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SIPHONOPHORES (CNIDARIA) AND SUMMER MESOSCALE FEATURES IN THE GULF OF MEXICO

Rebeca Gasca

ABSTRACT

The species composition and numerical abundance of siphonophores were studied in the southern Gulf of Mexico from epipelagic zooplankton samples collected during July, 1988. Thirty-one species of Siphonophora were recorded at 97 stations, with *Muggiaea kochi, Diphyes dispar, Bassia bassensis*, and *Eudoxoides spiralis* the most abundant overall. The presence of two warm-core anticyclonic eddies, one cold-core cyclonic eddy, and upwelling on the Yucatán shelf and in the southern Bay of Campeche were expected to influence patterns of siphonophore distribution. A relatively low siphonophore abundance was anticipated to be found within the oligotrophic anticyclonic eddies, whereas high density was expected within the local divergence created by the cyclonic eddy, and in the upwelling areas. Differences in overall density and in species composition of siphonophores were recorded between the two anticyclones, which probably reflect the ages of the two warm-core eddies. Nighttime densities of siphonophores were similar throughout July 1988, but daytime densities were higher within the cyclone and within the younger of the two anticyclones than those recorded in the other areas or mesoscale features. Siphonophores were absent or scarce in the area of main upwelling off northeastern Yucatán where cold waters reach the surface. Nevertheless, cluster analysis using the Bray-Curtis Index yielded just three distinct assemblages, which were correlated not with the mesoscale circulation regime but rather with distance offshore.

The regional circulation of the Gulf of Mexico is dominated by the Loop Current (LC), which enters the Gulf through the Yucatán Channel and leaves the Gulf through the Florida Strait, and by the mesoscale, anticyclonic Loop Current Eddies (LCEs) that are shed by this highly variable eastern Gulf current. For example, the northern periphery of the LC can range from 25–29°N (Vukovich et al., 1979): when it extends to the north, flow often becomes unstable and one or more LCEs are shed (Hulburt and Thompson, 1982). These eddies can drift toward the northern, central or northeastern portions of the Gulf, but most eventually end up in an "eddy graveyard" in the northwest Gulf, 25–28°N and 93–96°W (Vukovich and Crissman, 1986).

Up to three of these LCEs may be found at any one time west of 90°W (Kirwan et al., 1984a,b,c, 1988; Lewis et al., 1989). Those most recently detached from the LC can be detected by the presence of a high-salinity core of subtropical subsurface water at 150–200 m (Merrell and Morrison, 1981). Cyclonic eddies are often found in close association with these anticyclones, either as cyclone-anticyclone dipoles or as cyclone-anticyclone-cyclone triads (Vidal et al., 1992). These cyclones are areas of local divergence, in which colder, subsurface waters dome close to the base of, or sometimes reach the surface mixed layer (Merrell and Morrison, 1981; Merrell and Vásquez, 1983; Lewis and Kirwan, 1985). A semipermanent cyclonic eddy appears to be characteristic of the Bay of Campeche, southwest Gulf of Mexico. This cyclone is generally weaker in April and May, but when fully developed its counterclockwise circulation can cover up to 75% of the Bay (Vásquez de la Cerda, 1993). In addition, there is a seasonal upwelling off Cabo Catoche, along the northeastern portion of the Yucatán Peninsula. The zooplankton community of that upwelling region was described by Suárez-Morales and Gasca (1991), Gasca and Suárez-Morales (1991), Gasca (1992), Sánchez and Flores-Coto (1994), and Segura-Puertas and Ordóñez-López (1994).

Mesoscale circulation features have been reported to modify the abundance and distribution of several groups of the epiplankton (Wiebe et al., 1976; Hattori, 1991; Doyle et al., 1993; Ashjian, 1993), including the siphonophores (Pagès and Gili, 1992). Although decades of plankton studies have been carried out in the Gulf of Mexico, it is only since 1980 that plankton distribution and abundance have been studied concurrently with hydrographic surveys of the mesoscale cyclonic and anticyclonic eddies there (Biggs et al., 1988; Biggs et al., 1997).

In this work, the community structure of the siphonophores of the southern Gulf of Mexico is analysed as related to the regional circulation of the area, with special reference to mesoscale cyclonic and anticyclonic eddies, and upwelling during summer, 1988.

METHODS

Hydrographic and biological data were obtained during the JS8801 oceanographic cruise. It was carried out in 5–26 July 1988 by Mexico's Instituto Nacional de la Pesca and the Instituto de Investigaciones Eléctricas, on board the R/V JUSTO SIERRA, of the National University of Mexico (UNAM) (Fig. 1). Hydrographic data shown here have been contoured from T/S information presented by Vidal et al. (1988).

Zooplankton samples were collected by oblique hauls at 97 stations, from a maximum depth of 200 m, to the surface. Hauls were made using a Bongo net with a 0.33 mm mesh-size, and a 60 cm-mouth diameter; all samples were fixed and preserved in a 5% buffered formalin solution. Siphono-

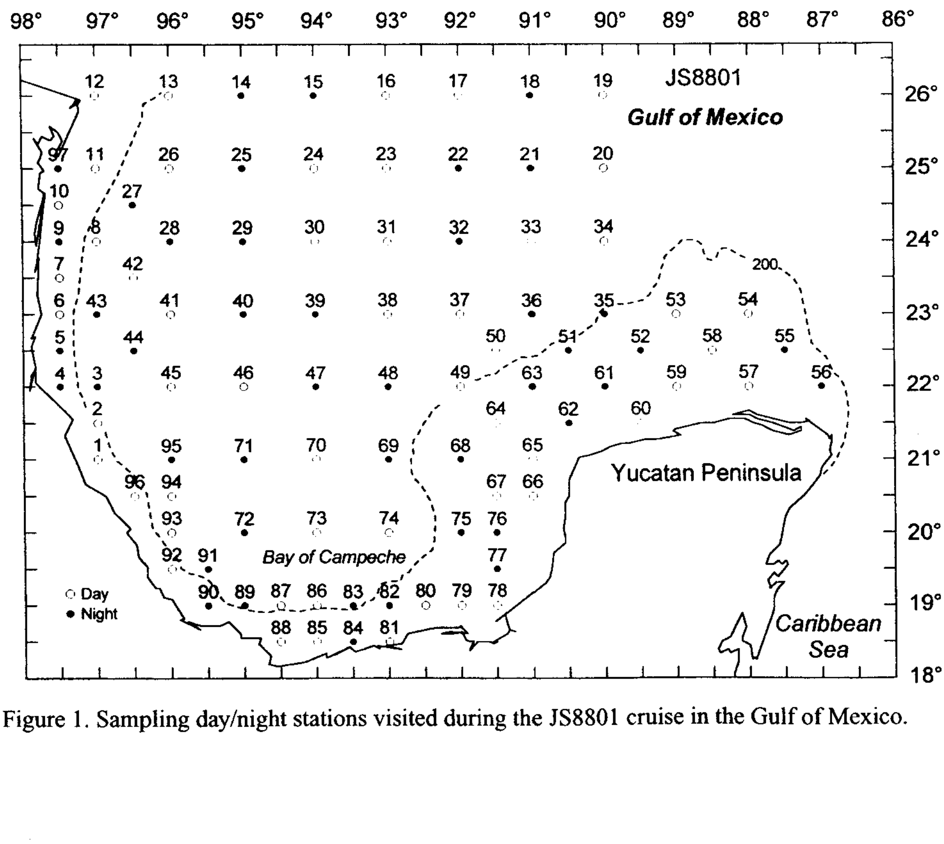

Figure 1. Sampling day/night stations visited during the JS8801 cruise in the Gulf of Mexico.

phores were sorted from a 25% subsample obtained with a Folsom Plankton Splitter, and then identified based on the works of Sears (1953), Totton (1965), and Daniel (1974), among others. Both eudoxid and polygastric stages were counted and density standardized into organisms/1000 m^3. However, these asexual vs sexual life history stages were considered separately for numerical analysis since the occurrence of large numbers of eudoxids can indicate favorable reproductive conditions. Density ranges used were modified from those suggested by Frontier (1981) to contrast abundant vs scarce. Diversity was estimated using the Shannon-Wiener Index (Krebs, 1978), and redundancy was also calculated as a measure of dominance (Parsons et al., 1975). Cluster Analysis was performed using the Bray-Curtis Index (Ludwig and Reynolds, 1988) to obtain groups of stations with similar features.

Results

Hydrography.—Surface temperature varied between 24.2°C at station 81 (18°29'N, 93°00.1'W), and 29.3°C at station 8 (23°59.9'N, 97°00'W) (Fig. 2), with an overall mean of 28.3°C. Salinity fluctuated between 36.9‰ at 25°55.0'N, 95°59.9'W, and 35.1‰ at 19°30.01'N, 95°30.0'W, with a mean of 36.28‰ (Fig. 3).

Subsurface temperatures generally covaried similarly, for example, the 22.5°C isotherm was as shallow as 9 m (22°00.2'N, 93°00'W), but deepened to 175 m (24°59.09'N, 90°00.01'W). Its mean depth was 53.5 m. This isotherm is a good proxy for upwelling when it shoals to less than 60 m. In July 1988, waters with a temperature of 22.5°C shoaled to less than 60 m over all of the continental shelf of Mexico, and this upwelling was particularly intense on the northeast Yucatán Shelf (Fig. 4).

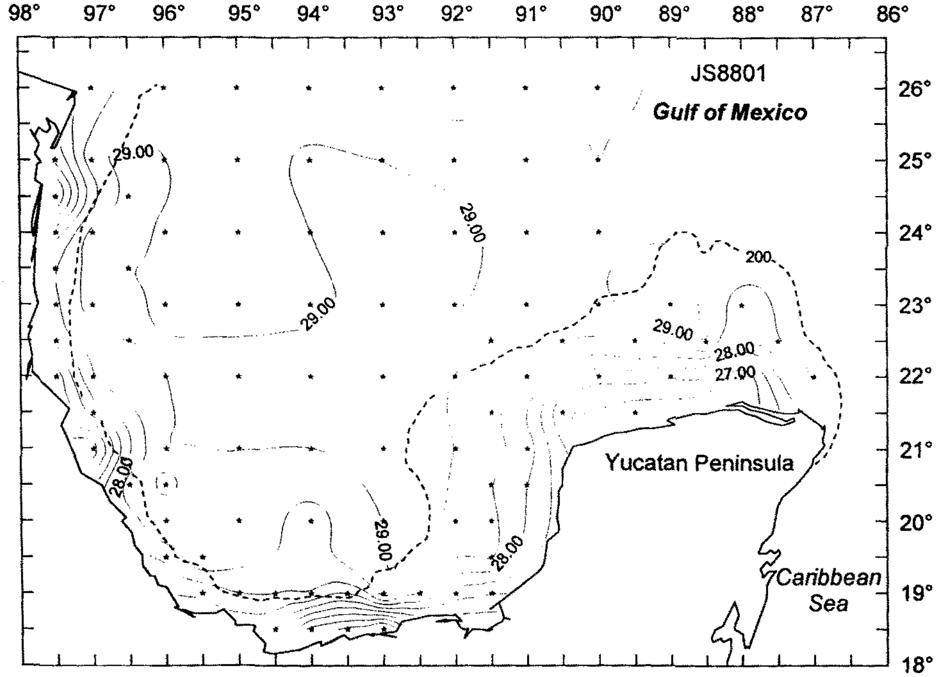

Figure 2. Surface temperature (°C) during the JS8801 cruise in the Gulf of Mexico.

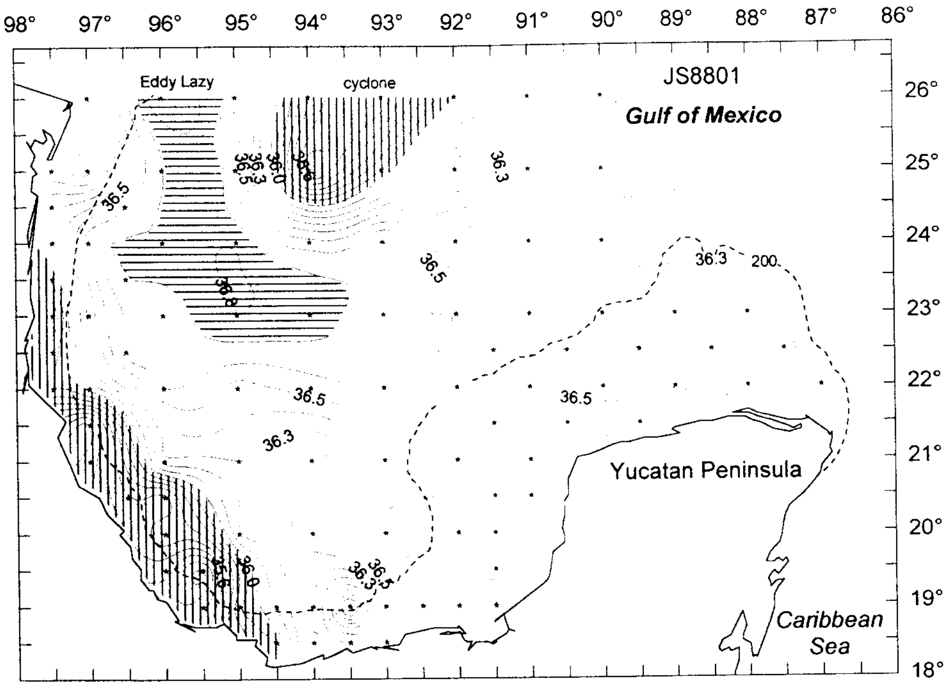

Figure 3. Surface salinity during the JS8801 cruise in the Gulf of Mexico.

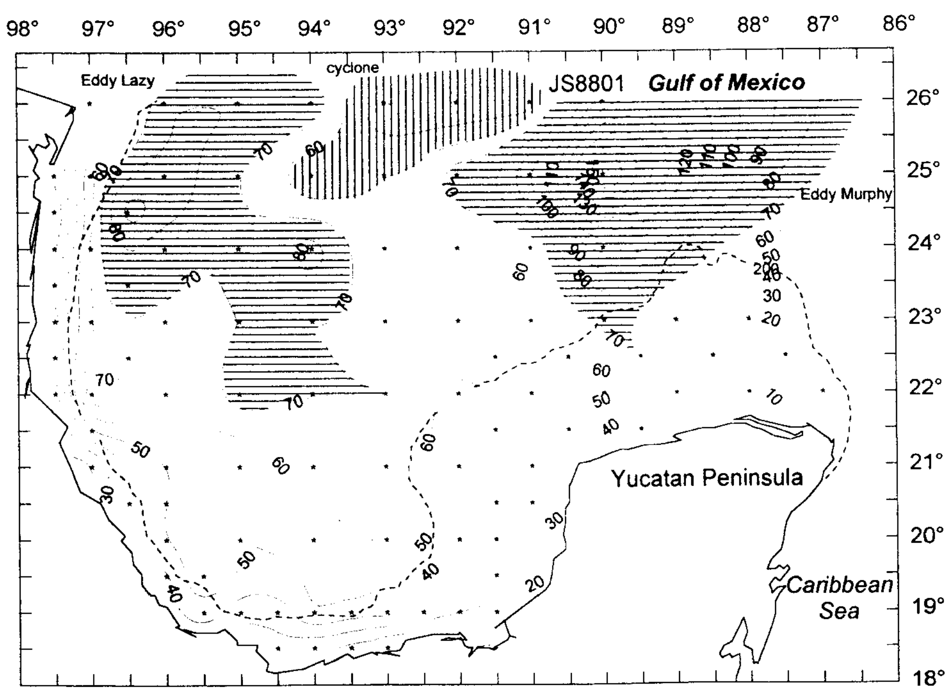

Figure 4. Topography of the 22.5°C isotherm during the JS8801 cruise in the Gulf of Mexico.

By comparing the topography of the 22.5°C (Fig. 4) with the 20°C (Fig. 5) temperature fields, several mesoscale hydrographic features can be detected in the surveyed area. There are two warm-core anticyclonic eddies, one with its core at station 20 (24°59.09'N, 90°00.01'W), and the other close to the coast at 24°N. A cyclonic eddy was present between the two anticyclones; the 22.5°C surface shoaled 70 m while the 20°C surface shoaled 140 m across this cyclone-anticyclone pair (<60 m in the cyclone and >200 m in both anticyclones).

The two LCEs had separated from the LC in the fall of 1987, and in the spring of 1988 (Berger, 1995). Each had been tagged with an Argos drifter, in order to monitor each eddy's westward movement across the southern Gulf (see SAIC, 1995). The easternmost and that more recently separated was named "Eddy Murphy" or "Eddy F", while the westernmost was known as "Eddy Lazy" or "Eddy E".

South of 22°N, in the deep water of the Bay of Campeche, the isotherm of 22.5°C was everywhere shallower than 70 m. It ranged in depth there between 40 and 65 m, indicating that this whole region was an area of divergence (Fig. 4). Over the continental shelf of the region, 22.5°C and 20°C surfaces shoaled locally to 20–30 m and 90 m, respectively.

Comparing Figure 3 with Figure 2 shows that surface salinity is more useful than surface temperature in locating summer mesoscale features. While surface temperature of the deep water off shelf was almost uniformly warm (28–29°C), two areas of locally low and locally high surface salinity show surface expression of the cyclone and of one of the anticyclones, respectively. The cyclone shows up as a "bulls eye" of locally low surface salinity (below 36‰), and the older of the two LCEs (Lazy Eddy) shows up as a region of locally high surface salinity (over 36.7‰).

Comparing Figure 4 with Figure 5, shows that in the upper 100 m, Lazy Eddy had

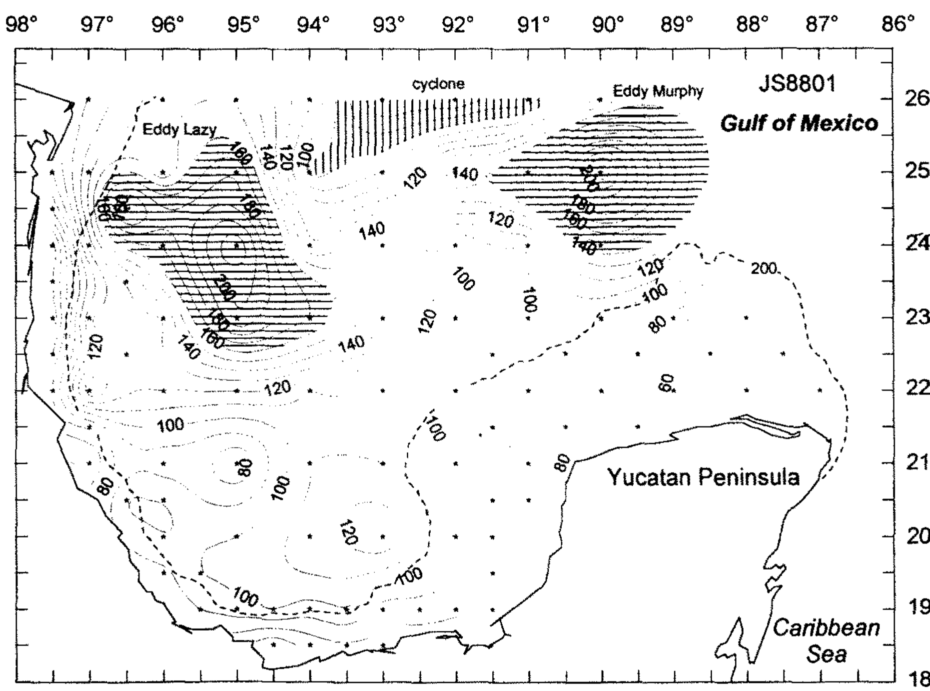

Figure 5. Topography of the 20°C isotherm during the JS8801 cruise in the Gulf of Mexico.

Table 1. Mean density of polygastric colonies and eudoxids (*) (per 1000 m^3) and number of siphonopore species/stages recorded in the environments considered herein. Day-Night (D-N) Eddy Lazy (EL), Eddy Murphy (EM), Cyclone at 26° N (CY), upwelling in the Campeche Bank (UP), non mesoscale feature-related oceanic stations (OO), all oceanic stations (AO), and neritic stations (EN).

	ELD	ELN	EMD	EMN	CYD	CYN	UPD	UPN	OOD	OON	AOD	AON	NED	NEN
Agalma okeni Eschscholtz, 1825	3	0	0	0	0	0	4	7	0	5	1	3	0	0
Halistemma rubrum (Vogt, 1825)	0	0	0	0	0	0	0	3	0	1	0	1	0	0
Nanomia bijuga A. Agassiz, 1865	2	0	0	0	0	0	0	0	0	0	0	0	0	5
Athorybia rosacea (Forskå l, 1775)	3	1	0	0	0	0	0	4	1	1	1	2	0	0
Amphicaryon ernesti Totton, 1954	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Desmophyes annectens * Haeckel, 1888	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hippopodius hippopus (Forskå l, 1776)	0	0	0	0	3	0	0	0	1	3	1	1	1	0
Vogtia glabra Bigelow, 1918	0	0	3	7	0	0	0	0	0	0	0	1	0	0
Sulculeolaria biloba (Sars, 1846)	0	0	0	0	0	0	0	0	0	0	0	0	3	6
S. turgida (Gegenbaur, 1853)	0	1	0	0	0	11	0	3	0	0	0	2	0	0
S. chuni (Lens & van Riemsdijk, 1908)	3	1	3	13	3	0	4	0	0	0	2	2	0	6
S. monoica (Chun, 1888)	0	0	0	0	0	0	0	0	0	2	0	1	0	0
Diphyes dispar Chamisso & Eysenhardt, 1821	27	16	10	0	82	0	18	0	15	7	26	8	417	579
D. dispar *	5	10	3	0	65	0	0	0	5	0	13	4	307	2,267
D. bojani (Eschscholtz, 1829)	17	9	48	7	10	0	5	14	10	16	16	12	49	26
D. bojani *	8	1	49	7	3	0	14	0	13	8	16	4	44	43
Lensia multicristata (Moser, 1925)	0	0	0	0	0	0	0	0	0	2	0	1	0	0
L. campanella (Moser, 1925)	0	16	11	0	10	11	16	15	12	2	10	9	31	22
L. cossack Totton, 1941	14	16	16	7	0	0	8	23	8	2	9	11	23	1
L. hotspur Totton, 1941	0	6	4	0	16	0	5	0	7	12	6	6	3	1
L. subtilis (Chun, 1886)	5	54	62	20	27	0	54	4	100	29	63	32	14	6
L. meteori (Leloup, 1934)	6	17	26	0	17	0	25	0	38	20	26	13	4	0
L. fowleri (Bigelow, 1911)	10	7	7	0	10	0	5	11	9	4	9	6	2	3
Muggiaea kochi (Will, 1844)	11	11	17	14	10	0	32	0	40	8	27	8	4,304	1,465
M. kochi *	0	0	0	0	0	0	0	0	0	0	0	0	2,535	0

Table 1. Continued.

	ELD	ELN	EMD	EMN	CYD	CYN	UPD	UPN	OOD	OON	AOD	AON	NED	NEN
M. kochi *	0	0	0	0	0	0	0	0	0	0	0	0	2,535	0
Dimophyes arctica (Chun, 1897)	0	6	10	20	20	0	23	36	23	17	17	16	0	0
Chelophyes appendiculata (Eschscholtz, 1829)	33	44	92	33	14	22	4	12	21	19	30	28	24	52
C. appendiculata *	0	0	0	0	0	0	0	0	0	0	0	0	0	25
Eudoxoides mitra (Huxley, 1859)	23	58	38	34	54	88	44	53	51	68	44	60	13	33
E. mitra *	39	33	51	75	64	44	48	75	58	46	54	48	41	48
E. spiralis (Bigelow, 1911)	48	59	146	33	143	88	22	22	65	85	79	62	117	57
E. spiralis *	10	29	88	0	34	0	0	14	17	47	26	29	122	149
Ceratocymba leuckarti * (Huxley, 1859)	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Abylopsis tetragona (Otto, 1823)	11	15	63	0	27	22	16	21	19	18	24	16	29	11
A. tetragona *	16	4	28	0	3	0	9	35	6	9	11	10	10	22
A. eschscholtzi (Huxley, 1859)	22	13	46	20	29	33	8	7	16	20	22	16	13	9
A. eschscholtzi *	13	13	45	20	17	22	8	33	29	19	25	19	50	85
Bassia bassensis (Quoy & Gaimard, 1834)	33	37	74	47	150	132	40	54	39	43	58	47	118	61
B. bassensis *	77	37	61	27	195	88	18	36	27	41	63	40	118	137
Enneagonum hyalinum Quoy & Gaimard, 1827	0	0	3	0	0	0	0	0	0	0	0	0	10	0
E. hyalinum *	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Mean density/environment	438	517	1,008	383	1,008	562	430	484	629	553	680	516	8,402	5,123
Standard deviation	261	157	68	136	387		91	221	229	371	314	251	19,196	8,912
Number of stations (n)	5	9	4	2	4	1	3	4	13	9	29	25	24	19
Number of species/stages	24	27	28	16	24	11	23	21	25	28	27	32	26	27

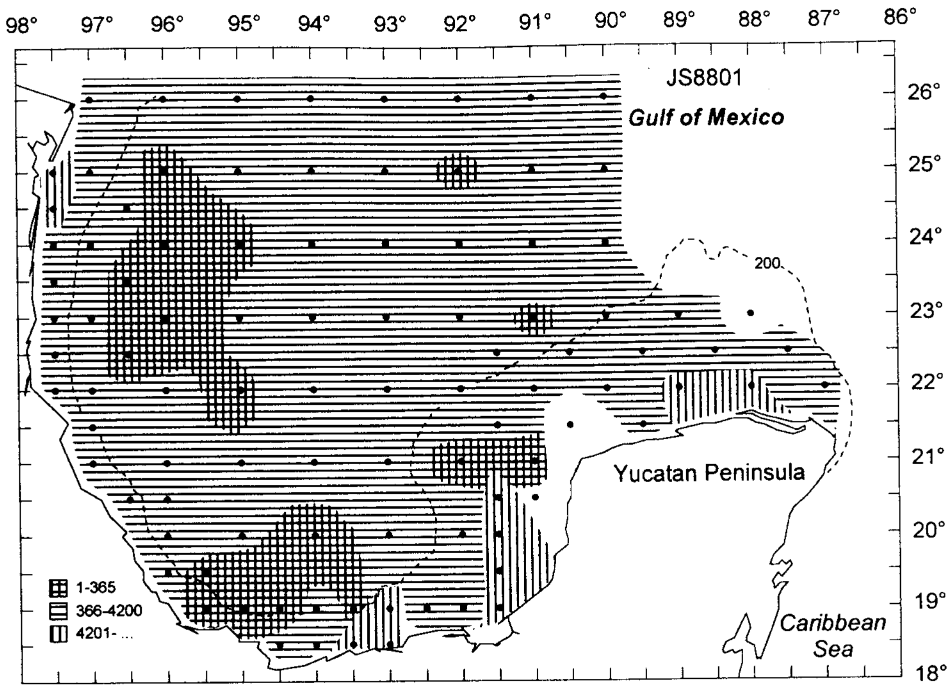

Figure 6. Total siphonophore density (1000 m^{-3}) distribution in the Gulf of Mexico during the JS8801 cruise.

reached depths of 180–205 m in both LCEs. As a younger anticyclone than Lazy Eddy, Eddy Murphy shows a twofold stronger warm core nature in the upper 100 m (Fig. 4).

Siphonophores.—Taxonomic analysis yielded a total of 31 species; mean densities (1000 m^{-3}), are reported separately for the various mesoscale features, in neritic and oceanic environments during night and day, in Table 1. Siphonophores were absent at three stations (54, 62, 66) (Fig. 6). The highest densities occurred over the continental shelf. The calycophores *Muggiaea kochi*, *Diphyes dispar*, *Bassia bassensis*, and *Eudoxoides spiralis* were overall the most abundant species, and together they constituted more than 89% of total siphonophore numbers (Table 1). The most frequent species (those occurring at more than 50% of the stations) were *E. spiralis*, *B. bassensis*, *E. mitra*, and *Abylopsis eschscholtzi*.

In contrast, lowest siphonophore densities (1–365 1000 m^{-3}) were recorded in the central-western and southern areas of the Gulf, at some stations near the northern Yucatán Peninsula, and at several coastal localities along the western coast of the Gulf of Mexico.

Siphonophores and Mesoscale Features.—Day versus night abundance in different environments were evaluated to determine whether siphonophore abundance varied among anticyclones, upwelling areas, the cyclone, or between neritic and oceanic areas. Day and night mean densities (± SD) of the siphonophore community in each environment are depicted in Figure 7. Densities at neritic stations were extremely variable (mean 8402 ± 19,196, n = 24 daytime and 5102 ± 8912, n = 19, at night). Densities at oceanic stations were less variable, and averaged an order of magnitude lower than those of the neritic zone, both in day (mean 680 ± 314, n = 29) and night (516 ± 251, n = 25).

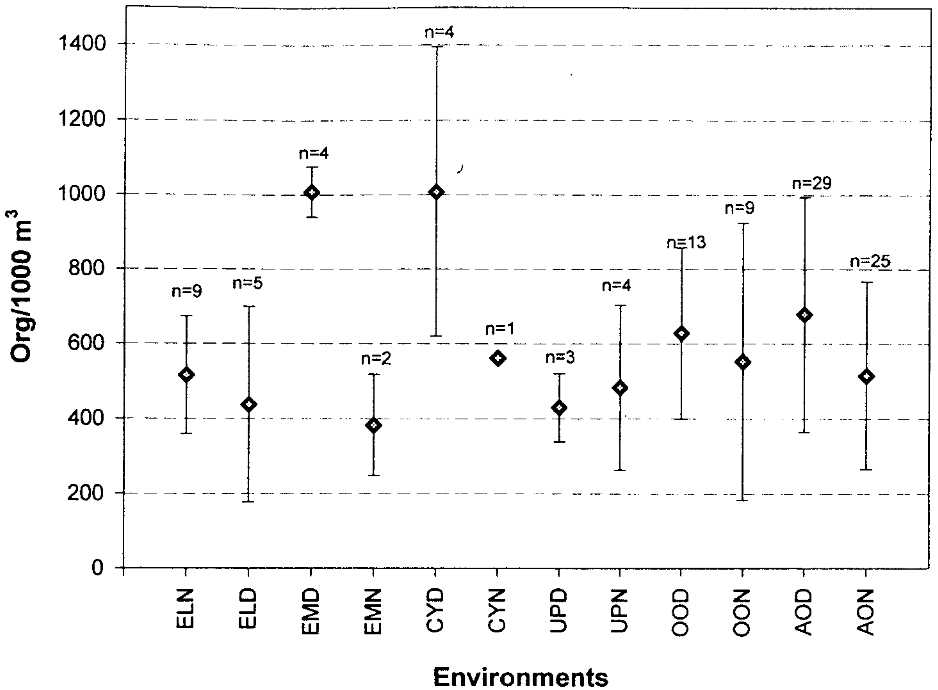

Figure 7. Mean siphonophore density (1000 m^{-3}) and standard deviation at each environment.

Density of siphonophores in the Eddy Murphy anticyclone during daytime were much higher than those recorded in most other areas. Rather surprisingly, siphonophore density in daytime there was comparable only to that in the daytime cyclone at 26°N. The cyclone at 26°N and Eddy Murphy exhibited the strongest changes in species richness between day (25, 28) and night (11, 16). In contrast, day and night density of siphonophores in Eddy Lazy was similar to that of all the other features (except to the daytime Eddy Murphy).

Except for high daytime concentrations in the cyclone and in Eddy Murphy siphonophore composition was quite uniform along the various mesoscale features. However, some inshore versus offshore patterns were evident among the most abundant species: *D. dispar* and *M. kochi* were more abundant in the neritic than in all the oceanic stations. Eudoxids of *D. dispar* were denser at night than in daytime in neritic stations; the opposite occurred in the oceanic stations. Eudoxids of the neritic *M. kochi* occurred only in daytime samples of the neritic zone.

Assemblages.—Clustering of stations with the Bray-Curtis Index yielded three station groups (Fig. 8). Group I included neritic stations of the Yucatán Shelf and the northeastern portion of Mexico, with low mean diversity (1.0 bits ind^{-1}), low species number (ca. 4, on average), and with *Muggiaea kochi* and *Diphyes dispar* as the dominant species. The highest overall mean densities (12,050 1000 m^{-3}) were included in this cluster. The stations with redundancy values over 0.7, were those with a high dominance of *M. kochi* (stations 59, 60, 78, 84), and of *D. dispar* (stations 65, 82).

Other neritic stations clustered together as Group II. These were farther from the coast than those in the first group; most had medium and high diversity values (average 3.01 bits ind^{-1}), and mean species number was three-fold higher than in the first group. Mean

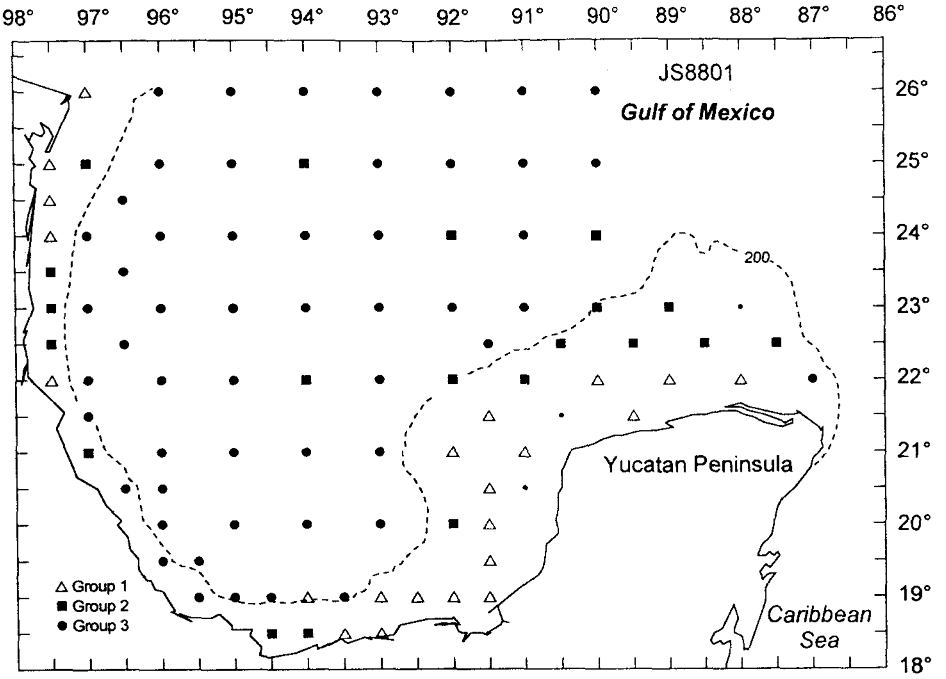

Figure 8. Distribution of station clusters generated from the Bray-Curtis Index.

density was 1840 1000 m^{-3}, with *Eudoxoides spiralis*, *B. bassensis*, *D. dispar*, and *A. eschscholtzi* being the most abundant species in this cluster.

Group III were mostly oceanic stations. It comprised 52 of the 97 stations of this survey. This group had the highest mean diversity (3.26 bits ind^{-1}), the highest average number of species (13), and the lowest mean density (571 1000 m^{-3}). The most abundant species in this group were *Eudoxoides mitra*, *B. bassensis*, *E. spiralis*, and *Lensia subtilis*. Several other species of *Lensia*, *Dimophyes arctica*, and *Chelophyes appendiculata* were also included in Group III.

Discussion

Siphonophore densities were generally moderate (366–4200 1000 m^{-3}) in most of the oceanic zone (Fig. 6); these values are similar to those recorded in surface oceanic waters of the Caribbean Sea (Michel and Foyo, 1976) and in previous work in the Gulf of Mexico (Gasca, 1993). Stations with lower density were mostly those in the central western portion of the Gulf. These were in or near the anticyclonic "Eddy Lazy", which had detached from the Loop Current in the fall of 1987. Low chlorophyll and zooplankton biomass have been reported to be typical of warm-core rings in the Gulf of Mexico (Biggs, 1992), and in other areas (Hattori, 1991). In July 1983, nitrate concentrations at stations within Lazy Eddy were very low (close to 0) through the 0–100 m layer, whereas in adjacent areas the nitracline occurred at a shallower depth (Vidal et al., 1988). As might be expected from Figure 4, the sigma-t density of the uppermost 100 m within Lazy Eddy did not vary from that of adjacent oceanic water. This presumably was a consequence of the fact that that this eddy was old and progressively mixing with the adjacent oceanic waters, even though it still had locally salty surface water (Fig. 3)

The other anticyclone, Eddy Murphy, which had more recently separated from the Loop Current, was expected to have even more oligotrophic upper waters, and lower zooplankton biomass. Rather surprisingly, daytime siphonophore densities within Eddy Murphy were on average two fold higher than in most of the other oceanic environments. In fact, daytime densities in Eddy Murphy were quite similar to those in the cyclone at 26°N. At night, mean siphonophore density within Eddy Murphy was similar to the rest of the oceanic Gulf, probably as a result of downward vertical migration toward deeper waters of several species of *Lensia*, and of both polygastric and eudoxids of *D. dispar*, *A. tetragona* and *E. hyalinum*. Densities of *D. bojani* and *E. spiralis* in the upper 200 m decreased sharply from day to night.

Based on previous reports by Biggs (1992), Biggs and Müller-Karger (1994), and Biggs et al. (1988), locally higher zooplankton densities were expected in the cyclonic cold-core eddy than in either of the two anticyclones. These cyclonic eddies have shallower nitraclines than do anticyclones, or the adjacent waters in the Gulf of Mexico (Biggs, 1992). In fact, there was locally high siphonophore density within the cyclone at 26°N during daytime, and during the day, 25 species/stages were recorded vs 11 at night. This could be a result of the combined effect of the migration patterns of the siphonophore species out of the photic layer during the night, and the presumed influence of the nutrient enriched cyclone water on plant production there, promoting an overall increase in numbers of herbivorous zooplankton and the siphonophores than in turn prey on the herbivorous.

Low siphonophore densities (1–365 1000 m^{-3}), and even absence of them were recorded in the northwestern coastal portion of the Yucatán Peninsula, where a low-density zone sharply separated two high siphonophore density areas (Fig. 6). Separation of two high-density zones in this coastal area has been previously observed for zooplankton biomass by De la Cruz (1972), who found them joined together only during summer season out of four seasonal surveys. This author hypothesized that periods of continuity between the two zones result from the northwards displacement of the southern high-density zone. This seems to indicate that the causes generating high siphonophore densities in the northern and western portions of the Yucatán shelf are not the same. The July 1988 hydrographic data show that nitrate in the water column in stations of the innermost zone of the Yucatán shelf is virtually absent (Vidal et al., 1988). This probably is a result of nitrate depletion after spring upwelling (Merino, 1997). As a corollary, high siphonophore densities during summer perhaps lag any local chlorophyll enrichment produced by this upwelling (Gasca and Suárez-Morales, 1991; Gasca, 1990; 1997). It remains problematic why there is a relatively low-density area between these high-density zones, but this has been reported previously also for other gelatinous zooplankton in this upwelling area (Gasca and Suárez-Morales, 1991; Segura-Puertas and Ordóñez-López, 1994).

Another siphonophore low-density region was found in the southern portion of the Gulf (Fig. 6). In this area, the 22.5°C isotherm appears to be deeper than in other neritic zones, and salinity (Fig. 3) tends to be low as a result of continental runoff. This low salinity may limit the distribution of siphonophores along the inner reaches of the shelf in the Bay of Campeche.

In neritic environments, the largest changes in siphonophore densities were caused by changes of a few species, namely *D. dispar*, *M. kochi* and *D. bojani*. These are three of the most characteristic species of neritic waters of the Gulf of Mexico (Gasca, 1993). On the Yucatán shelf, which had especially low diversity values, several stations were strongly dominated by *M. kochi* and *D. dispar*. Populations of both species seem to reach their highest concentrations in the uppermost 0–25 m layer in the Gulf of Mexico, as recorded by Vasiliev (1974). So, these two species are presumably the best adapted to these warm, shallow, low-nutrient conditions, showing even high densities as in the western portion of the Yucatán shelf. The relatively high densities of eudoxids of these species on the Yucatán shelf indicates that they were actively reproducing.

In both, cyclonic and anticyclonic eddies there were distributional peculiarities of some siphonophore species. *Dimophyes arctica* showed a wide distribution in the Gulf; apparently, the occurrence of this deep-living species (Stepanjants, 1975) at surface layers is a result of mixing of deep with surface waters generated by the upwelling effect of the cyclonic eddies, especially in the Bay of Campeche (Vásquez de la Cerda, 1993). *Muggiaea kochi*, which is a typical neritic species (Mackie et al., 1987), was recorded in fully oceanic zones north of the Yucatán Peninsula and off the western coast of the Gulf. This unusual phenomenon seems to be related to the effect of the mesoscale circulation in both areas. In the first case, waters from Eddy Murphy, and those from the LC, apparently advected water from the Yucatán Shelf and so passively transported *M. kochi* northwestwards into the oceanic zone. In the second case, the combined effect of the anticyclone present off Tamaulipas ("Lazy"), and the cyclone north of it seems to have entrained *M. kochi* from neritic waters off Tamaulipas or from south Texas into a confluence flow reaching the central oceanic portion of the Gulf of Mexico. The net transport is a NW–SE flow of neritic waters off the shelf, which then deflects southwards. This offshore flow has been reported previously for other cyclone-anticyclone geometries in the Gulf of Mexico (Brooks and Lageckis, 1982; Vidal et al., 1992; Biggs and Müller-Karger, 1994). However, eudoxids of *M. kochi* were only recorded in neritic samples, indicating that it does not reproduce in oceanic conditions.

The three assemblages resulting from the Bray-Curtis ordination (Fig. 8) reflect only the broadest hydrographic main environmental conditions in the Gulf and the corresponding community of siphonophores. The first one is evidence of the occurrence of warm waters, enriched by the presence of upwelling, and producing high densities of several species of siphonophores. The second group, located adjacent to the first one, represents a transitional zone in which siphonophore diversity and density are relatively higher, but in which temperature and salinity do not reach very high values. The third assemblage is definitely an oceanic one, with high temperature, high salinity, and high siphonophore species diversity but low siphonophore densities. It is apparent that these principal changes of siphonophore density and composition are more related to distance offshore rather than to the effect of mesoscale circulation features, and/or day and night variability. Mesoscale circulation and diel vertical migration appear to have but limited effect on the siphonophore community composition in the Gulf of Mexico.

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ADDRESS: *El Colegio de la Frontera Sur (ECOSUR), Unidad Chetumal, A.P. 424, Chetumal, Quintana Roo 77000, Mexico. E-mail: rgasca@ecosur-qroo.mx.*