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PRIMARY RESEARCH PAPER

Cross-shelf and vertical distribution of siphonophore assemblages under the influence of freshwater outflows in the southern Gulf of Mexico

Laura Sanvicente-Añorve · Claudia Alba · Miguel A. Alatorre · César Flores-Coto

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Abstract Siphonophores are exclusively marine cnidaria and their predatory role in plankton food-webs is well recognised. In this study, we analyse the structure and the spatial extent of siphonophore assemblages in relation to changes in freshwater outflows and food availability in the southern Gulf of Mexico during a high (October) and a low (April) outflow periods. A total of 149 samples were collected using a 505 μm multiple closing net at 1–6 levels (0–100 m) of the water column, depending on the bathymetry. Data on siphonophore species biovolumes (ml 100 m^{-3}) were treated by means of the Bray-Curtis Dissimilarity Index, and two distinctive assemblages were identified: the 'inner' and the 'outer' assemblages, located over the inner and outer shelves. Temperature, salinity, zooplankton biomass, and siphonophore species were included in a Principal Component Analysis (PCA) to identify the factors associated with each assemblage. Geographical distribution of the assemblages practically remained the same during both seasons and its cross-shelf variability was stronger than the vertical one. Seasonally, diversity values were higher in October, when the highest river discharges occur. Spatially, the lowest diversity and mean siphonophore biovolumes values were registered in the 'inner assemblage', where the highest and lowest salinity values were recorded. We suggest that even when extreme salinity values (>36.5 or <34) might depress siphonophore populations in the coastal area, enough food availability in the concerned areas might mitigate the negative effect of salinity, since a positive and significant ($p < 0.05$) relationship was found between siphonophores biovolume and zooplankton biomass. *Bassia bassensis*, *Diphyes dispar* and *Enneanogum hyalinum*, present in both assemblages during both seasons, were able to survive in a wide range of salinity values, following perhaps, their prey. All the 23 species here registered were found in the 'outer assemblage'; however, *Abylopsis eschscholtzi*, *Chelophyes appendiculata* and *Diphyes bojani* were more associated with the 'outer' group according to the PCA results. *Enneagonum hyalinum* was the only species frequently encountered and abundant in the 'inner assemblage' during both seasons and, supporting previous observations, this species might be considered as an indicator of nearshore waters.

Keywords Siphonophora · Assemblages · *Enneagonum hyalinum* · Seasonality · River discharges · Gulf of Mexico

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L. Sanvicente-Añorve (✉) · C. Alba · M. A. Alatorre · C. Flores-Coto
Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico City, Mexico
e-mail: lesa@servidor.unam.mx

Introduction

The southern Gulf of Mexico is a very productive regime due to the influence of continental discharge, to a wide continental shelf, and to a high diversity of primary and secondary producers (Flores-Coto et al., 1988; Okolodkov, 2003). Seasonally, hydrological features in this area are highly dynamic as a consequence of riverine inputs, especially coming from the Grijalva-Usumacinta River. Along the Mexican Gulf coast, this system represent the most important discharge of continental waters over the adjacent neritic zone, with the highest water outflows (7 – 10×10^9 m^3 $month^{-1}$) from July to November, and the lowest ($1.6–4 \times 10^9$ m^3 $month^{-1}$) from December to June (Czitrom et al., 1986). Water circulation in the southern Gulf is predominantly cyclonic (Vázquez-de-la-Cerda et al., 2005); however, during the fall-winter period, two opposite currents meet and an offshore transport of water occur (Zavala-Hidalgo et al., 2003).

Seasonal variability in hydrological conditions have profound effects on zooplankton community structure (Viitasalo et al., 1995; Kimmel & Roman, 2004), and changes in biomass, composition, abundance, distribution, and diversity of zooplankters are particularly evident in coastal ecosystems influenced by continental waters (Alvariño, 1968; Qureshi, 1997). In spite of the high biological production off the Grijalva-Usumacinta River, knowledge on the water column biota, especially that concerning siphonophores, is still poorly known. These gelatinous animals are widespread in the oceans, comprise a significant portion of the macrozooplankton, and are among the most important predators of the plankton food-webs (Purcell, 1997; Pugh, 1999). Environmental factors affecting their distribution and assemblages structure depend on the sites, times, and studied scales. Several authors (Lo & Biggs, 1996; Gasca, 1999; Suárez-Morales et al., 2002; Thibault-Botha et al., 2004) have recognised the importance of upwellings, eddies, main currents, distance offshore, and depth of the mixed layer on the spatio-temporal changes of siphonophore assemblages. However, the influence of continental water discharges is scarcely known (Alvariño, 1968). Since siphonophores are exclusively marine animals and voracious predators in the plankton ecosystem, it is our aim to test the influence of freshwater outflows and food availability on the structure (diversity, abundance, and composition) and spatial extent of siphonophore assemblages off the Grijalva-Usumacinta River during two contrasting outflow periods: April and October 2001.

Materials and methods

The study area comprised neritic waters of the southern Gulf of Mexico, between 18°30–20° North latitude, and 92°–93° West longitude. Sampling stations were arranged into six transects covering mainly neritic waters off the Grijalva-Usumacinta River (Fig. 1). Zooplankton samples were collected on two oceanographic cruises conducted during two periods: 19–29 April and 10–20 October 2001. Samples were taken over 23 stations with a multiple opening and closing net equipped with 75 cm diameter and 500 μm mesh size nets. Six strata were sampled (0–10, 10–20, 20–30, 40–60, 60–80, and 80–100 m), and the number of sampled levels depended on the bathymetry. Temperature and salinity measurements were taken with a CTD probe. In total, 76 zooplankton samples were collected during April, and 73 during October. Total zooplankton biomass was determined as wet weight (g 100 m^{-3}). Siphonophores were separated from samples, but due to inherent problems in accounting colonial organisms (Pugh, 1999) they were measured as wet displacement volume (WDV, as ml 100 m^{-3}). To define main siphonophore assemblages, similarity among stations was estimated using the Bray-Curtis Index (Bray & Curtis, 1957). Then, species richness and ($\log_2$) Shannon Diversity Index (Magurran, 1988) were estimated in each assemblage during both seasons. Moreover, environmental variables (temperature, salinity, zooplankton biomass) and siphonophore species were included in a Principal Component Analysis (PCA) to identify the factors associated with each of the groups defined by the cluster analyses during the two studied periods. Also, salinity data recorded in the water column were

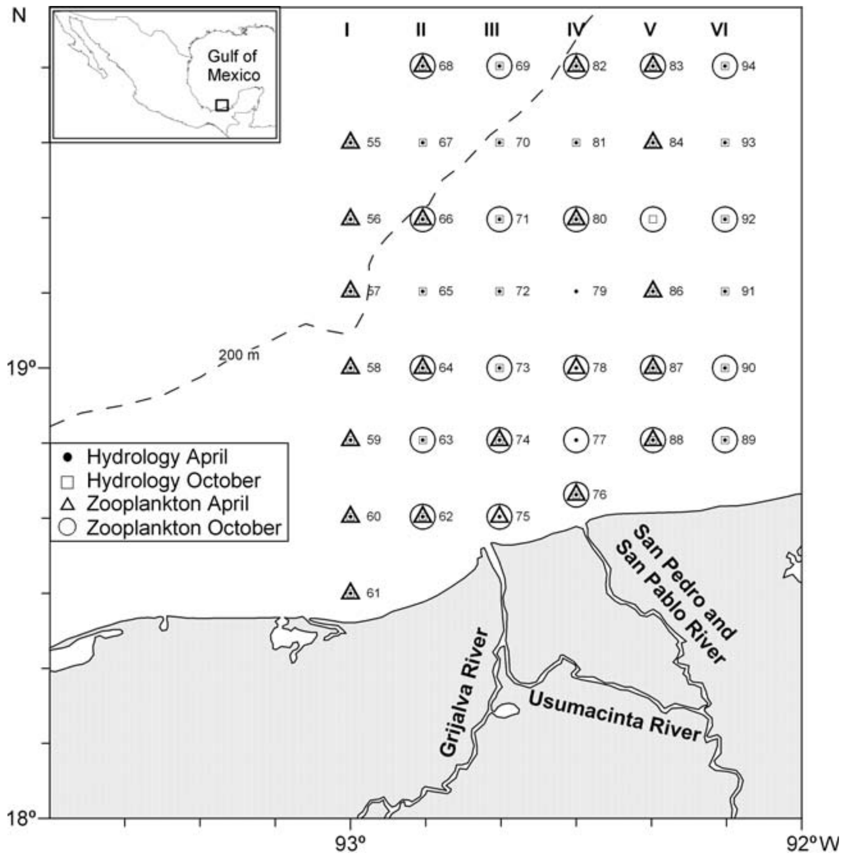

Fig. 1 Location of sampling stations in the southern Gulf of Mexico in April and October 2001. Transects are identified by Roman numerals, and run from north to south

treated by means of the 'triangulation with linear interpolation' method using the Surfer Program (Golden Software, Inc) in order to visualise in each transect the influence of the riverine system. Information on surface circulation during the two studied months was taken from the University of Colorado website (http://argo.colorado.edu/~realtime/gom-real-time_velmag/).

Results

In total, 23 siphonophore species were identified in the surveyed area. The overall five most abundant species were the calycophorans *Diphyes dispar*, *Abylopsis eschscholtzi*, *A. tetragona* and *Enneagonum hyalinum*, and the physonect *Agalma okeni*. Together their WDV accounted for 70% of the total biovolume. *Dyphyes dispar, A. okeni*, *A. eschscholtzi*, and *E. hyalinum*, as well as *Amphicaryon ernesti, Chelophyes appendiculata* were substantially more numerous in October, while *Bassia bassensis*, *Eudoxoides spiralis*, and *Lensia cossack* were significantly (Mann–Whitney test, $p < 0.05$) more abundant in April.

Cluster analysis defined two main groups of stations, called 'inner' and 'outer' assemblages (Figs. 2, 3). Geographically, these groups occurred in the same locations during both seasons. The first assemblage mainly was found at shallow depths (0–20 m) over the inner shelf, while the 'outer assemblage' was found at all depths over the middle and outer shelves and the upper continental slope (Figs. 4, 5). Results from PCA exhibited the highest temperatures always associated with the 'inner assemblage', whereas the highest salinity values were associated with the 'inner' group during April and with the 'outer

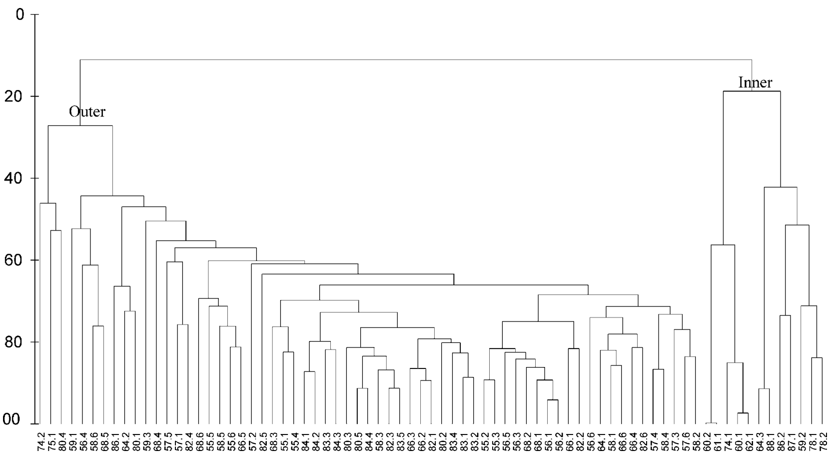

Fig. 2 Dissimilarity dendrogram based on the Bray-Curtis Index applied to the siphonophore/ stations April matrix. Integers indicate the station number, and decimals the depth sampled

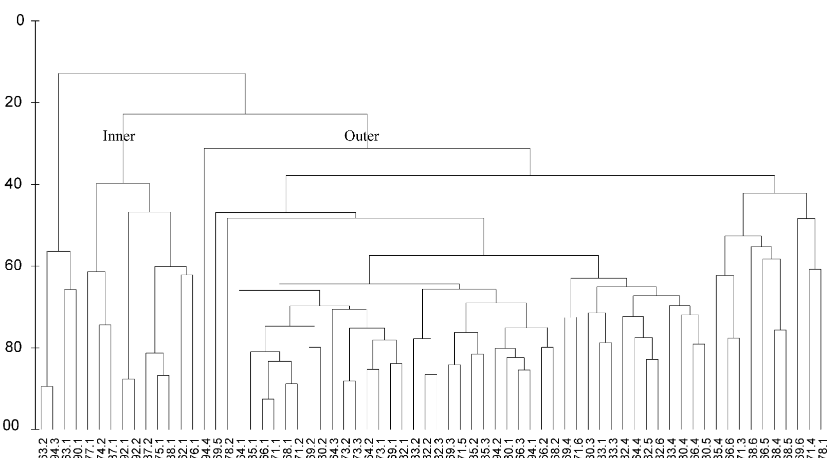

Fig. 3 Dissimilarity dendrogram based on the Bray-Curtis Index applied to the siphonophore/ stations October matrix. Integers indicate the station number, and decimals the depth sampled

assemblage in October (Table 1). These results indicated that the 'inner assemblage' was the only supporting a wide range of salinity conditions (30.7–37; Table 1). The Spearman rank correlation developed between zooplankton and the overall siphonophore biomass showed a significant ($p < 0.05$) and positive relationship.

In general, mean WDV was higher in the 'outer assemblage' (Table 2). Spatially, mean species richness and Shannon diversity index were lower in the 'inner assemblage' during the two studied periods. Seasonally, October registered the highest diversity values in both assemblages (Table 1). The 'outer assemblage' contained all 23 species identified in this study, whereas the 'inner assemblage' contained four species in April, and nine in October (Table 2). Among them, *B. bassensis*, *D. dispar*, and *E. hyalinum* occurred in both assemblages during both seasons, but only *E. hyalinum* showed a significantly (Mann-Whitney test, $p < 0.05$) higher mean biovolume in the 'inner' group. In fact, results from the PCA consistently showed this species to be associated with the 'inner assemblage' (Table 2). PCA also showed *A. eschscholtzi*, *C. appendiculata* and *Diphyes bojani* more associated with the 'outer assemblage', even if they were also registered in the 'inner' one during October. *Hippopodius hippopus*, *Lensia fowleri*, and species of *Abyla* and *Amphycarion* were among the taxa only present in the 'outer assemblage' (Table 2).

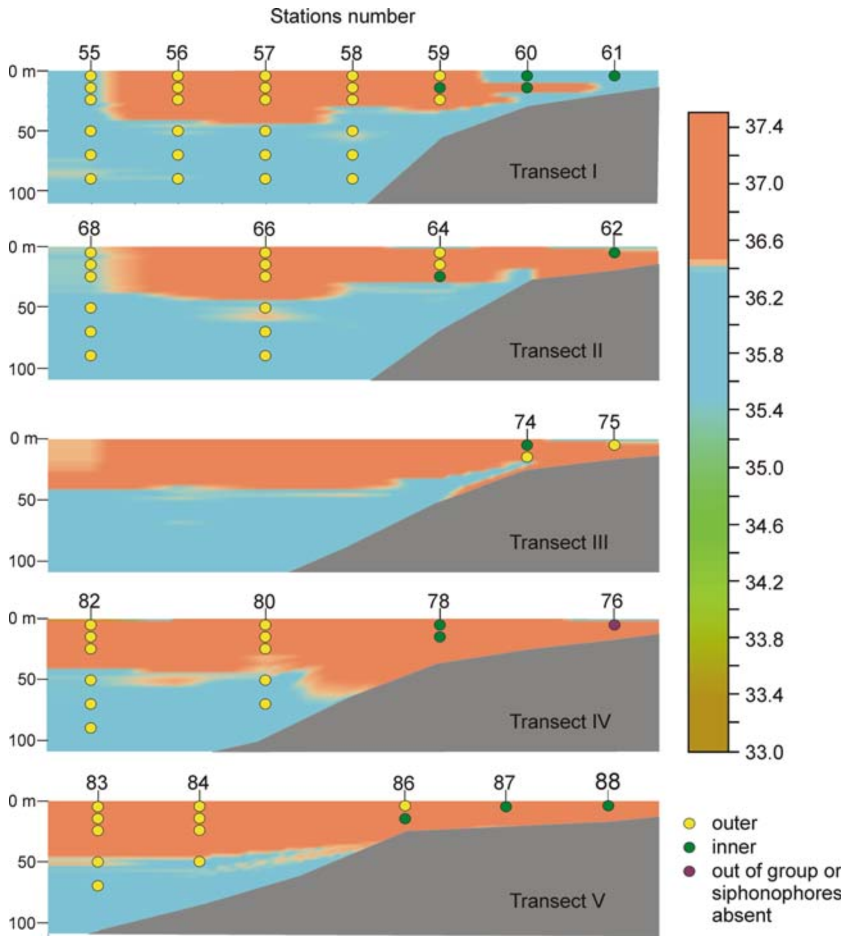

Fig. 4 Location of siphonophore assemblages over vertical salinity profiles in the southern Gulf of Mexico during April 2001

Discussion

Geographical distribution

Cross-shelf variability in siphonophore assemblages was greater than vertical changes (Figs. 4, 5). Geographically, the extent of the 'inner assemblage' was very similar during both seasons, indicating that, in addition to seasonal changes in hydrological conditions, other phenomena could explain the spatial extent of the assemblages during the two studied periods. Since siphonophores are exclusively marine cnidaria (Margulis, 1972), one might expect a more restricted distribution of the 'outer assemblage' during October, a month in which there is typically higher river discharges to the shelf than in April (Czitrom et al., 1986; Fig. 5). In contrast, however, in spite of the lowest salinity values over the inner shelf in October, the 'outer assemblage' occupied waters over the middle and outer shelves. Although April did in fact have higher salinity values (Fig. 4), the geographical occupancy of assemblages practically remained the same. Surface circulation pattern during the period studied exhibited a flow confluence moving offshore during October *versus* and onshore transport in April (Fig. 6). Zooplankton biomass distribution was in accordance with this circulation pattern, since highest mean values were registered in the 'inner assemblage' during April and in the 'outer assemblage' in October (Table 1).

It is well known that siphonophores are carnivorous zooplankton, consuming mainly co-

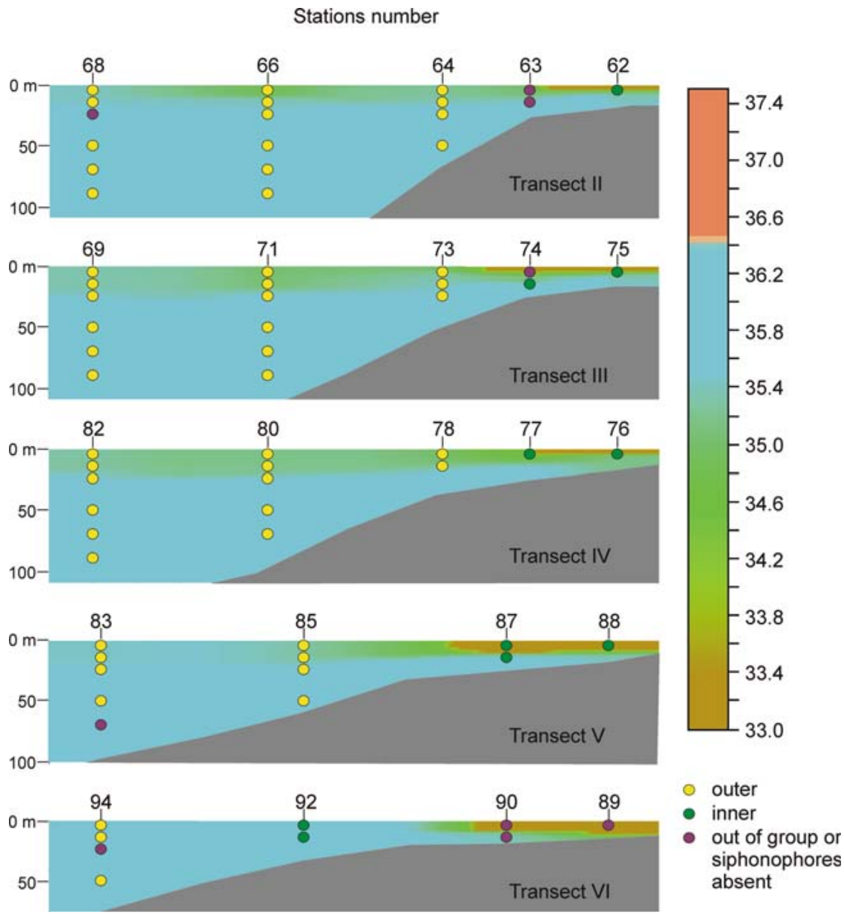

Fig. 5 Location of siphonophore assemblages over vertical salinity profiles in the southern Gulf of Mexico during October 2001

pepods, the major constituent of the zooplankton community (Purcell, 1997). This fact led us to suppose that zooplankton biomass distribution over the study area also plays an important role on the spatial distribution of siphonophore assemblages. From a field study, Purcell (1981, 1997) concluded that the spatial distribution of siphonophores follows that of their prey, so closely that, in some areas, a single species of siphonophore is able to remove between 2.9 and 69.3% of the small-copepod-size biomass (Pagès et al., 2001). We suggest that even when seasonality in continental water discharges could depress siphonophore populations in the southern Gulf of Mexico coastal area, enough food availability in the concerned areas might mitigate the negative effect of low or high salinity waters, given the positive and significant relationship between siphonophore WDV and zooplankton wet weight biomass ($p < 0.05$). Our distributional records indicated that populations of *B. bassensis*, *D. dispar*, and *E. hyalinum* are able to survive in a wide range of salinity values, following, perhaps, their prey. Studies concerning siphonophore assemblages at larger spatial scales emphasise the importance of mesoscale features, such as currents, mixing of water masses, upwellings, eddies, and coastal processes in the spatial distribution of siphonophore assemblages (Lo & Biggs, 1996; Gasca, 1999; Gibbons & Thibault-Botha, 2002; Suárez-Morales et al., 2002; Thibault-Botha et al., 2004). At finer scales, or within hydrologically homogeneous waters, it has been established that biological processes, such as productivity or prey selection, could have a more important effect on their distribution (Margulis,

Table 1 Species richness (S), Shannon diversity index (H'), zooplankton biomass (g 100 m^{-3}; Zoo), salinity (Sal) and temperature (°C; Tem) values registered in the two siphonophore assemblages identified in the southern Gulf of Mexico during April and October 2001

	Inner			Outer		
April						
	Min	Max	Mean	Min	Max	Mean
S	1	3	1.5	1	12	6.8
H'	0	1.29	0.26	0	3.03	2.01
Zoo	0.74	17.43	*5.41	0.44	16.27	3.77
Sal	35.95	37.03	*36.62	36.03	36.97	36.52
Tem	21.68	26.96	*25.80	18.18	27.73	24.45
October						
S	1	9	3.9	4	13	8.7
H'	0	1.05	0.77	1.16	3.06	2.32
Zoo	0.78	8.60	3.91	0.27	17.84	*4.44
Sal	30.71	36.23	33.74	33.4	36.4	*36.64
Tem	27.08	29.19	*27.96	21.48	28.78	26.81

* variable positively associated with this assemblage according to the PCA

1972; Mackie et al., 1987). The data in this study are consistent with this possibility.

Diversity

Seasonally, the highest number of siphonophore species was identified in October (Table 1). As in the case of the spatial extent of assemblages, we hypothesise that the higher species richness observed in both assemblages in this month might be due to a high food supply during this period in the overall study area, as a consequence of the nutrient-enrichment of the neritic area (Flores-Coto et al., 1988). In accordance, Alvariño (1968) found a larger number of siphonophore species during the period of maximum outflow of the Amazon River off the northeast South America coast. Several theoretical and experimental studies (Rozensweig & Abramski, 1993; Kassen et al., 2000) support the correlation between biological

Table 2 List of species occurring in the siphonophore assemblages identified in the southern Gulf of Mexico during April and October 2001

Species	April				October			
	Inner (n = 12)		Outer (n = 63)		Inner (n = 10)		Outer (n = 54)	
	X	*F*	*X*	*F*	*X*	*F*	*X*	*F*
Abyla haeckeli	—	—	0.001	3.2	—	—	0.002	7.4
Abyla trigona	—	—	0.001	3.2	—	—	0.001	1.9
Abylopsis eschscholtzi	—	—	*0.030	81.0	0.005	40.0	*0.141	98.1
Abylopsis tetragona	—	—	*0.074	87.3	0.001	20.0	0.083	96.3
Agalma okeni	—	—	0.007	11.1	—	—	0.180	87.0
Amphicaryon acaule	—	—	0.001	1.6	—	—	—	—
Amphicaryon ernesti	—	—	—	—	—	—	0.006	22.2
Bassia bassensis	<0.001	8.3	0.044	81.0	0.001	20.0	0.017	51.9
Ceratocymba dentata	—	—	—	—	—	—	0.011	3.7
Chelophyes appendiculata	—	—	*0.017	47.6	0.002	20.0	*0.117	98.1
Diphyes bojani	—	—	*0.063	81.0	0.005	30.0	*0.042	87.0
Diphyes dispar	0.081	58.3	0.110	73.0	*0.758	90.0	0.239	92.6
Enneagonum hyalinum	*0.134	66.7	0.014	15.9	*0.402	100.0	0.028	66.7
Eudoxoides mitra	—	—	0.023	52.4	<0.001	10.0	0.013	46.3
Eudoxoides spiralis	—	—	*0.101	98.4	<0.001	10.0	0.007	75.9
Hippopodius hippopus	—	—	0.010	3.2	—	—	0.001	1.9
Lensia campanella	—	—	<0.001	4.8	—	—	—	—
Lensia cossack	0.002	16.7	0.001	25.4	—	—	<0.001	11.1
Lensia fowleri	—	—	<0.001	4.8	—	—	<0.001	1.9
Muggiaea kochi	—	—	—	—	—	—	<0.001	3.7
Physophora hydrostatica	—	—	—	—	—	—	<0.001	1.9
Sulculeolaria chuni	—	—	—	—	—	—	0.001	3.7
Vogtia spinosa	—	—	<0.001	1.6	—	—	—	—

X = mean wet displacement volume (ml 100 m^{-3}); *F* = frequency of occurrence (%). * positively associated with this assemblage according to the PCA

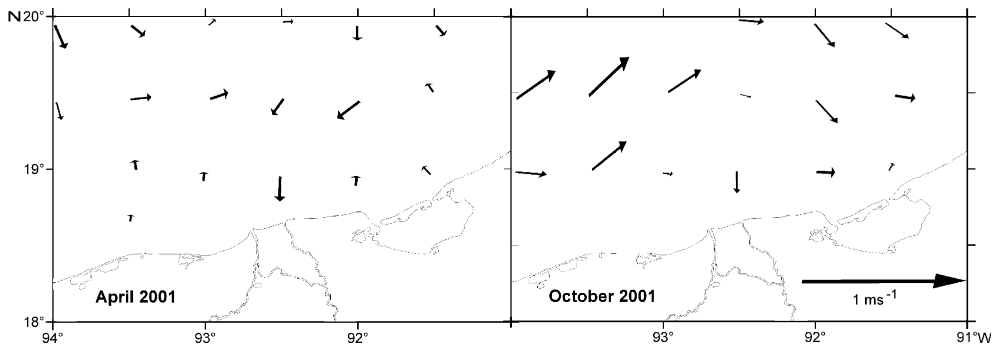

Fig. 6 Surface circulation pattern during April and October 2001. Modified from the University of Colorado website (http://argo.colorado.edu/~realtime/gom-real-time_velmag/)

productivity and diversity, indicating a convex-shaped functional relationship. In addition, we think that seasonality in zooplankton biomass might be a control mechanism of seasonal cycles of the major gelatinous predators, and in consequence, affect the number of siphonophore species collected. Mackie et al. (1987) argued that seasonal changes of siphonophore populations are more correlated with changes in hydrological conditions, but observations of Silguero & Robison (2000) seem to support our conclusion, since they noted a six-week lag between the primary production and calycophoran peaks in Monterey Bay. As in this study, Moore (1949) and Lo & Biggs (1996) observed a marked seasonality for *A. eschscholtzi, B. bassensis*, *E. spiralis*, and *C. appendiculata* in Bermuda waters. However, information about seasonal changes of gelatinous organisms and their relationship with biophysical processes is still lacking, especially in tropical areas, where the largest number of siphonophore species inhabit.

Spatially, the lowest diversity values were registered in the 'inner assemblage', especially during April (Table 1). Our results indicate that coastal waters characterised by high or low salinity values could reduce the siphonophore species richness. In agreement, Pugh (1999) stated that in high salinity regions, such as the Red Sea, species diversity is greatly reduced. Thibault-Botha et al. (2004) also found the lowest diversity and evenness values in the nearshore siphonophore assemblage in waters around southern Africa, and Gasca (1999) reported the highest diversity values in the oceanic environment, and the lowest over the shelf in the southern Gulf of Mexico. These results indicate an ocean-coastal gradient of species richness and diversity values, which become stronger when the nearshore waters are influenced by riverine systems.

Composition

All the 23 species here registered have a wide distribution at tropic-equatorial latitudes of the Atlantic Ocean (Pugh, 1999) and have been previously reported in the southern Gulf of Mexico (Gasca, 1993, 1999; Alba-Hurtado, 2001).

A. eschscholtzi, *C. appendiculata* and *Diphyes bojani*, present in both assemblages, were more associated with the 'outer' group according to the PCA results. These species have been found among the four most important species of both neritic and oceanic environments in the Mexican Caribbean Sea (Gasca, 1997). The infrequently encountered and lowest abundance calycophoran species, like *Abyla haeckeli*, *A. trigona*, *Ceratocymba detanta, A. ernesti*, *A. acaule*, *H. hippopus*, *L. fowleri*, *L. campanella*, *Muggiaea kochi*, *Sulculeolaria chuni*, and *Vogtia spinosa* did not reach the 'inner assemblage' at any time (Table 2). Analysing the siphonophore assemblages from South Africa, Gibbons & Thibault-Botha (2002) indicated the last eight species to be more frequent in the oceanic than in the neritic realm, a fact that could explain their absence in the 'inner assemblage'. Alba-Hurtado (2001), who for her thesis research studied the upper 200 m layer of both neritic and oceanic provinces from the southern Gulf of Mexico, found

A. ernesti, *H. hippopus*, *V. spinosa* and *Lensia* spp to be more frequent in the oceanic environment.

All the species registered in the 'inner assemblage' were also found in the 'outer' one (Table 2). Gibbons & Thibault-Botha (2002) found *Abylopsis tetragona, B. bassensis, C. appendiculata, D. dispar, E. hyalinum*, and *E. spiralis* to be widely distributed in the oceanic realm, but also in the nearshore waters around southern Africa. In accordance, all these species were also registered in the 'inner assemblage' (Table 2), where extreme salinity values were recorded (Table 1). *E. hyalinum* was the only showing a significantly ($p < 0.05$) higher mean biovolume in the 'inner' group. Along the east coast of South Africa, Thibault-Botha et al. (2004) also found this species to be more common in the nearshore assemblage, so this species is probably a good indicator species for nearshore waters.

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References

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

Alvariño, A., 1968. Los quetognatos, sifonóforos y medusas en la región del Atlántico ecuatorial bajo la influencia del Amazonas. Anales del Instituto de Biología. Universidad Nacional Autónoma de México 39, Serie Ciencias del Mar y Limnología 1: 41–76.

Bray, J. R. & J. T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349.

Czitrom, S. P. R., F. Ruiz, M. A. Alatorre & A. R. Padilla, 1986. Preliminary Study of a front in the Bay of Campeche, Mexico. In Nihoul, J. C. J. (ed.), Marine interfaces ecohydrodynamics. Elsevier Oceanography Series, Liege, 301–311.

Flores-Coto, C., L. Sanvicente-Añorve, R. Pineda-López & M. A. Rodríguez Van Lier, 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. Caribbean Journal of Science 29: 220–225.

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

Gasca, R., 1999. Siphonophores (Cnidaria) and the summer mesoscale features in the Gulf of Mexico. Bulletin of Marine Science 65: 75–89.

Gibbons, M. J. & D. Thibault-Botha, 2002. The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. Journal of the Marine Biological Association of the United Kingdom 82: 801–810.

Kassen, R., A. Bucling, G. Bell & P. B. Rianey, 2000. Diversity peaks at intermediate productivity in laboratory microcosms. Nature 406: 508–512.

Kimmel, D. G. & M. R. Roman, 2004. Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. Marine Ecology Progress Series 267: 71–83.

Lo, W. T & D. C. Biggs, 1996. Temporal variability in the night-time distribution of epipelagic siphonophores in the North Atlantic Ocean at Bermuda. Journal of Plankton Research 18: 923–939.

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

Magurran, A. E., 1988. Ecological diversity and its measurement. Princeton University Press, Princeton.

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, H. B., 1949. The zooplankton of the upper waters of the Bermuda area of the North Atlantic. Bulletin of the Bingham Oceanography Collection, Yale University 12: 1–97.

Okolodkov, Y. B., 2003. A review of Russian plankton research in the Gulf of Mexico and the Caribbean Sea in the 1960–1980s. Hidrobiológica 13: 207–221.

Pagès, F., H. E. González, M. Ramón, M. Sobarzo & J. M. Gili, 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). Marine Ecology Progress Series 210: 13–24.

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

Purcell, J. E., 1981. Dietary composition and diel feeding patterns of epipelagic siphonophores. Marine Biology 65: 83–90.

Purcell, J. E., 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. Annales de l'Institut Océanographique Paris 73: 125–137.

Qureshi, N. A., 1997. Distribution, abundance and diversity of mesozooplankton from surface waters of the inner continental shelf of northern Gulf of Mexico. Pakistan Journal of Zoology 29: 391–403.

Rosenzweig, M. L. & Z. Abramsky, 1993. How are diversity and productivity related? In Ricklefs, R. E. & D. Schluter (eds), Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, 52–65.

Silguero, J. M. B. & B. H. Robison, 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. Journal of Plankton Research 22: 1139–1153.

Suárez-Morales, E., R. Gasca, L. Segura-Puertas, & D. C. Biggs, 2002. Planktonic cnidarians in a cold-core ring in the Gulf of Mexico. Anales del Instituto de Biología, Universidad Nacional Autónoma de México (Zoología) 73: 19–36.

Thibault-Botha, D., J. R. E. Lutjeharms & M. J. Gibbons, 2004. Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. Journal of Plankton Research 26: 1115–1128.

Vázquez-de-la-Cerda, A. M., R. O. Reid, S. F. DiMarco & A. E. Jochens, 2005. Bay of Campeche circulation: an update. In Sturges, A. & A. Lugo-Fernández (eds), Circulation in the Gulf of Mexico: observations and models. Geophysical Monograph Series 161, American Geophysical Union, Washington, DC, 279–294.

Viitasalo, M., I. Vuorinen & S. Saesmaa, 1995. Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. Journal of Plankton Research 17: 1857–1878.

Zavala-Hidalgo, J., S. L. Morey & J. J. O'Brien, 2003. Seasonal circulation on the western shelf of the Gulf of Mexico using a high-resolution numerical model. Journal of Geophysical Research 108(C12) 3389 doi: 10.1029/2003JC001879 2003.