15. Siphonophore communities in the southern Gulf of Mexico during April-May, 1986.

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KEY WORDS: Siphonophora, distribution, Gulf of Mexico, upwelling.

ABSTRACT

From zooplankton samples taken at sixty-nine stations with a standard plankton net (0.3 mm mesh-size) in April-May, 1986, the community of siphonophores was analyzed in relation to the hydrologic conditions in the southern Gulf of Mexico. Thirty-three species were identified, with *Eudoxoides spiralis, Diphyes bojani, D. dispar, Muggiaea kochi* and *Bassia bassensis* being the most abundant, representing more than 83% of total siphonophore numbers. Quantitative analyses included calculation of diversity, dominance and percentage of similarity indexes. Highest siphonophore densities (> 5000 ind.1000m^{-3}) were observed in shelf environments. Station clustering (Bray-Curtis Index) revealed the presence of five distinct assemblages: I) stations within warm water or local upwelling areas, generally characterized by quite low densities (mean density: 422 ind.1000m^{-3}) and high diversity. II) stations adjacent to upwelling areas, with high densities (>3000 ind.1000m^{-3}) and high species richness. III) continental margin stations with moderate densities (mean density: 2954 ind.1000m^{-3}), a mixture of species of *Diphyes, Lensia, Eudoxoides* and *Abylopsis*, among others. IV) oceanic stations with a composition as in group III, but with a lower mean density (1271 ind.1000m^{-3}). V) stations on the western Campeche Shelf (depht < 50m), with *Diphyes dispar* dominating, representing 67.4% of the siphonophores. Siphonophore communities in the Gulf of Mexico are influenced mainly by the presence or absence of upwelling in shelf areas, and by mesoscale eddies and internal currents.

INTRODUCTION

Various authors have given species lists of siphonophores from the Caribbean Sea and the Gulf of Mexico, (Alvariño, 1972; Phillips, 1972; Vasiliev, 1974; Stepanjants, 1975; Gasca & Suárez, 1989, 1991; Gasca, 1993, among others). However, there have been few efforts to relate the composition, distribution and abundance of Gulf of Mexico siphonophores to specific water masses, or to explain how siphonophore assemblages might vary in time and space as a reflexion of the complex hydrography of the Gulf of Mexico.

The Gulf of Mexico is a semi-enclosed basin with only two openings: inflow comes via the Yucatan Channel and outflow through the Florida Straits. The flow through the two ports is restricted to the depths of 1760 m and 800 m, respectively. The circulation in the eastern gulf is dominated by the Loop Current, which can sometimes penetrate as far north as 27-28°N and then shed an anticyclonic eddy before returning again to the south. As this Loop Curent flows into the eastern Gulf it contributes to upwelling along the northeastern edge of the Yucatan Peninsula and the central portion of the Campeche Bank; its strength is proportional to the intensity and speed of the Yucatan Current (Merino, 1992). The anticyclonic eddies propagate westward across the Gulf and ultimately collide with the continental margin. As they spin down, these anticyclones may spawn counterclockwise (cyclonic) eddies, in which nutrient-rich midwater comes close to the surface (Lewis & Kirwan, 1985).

The siphonophore composition of near surface waters of the Gulf of Mexico was studied during April, 1986 as related to hydrographic conditions in the Gulf, including local upwelling and in cyclonic and anticyclonic gyres.

Methods

Zooplankton was collected during the oceanographic cruise JS8601 (April 11 to May 3, 1986) to the Mexican Economic Exclusive Zone of the Gulf of Mexico by the Instituto Nacional de la Pesca, Mexico (Fig. 1). Sixty-nine zooplankton samples were collected in oblique hauls to 200 m, using a Bongo net with a 0.3 mm mesh. A flowmeter was attached to the net's mouth to estimate the volume of water filtered. Salinity and temperature were measured at different depths at each station. Siphonophores were sorted from a 0.25% aliquot and then identified and counted. Polygastric and eudoxid phases were counted separately for all community analyses. Siphonophore communoiy structure was described on the basis of the following parameters: the number of species, the abundance of each species or phase, the Shannon-Wiener Diversity (H') (Pielou, 1966) and the Patten Redundancy indexes (Parsons, Takahashi & Hargrave, 1977). The Bray-Curtis analysis of Similarity (Ludwig & Reynolds, 1988), using the abundance data of siphonophores standardized to ind.1000m^{-3}, was performed to cluster similar stations.

Results

The analysis of hydrographic data allowed the detection of upwelling and downwelling areas related to cyclonic and anticyclonic eddies in oceanic areas; local upwellings also occurred over the continental shelf (Fig. 2). Surface waters were generally warm and salty, but temperatures at 100 m ranged between 15°C (station 150-100) and 26°C (stations 60-240 and 80-240), salinities at 100 m were between 36.64 ‰ (stations 60-50) and 35.87 ‰ (station 140-80).

Thirty-three species of siphonophores were collected (Table 1). The five most abundant (relative densities over 8%) were *Eudoxoides spiralis, Diphyes bojani, D. dispar, Muggiaea kochi* and *Bassia bassensis*, representing more than 83% of total siphonophore numbers. *Eudoxoides spiralis, D. bojani,* and *B. bassensis* were widely distributed in the studied area, while

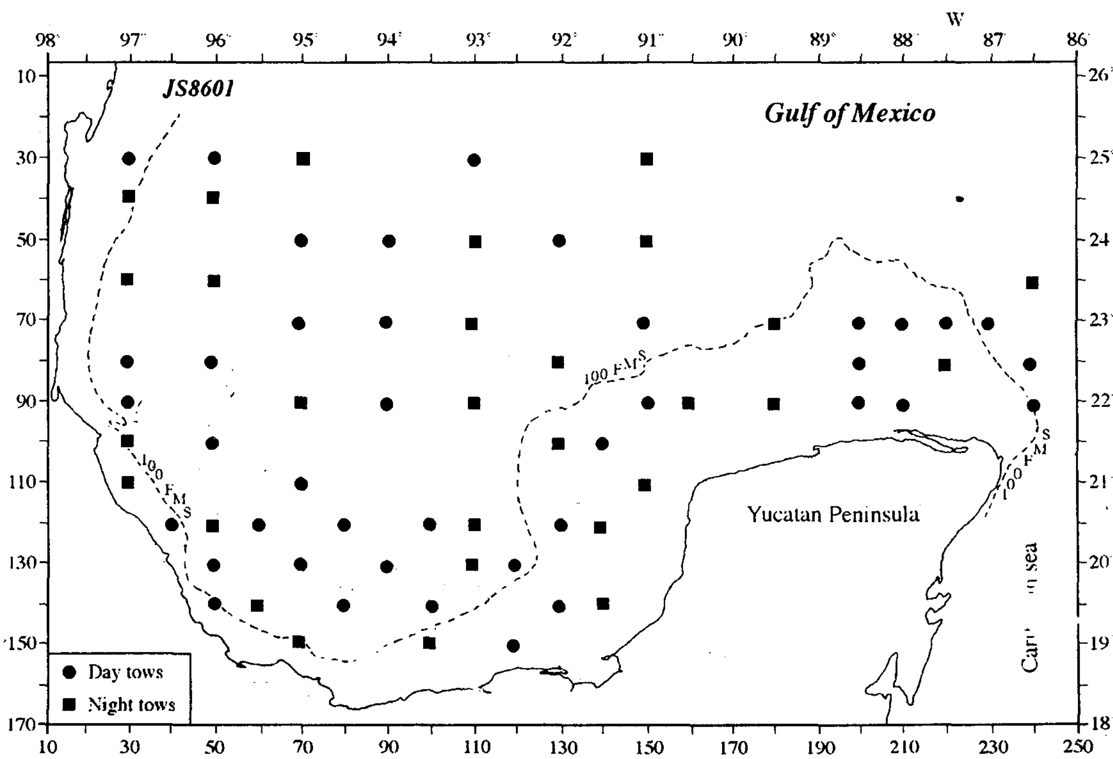

Fig. 1. Study area, with sampling stations during the JS8601 cruise in the southern Gulf of Mexico. Stations number are coordinates in the y-x axis.

the other two occurred mainly in neritic waters.

Most of the siphonophore species which were recorded in the Gulf of Mexico as the most abundant during the study period (Table 1) occurred as both polygastric (asexual) and eudoxoid (sexual) phases, with a wide distribution.

Lowest total siphonophore densities (<3000 ind.1000m^{-3}) occurred at oceanic stations and at neritic stations over the upwelling zones. Highest densities (>3000 ind.1000m^{-3}) were observed in shelf or shelf border areas near the upwellings, but not directly over the main upwelling area.

Highest diversity values occurred in almost all the oceanic stations and in some localities of the northern Yucatan Shelf. Lowest diversity values occurred mainly over the western Yucatan Shelf, and also in some localities of the northern shelf. Redundancy Index values (which are positively related to dominance) were low throughout most of the area: at only two stations (150-120, 190-140) were high redundancy values > 0.7, and at only 31% of the stations were values > 0.3. The Bray-Curtis ordination analysis produced five clusters of stations (Fig. 3), which were well correlated with environmental variables, as will be explained.

Discussion

Standing stocks of siphonophores were locally low in regions of shelf upwelling. In regions of the Yucatan Shelf, where there is upwelling, cooler midwater dominates the shallow water column; this "invasion" of cold waters generally resulted in a drastic decline of siphonophore numbers. This reflects the fact that the dominant species over the shelf are all warm-water, surface (0-50 m) dwellers. Such a dilution effect has been described for siphonophores by Michel & Foyo (1976) in the Caribbean Sea, and by Gasca & Suárez (1991) in the Yucatan Shelf. Several other gelatinous predators seem to respond in the same way in this area (Segura-Puertas & Ordóñez-López, 1994). However, it is relevant to mention that highest total siphonophore numbers were recorded adjacent to these areas of siphonophore absence. High standing stocks of siphonophores were also recorded along the shelf edge of the western Yucatan Peninsula and even within the Gulf. The general dis-

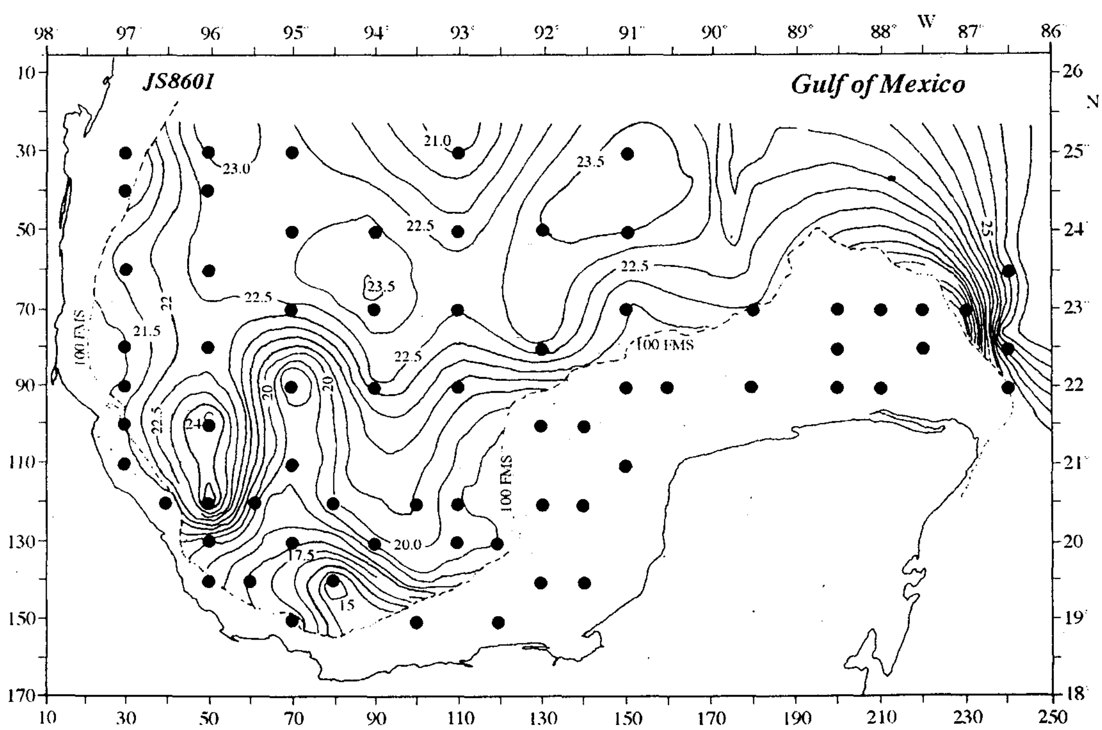

Fig. 2. Isotherm lines at the 100 m depth. Upwelling and mesoscale cold and warm-core eddies can be observed.

Table 1. Mean density of polygastric colonies or eudoxids (per 1000 m^3), total numeric (siphonophores in all stations) and relative (%) abundance, and frequency (number of positive stations and percentage) of the siphonophores species recorded in the surveyed area.

Species	Abundance			Frequency	
	ind.1000m^{-3}	total	%	no. stat.+	%
Agalma okeni Eschscholtz, 1825	3.36	232	0.11	12	17.39
A. elegans (Sars, 1846) Fewkes, 1880	2.33	161	0.07	4	5.80
Nanomia bijuga A. Agassiz, 1865	4.66	318	0.15	9	13.04
Athorybia rosacea (Forskål, 1775)	0.19	13	0.01	1	1.45
Amphicaryon ernesti Totton, 1954	1.10	76	0.04	4	5.80
Hippopodius hippopus (Forskål, 1776)	0.33	23	0.01	3	4.35
Vogtia spinosa Kefferstein and Ehlers, 1861	0.12	9	0.00	1	1.45
V. pentacantha Kölliker, 1853	0.33	23	0.01	2	2.90
V. glabra Bigelow, 1918	1.17	81	0.04	6	8.70
Sulculeolaria quadrivalvis Blainville, 1834	2.52	174	0.08	2	2.90
S. biloba (Sars, 1846)	0.58	40	0.02	3	4.35
S. turgida (Gegenbaur, 1853)	1.59	50	0.02	3	4.35
S. chuni (Lens & van Riemsdijk, 1908)	2.11	146	0.07	4	5.80
Diphyes dispar Chamisso & Eysenhardt, 1821 P*	165.23	11401	5.27	30	43.48
D. dispar E**	257.09	17739	8.20	27	39.13
D. bojani (Eschscholtz, 1829) P	205.04	14148	6.54	60	86.96
D. bojani E	257.71	17782	8.22	52	75.36
Lensia campanella (Moser, 1925)	6.49	448	0.21	14	20.29
L. cossack Totton, 1941	5.11	353	0.16	10	14.49
L. hotspur Totton, 1941	14.25	983	0.45	22	31.88
L. subtilis (Chun, 1886)	34.88	2406	1.11	40	57.97
L. meteori (Leloup, 1934)	6.49	448	0.21	14	20.29
L. fowleri (Bigelow, 1911)	4.94	341	0.16	17	24.64
Muggiaea kochi (Will, 1844) P	495.45	34186	15.80	15	21.74
M. kochi E	75.48	5208	2.41	1	1.45
Dimophyes arctica (Chun, 1897)	6.97	481	0.22	14	20.29
Chelophyes appendiculata (Eschscholtz, 1829) P	34.17	2357	1.09	42	60.87
Eudoxoides mitra (Huxley, 1859) P	90.91	6272	2.90	52	75.36
E. mitra E	99.15	6842	3.16	57	82.61
E. spiralis (Bigelow, 1911) P	389.95	26907	12.44	56	81.16
E. spiralis E	488.23	33688	15.57	56	81.16
Ceratocymba leuckarti (Huxley, 1859) P	0.33	23	0.01	2	2.90
C. leuckarti E	1.21	83	0.04	4	5.80
C. sagittata (Quoy & Gaimard, 1827) P	0.18	13	0.01	1	1.45
C. sagittata E	1.84	127	0.06	5	7.25
Abyla trigona Quoy & Gaimard, 1827 P	1.05	72	0.03	4	5.80
Abylopsis tetragona (Otto, 1823) P	49.98	3448	1.59	53	76.81
A. tetragona E	44.26	3054	1.41	48	69.57
A. eschscholtzi (Huxley, 1859) P	30.11	2077	0.96	42	60.87
A. eschscholtzi E	66.43	4583	2.12	52	75.36
Bassia bassensis (Quoy & Gaimard, 1834) P	133.37	9203	4.25	50	72.46
B. bassensis E	148.68	10259	4.47	54	78.26
Enneagonum hyalinum Quoy & Gaimard, 1827 P	0.79	55	0.03	2	2.90
E. hyalinum E	0.60	41	0.02	1	1.45

*P=Poligastric phase **E=Eudoxic phase

tribution of siphonophore highest densities could have resulted from the circulation pattern of one of the main branches of the Yucatan Current, the Intrusion Current (Vázquez-De la Cerda, 1993), which would shed these upwelled productive waters along the neritic areas of the southern Gulf of Mexico.

Oceanic upwellings in the Gulf of Mexico are associated with cyclonic cold-core gyres, which seem to be more productive than the surrounding oligotrophic waters (Biggs, 1992). However, during the spring of 1986, total siphonophore numbers in stations associated with cyclonic eddies were low, similar to the other oceanic localities. This

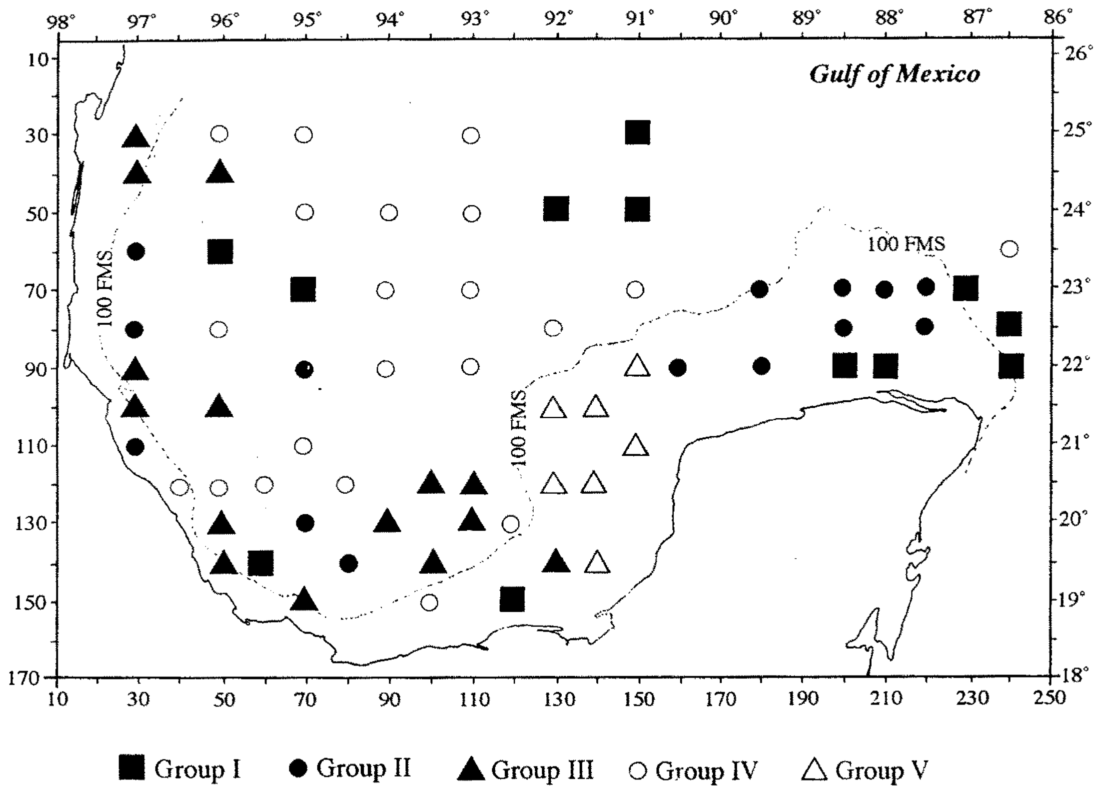

Fig. 3. Distribution of station groups resulting from the Bray-Curtis Index.

could reflect the limited vertical range of the cold waters of the cyclonic eddies (i.e. more prominent in midwater than in surface waters) or their limited persistence in time or space. Oceanic waters of the rest of the Gulf of Mexico, outside the cyclonic eddies, have been described as oligotrophic (Biggs, 1992); low siphonophore densities were the rule in these areas during the period surveyed.

The distribution patterns of some species showed positive functional relations to certain hydrologic or ecologic characteristics. *Diphyes dispar* and *M. kochi* showed a quasi-neritic distribution. The first one has not been previously reported with neritic affinities in the Gulf of Mexico, though it has been reported to be a common zooplankter of surface waters in the Gulf (Stepanjants, 1975) and the Caribbean Sea (Michel & Foyo, 1976). On the other hand, *M. kochi* is a typical neritic species (Mackie et al., 1987), although it was also found at some oceanic stations in the southernmost Gulf of Mexico. Such distributions may be a consequence of seaward transport by the Intrusion Current.

Most of the remaining species were more or less randomly distributed in neritic as well as oceanic waters. One peculiar species in this survey, however, was *Dimophyes arctica*, which has been described as eurybiotic (Mackie et al., 1987), which previously has been reported inhabiting the Gulf of Mexico only between 200-500 m (Stepanjants, 1975). In this study, *D. arctica* was captured in the upper 200 m at 14 oceanic localities of the Gulf, close to the shelf border. Its occurrence in near surface waters was probably a result of mixing of Equatorial Underwater (with salinities over 36.5 ‰) with oceanic Gulf Common Waters, which together constitute the Gulf Typical Waters (Morrison et al., 1983).

Clustering data by stations using the Bray-Curtis Index revealed five distinct groups. Group I: stations within regions of local upwelling, generally characterized by quite low numerical densities (mean density: 422 ind.1000m^{-3}), but with high species diversity. Clustered with this group was a neritic station with warm near surface temperatures and with the highest siphonophore density encountered in this study (>10000 ind.1000m^{-3}, mainly composed of *M. kochi*), and three oceanic stations with very low densities. Group II): stations generally adjacent to upwelling areas, high densities (>3000 ind.1000m^{-3}), jointly with high species richness. It is hypothezised that this group of stations, characterized by high densities of *E. spiralis, E. mitra, D. bojani, A. tetragona, A. eschscholtzi* and *B. bassensis*, was probably the most affected by the enrichment of the upwelling. Group III) continental margin stations with moderate densities (mean density: 2954 ind.1000m^{-3}) of a mixture of species including *Diphyes, Lensia, Eudoxoides, Abylopsis*. These stations appear to be areas of mixing between oceanic and neritic waters, which I hypothesize should be lower in biological production than Group II but more productive than the adjacent oceanic waters. Group IV: oceanic stations with a mixed composition as in group III, but with a lower mean density (1271 ind.1000m^{-3}). This group included the largest number of stations, and was "typical" of the oligotrophic oceanic waters of the Gulf of Mexico. Group V: shallow stations (depth < 50 m) on the western Yucatan Shelf, characterized by temperatures over 25°C and salinities over 36.6‰. *Diphyes dispar* was very abundant at those stations, where it represented 67.4% of the total siphonophores. *Diphyes bojani, M. kochi, B. bassensis, N. bijuga* and *L. campanella* also occurred in these stations. It is interesting to note that species that are widely distributed in the Gulf of Mexico, such as *A. tetragona, A. eschscholtzi, C. appendiculata, E. mitra*, and *E. spiralis*, and all *Lensia* species (except *L. campanella*), were absent from these Group V stations. This region has previously been described as a very productive area, in which pteropods, copepods and siphonophores have been found very abundantly (De la Cruz, 1971; Gasca, 1993; Suárez & Gasca, 1992; Suárez, 1992).

In summary then, the numerical abundance and species richness of siphonophore communities in the Gulf of Mexico are influenced mainly by the presence or absence of upwelling in shelf areas, and by the presence or absence of mesoscale eddies and the velocity of internal currents over the continental margin. Since the horizontal and vertical distributions of temperature and salinity are locally different between shelf upwelling regions and regions influenced by anticyclonic and cyclonic eddies, both temperature and salinity are useful tracers of differences in siphonophore assemblages.

ACKNOWLEDGMENTS

Zooplankton sampling was granted by Biol. Rosario Guadarrama Granados of the Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México. Douglas C. Biggs made valuable comments on the manuscript. SCOR provided the support to attend the ICoPB; Ms. Wesley Anne Ross kindly made the arrangements.

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