the Costa Rican waters is *ca.* 90 species (Alvariño 1972, 1974, Stepanjants 1977, Gasca 2002), representing 42% of the species reported from this area. Roughly seven species have been reported from the Caribbean Sea of Costa Rica, which represents only 10% of the 70 species known from the Caribbean region (Alvariño 1972, 1974, Owre & Foyo 1972, Stepanjants 1975, Michel & Foyo 1976, Gasca 2002). These data show the need to increase surveys of the zooplankton community in both coasts of Costa Rica, but particularly in the Caribbean waters.

Specialists

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Collections

Specimens of most of the species reported herein are deposited in a collection kept by K. Rodríguez as part of her Master thesis research. This material is held at CIMAR, Universidad de Costa Rica, San José. A few specimens, collected in previous projects, are deposited in the Museo de Zoología of the Universidad de Costa Rica.

Conclusions

One of the reasons for the relatively low biodiversity found in the Caribbean coast of Costa Rica with respect to the Pacific coast is the scarcity of research in those waters. Additional collections of gelatinous zooplankton in both oceanic and coastal waters are necessary, including estuaries, but emphasizing the neritic and oceanic areas. The same recommendation is valid for the rest of Central America. Through understanding the ecology and distribution of siphonophores as an important group of predators, it will be easier to evaluate the processes determining the dynamics of the marine planktonic biota of Costa Rica, including the ecology and development of local fisheries.

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Species List 8.1 Siphonophores collected in Caribbean of Costa Rica following the taxonomic arrangement and nomenclature proposed by Totton (1965) and Pagès et al. (1992)

Species	World distribution[a]	Central America[b]	Costa Rica[c]	Oceanic distribution[d]	Depth[e](m)	Habitat/ Community[f]	References[g]
Order CYSTONECTAE							
Family PHYSALIIDAE							
Physalia physalis (Linnaeus, 1758)	ct-t	n.a.	CC	ep	0	p	[1, 2, 6, 7]
Order CALYCOPHORAE							
Family DIPHYIDAE							
Abylopsis eschscholtzi (Huxley, 1859)	ct-t		CC	Ep	0–200	wc	[1, 2, 5, 6][h]
Chelophyes appendiculata (Eschscholtz, 1829)	ct-t	N,H	CC	Ep	0–300	wc	[1, 2]
Chelophyes contorta (Lens and van Riemsdijk, 1908)	t-t		IU	ep	0–200	wc	[1, 2, 9][h]
Enneagonum hyalinum Quoy and Gaimard, 1827	ct-s		CC	ep	300–1000	wc	[2, 4, 5]
Muggiaea atlantica Cunningham, 1892	EA,Med,WA	CA	IU	Ep	0–100	wc	[1, 2, 4, 5][h]
Sulculeolaria quadrivalvis Blainville, 1834	ct-s	G,P	CC	ep	0–100	wc	[2, 3, 7, 9][h]

[a] ct = circumtropical; ct-t = circumtropical-temperate; ct-s = circumtropical-subtropical; t-t = tropical-temperate; EA = eastern Atlantic; EP = eastern Pacific; Med = Mediterranean; WA = western Atlantic

[b] CA = all Central American countries; G = Guatemala; H = Honduras; N = Nicaragua; P = Panama

[c] CC = Caribbean coast; IU = Isla Uvita

[d] ep = epipelagic

[e] Uppermost and lowermost occurrences (in meters)

[f] wc = water column; p = pleuston

[g] References are indicated by numbers according to the Reference list.

[h] Rodríguez, K. unpublished data

Species List 8.2 Siphonophores collected in Pacific waters of Costa Rica. The systematic arrangement and nomenclature used was that proposed by Totton (1965) and Pagés *et al.* (1992)

Species	World distribution[a]	Central America[b]	Costa Rica Pacific[c]	Oceanic distribution[d]	Depth[e] (m)	Habitat/ Community[f]	References[g]
Order CYSTONECTAE							
Family PHYSALIIDAE							
Physallia physalis Linnaeus, 1758	ct-t		GP,ICñ	surface	0	p	[2, 6, 7, F. Pagès, 2000 personal communication]
Family RHIZOPHYSIDAE							
Rhysophysa eysenhardti Gegenbaur, 1859	ct		GP	ep,mp	n.a.	wc	[8, 9]
Order PHYSONECTAE							
Family AGALMIDAE							
Agalma elegans (Sars, 1846)	ct-t		D,GP	ep,mp	0–200	wc	[2, 6, 8]
Agalma okeni Eschscholtz, 1825	ct-t	CA	D,GP	ep	0–200	wc	[2, 6, 8]
Halistemma sp. Hexley, 1859	n.a.		IC	mp	n.a.	wc	[8]
Nanomia bijuga (Chiaje, 1841)	ct-t		D,GP	ep,mp	0–200	wc	[2, 8]
Family FORSKALIIDAE							
Forskalia edwarsi Kolliker, 1853	ct-t		GP	ep	0–250	wc	[8, 9]
Family PHYSOPHORIDAE							
Physophora hydrostatica Forskål, 1775	ct-t		D	ep	0–200	wc	[2]
Order CALYCOPHORAE							
Family PRAYIDAE							
Amphicaryon ernesti Totton, 1954	ct-s		D	ep	0–200	wc	[2]
Rosacea cymbiformis (Chiaje, 1822)	EA,Med,WA		GD	ep,mp	0–675	wc	[4, 5]
Rosacea flaccida Biggs, Pugh & Carré, 1978	n.a.		GP	ep	0–50	wc	[8]

Family HIPPOPODIIDAE							
Hippopodius hippopus (Forskål, 1776)	ct-s		D	ep	0–200	wc	[2, 9]
Vogtia pentacantha Kolliker, 1853	ct-t		D	mp	300–500	wc	[2, 4]
Family DYPHIDAE							
Sulculeolaria biloba (Sars, 1846)	ct-s		D	ep	0–200	wc	[2, 4]
Sulculeolaria chuni (Lens & van Riemsdijk, 1908)	ct-s		D,GD,GP	ep	0–200	wc	[2, 5, 8, 9]
Sulculeolaria quadrivalvis Blainville, 1834	ct-s		D,GD,GP	ep	0–200	wc	[2, 4, 5, 8]
Sulculeolaria turgida (Gegenbaur, 1853)	ct-s.		D	ep	0–200	wc	[2, 4]
Chelophyes appendiculata (Eschscholtz, 1829)	ct-t		D	ep	0–500	wc	[2]
Chelophyes contorta (Lens & van Riemsdijk, 1908)	t-t		D,GD,GP,IC	ep	0–200	wc	[2, 8, 9]
Diphyes bojani (Eschscholtz 1829)	ct-t	G	D,GD,GP,IC	ep	0–500	wc	[2, 5, 8, 9]
Diphyes dispar Chamisso & Eysenhardt, 1821	ct-t	N	GD,GP	ep	0–500	wc	[4, 5, 8, 9]
Eudoxoides mitra Huxley, 1859	ct-t		D,GD,GP,IC	ep	0–200	wc	[2, 8]
Lensia campanella (Mosser, 1925)	ct-s		D,GD	ep	0–200	wc	[2, 6, 9]
Lensia challengeri Totton, 1954	EA,EP,IO, WA,WP		D	ep	0–500	wc	[2, 9]
Lensia conoidea (Keferstein & Ehlers, 1860)	temperate		D	ep	0–300	wc	[2, 9]
Lensia cossack Totton, 1941	ct-s		D	ep,mp	0–200	wc	[2, 9]
Lensia hotspur Totton, 1941	ct-s		D	ep	0–200	wc	[2, 4]
Lensia subtilis (Chun, 1886)	ct-s		D,GD	ep	0–200	wc	[2, 5, 9]

(continued)

Species List 8.2 (continued)

Species	World distribution[a]	Central America[b]	Costa Rica Pacific[c]	Oceanic distribution[d]	Depth[e] (m)	Habitat/ Community[f]	References[g]
Muggiaea atlantica Cunningham, 1892	EA,Med,WA		D,GD,GP,IC	ep	0–100	wc	[2, 4, 5, 8]
Sphaeronectes gracilis (Claus, 1873)	n.a.		GD	ep	0–100	wc	[5, 6]
Family ABYLIDAE							
Abyla haeckeli Lens & van Riemsdijk, 1908	ct-s		D	ep	0–200	wc	[2, 9]
Abylopsis eschscholtzi (Huxley, 1859)	ct-t		GD,GP,IC,D	ep	0–200	wc	[2, 5, 6, 8]
Abylopsis tetragona (Otto, 1823)	ct-t,Med	P	GP	ep	0–200	wc	[6, 8]
Bassia bassensis (Quoy & Gaimard, 1827)	ct-s	N	GD	ep	0–200	wc	[4, 5]
Ceratocymba leuckarti (Huxley, 1859)	ct-s		D	ep	0–200	wc	[2, 9]
Enneagonum hyalinum Quoy & Gaimard, 1827	ct-s		D	ep	0–200	wc	[2, 4, 5]

n.a. = information not available

[a] Ant = Antarctic; Arc = Arctic; cp = cosmopolitan; ct = circumtropical; ct-t = circumtropica-temperate; ct-s = circumtropical-subtropical; t-t = tropical-temperate; EA = eastern Atlantic; EP = eastern Pacific; IO = Indian Ocean; IP = Indo-Pacific; Med = Mediterranean; WA = western Atlantic; WP = western Pacific

[b] CA = all Central American countries; G = Guatemala, N = Nicaragua; P = Panama

[c] D = Costa Rica Dome; GD = Golfo Dulce; GP = Golfo de Papagayo; IC = Isla del Coco; ICñ = Isla del Caño

[d] ep = epipelagic; mp = mesopelagic; n = neritic

[e] Uppermost and lowermost occurrences (in meters)

[f] wc = water column; p = pleuston

[g] References are indicated by numbers according to the reference list