Siphonophores off a riverine system in the southern Gulf of Mexico: factors affecting their distribution and spatial niche breadth and overlap

Laura Sanvicente-Añorve · Claudia Alba ·
César Flores-Coto · Manuel Castillo-Rivera

Abstract Environmental factors determining the spatial pattern of the whole siphonophore community, as well as the hydrological occurrence ranges, small-scale vertical distribution, and spatial niche breadth and overlap of 23 siphonophore species collected off a riverine system in the southern Gulf of Mexico were analysed. A total of 149 zooplankton samples were collected in different strata of the water column (from 0 to 100 m) over a grid of 23 oceanographic stations during low (April) and high (October) rainy periods. Temperature and salinity measurements were taken with a CTD probe. Considering both seasons, salinity fluctuated between 30.7 and 37.0, and temperature between 18.2 and 29.0°C. Under these conditions, the hydrological occurrence ranges of species were analysed. Data on siphonophore biovolumes in the upper 30-m layer were subjected to a regression tree (RT) analysis taking the zooplankton biomass, the distance to the shore, the temperature, and the salinity as predictable variables. Results of the RT analysis showed that the distance from the shore, food availability, and temperature were among the most important factors affecting siphonophore spatial distribution. Food availability had a positive influence on the siphonophores distribution, whereas temperatures higher than 28.1°C seemed to depress most siphonophore populations. *Diphyes dispar* moderately dominated the community and represented 30% of the total biovolume. The calycophorans *Abylopsis tetragona, A. eschscholtzi, Diphyes bojani*, and *Chelophyes appendiculata* were the most generalist species as revealed by their niche breadth values, and *Enneagonum hyalinum* endured the widest salinity conditions (30.7–37.0) and was mainly distributed in coastal waters. The second most abundant species, the physonect *Agalma okeni*, exhibited a low mean niche overlap value with the calycophoran species. We hypothesise that differences in diet composition between physonects and calycophorans are the main cause of those low niche overlap values.

Keywords Environmental tolerances ·
Freshwater outflows · Grijalva-Usumacinta River ·
Siphonophora · Vertical distribution

L. Sanvicente-Añorve (✉) · C. Alba · C. Flores-Coto
Instituto de Ciencias del Mar y Limnología, Universidad
Nacional Autónoma de México, Apdo. Postal 70-305,
04510 Mexico, D.F, México
e-mail: sanvi@mar.icmyl.unam.mx

M. Castillo-Rivera
División de Ciencias Biológicas y de la Salvel,
Universidad Autónoma Metropolitana, Unidad Iztapalapa,
Apartado Postal 55-535, 09340 México, D.F, Mexico

Introduction

Siphonophores, a group of complex colonial organisms of about 160 described species, are among the most abundant predators of macroplankton and constitute an important link in pelagic food-chains (Boucher and

Thiriot 1972; Alvariño 1985; Pugh 1999). These animals are strictly carnivorous, consuming mainly copepods (Purcell 1981; Pagès et al. 2001), as well as euphausiids, decapods, pteropods, and fish larvae and eggs (Alvariño 1985). Predation on other cnidarians or ctenophores is not common among siphonophores, and no species is known to eat only gelatinous zooplankton (Purcell 1991). In spite of their gelatinous nature, siphonophores are eaten by a variety of vertebrate and invertebrate carnivores, such as sea turtles, fishes, sea stars, molluscs, medusae, ctenophores, and other siphonophores (den Hartog 1980; Purcell 1991; Lauerman 1998; Pugh 1999).

Siphonophores are widespread in the oceans. Most species are truly oceanic, a few are mainly neritic, and some rarely appear inshore (Pugh 1999). Due to their limited mobility, earlier studies (Moore 1949; Alvariño 1971, 1981; Margulis 1972; Vasiliev 1974) considered these gelatinous animals as indicators of water masses. However, Pugh (1999) found no clear correlations between hydrographical features and siphonophore populations. In the water column, most species are epipelagic (Pugh 1974), comprising a significant portion of the near-surface zooplankton biomass when measured as volume (Grice and Hart 1962); others are deep-living, bathypelagic species occurring at almost any latitude, where temperature does not vary greatly (Pugh 1999). Factors affecting vertical distribution of these animals vary depending on the time and localities. Pugh (1977, 1999) indicated that diel changes in the vertical distribution of siphonophores are mainly correlated to migrational patterns of their prey, whereas Silguero and Robison (2000) found that seasonal changes on their vertical distribution were associated to the upwelling process.

The southern Gulf of Mexico is a dynamic area where marked seasonal changes occur in both hydrological and biological features. The variety of physical phenomena, such as haline fronts, upwelling processes, changes in the direction of surface currents, and continental water discharges (Czitrom et al. 1986; Zavala-Hidalgo et al. 2003, 2006) generate a high heterogeneity in the marine habitats. Our knowledge on siphonophore fauna, or indeed of any zooplankter, in this region is limited. Gasca (1993) and Alba-Hurtado (2001) studied the composition and abundance of siphonophores of both neritic and oceanic waters; Gasca (1999) focussed on the distribution of several species and identified the main physical factors determining siphonophore assemblages at a mesoscale, and Sanvicente-Añorve et al. (2007) analysed the diversity and composition of the assemblages defined from the same data set treated in this study. Several authors (Alvariño 1981; Pugh 1999; Gibbons and Thibault-Botha 2002) emphasise that siphonophores are exclusively marine animals and that only few species are able to support the highly complex and variable environmental conditions of coastal waters. However, ecological studies are scarce and have hardly focussed on coastal populations under the influence of riverine inputs (Alvariño 1968). Hence, in this work we analyse the main biological and physical features affecting distributional patterns of the overall siphonophore community, we document the hydrological preferences of 23 species, assess their small-scale vertical distribution, and define their niche breadth and overlap through the analysis of 149 samples collected off the Grijalva-Usumacinta River during two contrasting outflow periods in the southern Gulf of Mexico.

Materials and methods

Study area

The studied area is located in neritic waters of the southern Gulf of Mexico (18°30′ to 20° N, 92° to 93° W), off the most important riverine system in the area, the Grijalva-Usumacinta River (Fig. 1). This is a highly dynamic area due to the influence of continental water discharges and oceanic processes that induce water-mass mixing and turbulent environments. The large amount of continental water discharges (7–10×10^9 m^3 month^{-1} from July to November and 1.6–4×10^9 m^3 month^{-1} from December to June) coming from the Grijalva-Usumacinta system into the adjacent neritic zone generates a thermo-haline front persisting throughout the year (Czitrom et al. 1986). Surface circulation on the shelf is influenced by southerly and southeasterly winds during summer and by northwesterly cold winds during the autumn-winter (Zavala-Hidalgo et al. 2006). As a result, circulation is westwards throughout the year, but during the autumn–winter period a counter-clock-wise current reaches the southern Bay of Campeche, where it encounters an opposite current and results in an offshore transport of water (Zavala-Hidalgo et al. 2003).

Fig. 1 Study area and location of oceanographic stations, southern Gulf of Mexico
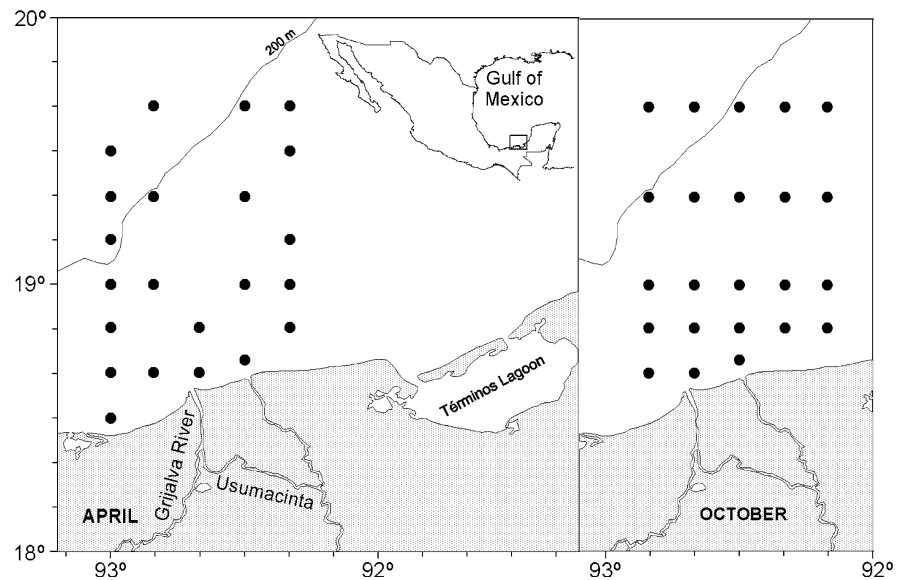
Sampling and laboratory analysis

Sampling was carried out during April and October 2001 on a grid of 23 oceanographic stations located over neritic waters of the southern Gulf of Mexico (Fig. 1). Samples were taken using a multiple opening/closing net with 75-cm diameter and 500-μm mesh size, and towed for approximately 10 min. A flowmeter was placed in each net to measure the volume of water filtered, and six strata were sampled: 0–10, 10–20, 20–30, 40–60, 60–80, and 80–100 m. Salinity and temperature measurements were also taken with a CTD probe. In total, 149 zooplankton samples were collected during both seasons, and fixed with 4% formalin neutralised with sodium borate.

In the laboratory, zooplankton biomass was estimated as wet weight (g 100 m^{-3}) using an analytical balance (0.001 g precision). Before this, all siphonophore pieces were separated from samples, without taken aliquot parts, and determined to the species level using specialised literature (Sears 1954; Totton and Bargmann 1965; Trégouboff and Rose 1957; Alvariño 1981; Pugh 1999, among others). Because siphonophores are highly polymorphic colonies and the number of individuals might not be the best way to compare populations of widely different size organisms (Whittaker 1975), siphonophores were quantified as displacement volume (ml 100 m^{-3}). Other authors (Vollmer and Edmunds 2000; Alcaraz

et al. 2003; Kaspari 2005) also emphasised the importance of biomass measurements in the study of community dynamics.

Data analysis

Since siphonophores were most abundant in the upper 30-m layer, we decided to analyse environmental factors affecting their distribution in this stratum. For this purpose, a regression tree (RT) analysis was applied to data matrices from each season, using the distance from the shore, the temperature, the salinity, and the zooplankton biomass as predictable variables, and the siphonophore biovolume as response variable. For this purpose, data on zooplankton and siphonophores were log-transformed, and mean vertically integrated values of environmental variables were estimated as:

$$Mx = \frac{1}{30} \int_0^{30} x(z)\,\mathrm{d}z$$

where Mx = mean integrated value (0–30 m) of the variable x (temperature, salinity, zooplankton biomass, siphonophore biovolume); z = depth.

The niche breadth (B) of each species and the niche overlap (C) between pairs of species were also calculated. Niche breadth can be estimated by measuring the uniformity of the distribution of their individuals over the resource state matrix (Colwell and Futuyma 1971). In this study, a 'resource state'

represents each of the oceanographic stations and depth sampled at a given time, and the resource state matrix was constructed considering both seasons (149 samples × 23 species). The B value was estimated according to the equation given by Levins (1968) and standardised by Colwell and Futuyma (1971):

$$B_i = \frac{1}{n-1}\left[\frac{1}{\sum\limits_{j} p_{ij}^2} - 1\right]$$

where p_{ij} = proportion of the individuals of species i that is associated with resource state j; n = number of resources.

The niche breadth measurement maximises when an equal number of individuals of the species is associated with each resource state. It ranges from 0 (use of a single resource) to 1 (equal usage of resources).

Niche overlap (C) between two species can be estimated by comparing the distribution of the individuals of the two species over the resource state matrix (Colwell and Futuyma 1971). It was calculated as:

$$C_{ih} = 1 - \frac{1}{2}\sum_{j} |p_{ij} - p_{hj}|$$

where p_{ij} = the same as before; p_{hj} = proportion of the individuals of species h that is associated with resource state j.

The niche overlap measurement takes its minimum value of 0 when the two species do not share any resource state, and its maximum value of 1 when the proportional distributions of both species over the resource states are exactly the same.

Results

Hydrological conditions and zooplankton biomass

In general, the highest temperatures and the lowest salinity values were observed during the rainy season (October). In the upper 100-m layer, where the sampling was done, salinity varied between 30.7 and 36.5 during October and between 35.9 and 37.0 in April. Temperature fluctuated from 21.5 to 29.0°C in October, and from 18.2 to 27.7°C in April.

Mean vertically integrated values of hydrological data in the upper 30-m layer showed that, during April, temperature varied from 23.3°C near the shore, to

26.1°C over the external shelf. During October, warm waters (27.5–28.6°C) were observed over the entire shelf (Fig. 2). Salinity values in April varied between 36.3 and 36.9. During October, salinity decreased greatly, showing the lowest values (33.2) near the shore, and the highest (35.8) offshore (Fig. 3).

Mean integrated values of zooplankton biomass (g 100 m^{-3}) during April showed the highest values near the shore, mostly towards the west. During October, the highest values were more homogeneously distributed over the shelf (Fig. 4). However, no significant differences were detected between the two seasons (t-test, $P > 0.05$).

Factors affecting the overall siphonophore distribution

Mean vertically integrated values of siphonophore biovolume (ml 100 m^{-3}) in the upper 30 m layer indicated that, in April, the highest values (>0.9 ml 100 m^{-3}) were found over the middle shelf, especially to the west. During October, waters over the middle and external shelves showed the highest siphonophore biomass. No significant differences (t-test, $P > 0.05$) were observed between the two seasons.

RT analysis applied to the April data revealed that distance from the shore and zooplankton biomass are the main factors influencing distributional patterns of the overall siphonophore community (Fig. 5). The analysis separated inshore stations (<22.4 km from the shore), characterised by low siphonophore biovolume, from the offshore stations. In turn, the group of stations far from the shore was subdivided as the zooplankton biomass predicted. During October, distance from the shore was also the main factor grouping high (>41.4 km from the shore) and low siphonophore biovolume values. At lower levels of the RT hierarchical structure, temperature appeared to be an important factor subdividing the inshore group (Fig. 6).

Species composition, hydrological occurrence ranges, niche breadth and overlap

In total, 23 species were identified. Considering both studied seasons, the species with the highest biovolumes were *Diphyes dispar* (30% of the total biovolume), *Agalma okeni* (11%), *Abylopsis eschscholtzi* (10%), *Abylopsistetragona* (9.7%),

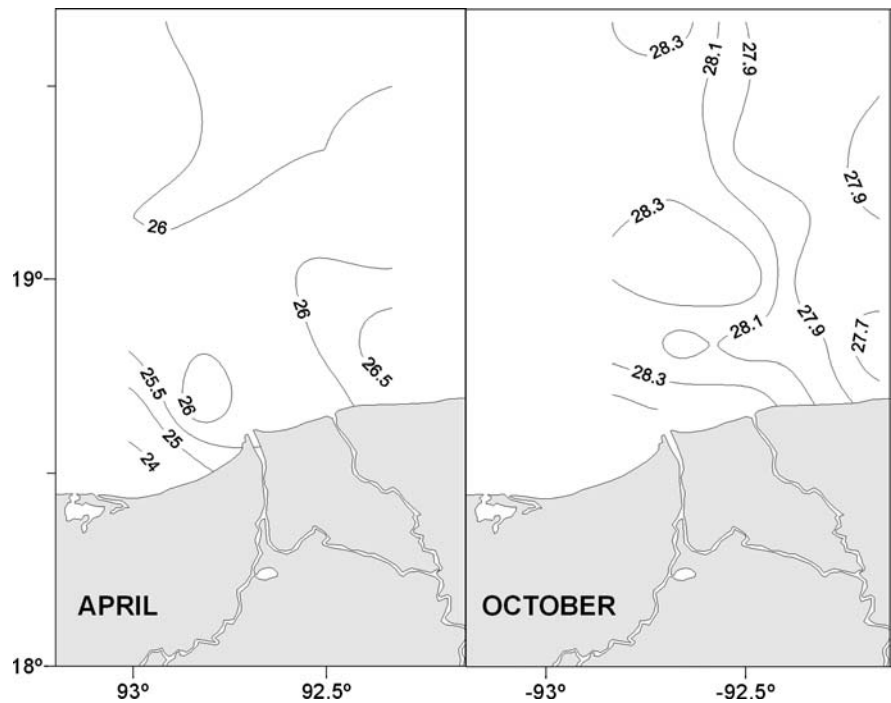Fig. 2 Mean integrated values (0–30 m) of temperature during April and October 2001 in the southern Gulf of Mexico

Fig. 3 Mean integrated values (0–30 m) of salinity during April and October 2001 in the southern Gulf of Mexico
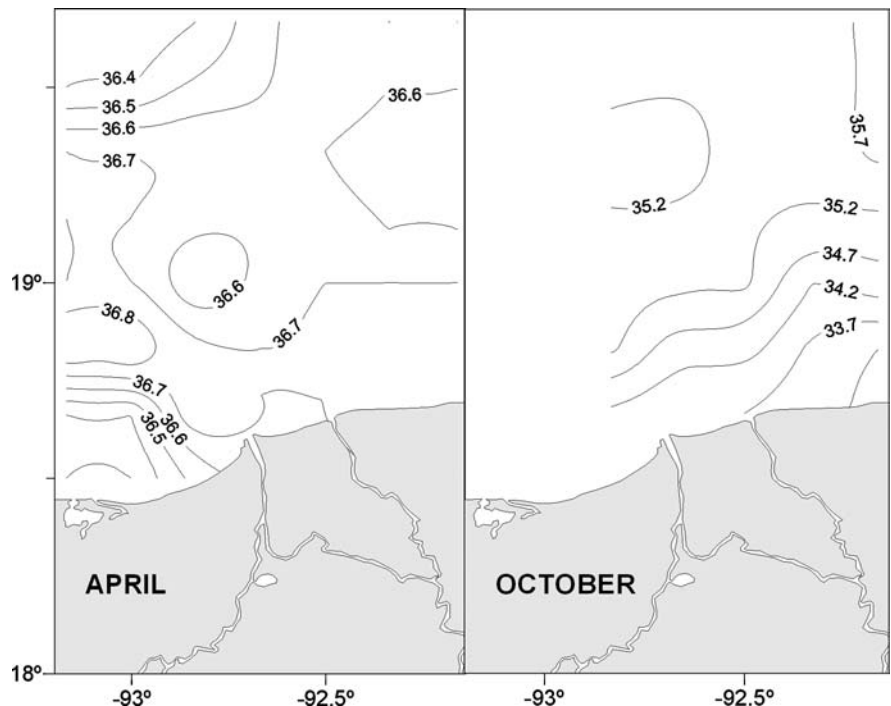
Enneagonum hyalinum (8.6%), *Chelophyes appendiculata* (8%), *Eudoxoides spiralis* (7%), and *Diphyes bojani* (7%). The species *Bassia bassensis* and *Eudoxoides mitra* together accounted for 6.3% of the total biovolume. These 10 species showed the highest spatial niche breadth values ($B > 0.088$): *A. tetragona* (0.349), *A. eschscholtzi* (0.235), *D. bojani* (0.230), and *C. appendiculata* (0.198). The highest hydrological occurrence ranges were shown by the last two species and *E. hyalinum*. This species,

Fig. 4 Mean integrated values (0–30 m) of zooplankton biomass (g 100 m^{-3}) during April and October 2001 in the southern Gulf of Mexico
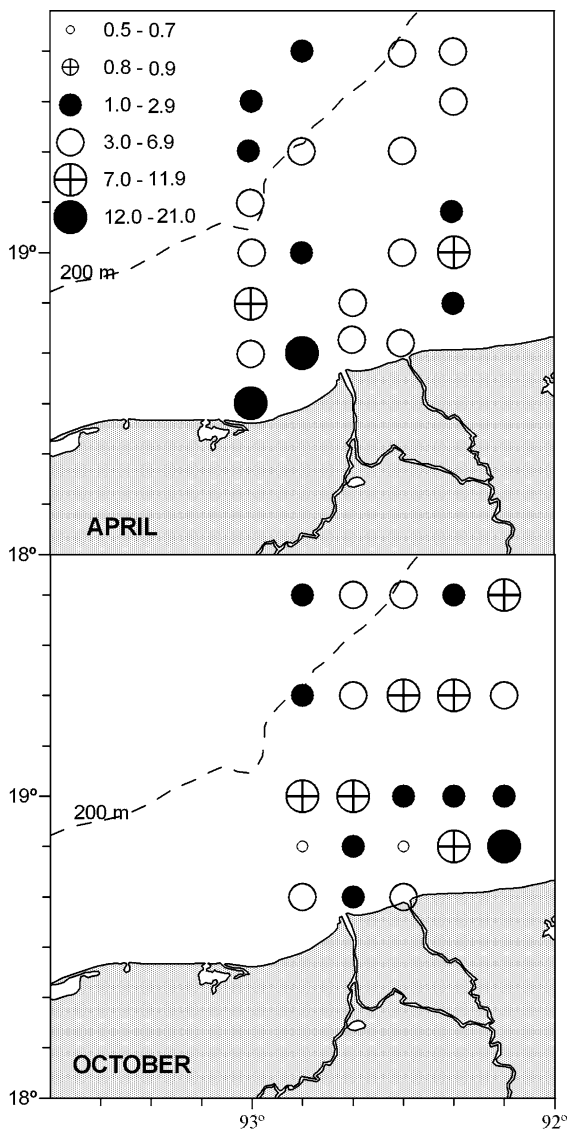

Fig. 5 a Regression tree analysis applied to the log-transformed siphonophore biovolume as response variable, and distance from the shore, temperature, salinity, and log-transformed zooplankton biomass, April 2001. Mean siphonophore biovolume (ml 100 m^{-3}) in parenthesis. b Geographical location of the groups defined by the analysis

registered in salinity and temperature ranges of 30.7–37.0 and 19.1–29.2°C (Table 1), showed its highest biovolume values in coastal waters. The remaining 13 species accounted for 2.5% of the total biovolume (Table 1), from these species, only *Lensia cossack* had a wide distribution in the water column and a relatively high *B* value (0.092), similar to the 10 most abundant species (Table 2). The three shallowest depths contained the highest overall values of siphonophore biovolume. Most species were found in the polygastric stage (Table 1).

The highest values of species niche overlap (>40%) were generally observed between several pairs of the 10 most abundant species (Table 3). The pair *H. hippopus/V. spinosa* registered the highest value (Table 1). Congeneric species showed a variety of niche overlap values. Hence, the pair *A. eschscholtzi/A. tetragona* had the highest (51.3%) niche overlap, the pairs formed by species of *Abyla*, *Diphyes*, and *Eudoxoides* had intermediate values (16.7–28.5%), whereas species of *Amphicaryon* and *Lensia* exhibited the lowest niche overlap values (0–4.1%) (Table 3).
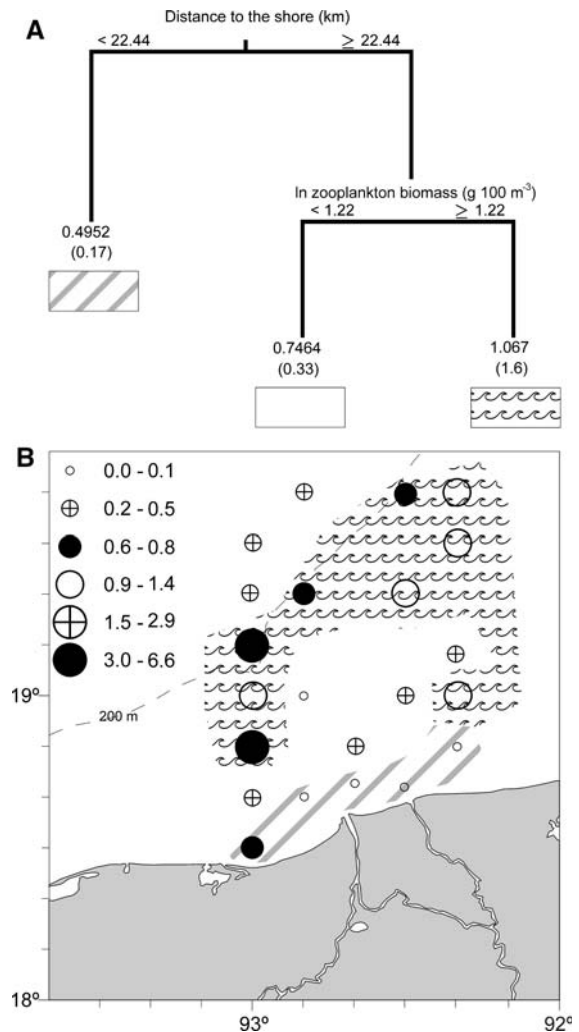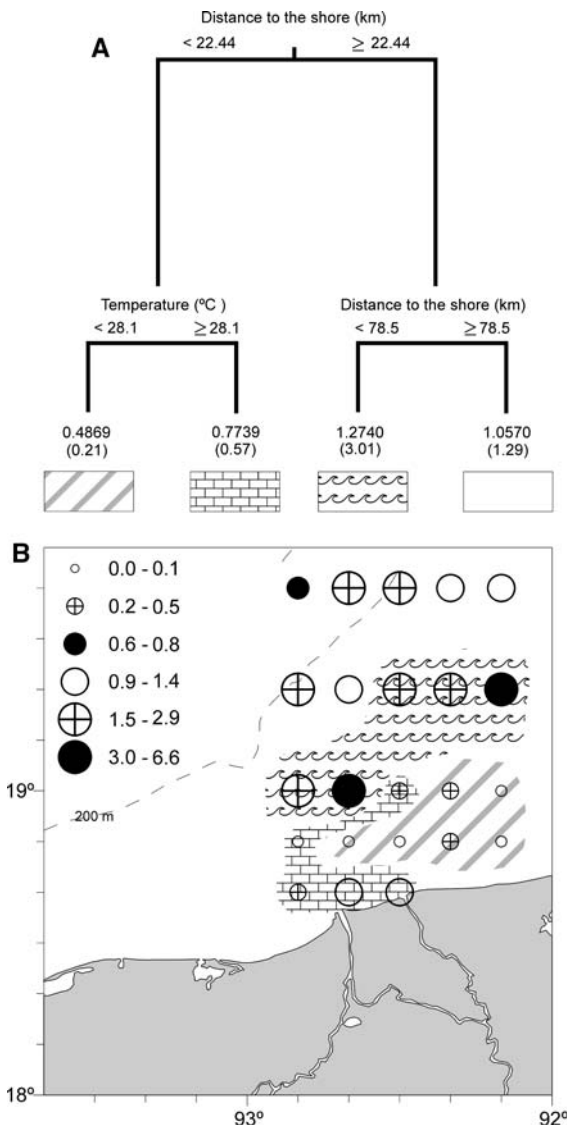
Fig. 6 a Regression tree analysis applied to the log-transformed siphonophore biovolume as response variable, and distance from the shore, temperature, salinity, and log-transformed zooplankton biomass, October 2001. Mean siphonophore biovolume (ml 100 m^{-3}) in parenthesis. b Geographical location of the groups defined by the analysis

Discussion

Factors affecting siphonophore distribution

RT analyses applied to data matrices of each season showed the distance from the shore as one of the most important factors determining siphonophore spatial patterns (Figs. 5 and 6). Many factors vary along with offshore distance. In the study area, turbulence of

waters and changes in salinity induced by the river discharges probably constitute the most important coastal processes influencing siphonophore distribution, since they are exclusively marine animals. Comparisons on abundance and diversity of siphonophores in a coastal-ocean gradient of the southern Gulf of Mexico revealed that neritic waters have the highest abundance but the lowest diversity (Gasca 1993; Alba-Hurtado 2001). In the western Mediterranean, in an area influenced by the inflow of continental waters, Gili et al. (1988) also found the greatest variability in the cnidarian community from the coast to the open sea. Zooplankton biomass distribution (Fig. 4) was also an important factor influencing the spatial patterns of siphonophores, especially during April (Fig. 5). Purcell (1981) established that prey distribution greatly determines the distribution of siphonophores, and Pugh (1991) also found a clear relation between hippopodiids and ostracods, their main prey. Like the aforementioned abiotic factors, zooplankton biomass distribution has also a strong coastal-ocean gradient in the southern Gulf (Flores-Coto et al. 1988), associated to nutrient enrichment of the coastal area due to river discharges (Czitrom et al. 1986). Hence, factors varying with distance from the shore may have either a direct (salinity, turbulence) or indirect (nutrients) effect over siphonophores distribution.

RT analysis also indicated the temperature as another important factor affecting spatial distribution of siphonophores during October (Fig. 6a). During this month, the group of stations close to the shore (<41.4 km) was subdivided by the 28.1°C isotherm. At temperatures higher than this value, most siphonophore populations were depressed and only *Enneagonum hyalinum* and *Diphyes dispar* registered high biovolumes. Sanvicente-Añorve (1990) also found low zooplankton biomass associated with high temperature values in the southern Gulf of Mexico. At a planetary scale, Margulis (1972) stated that temperature has a profound impact on siphonophores distribution. Results of the present study showed that its effects are also important at smaller spatial scales.

Hydrological occurrence ranges and niche breadth and overlap

Hydrological conditions in the study area were highly variable as a consequence of changes in continental

Table 1 Biovolume, frequency of occurrence, hydrological tolerances, and spatial niche breadth and overlap of 23 siphonophore species collected in the southern Gulf of Mexico during two seasons

Code	Species	Biovolume ($n = 149$)			Hydrological occurrence ranges				Niche breadth (B)	$\overline{C}$	Main phase
					Salinity		Temperature (°C)				
		TB	PB	N	Min	Max	Min	Max			
Aha	*Abyla haeckeli*	0.16	0.17	6	35.4	36.7	22.4	28.0	0.029	5.2	E
Atr	*Abyla trigona*	0.12	0.13	3	36.2	36.4	19.8	27.2	0.006	3.1	P
Aes	*Abylopsis eschscholtzi*	9.52	10.15	108	32.2	37.0	19.1	28.8	0.235	17.3	E
Ate	*Abylopsis tetragona*	9.12	9.73	109	33.4	37.0	18.2	28.8	0.349	18.9	P
Aok	*Agalma okeni*	10.19	10.86	54	34.2	36.7	19.1	28.8	0.089	13.4	O
Aac	*Amphicaryon acaule*	0.05	0.05	1	36.3	36.3	20.0	21.6	0.000	0.5	P
Aer	*Amphicaryon ernesti*	0.30	0.32	12	34.6	36.4	21.8	28.1	0.033	6.6	P
Bba	*Bassia bassensis*	3.70	3.94	82	33.7	37.0	18.8	28.8	0.155	14.9	E P
Cde	*Ceratocymba dentate*	0.59	0.63	2	36.2	36.4	22.5	28.0	0.002	1.9	E P
Cap	*Chelophyes appendiculata*	7.40	7.89	85	30.9	36.7	18.8	28.8	0.198	15.4	P
Dbo	*Diphyes bojani*	6.26	6.68	101	34.2	36.7	18.8	28.8	0.230	16.7	E P
Ddi	*Diphyes dispar*	28.46	30.34	116	30.7	37.0	18.2	29.0	0.118	12.4	E P
Ehy	*Enneagonum hyalinum*	8.04	8.57	65	30.7	37.0	19.1	29.2	0.088	7.2	E P
Emi	*Eudoxoides mitra*	2.19	2.34	59	34.5	37.0	18.2	28.8	0.150	12.6	P
Ees	*Eudoxoides spiralis*	6.75	7.20	104	34.2	37.0	18.2	28.8	0.173	12.3	P
Hhi	*Hippopodius hippopus*	0.69	0.74	3	36.1	36.4	21.4	27.3	0.003	6.3	P
Lca	*Lensia campanella*	0.02	0.02	3	36.7	37.0	24.4	26.1	0.013	1.3	P
Lco	*Lensia cossack*	0.12	0.13	24	34.8	37.0	18.2	28.1	0.092	9.3	P
Lfo	*Lensia fowleri*	0.01	0.01	4	36.2	36.4	18.8	22.6	0.018	0.4	P
Mko	*Muggiaea kochi*	0.01	0.01	2	33.4	34.8	27.8	27.9	0.007	0.4	P
Phy	*Physophora hydrostatica*	0.02	0.02	1	35.5	35.8	28.3	28.5	0.000	0.8	O
Sch	*Sulculeolaria chuni*	0.03	0.03	2	35.8	36.3	22.2	27.9	0.002	1.2	P
Vsp	*Vogtia spinosa*	0.02	0.02	1	36.2	36.4	21.4	23.1	0.000	3.9	P

TB = total biovolume (ml 100 m^{-3}), PB = percentage of total biovolume, N = number of samples where the species occurred, n = total number of samples, $\overline{C}$ = mean niche overlap

Main stage encountered P = polygastric, E = eudoxid, O = adult colony

Note that hydrological ranges of species found once correspond to the minimum and maximum values of the stratum where they were found

discharges and dominant winds. Considering the two contrasting freshwater outflow periods, salinity fluctuated between 30.7 and 37.0, and temperature between 18.2 and 29.0°C; under these conditions, the hydrological occurrence ranges of the 23 species were analysed (Table 1). These species are widely distributed in tropic-equatorial latitudes of the Atlantic Ocean (Pugh 1999), including the southern Gulf of Mexico (Gasca 1993, 1999; Alba-Hurtado 2001).

With 30% of the total biovolume, *Diphyes dispar* moderately dominated the siphonophore community. Dominance of this species might be due to its hydrological tolerance, since the species was

registered in a wide range of salinity and temperature conditions (Table 1). However, its relatively low niche breadth value ($B = 0.118$) indicates a lack of uniformity in the species distribution, being more concentrated in the upper 30 m layer (Table 2). Vasiliev (1974) and Gasca (1993) also registered this species as the most abundant in the oceanic region of the Gulf of Mexico. In the water column, Pugh (1999) found this species in the epipelagic region.

The group of *Agalma okeni*, *Abylopsis eschscholtzi*, *Abylopsis tetragona*, *Enneagonum hyalinum*, *Chelophyes appendiculata*, *Eudoxoides spiralis*, and *Diphyes bojani* species showed similar biovolumes,

Table 2 Mean biovolume (ml 100 m^{-3}) of siphonophore species collected at several strata in the southern Gulf of Mexico during two seasons

Species	April						October					
	Level 1	Level 2	Level 3	Level 4	Level 5	Level 6	Level 1	Level 2	Level 3	Level 4	Level 5	Level 6
Abyla haeckeli	–	0.26	–	0.26	–	–	–	–	0.32	0.19	0.49	–
Abyla trigona	–	–	–	0.80	0.08	–	–	–	–	–	0.43	–
Abylopsis eschscholtzi	1.60	2.34	4.87	4.00	1.38	0.41	9.97	19.02	12.18	4.45	4.64	1.36
Abylopsis tetragona	3.18	4.93	11.72	8.52	6.26	4.69	2.19	8.54	8.53	8.08	9.35	4.44
Agalma okeni	0.25	0.18	2.76	0.09	0.38	–	4.13	25.88	16.88	14.83	9.60	7.36
Amphicaryon acaule	–	–	–	–	–	0.76	–	–	–	–	–	–
Amphicaryon ernesti	–	–	–	–	–	–	–	0.43	0.11	1.28	0.73	0.74
Bassia bassensis	1.11	3.05	6.55	4.69	8.27	0.70	0.54	1.85	2.59	1.64	0.29	0.14
Ceratocymba dentata	–	–	–	–	–	–	–	–	–	1.10	6.91	–
Chelophyes appendiculata	0.52	1.12	3.13	2.16	1.68	0.80	6.57	16.06	9.29	5.90	4.91	2.35
Diphyes bojani	3.20	5.90	12.70	5.03	2.42	1.11	3.13	5.89	3.33	0.90	1.44	0.25
Diphyes dispar	3.20	24.91	17.71	5.37	1.73	5.84	37.04	52.18	23.03	3.05	3.72	0.94
Enneagonum hyalinum	3.88	4.77	7.03	0.30	0.19	0.13	13.37	10.63	4.53	0.80	0.66	0.18
Eudoxoides mitra	0.13	0.96	1.77	3.92	4.74	3.44	0.11	1.02	1.21	1.64	1.86	2.08
Eudoxoides spiralis	5.50	7.33	16.63	10.32	7.83	3.90	0.15	0.55	0.34	0.98	0.70	1.03
Hippopodius hippopus	–	–	–	0.80	6.40	–	–	–	–	0.34	–	–
Lensia campanella	–	0.08	0.04	–	–	–	–	–	–	–	–	–
Lensia cossack	0.11	0.07	0.12	0.09	0.31	0.23	0.02	0.03	0.07	0.04	–	0.05
Lensia fowleri	–	–	–	–	–	0.11	–	–	–	–	–	0.06
Muggiaea kochi	–	–	–	–	–	–	0.04	–	–	–	–	–
Physophora hydrostatica	–	–	–	–	–	–	–	–	0.17	–	–	–
Sulculeolaria chuni	–	–	–	–	–	–	–	0.16	–	–	–	0.09
Vogtia spinosa	–	–	–	–	0.21	–	–	–	–	–	–	–

Values are multiplied by 10^2

that is, between 7 and 11% (Table 1). *Agalma okeni* has been scarcely registered in the oceanic waters of the southern Gulf of Mexico (Gasca 1999) and the Caribbean (Lewis and Fish 1969). In this study, it was the second most abundant species, mainly found during October in the 10–60-m stratum in salinities higher than 34.2 and in a wide range of temperatures (Tables 1 and 2), but it was concentrated in the 26–28.8°C range (74% of their occurrences). In situ studies by Biggs (1976) registered the species in water lenses 0.5–1.2°C warmer than the surrounding waters, indicating that the temperature exerts a strong influence on its distribution. These observations might explain the differences in rank abundance of this species in neritic and oceanic waters. *Abylopsis tetragona* had the highest spatial niche breadth value ($B = 0.349$), but not the widest hydrological

occurrence ranges (Table 1). Conversely, its congener *A. eschscholtzi* showed a wider tolerance range to salinity and a smaller niche breadth value ($B = 0.235$), indicating that the species was more concentrated in the upper levels (Table 3). *Abylopsis tetragona* was found in all the sampled levels (Table 2) and its B value indicated a high degree of uniformity in its distribution, in areas with salinities higher than 33.4. In the western Mediterranean, this species was also found homogeneously distributed along the Catalan coast (Gili et al. 1988). In the southern Gulf of Mexico, these congeneric species were recorded widely distributed in the oceanic environment (Gasca 1993). From this group of species, *E. hyalinum* and *C. appendiculata* showed relatively high spatial niche breadth values and the widest tolerance to salinity and temperature (Table 1). Pugh (1999) established that the main habitat of

Table 3 Niche overlap (in percentage) of the 23 siphonophore species collected in neritic waters of the southern Gulf of Mexico during two seasons

	Aha	Atr	Aes	Ate	Aok	Aac	Aer	Bba	Cde	Cap	Dbo	Ddi	Ehy	Emi	Esp	Hhi	Lca	Lco	Lfo	Mko	Phy	Sch	Vsp
Aha	100.0	16.7	2.7	8.7	15.1	0.0	14.2	4.6	12.8	6.2	3.2	1.1	0.6	3.5	3.0	16.5	0.0	5.6	0.0	0.0	0.0	0.0	0.0
Atr		100.0	1.2	5.3	1.3	0.0	12.3	1.4	0.0	1.4	0.8	0.5	0.3	5.7	1.7	11.6	0.0	8.0	0.0	0.0	0.0	0.0	0.0
Aes			100.0	51.3	44.6	0.1	9.3	35.1	1.1	56.1	49.6	44.0	18.2	25.6	23.9	0.9	0.6	12.3	0.2	0.5	2.4	1.1	0.2
Ate				100.0	38.7	1.3	16.0	42.0	0.8	43.6	48.8	27.8	15.7	35.2	44.7	4.8	2.9	22.2	1.4	0.4	0.5	2.4	0.4
Aok					100.0	0.0	17.6	17.3	2.4	36.8	27.2	26.7	12.6	17.7	9.6	4.4	0.0	16.9	0.3	0.9	4.0	1.8	0.0
Aac						100.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	5.6	0.5	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0
Aer							100.0	3.8	17.5	10.5	5.8	3.0	1.7	11.1	2.1	4.9	0.0	4.0	1.0	0.0	0.0	0.0	0.0
Bba								100.0	0.1	27.7	47.8	22.2	13.6	33.4	48.8	2.6	3.9	21.2	0.9	0.1	1.0	11.3	0.8
Cde									100.0	0.9	0.2	0.1	0.1	4.4	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Cap										100.0	46.0	28.3	10.3	28.3	19.1	1.1	0.3	16.5	0.6	1.2	0.5	0.0	0.0
Dbo											100.0	28.5	11.0	23.9	51.9	1.0	1.4	17.0	0.5	0.6	0.6	3.1	0.5
Ddi												100.0	43.1	13.7	10.3	0.3	3.1	13.2	0.1	0.5	5.2	0.7	0.0
Ehy													100.0	5.4	3.6	0.2	10.4	7.2	0.1	0.0	3.4	1.4	0.0
Emi														100.0	27.4	2.4	2.2	27.7	1.1	0.2	0.0	0.1	0.4
Esp															100.0	1.9	0.4	17.6	2.0	0.1	0.1	3.0	0.9
Hhi																100.0	0.0	2.4	0.0	0.0	0.0	0.6	83.5
Lca																	100.0	4.0	0.0	0.0	0.0	0.0	0.0
Lco																		100.0	1.6	3.2	0.0	0.0	0.0
Lfo																			100.0	0.0	0.0	0.0	0.0
Mko																				100.0	0.0	0.0	0.0
Phy																					100.0	0.0	0.0
Sch																						100.0	0.0
Vsp																							100.0

See Table 1 for the code of species

E. hyalinum is the 300–1,000-m layer. However, Thibault-Botha et al. (2004) found this species in coastal waters east of South Africa, indicating even the possibility of considering this species as indicative of near shore waters. Our results also showed this species to be very abundant in the epipelagic layer, especially in the upper 30-m layer (Table 2) near the coast. These discrepancies suggest that further studies are needed to document its vertical distribution.

In our study area, *C. appendiculata* was most abundant during October, mainly in the 30 m surface layer (Tables 1 and 2). Vasiliev (1974) reported this species to be strictly oceanic; however, our distributional records showed its major abundance nuclei over the middle and outer shelves bearing salinities as low as 30.9 (Table 1). *Eudoxoides spiralis* and *D. bojani* were here registered in a wide range of temperatures in all the levels sampled (Tables 1 and 2). Both species were considered by Gasca (1993) as dominant in surface waters (0–50 m) of the oceanic region of the southern Gulf of Mexico during January. While present in neritic waters, our records indicate that these two species do not tolerate salinities lower than 34.2 (Table 1).

The species *Eudoxoides mitra* and *Bassia bassensis*, accounting for 6.3% of the total biovolume, revealed relatively high niche breadth values ($B \sim 0.15$); the first was mainly distributed at the three lowest depths and the second at intermediate depths (Table 2). Studying neritic and oceanic waters of the southern Gulf of Mexico, Gasca (1999) found *B. bassensis* among the most abundant siphonophores, and *E. mitra* among the most frequent species. Off the coast of Chile, *B. bassensis* has been found most abundant in the 50-m surface stratum, especially in oceanic waters (Pagès et al. 2001). Our finer sampling indicates that these species inhabit mainly the 20–80-m stratum (Table 2). Around southern Africa, Gibbons and Thibault-Botha (2002) registered these two species in both neritic and oceanic provinces, more frequently in the latter. These findings could explain their low biovolume in the studied area.

According to Lane (1975), the niche breadth value *(B)* is a measure of the degree of generalisation of the species. In this context, the calycophorans *A. tetragona, A. eschscholtzi, D. bojani*, and *C. appendiculata*, were the most generalist species and, in consequence, exhibited the highest mean niche overlap values ($\overline{C}$) with the remainder 22 species (Table 1). The highest observed *C* value (83.5%) was between the two rare hippopodiids *H. hippopus/V. spinosa.* This fact is probably rather due to a chance co-occurrence of species than to dietary preferences, since both consume mainly ostracods (Pugh 1991). In spite of being the second most abundant species, the physonect *A. okeni* exhibited low niche overlap *(C)* values (<40%) with almost all the species (Table 3). Due to differences in gastrozoid sizes and nematocyst types, most physonect species consume large crustacean zooplankters, whereas calycophorans feed mainly on small copepods (Purcell 1980; Mackie et al. 1987). This fact could explain the low *C* values of *A. okeni* with the calycophoran species. Phylogenetically, Dunn et al. (2005) also showed that caycophorans and physonects are quite distant groups.

Congeneric species found in this study are very similar morphologically, which would predict their ecological overlap. However, among the most abundant congeneric pairs in this study, *A. tetragona* and *A. eschscholtzi* exhibited a high *C* value, whereas *D. dispar* and *D. bojani* had a lower one (Table 3). This variety of *C* values within genera is difficult to explain due, in part, to the lack of data. Besides the feeding habits and environmental tolerances of the species, their life history and phylogenetic relationships might determine their coexistence. However, the degree of importance of the phylogeny and ecology in determining the geographic distribution and hydrological tolerances of species is difficult to assess. As modern historical ecologists stated (Brooks and McLennan 1994), we think that both disciplines must collaborate actively to explain spatial patterns and processes which determine the co-occurrence of species.

References

Alba-Hurtado C (2001) Composición, abundancia y distribución de los sifonóforos (Cnidaria: Hydrozoa), en la Bahía de Campeche, México. Bch. Thesis FES Zaragoza, Universidad Nacional Autónoma de México

Alcaraz M, Saiz E, Calbet E, Trepat I, Broglio E (2003) Estimating zooplankton biomass through image analysis. Mar Biol 143:307–315

Alvariño A (1968) Los quetognatos, sifonóforos y medusas en la región del Atlántico ecuatorial bajo la influencia del Amazonas. An Inst Biol Univ Nal Autón Méx 39, Ser Cienc del Mar y Limnol 1:41–76

Alvariño A (1971) Siphonophores of the Pacific, with a review of the world distribution. Bull Scripps Inst Oceanogr Univ Calif 16:1–432

Alvariño A (1981) Siphonophora. In: Boltovskoy D (ed), Atlas de zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino. INIDEP, Mar de Plata, pp 383–442

Alvariño A (1985) Predation in the plankton realm, mainly with reference to fish larvae. Invest Mar CICIMAR 2:1–122

Biggs D (1976) Nutritional ecology of *Agalma okeni* and other siphonophores from the epipelagic Western North Atlantic. PhD Thesis, WHOI-MIT joint program, 141 pp

Boucher J, Thiriot A (1972) Zooplancton et micronecton estivaux des deux cents premiers mètres en Méditerranée Occidentale. Mar Biol 15:47–56

Brooks DR, McLennan DA (1994) Historical ecology a research programme: scope, limitations and the future. In: Eggleton P, Vane-Wrigth RI (eds) Phylogenetics and ecology. Linnean Society Symposium Series 17. Academic Press, London, pp 1–27

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567–576

Czitrom SPR, Ruiz F, Alatorre MA, Padilla AR (1986) Preliminary study of a front in the Bay of Campeche, Mexico. In: Nihoul JCJ (eds) Marine interfaces ecohydrodynamics. Elsevier Oceanography Series, Liege, pp 301–311

den Hartog JC (1980) Notes on the food of sea turtles: *Eretmochelysimbricata* (Linnaeus) and *Dermochelyscoriacea* (Linnaeus). Neth J Zool 30:595–610

Dunn CW, Pugh PR, Haddock SHD (2005) Molecular phylogenetics of the Siphonophora (Cnidaria), with implications for the evolution of functional specialization. Syst Biol 54:916–935

Flores-Coto C, Sanvicente-Añorve L, Pineda-López R, Rodríguez Van Lier MA (1988) Composición, distribución y abundancia ictioplanctónica del sur del Golfo de México. Universidad y Ciencia 5:65–84

Gasca R (1993) Especies y abundancia de sifonóforos (Cnidaria: Hydrozoa) en la región sur del Golfo de México. Caribb J Sci 29:220–225

Gasca R (1999) Siphonophores (Cnidaria) and the summer mesoscale features in the Gulf of Mexico. Bull Mar Sci 65:75–89

Gibbons MJ, Thibault-Botha D (2002) The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. J Mar Biol Assoc UK 82:801–810

Gili JM, Pagès F, Sabatés A, Ros JD (1988) Small-scale distribution of a cnidarian population in the western Mediterranean. J Plankton Res 10:385–401

Grice GD, Hart AD (1962) The abundance, seasonal occurrence and distribution of the epipelagic zooplankton between New York and Bermuda. Ecol Monogr 32:287–309

Kaspari M (2005) Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. Proc Natl Acad Sci USA 102:5079–5083. doi: 10.1073/pnas.0407827102

Lane P (1975) The dynamics of aquatic systems: a comparative study of the structure of four zooplankton communities. Ecol Monogr 45:307–336

Lauerman LML (1998) Diet and feeding behaviour of the deep-water sea star *Rathbunaster californicus* (Fisher) in the Monterey Submarine Canyon. Bull Mar Sci 63:523–530

Levins R (1968) Evolution in changing environments. Princeton University Press, Princeton

Lewis JB, Fish AG (1969) Seasonal variation of the zooplankton fauna of surface waters entering the Caribbean Sea at Barbados. Caribb J Sci 9:1–24

Mackie GO, Pugh PR, Purcell JE (1987) Siphonophore Biology. Adv Mar Biol 24:97–262

Margulis R.Y (1972) Factors determining the large-scale distribution of siphonophores of the suborders Physophorae and Calycophorae in the Atlantic Ocean. Oceanology 12:420–425

Moore HB (1949) The zooplankton of the upper waters of the Bermuda area of the North Atlantic. Bull Bingham Oceanogr Collect Yale Univ 12:1–97

Pagès F, González HE, Ramón M, Sobarzo M, Gili JM (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). Mar Ecol Prog Ser 210:13–24

Pugh PR (1974) The vertical distribution of the siphonophores collected during the SOND cruise, 1965. J Mar Biol Assoc UK 45:25–90

Pugh PR (1977) Some observations on the vertical migration and geographical distribution of siphonophores in the warm waters of the North Atlantic Ocean. Proc Symp Warm Water Zoopl NIO, Goa, pp 362–378

Pugh PR (1991) Co-occurrence of hippopodiid siphonophores and their potential prey. Hydrobiologia 216/217:327–334

Pugh PR (1999) Siphonophorae. In: Boltovskoy D (ed) South atlantic zooplankton. Blackhuys Publishers, Leiden, pp 467–511

Purcell JE (1980) Influence of siphonophore behaviour upon their natural diets: evidence for aggressive mimicry. Science 209:1045–1047

Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar Biol 65:83–90

Purcell JE (1991) A review of cnidarian and ctenophores feeding on competitors in the plankton. Hydrobiologia 216/217:335–342

Sanvicente-Añorve L (1990) Comunidades ictioplanctónicas en el suroeste del Golfo de México. M.Sc. Thesis, Universidad Nacional Autónoma de México

Sanvicente-Añorve L, Alba C, Alatorre MA, Flores-Coto C (2007) Cross-shelf and vertical distribution of siphonophore assemblages under the influence of freshwater outflows in the southern Gulf of Mexico. Hydrobiologia. doi:10.1007/s10750-006-0492-6

Sears M (1954) Siphonophores in the Gulf of Mexico. Fish Bull (Fish Wildl Serv) 55:275–276

Silguero JMB, Robison BH (2000) Seasonal abundance and vertical distribution of mesopelagic calycophoran

siphonophores in Monterey Bay, CA. J Plankton Res 22:1139–1153

Thibault-Botha D, Lutjeharms JRE, Gibbons MJ (2004) Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. J Plankton Res 26:1115–1128

Totton AK, Bargmann HE (1965) A synopsis of the Siphonophora. Trust Brit Mus Nat Hist, London

Trégouboff G, Rose M (1957) Manuel de Planctonologie Méditerranéenne II. CNRS, Paris

Vasiliev V (1974) Distribución de los sifonóforos en el Golfo de México durante el periodo de primavera-verano en el año de 1969. Invest Mar 8:1–51

Vollmer SV, Edmunds PJ (2000) Allometric scaling in small colonies of the scleractinian coral *Siderastrea sinerea* (Ellis and Solander). Biol Bull 199:21–28

Whittaker RH (1975) Communities and ecosystems. MacMillan Publ, New York

Zavala-Hidalgo J, Morey SL, O'Brien JJ (2003) Seasonal circulation on the western shelf of the Gulf of Mexico using a high-resolution numerical model. J Geophys Res 108(C12) 3389. doi:10.1029/2003JC001879

Zavala-Hidalgo J, Gallegos-García A, Martínez-López B, Morey SL, O'Brien JJ (2006) Seasonal upwelling on the western and southern shelves of the Gulf of Mexico. Ocean Dyn. doi:10.1007/s10236-006-0072-3