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javierd@ibiologia.unam.mx
Universidad Nacional Autónoma de México
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Suárez MORALES, E.; Gasca, R.; Segura PUERTAS, L.; Biggs, D. C.
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# Planktonic cnidarians in a cold-core ring in the Gulf of Mexico

E. Suárez-Morales*
R. Gasca*
L. Segura-Puertas**
D.C. Biggs***

**Resumen.** Se analizó la composición específica y la abundancia de medusas y sifonóforos recolectados en marzo 1993 al cruzar un anillo ciclónico de núcleo frío en el Golfo de México (CCR por sus siglas en inglés). Las muestras se obtuvieron mediante arrastres oblicuos (de 100m a la superficie) con una red de plancton. Se encontraron 12 especies de medusas cuya abundancia global fue similar dentro y fuera del CCR. Sin embargo, las dos especies que en conjunto conformaron más del 66% de las medusas dentro del CCR (*Nausithoë punctata* y *Liriope tetraphylla*) fueron raras fuera de éste. Las más comunes dentro del CCR (en conjunto >66% de las medusas fuera del CCR) no se encontraron o fueron raras dentro del CCR. Los sifonóforos estuvieron representados por 25 especies; las siete más abundantes dentro del CCR lo fueron también fuera. Debido a los patrones de migración día/noche, se encontró que la abundancia nocturna de sifonóforos es consistentemente mayor en el estrato de los primeros 100m de profundidad. El análisis de agrupamiento confirmó estas diferencias en la composición y abundancia de los sifonóforos entre las muestras diurnas y las nocturnas y entre las nocturnas dentro y fuera del CCR. No obstante que fueron poco comunes, dentro del CCR se encontraron dos especies relativamente raras de *Lensia* y de *Ceratocymba* y fuera del CCR, otras dos de *Lensia*,una tercera de *Ceratocymba*, y otras cuatro especies, también raras. La diferencia de especies sugiere que estos cnidarios no están distribuidos de modo uniforme en esta zona del Golfo de México; muestran variaciones como respuesta a cambios a mesoescala en su ambiente físico.

Palabras clave: medusas, sifonóforos, ecología, giros, mesoescala

*El Colegio de la Frontera Sur-Unidad Chetumal, Apartado postal 424, Chetumal 77000, Quintana Roo, México.

**Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Estación Puerto Morelos, Apartado postal 1152, Cancún, Quintana Roo. México.

*** Texas A&M University, Department of Oceanography, College Station, 77843-3146, Texas, U.S.A.

**Abstract.** The species composition and abundance of medusae and siphonophores collected in March 1993 across a Gulf of Mexico cold-core ring (CCR) were analysed. Samples were collected in day and night time by oblique tows (100 m to surface) with a plankton net. Medusae were represented by 12 species, which by combined numbers were almost equally abundant within and outside the CCR. However, the two species that together comprised >66% of all medusae inside the CCR (*Nausithoë punctata* and *Liriope tetraphylla*) were rare outside the CCR and species most common outside (combined >66% of all medusae outside) were either absent or rare inside the CCR. Siphonophores were represented by 25 species; the seven most abundant within the CCR were also those most abundant outside. Because of day/night migrational patterns, consistently greater total numbers of siphonophores were found at night in the upper 100m layer. Cluster analysis confirmed these differences in siphonophore composition and abundance between daylight and night samples but also showed differences between night samples inside and outside the CCR. Although they were uncommon within the CCR, two rare species of *Lensia* and two of *Ceratocymba* were found only in collections inside this feature. Two other species of *Lensia*, a third species of *Ceratocymba*, and four other overall uncommon siphonophores were found only outside the CCR. Thus, differences at the species level indicate that pelagic cnidarians are not uniformly distributed in this zone of the gulf, but rather they vary in response to mesoscale changes in their physical environment.

Key words: medusae, siphonophores, ecology, mesoscale eddy

## Introduction

In the Gulf of Mexico the mesoscale circulation is dominated by the loop current (LC) and by a dynamic eddy field that is created as meanders in the LC that result in eddy separation events (Lewis & Kirwan 1985). These eddies, also called rings, can be warm-core (anticyclonic) or cold-core (cyclonic). The cold-core rings (CCRs) are local regions in which primary productivity in near-surface waters is relatively higher than in the oligotrophic areas outside and so they are analogous to oceanic oases. Conversely, the warm-core rings (WCRs) are nutrient-limited, low productivity areas whose surface waters are analogous to ocean deserts (Biggs *et al.* 1988; Biggs 1992; Wormuth *et al*. 2000).

Siphonophores and medusae are among the most abundant groups of gelatinous zooplankton in the oceanic realm. The general composition and distributional patterns of these two groups in the oceanic waters of the Gulf of Mexico are relatively well-known (Phillips 1972; Gasca & Suárez-Morales 1991; Segura-Puertas 1992; Gasca 1993, 1999). Recent work has suggested that siphonophores and medusae show distributional patterns related to the influence of different water masses and to mesoscale features such as upwelling and eddies (Gasca 1999; Gasca

& Suárez-Morales 1991; Segura-Puertas 1992; Segura-Puertas & Ordóñez-López 1994). However, quantitative information on the oceanic cnidarian zooplankton community as related to these eddies is still scarce (Gasca 1999). Therefore, in order to determine if the hydrographic conditions set by a mesoscale cyclonic eddy are reflected in the gelatinous zooplankton community, this study describes changes in the numerical abundance, composition, and species diversity of the medusae and siphonophores collected during the transit of the research vessel Gyre across a CCR in March, 1993, in the Gulf of Mexico.The eddy surveyed was located in the western central Gulf of Mexico between the 26º 30N, 93º 30W and 25º 30'N, 92º 56'W (Fig. 1). The CCR was detected from space as a region of surface temperatures 1-2 °C cooler than the adjacent oceanic waters and as an elliptical local depression in sea surface height (SSH) (see Biggs *et al*., 1997; Wormuth *et al*., 2000).

## Methods

During transit from Texas to the Campeche Bank by R/V Gyre, operated by Texas A&M University, 33 expendable bathythermograph probes (XBTs) were dropped and 8 net tows were made as the ship crossed the CCR (Fig. 1; see also Biggs *et al*., 1997). The net tows were oblique hauls (0-100 m) with a standard plankton net (0.33 mm mesh-size, diameter of mouth 1m). Net tows were made at every third XBT site of the hydrographic transect beginning at 27°00' N. Data from a 153 kHz accoustic Doppler current profiler (ADCP) were also logged by the research vessel allowing sampling of near-surface currents from 8-250 m below the surface. The geographic position, date and time of collection, and the volumes of water filtered by the net at each station are presented in Table 1. A mechanical flowmeter was attached to the net mouth to estimate the volume of water filtered (this ranged between 450-800 $m^3$ per haul). This net allowed collection of small and medium-sized medusae and siphonophores. Zooplankton samples were fixed and preserved in a buffered 4 % formalin solution (Smith & Richardson 1979). Zooplankton samples were collected in day and nighttime, upon arrival to the designed station. Four of the eight tows were made during daylight hours (station1,5-7) and the other 4 were made at night. The first tow was made in daylight outside and to the northwest of the CCR, and then tows 2-4 were at night within the CCR. Tows 5-7 were daylight tows outside the CCR and tow 8 was outside the CCR, at night ( Fig. 1).

Medusae and siphonophores were sorted from 25% aliquots and then identified to species level. Siphonophores were quantified following Gasca & Suárez-Morales (1991). Density data were calculated as number of organisms per 1000$m^3$ for all species. Analysis of the numerical abundance of medusae and siphonophores was made after logarithmic transformation (log [x+1] ) of data to reduce both the effects of abundant species relative to rare species and the possibility that significant differences among stations could be due to chance (Clarke 1993). Sh-

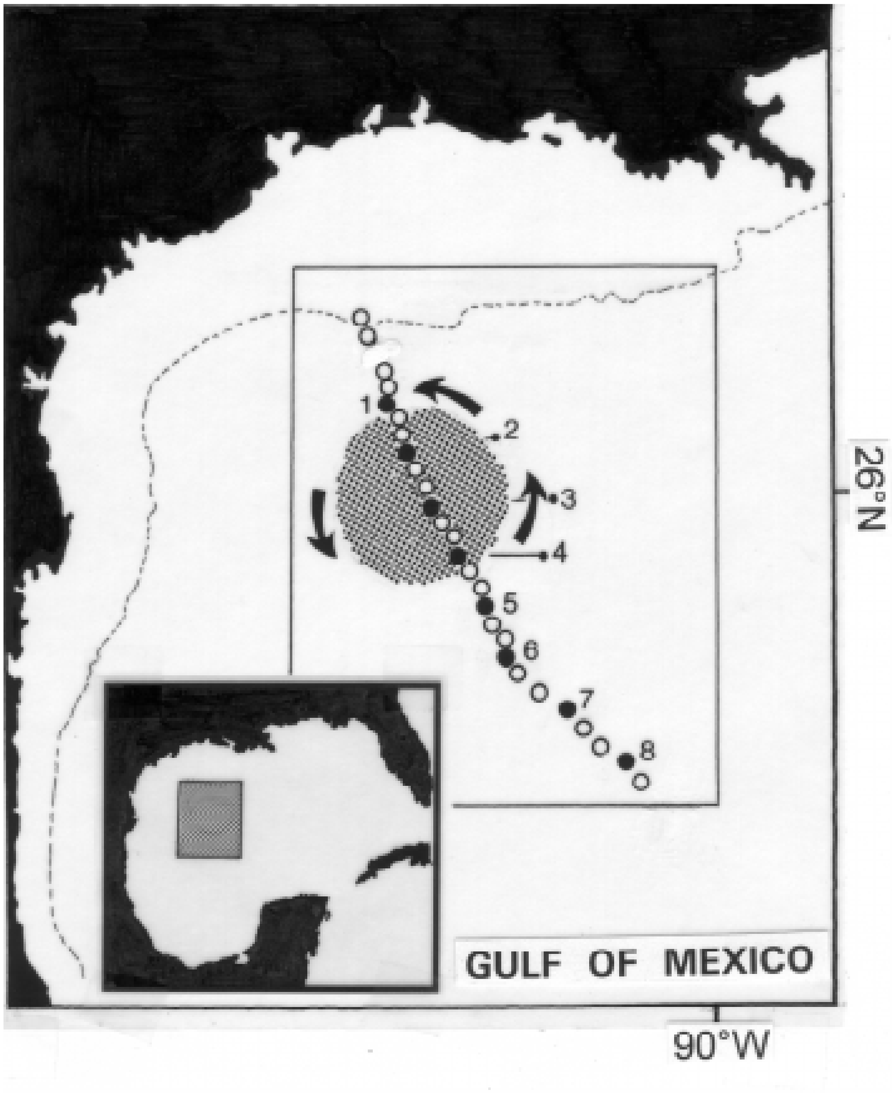

Fig. 1. Surveyed area showing arrangement of hydrographic (open circles) and zooplankton sampling stations (filled circles), during transit of a CCR in the central western Gulf of Mexico. Arrows indicate the direction of surface currents associated with the cyclone.

**Table 1.** Data of zooplankton sampling during the R/V “Gyre” cruise in March, 1993

| Station | Date | Time | Filtered volume(m3) | Salinity o/oo | Temp. °C | Biomass gr/1000m3 |
|---|---|---|---|---|---|---|
| 1 | 10-03-93 | 12:12 | 810 | 35.95 | 23.1 | 125.98 |
| 2 | 10-03-93 | 15:52 | 559 | 35.97 | 23.4 | 34.92 |
| 3 | 10-03-93 | 19:29 | 584 | 36.15 | 22.7 | 76.03 |
| 4 | 10-03-93 | 23:18 | 508 | 36.03 | 22.0 | 94.57 |
| 5 | 11-03-93 | 03:08 | 485 | 36.07 | 22.3 | 99.05 |
| 6 | 11-03-93 | 07:03 | 454 | 36.19 | 22.7 | 41.94 |
| 7 | 11-03-93 | 11:10 | 670 | 36.18 | 23.9 | 31.70 |
| 8 | 11-03-93 | 16:08 | 616 | 36.17 | 23.8 | 43.64 |
| 9 | 11-03-93 | 21:17 | 686 | 36.26 | 23.4 | 76.44 |

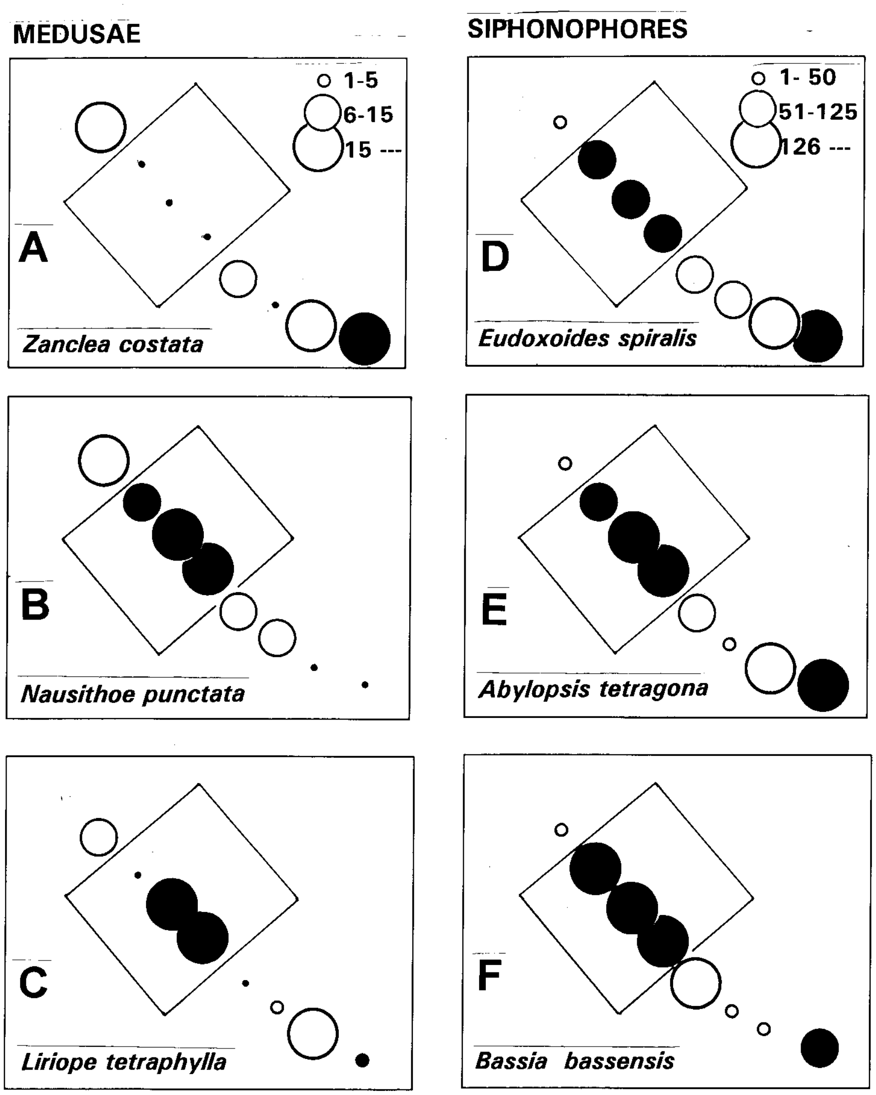

Fig. 2A-F. Numerical abundance (org./1000m$^3$) of selected medusae and siphonophores at each of the sampling stations across the CCR. Open circles indicate daytime samples, filled circles are nighttime samples.

**Table 2.** Density (org./1000m$^3$) of the medusae collected in the upper 100 m during March, 1993 on board the R/V Gyre

| Species/Stations | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | TD | AD | RA |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nausithoe punctata* Kølliker, 1853 | 21.4 | 13.6 | 86.4 | 24.8 | 8.8 | 6 |  |  | 161 | 20.1 | 20 |
| *Liriope tetraphylla*(Cham. & Eysen. 1821) | 14.4 |  | 39.2 | 41.2 |  | 6 | 19.2 | 6 | 126 | 15.8 | 15.6 |
| *Zanclea costata* Gegenbaur 1856 | 21.4 |  |  |  | 8.8 |  | 192 | 112 | 334.2 | 41.8 | 41.3 |
| *Rhopalonema velatum* Gegenbaur 1856 | 21.6 |  | 8 | 8 |  |  |  | 6 | 43.6 | 5.5 | 5.4 |
| *Euphysora gracilis*(Brooks 1882) | 7.2 |  |  |  |  |  |  |  | 7.2 | 0.9 | 0.9 |
| *Solmundella bitentaculata*(Quoy & Gaim. 1833) |  |  | 8 |  |  |  |  |  | 8 | 1 | 1 |
| *Amphinema rugosum*(Mayer 1900) |  |  | 8 |  |  |  |  |  | 8 | 1 | 1 |
| *Bougainvillia platygaster* (Haeckel 1879) | 7.2 |  | 8 |  |  | 12 | 12.8 |  | 40 | 5 | 4.9 |
| *Cunina octonaria* McCrady 1857 | 7.2 | 8 |  |  |  | 6 |  |  | 21.2 | 2.7 | 2.6 |
| *Pegantha triloba* Haeckel 1879 |  |  |  | 24.8 |  |  |  |  | 24.8 | 3.1 | 3 |
| *Euphysora furcata* Kramp 1948 |  |  |  | 16 |  |  | 12.8 |  | 28.8 | 3.6 | 3.5 |
| *Cytaeis tetrastyla* Eschscholtz 1829 |  |  |  |  |  |  |  | 6 | 6 | 0.8 | 0.7 |
| *Total* | 100.5 | 21.6 | 157.6 | 114.8 | 17.6 | 30 | 236.8 | 130 |  |  | 100 |

TD=Total density; AD= Average density; RA= Relative abundance.

annon-Wiener's Diversity was determined, and the Bray-Curtis Similarity Index was used to cluster stations with similar density and composition (Ludwig & Reynolds 1988). These indices were calculated using the ANACOM software (De la Cruz 1997).

## Results

*Hydrography*

The ADCP-measured currents were anti-clockwise in direction around the CCR and were in close agreement in speed with those computed from the along-track horizontal geopotential gradient in relation to a reference level of 800 db. The CCR was manifested as a 14 cm difference in sea surface height (SSH) from the surrounding water (a low 88 dyn cm in the interior of the CCR versus 102 dyn cm to the north and south). Both TOPEX Cycle 18 and TOPEX Cycle 17 linages from 10 days earlier confirmed the location of this cold-core ring (see Biggs *et al.*, 1997). The CCR measured about 150 km in diameter and in its interior the 8°C isotherm domed to <500 m and the 15°C isotherm to < 150 m.

Results of our taxonomic and ecologic analysis of medusae and siphonophores in the eight plankton tows are reported separately, by taxonomic groups, as follows:

*Medusae*

The highest total density of medusae was recorded during tow 7, followed by tows 3 and 8 (Table 2).The average density during daylight samples (96 org./1000m$^3$) was slightly less than the nighttime average (106 org./1000m$^3$) (Table 2).

Medusae were represented by 12 species (see Table 2). On average, 77 % of the medusae were represented by a group of three dominant species: *Zanclea costata* (41 % of total medusae numbers; mean density: 42 org./1000m$^3$), *Nausithoë punctata* (20 %; 20 org./1000m$^3$), and *Liriope tetraphylla* (16 %; 16 org./1000m$^3$). The density of medusae at each trawl is shown in table 2. Note that *Liriope tetraphylla* and *N. punctata* both occurred at six of the eight sampling stations where net tows were performed.

Cumulatively, the numerical abundance of medusae was similar within and outside the CCR. Medusae averaged 98 org./1000m$^3$ within the CCR (night: station 2-4), 100 org./1000m$^3$ at station 1 (daylight: NW of CCR), and 94 org./1000m$^3$ at stations 5, 6, and 7 (daylight:SE of CCR). In all, about 36% of the total medusae were collected within the CCR. The average abundance was slightly higher inside (93.2 org/1000m$^3$) than outside (86.5 org/1000m$^3$) the CCR.

However, the two most abundant medusan species in the CCR (*N. punctata* and *L. tetraphylla*) reached an abundance 3-6 times higher within the CCR than outside it (*N. punctata*: 42 org/1000m$^3$ inside vs 7org/1000m$^3$ outside CCR; *L. tetraphylla*: 27org/1000m$^3$ inside vs 9 org/1000m$^3$ outside CCR). Although these differences

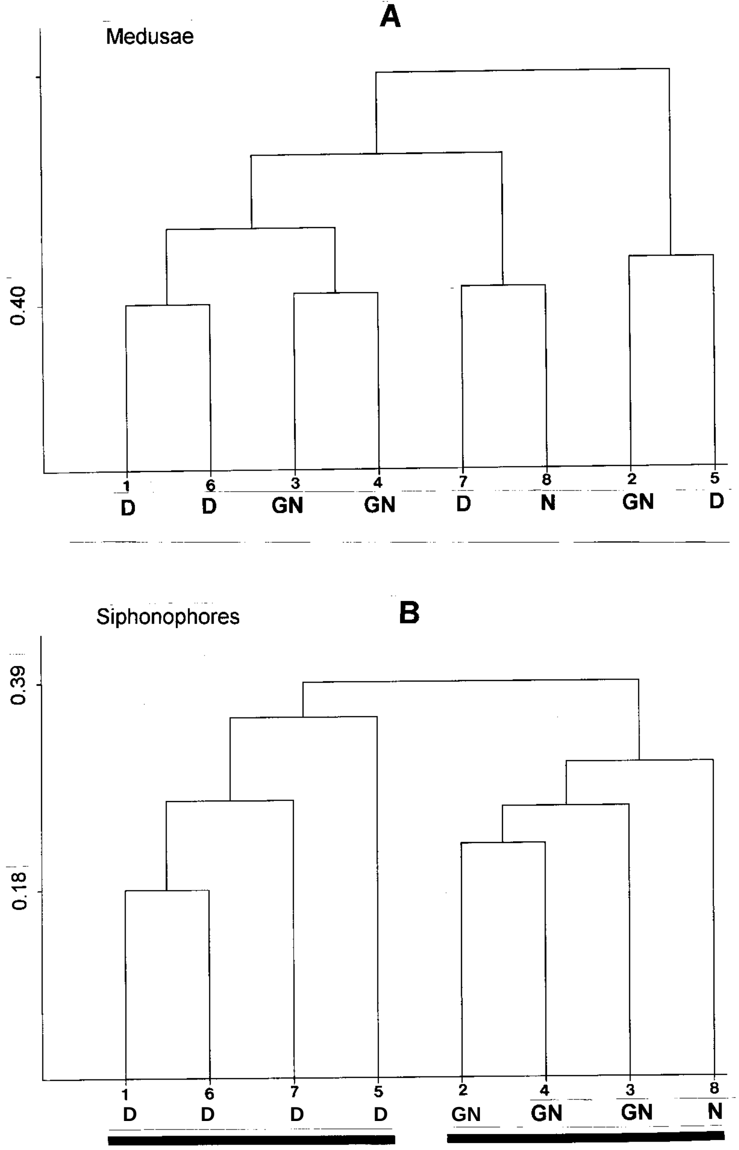

Fig. 3. Dendrograms showing clusters of stations from the Bray-Curtis Index for: A) medusae, and B) siphonophores during the surveyed period. Each branch indicates the station number and distinguishes day (D), night (N), and within cold-core ring at night (GN) samples.

were found to be not statistically significant, about 75% of the overall numerical abundance of *N. punctata* was recorded within the CCR and about 63 % that of *L. tetraphylla*. The most abundant species elsewhere in this survey, *Z. costata*, was not recorded within the CCR. This species was recorded in four of the five collections made outside the CCR ( Figs. 2A-C, Table 3). Table 3 shows that the two species that together comprised over 66% of all medusae inside the CCR (*N. punctata* and *L. tetraphylla*) were rare outside it and some of the species most common outside (combined >66% of all medusae outside) were either absent (*Z. costata, C. tetrastyla*) or rare (*E. gracilis, B. platygaster*) inside the CCR.

Mean diversity was low overall, averaging <1.8 bits/ind. Shannon-Wiener diversity averaged slightly higher (1.14) at the three stations within the CCR than at the five outside it (0.85). Clustering revealed three station groups showing a mixture of day and night stations, and stations within and outside the CCR (Fig. 3A).

### *Siphonophora*

The highest density of siphonophores was recorded during tow 8, followed by tows 7 and 4 (Table 4). The average siphonophore density during daylight samples ( 393org./1000m$^3$) was about 60% that of the average nighttime figure ( 645org./ 1000m$^3$).

A total of 25 species of Siphonophora were collected in the surveyed area (Table 4). Seven species, when added together, comprised >90% of all the siphonophores at most of the eight stations. These were two species of *Eudoxoides*, two of *Abylopsis*, *Bassia bassensis*, *Chelophyes appendiculata*, and *Diphyes bojani* ( Table 4). On average, 76 % of the siphonophores were represented by just three of the seven species mentioned above: *Eudoxoides spiralis*, *Abylopsis tetragona,* and *Bassia bassensis* (Table 4). In contrast to what was found for the medusae, the most abundant siphonophore species within the CCR were also the most abundant outside (together, the seven species above represented 92% of siphonophores within the CCR, and 88% outside the CCR). In terms of percent abundance the seven most abundant siphonophores during the day were the same as those most abundant at night.

The average density/station of siphonophores within the CCR (579 org./1000m$^3$) was higher than that recorded at the non-CCR stations ( 483org./1000m$^3$). However, the average of the night CCR stations (579 org./1000m$^3$ ) was lower than the abundance recorded in the other night trawl (840 org./1000m$^3$). The three most abundant species outside the CCR showed lower values of mean density and percent abundance inside it ( Table 5). Four species of siphonophores were obtained only inside the CCR, and seven species occurred outside, but were absent inside the CCR (Table 5). Two species of *Lensia* (*L. challengeri*, *L. fowleri*) and two of *Ceratocymba* (*C. leuckarti*, *C. sagittata*) were found only within the CCR. Conversely, two other uncommon species of *Lensia* (*L. hotspur*, *L. cossack*), a third species of *Ceratocymba* (*C. dentata*), and four other uncommon species (*Sulculeolaria turgida*, *S. chuni*, *Abyla haeckeli*, and *A. rosacea*) were found only outside the CCR. The distribution of the most abundant species is shown in Figs. 2D-F.

**Table 3.** Inside vs. outside cold-core ring (CCR)density values of species of medusae

| | Inside CCR | / | Outside CCR | |
|---|---|---|---|---|
| Species/ Stations | Mean density (org/1000 m$^3$) | Relative density % | Mean density (org/1000 m$^3$) | Relative density % |
| *Nausithoe punctata* | 41.6 | 41.9 | 6.8 | 7.04 |
| *Liriope tetraphylla* | 26.8 | 27.0 | 7.6 | 7.8 |
| *Zanclea costata* | — | — | 55.7 | 57.1 |
| *Rhopalonema velatum* | 5.33 | 5.37 | 4.6 | 4.7 |
| *Euphysora gracilis* | 1.2 | 1.21 | — | — |
| *Solmundella bitentaculata* | 2.7 | 2.6 | — | — |
| *Amphinema rugosum* | 2.7 | 2.6 | — | — |
| *Bougainvillia platygaster* | 2.7 | 2.6 | 5.33 | 5.47 |
| *Cunina octonaria* | 2.7 | 2.6 | 2.2 | 2.25 |
| *Pegantha triloba* | 8.3 | 8.3 | | |
| *Euphysora furcata* | 5.3 | 5.4 | 12.8 | 13.3 |
| *Cytaeis tetrastyla* | — | — | 1.0 | 1.02 |
| *Aurelia aurita* | — | — | 1.33 | 1.36 |

— absence of the species either within or outside the CCR.

Mean diversity was moderate overall, at just over 2.0 bits/ind. However, average siphonophore diversity was similar within the CCR (1.83) than outside it (1.76). Clustering revealed two station groups. The first one included all the daylight collections outside the CCR. The second assemblage contained all the night stations, including a subgroup containing three within-CCR stations and an isolated subgroup with night station 8 (Fig. 3B).

## Discussion

*Medusae*

All the species of medusae collected during this survey have been recorded previously in the Gulf of Mexico (Phillips 1972; Segura-Puertas 1992; Segura-Puertas & Ordóñez-López 1994). Segura-Puertas and Ordóñez-López (1994) reported six species (*A. hemistoma*, *L. tetraphylla*, *N. punctata*, *R. velatum*, *E. gracilis*, and *Z. costata*) as being the most representative in surface waters of the southern Gulf of Mexico. Results of our survey largely agree with this scheme. At least two of these species (*N. punctata*, *Z. costata*) have been reported as highly abundant in other Atlantic areas as well (Gili & Pagès 1987; Gili *et al*. 1988). As recorded herein, the medusan fauna of the western central Gulf of Mexico seems to be a typical oceanic assemblage with the presence of some neritic forms.

The community structure of the medusae within and outside the CCR showed some variation in terms of species richness and density. The two species of medusae that comprised over two-thirds of all medusae inside the CCR were rare outside this feature (combined, their numbers are less than 15% of total numbers of medusae outside). Conversely, those species that combined represented over two-thirds of all medusae outside were either absent or rare inside the CCR. Since *N. punctata* was absent in the only non-CCR night sample (station 8), we speculate that this species finds better conditions within the CCR, where more than 75 % of the individuals of this species were captured. However, this distribution could be due to the migratory pattern of this species if it was transported upwards from subsurface waters into the upper 100 m as a consequence of the doming of isotherms within the ring. On the other hand, the absence of *Z. costata* within the CCR does not seem to be related to migrational patterns during nighttime collections because in the other nighttime sample (station 8, outside the CCR) this species was highly abundant (Table 2). Hence, the absence of *Z. costata* may indicate the presence of local cyclonic circulation in the Gulf of Mexico. In fact, Segura-Puertas & Ordóñez-López (1994) pointed out that some species of medusea apparently avoid upwelled waters with locally cool surface temperature in the Bay of Campeche, located to the SSW of our study area.

Three medusan species (*S. tentaculata*, *A. rugosum*, *P. triloba*) occurred exclusively within the CCR, probably as a result of migrational behavior because they were not present in station 8. Two species (*C. tetrastyla* and *E. gracilis*) were present

**Table 4.** Density (org./1000m$^3$) of the siphonophores collected in the upper 100 m during March, 1993 on board the R/V Gyre

| Species\ Station | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | TD | AD | % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Agalma okeni* Eschscholtz 1825 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 6 | 13 | 1.6 | 0.28 |
| *A. elegans* (Sars, 1846) Fewkes 1880 | 0 | 7 | 0 | 8 | 0 | 0 | 0 | 6 | 21 | 2.6 | 0.47 |
| *Athoribia rosacea* (Forskål 1775) | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 6 | 0.7 | 0.14 |
| *Amphicaryon ernesti* Totton 1954 | 7 | 0 | 16 | 8 | 0 | 18 | 19 | 6 | 74 | 9.2 | 1.66 |
| *Hippopodius hippopus* (Forskål 1776) | 0 | 7 | 8 | 0 | 0 | 0 | 0 | 6 | 21 | 2.6 | 0.46 |
| *Sulculeolaria turgida* (Gegenb. 1853) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 6 | 0.7 | 0.13 |
| *S. chuni* (Lens & van Riemsdijk 1908) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 12 | 1.4 | 0.26 |
| *Diphyes dispar* Cham. & Eysen. 1821 | 0 | 0 | 8 | 25 | 0 | 6 | 0 | 35 | 74 | 9.2 | 3.18 |
| *D. bojani* (Eschscholtz 1829) | 14 | 55 | 32 | 25 | 18 | 12 | 25 | 0 | 181 | 22.6 | 4.04 |
| *Lensia campanella* (Moser 1925) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0.6 | 0.11 |
| *L. challengeri* Totton 1954 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 8 | 1 | 0.18 |
| *L. hotspur* Totton 1941 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 6 | 15 | 1.8 | 0.33 |
| *L. subtilis* (Chun 1886) | 0 | 0 | 0 | 8 | 9 | 0 | 13 | 12 | 42 | 5.2 | 0.93 |
| *L. fowleri* (Bigelow 1911) | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | 16 | 2 | 0.35 |
| *L. cossack* Totton 1941 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 6 | 0.7 | 0.13 |
| *Chelophyes appendiculata* (Esch.1829) | 43 | 7 | 39 | 8 | 0 | 6 | 45 | 58 | 207 | 25.8 | 4.62 |
| *Eudoxoides mitra* (Huxley 1859) | 36 | 48 | 8 | 49 | 53 | 12 | 32 | 193 | 430 | 53.7 | 9.61 |
| *E. spiralis* (Bigelow 1911) | 43 | 110 | 87 | 131 | 62 | 96 | 331 | 134 | 993 | 124 | 26.2 |
| *Ceratocymba leuckarti* (Huxley 1859) | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 8 | 1 | 0.18 |
| *C. sagittata* (Quoy & Gaimard 1827) | 0 | 0 | 8 | 8 | 0 | 0 | 0 | 0 | 16 | 2 | 0.36 |
| *C. dentata* (Bigelow 1918) | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 13 | 1.6 | 0.29 |
| *Abyla haeckeli* Lens & v. Riems. 1908 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 9 | 1.1 | 0.20 |
| *Abylopsis tetragona* (Otto 1823) | 29 | 110 | 141 | 214 | 88 | 24 | 156 | 198 | 960 | 120 | 21.7 |
| *A. eschscholtzi* (Huxley 1859) | 21 | 14 | 0 | 0 | 0 | 30 | 45 | 41 | 160 | 20 | 3.78 |
| *Bassia bassensis* (Quoy & Gaim. 1833) | 21 | 213 | 134 | 157 | 132 | 36 | 45 | 122 | 860 | 107 | 20.3 |
| Total | 215 | 575 | 504 | 660 | 379 | 245 | 734 | 840 | 4482 | 560 | 100 |

TD=Total density; AD= Average density; RA= Relative abundance.

only outside the CCR All in all, the region around the CCR had the highest species richness of medusae: seven species at station 1, and six at station 3, but only four at station 8. These results on the medusan composition, distribution and abundance, then, generally support the paradigm that these cyclonic systems are areas with near-surface faunal assemblages different from those dwelling in the oligotrophic oceanic waters outside them (Biggs *et al.*1997; Wormuth *et al*. 2000). Thus, differences at the species level indicate that planktonic medusae are not uniformly distributed in the central Gulf of Mexico, but rather they vary in response to mesoscale changes in their physical environment.

*Siphonophores*

All siphonophore species collected during this survey are tropical-subtropical forms. The three most abundant are part of a species group considered to be dominant in the entire Gulf of Mexico (Phillips 1972; Vasiliev 1974; Gasca 1990, 1993). As might be expected from the three samples representing 38% of the entire sampling, total siphonophore numbers collected within the CCR accounted for about 39% of the total numbers of siphonophores. Nevertheless, the community of siphonophores within and outside the CCR showed species-level variations in terms of composition, species richness, and density. Stations within the CCR showed differential abundance of the commonest species; only 33 % of *E. spiralis*, compared with 48% of *A. tetragona* and 58% of *B. bassensis,* were collected within the CCR.

Possibly, near surface conditions are sub-optimum within the CCR for the otherwise dominant *E. spiralis* and even for the two other species dominant outside ( Table 5). All three species had a lower numerical abundance inside the CCR.. *Eudoxoides spiralis* has a restricted vertical distribution, in which most individuals remain in day and nighttime within the 0-100 m layer (Moore, 1953; Vasiliev, 1974). Thus, we speculate that the low nighttime abundance of *E spiralis* is likely more an effect of the CCR than of any endogenous vertical migration pattern.

*Bassia bassensis* is relatively less abundant in warmer waters and has been regarded as a winter form (Moore 1953; Gasca & Suárez-Morales 1991). About half of the total numbers of this species occurred in the three stations within the CCR, and averaged higher within the CCR than in the night station outside the CCR. It is distributed mainly in the 0-100 m layer, and is a weak vertical migrator in the Gulf (Moore 1953; Vasiliev 1974). The higher inside-CCR density of this species is probably more related to its tendency to dwell in relatively cooler conditions than to its weak day/night migrational behavior (Fig. 2F).

The cluster analysis revealed that the daylight siphonophore community differs from the night one. However, it grouped together the three CCR night stations and separated the non-CCR station, thus suggesting differences between a typical night community and the CCR night community (Fig. 3B).

**Table 5.** Inside vs. outside CCR density values of species of Siphonophora

| Species | Mean density (org/1000 m$^3$) | Relative density % | Mean density (org/1000 m$^3$) | Relative density % |
|---|---|---|---|---|
| *Bassia bassensis* | 168.0 | 29.0 | 71.2 | 14.8 |
| *Abylopsis tetragona* | 155.0 | 26.7 | 99.0 | 20.6 |
| *Eudoxoides spiralis* | 109.3 | 18.9 | 133.2 | 27.7 |
| *Diphyes bojani* | 37.3 | 6.4 | 13.8 | 2.9 |
| *Eudoxoides mitra* | 35.0 | 6.0 | 65.2 | 13.6 |
| *Chelophyes appendiculata* | 18.0 | 3.1 | 30.4 | 6.3 |
| *Diphyes dispar* | 11.0 | 1.9 | 8.2 | 1.7 |
| *Amphycaryon ernesti* | 8.0 | 1.4 | 10.0 | 2.1 |
| *Abylopsis eschscholtzi* | 7.3 | 1.3 | 27.4 | 5.7 |
| *Ceratocymba sagittata* | 5.3 | 0.9 | — | — |
| *Lensia fowleri* | 5.3 | 0.9 | — | — |
| *Agalma elegans* | 5.0 | 0.9 | 1.2 | 0.2 |
| *Hippopodius hippopus* | 5.0 | 0.9 | 1.2 | 0.2 |
| *Ceratocymba leuckarti* | 2.7 | 0.5 | — | — |
| *Lensia subtilis* | 2.7 | 0.5 | 6.8 | 1.4 |
| *Lensia challengeri* | 2.7 | 0.5 | — | — |
| *Agalma okeni* | 2.3 | 0.4 | 1.2 | 0.2 |
| *Ceratocymba dentata* | — | — | 2.6 | 0.5 |
| *Sulculeolaria chuni* | — | — | 2.4 | 0.5 |
| *Lensia hotspur* | — | — | 1.8 | 0.4 |
| *Abyla haeckeli* | — | — | 1.8 | 0.4 |
| *Lensia cossack* | — | — | 1.2 | 0.2 |
| *Athorybia rosacea* | — | — | 1.2 | 0.2 |
| *Sulculeolaria turgida* | — | — | 1.2 | 0.2 |

In summary, the abundance and species composition of siphonophores across the CCR feature showed contrasting tendencies for different species. The lower abundance of *E. spiralis* in the relatively richer and cooler waters of the CCR (Table 5) supports the pattern described by Gasca & Suárez-Morales (1991) in which siphonophores tended to be less abundant in cooler, upwelled waters. An alternative explanation of the locally higher numerical abundance of *B. bassensis* within the CCR is its passive aggregation by the vertical displacement of cooler midwater into the surface layer. An opposite scenario for siphonophores is represented by anticyclonic, warm-core eddies (Gasca 1999). Perhaps because anticyclones are particularly oligotrophic systems, with low zooplankton concentrations (Hattori 1991; Wormuth *et al.* 2000), they have more typical subtropical siphonophore fauna. In fact, the highest species richness of siphonophores at any single station was found at night in station 8, outside the CCR, where 15 species were collected..

### *General remarks*

The broad distribution of tropical and subtropical cnidarian species indicates that they have high adaptability (Gili *et al.* 1988). This may explain the wide distribution of siphonophore and medusae species, and the fact that all have been previously reported from the Gulf of Mexico.We emphasize, though, that the most abundant species of cnidarians that we found in the central western Gulf of Mexico were not homogeneously distributed inside and outside the CCR. Instead, it appears to us that the CCR represents a discontinuity in which the cnidarian community changes shifting the dominance of the most abundant species. This is particularly evident in the distributional patterns shown by the medusae *N. punctata* and *Z. costata* and the siphonophore *E. spiralis* across the CCR. Such differences are not unique to plankton, for the distribution and abundance of one fish species is also a good indicator of frontal boundaries and hence of local regions of physical and biological interaction in the Gulf (Lamkin 1997).

If certain species of cnidarians are limited strongly by a 2°C surface temperature anomaly, then these forms may be local indicators of the anomalously cool surface conditions that are sometimes characteristic of Gulf of Mexico cyclonic eddies and/or of upwelling regions. For instance, the absence of siphonophores is a proxy for periods of locally intense upwelling over the Campeche Bank (Gasca & Suárez-Morales 1991). It appears that day-night variations were less important than differences within and outside the CCR.

As shown by Pagès & Gili (1988), there are differences in local abundance and distribution of cnidarians within mesoscale circulation features. The distribution and abundance of predators may ultimately reflect the distribution and abundance of their prey (Alvariño 1985). If the concentration of potential prey is enhanced by the hydrographic conditions and a relatively higher secondary productivity (zooplankton biomass) found within the CCR (Biggs *et al.* 1997; Wormuth *et al.* 2000) and in regional upwelling areas as well (Sánchez-Velasco & Flores-Coto 1994), then the numerical abundance of cnidarian zooplankton predators might be expected to follow this pattern. This is suggested by the slightly higher overall average numerical abundance of medusae but not by the lower numerical abundance of siphonophores within the CCR. Overall, the response of each of these two groups of cnidarians to the conditions set by the CCR is different, but even with our limited set of data, this differential response seems to be strong enough to be detected by the analysis of abundance and composition of these two cnidarian taxa. It should be considered also that besides these scales, at which the organisms interacts with its physical environment, we have to consider also the directed motility scale (i.e. search for food), and the ecological scale (see Denman, 1994). Hence, distributional surveys must have a strong background on the behavior and ecology of the organisms in order to allow sounder interpretations.

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