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SEASONAL OCCURRENCE OF REEF-RELATED MEDUSAE (CNIDARIA) IN THE WESTERN CARIBBEAN SEA

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ABSTRACT Seasonal fluctuations in composition and abundance of medusae collected in a reef lagoon of the Mexican Caribbean were analyzed. Plankton samples and hydrological data were taken monthly from January to September 1994 at 2 stations: coastal and near-reef. The highest densities of medusae were recorded in March (17,687 ind/100 m^3) and August (2,433 ind/100 m^3) at the coastal station. Medusae were less abundant at the near-reef station, but diversity indices were higher in comparison to the coastal station. Twenty-five species (24 hydroidomedusae and 1 scyphomedusa) were identified, with *Linuche unguiculata* (Swartz, 1788) and *Eirene lactea* (Mayer, 1900) being the most abundant. *Linuche unguiculata* was the dominant species, accounting for more than 84% of the total numbers of medusae in the coastal station and over 97% in the near-reef station. The co-occurrence of neritic and oceanic species in the reef-associated community of medusae is probably related to circulation patterns and wind regimes. *Dipurena ophiogaster* (Haeckel, 1879) and *Sarsia eximia* (Allman, 1859) were recorded for the first time in the Mexican Caribbean Sea.

INTRODUCTION

Generally, in tropical zones only small seasonal fluctuations in total abundance of zooplankton are common. In many cases, changes in numerical abundance of individual species can be associated with variable hydrographic conditions locally rather than with seasonal changes in production (Lewis and Fish 1969, Sale et al. 1978, Guzmán and Obando 1988). In dynamic ecosystems such as reef lagoons where the reef acts as a hydrodynamic barrier (Ogden and Gladfelter 1983), variations in planktonic communities are influenced by oceanographic factors (i.e., currents, temperature, salinity, substrate, and diel cycles) as well as by their own endogenous rhythm (Lefevre 1985).

The second largest barrier reef in the world is located along the Caribbean coast. This reef runs from Isla Contoy to Belize (Jordán 1993). Only a few studies have been conducted on the reef-related medusan fauna along this shallow barrier. Araneda (unpubl. data) analyzed diel variations of the medusan community in the fore-reef (oceanic) zone and in the reef lagoon in Puerto Morelos from June to December 1991. Suárez-Morales et al. (1999a) studied small-scale space and time variation in the medusan community of the Mahahual reef system. Gasca et al. (2003) described the community structure of the reef-related medusan fauna collected in Banco Chinchorro, a large oceanic atoll found off the southern part of the state of Quintana Roo, Mexico. In Belizean waters, Larson (1982) made a qualitative and quantitative study of medusae at Carrie Bow Cay between January and April 1978.

The present study describes changes in the numerical abundance, composition, and diversity of the reef-related medusae between January and September 1994 in the Puerto Morelos reef lagoon in the Mexican Caribbean Sea. The surveyed area is located at 20°52'N and 86°51'W on the northeastern coast of the Yucatan Peninsula. The oceanographic characteristics of this zone are influenced by the northward flow of the Yucatan Current and by a countercurrent that runs south very close to the continental slope which varys in strength and size throughout the year (Merino 1997). On the Caribbean coast the shelf is very narrow, ranging between 1 and 2 km and widening to the north of Puerto Morelos. The width of the reef lagoon (distance from sea shore to reef barrier) varies between 350 and 1600 m with an mean depth of 3 m and a maximum depth of 8 m (Merino and Otero 1991). The bottom is alternately covered by calcareous sand and large patches of seagrasses dominated by *Thalassia testudinum* (Banks ex König). The water column is highly transparent. Horizontal secchi disk readings as measured by the CARICOMP group in 1992–1993 averaged 15 m—a range of 5 to 20 m. Surface temperature during the same period ranged between 25 and 31 °C with almost constant salinity near 36 psu (Ruiz-Rentería et al. 1998). The tidal regime is mixed semi-diurnal, with a small range of 0.24 m (Instituto de Geofísica 1992).

MATERIALS AND METHODS

Field methods

Zooplankton samples and hydrological data were collected at monthly intervals from January to September 1994 between 18:00 and 19:30 h at 2 stations. Station A is about 20 m off the coast and station B is located near the reef about 800 m from the coast (Figure 1). Station B was not sampled in January and August due to bad weather. A near-surface horizontal haul of ~10 min duration following

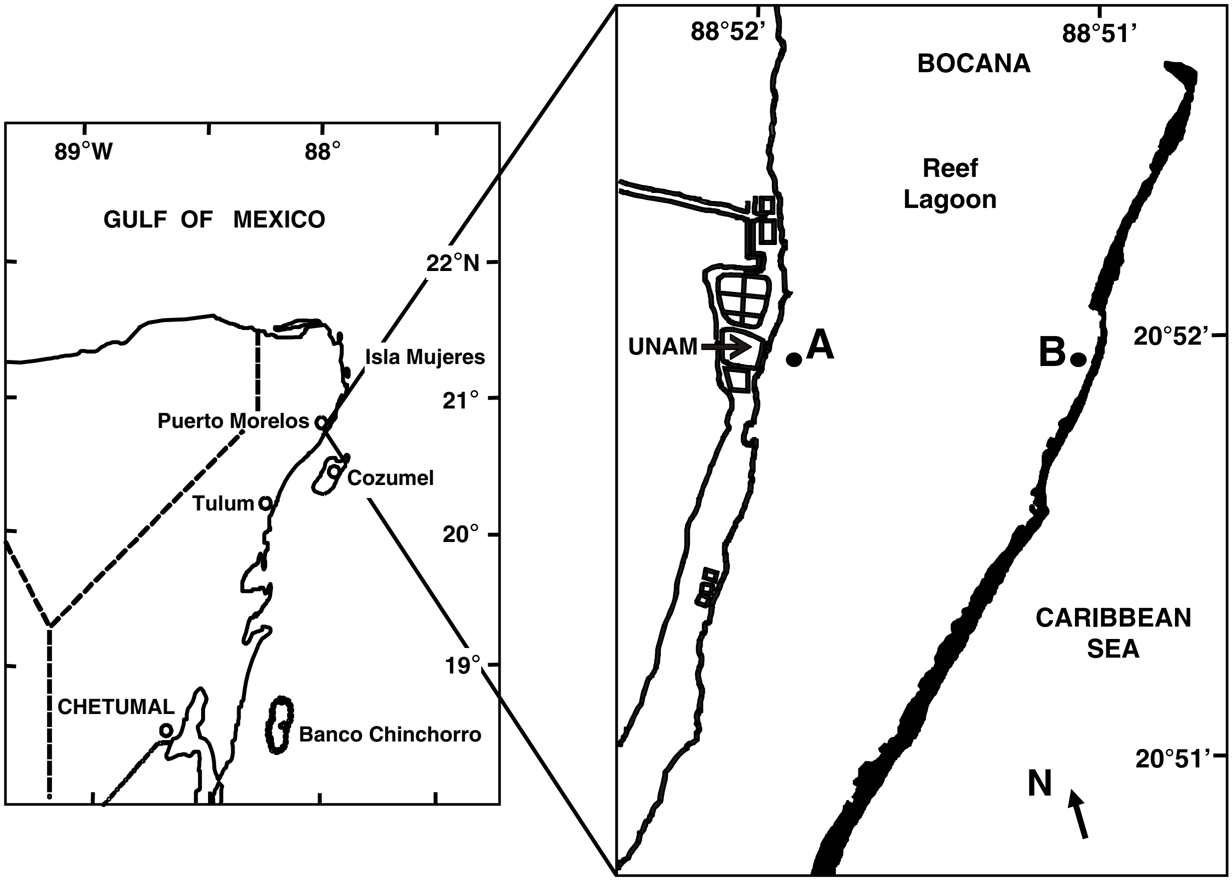

Figure 1. Location of the 2 sampling stations in the Puerto Morelos reef lagoon.

a circular path at 1.5 kn was made at each station with a conical plankton net (40 cm mouth diameter, 1.30 m length and 0.33 mm mesh-size). A digital flow-meter (General Oceanics, USA) was attached to the mouth to estimate the volume of water filtered. Zooplankton samples were fixed in a 4% formaldehyde solution buffered with sodium borate (Smith and Richardson 1979). Temperature was measured in situ with a bucket thermometer and salinity was measured in the laboratory using a Beckman induction salinometer.

Laboratory methods

All medusae were sorted, identified, and counted then the counts were standardized to number of individuals per 100 m^3. Taxonomic references for identifications and nomenclature follow Mayer (1910), Russell (1953), Kramp (1959, 1961), Bouillon (1985), and Bouillon and Boero (2000).

Because data were not distributed normally, a non-parametric paired sample Wilcoxon test (Zar 1974) was applied to evaluate differences in density between the 2 sampled stations. Additionally, a paired t-test (Zar 1974) was applied to log_{10}-transformed data after exclusion of the dominant species *Linuche unguiculata* (Swartz). Diversity was estimated using the Shannon-Wiener Index (Krebs 1985). The Pearson correlation coefficient (*r*) was used to infer relationships between species abundance and physical factors.

RESULTS

Surface temperatures during the survey period ranged from 27.2 to 30.9 °C, with minimum values in February and March and maximum values in August. The temperature was similar at the 2 stations, differing by less than 1 °C. Salinity ranged from 35.7 to 36.2 psu, with a minimum in February and September and a maximum in July (Figure 2).

Total density of medusae showed temporal variation throughout the survey period. Two density pulses were obseved at station A. The highest was recorded in March, with 17,687 ind/100 m^3 and was dominated by the scyphomedusa *L. unguiculata*. The second highest density occurred in August with 2,433 ind/100 m^3, with the most abundant species being the hydroidomedusa *Eirene lactea* (Mayer). The lowest density was recorded in January with

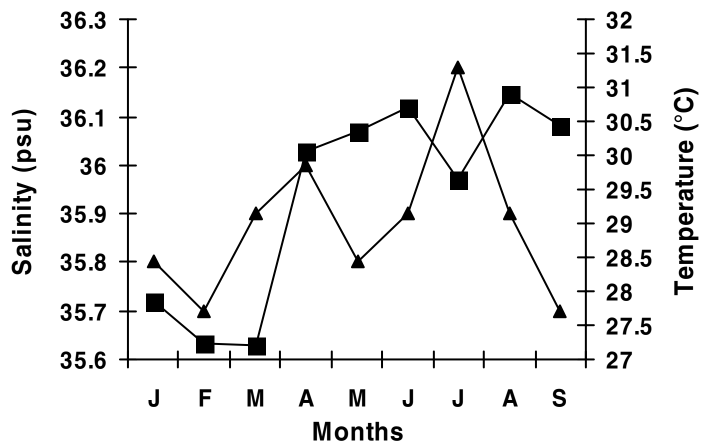

Figure 2. Monthly variation in the mean surface temperature (°C) and salinity (psu) in the study area during January to September 1994.

5 ind/100 m^3. At station B, the highest density was also observed in March with 9,478 ind/100 m^3 again dominated by *L. unguiculata*. The lowest density at station B occurred in May with 8 ind/100 m^3 (Figure 3). There was no significant difference in the mean density between the 2 sampled stations when *L. unguiculata* was included in the analysis ($z = 1.352$, $P = 0.176$, $n = 7$) or when it was excluded ($t = 0.647$, $P = 0.117$, $n = 7$). There was no significant correlation between water temperature or salinity and the overall density of medusae at either station. Indices for temperature were $r = 0.44$, $P = 0.24$; $r = 0.1$, $P = 0.94$ and for salinity $r = 0.09$, $P = 0.99$; $r = -0.21$, $P = 0.48$.

A total of 25 species (24 hydroidomedusae and 1 scyphomedusa) were recorded in the surveyed area (Tables 1 and 2). *Linuche unguiculata* was by far the most abundant species, accounting for more than 84% of the total population of medusae at the coastal station and over 97% at the near-reef station. *Eirene lactea* was the second most abundant species, representing 14% of the total number of medusae at the coastal station. By contrast, other species such as *Amphinema rugosum* (Mayer), *Dipurena halterata* (Forbes), *Zanclea costata* (Kramp), *Clytia hemisphaerica* (Linné), and *Aglaura hemistoma* Péron and Lesueur were recorded only once during the entire survey. The collection

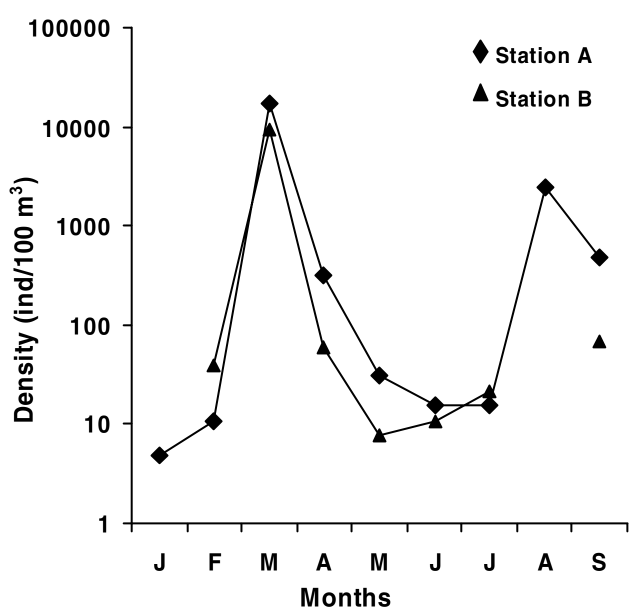

Figure 3. Monthly density (ind/100 m^3) of medusae recorded at 2 sampling locations during January to September 1994.

TABLE 1

Density (ind/100 m^3), relative abundance (RA), and relative frequency (RF) of the species of medusae collected monthly at station A in the Puerto Morelos reef lagoon in 1994. *First record for the Mexican Caribbean Sea.

SPECIES	J	F	M	A	M	J	J	A	S	TOTAL	RA	RF
Hydractinia carnea (M. Sars, 1846)					1.6					1.6	0.0	11.1
Hydractinia minuta (Mayer, 1900)				14.7	6.6					21.2	0.1	22.2
Amphinema dinema (Péron and Lesueur, 1809)								1.5		1.5	0.0	11.1
**Dipurena ophiogaster* Haeckel, 1879				91.6						91.6	0.4	11.1
Sarsia angulata (Mayer, 1900)			6.3	12.8	1.6			1.5	3.1	25.4	0.1	55.5
**Sarsia eximia* (Allman, 1859)	1.6	3.1	6.3	137.4	8.2	1.7		3.09	3.1	164.5	0.8	88.8
Sarsia prolifera Forbes, 1848	1.6	1.6		5.5						8.6	0.0	33.3
Vannuccia forbesii (Mayer, 1894)					1.6					1.6	0.0	11.1
Euphysa sp. Bouillon, 1974		1.6								1.6	0.0	11.1
Eirene lactea (Mayer, 1900)				29.3	3.3		7.8	2422.2	463.1	2925.6	13.9	55.5
Eucheilota paradoxica Mayer, 1900				3.7	3.3					6.9	0.0	22.2
Clytia discoida (Mayer, 1900)				3.7				1.5	15.5	20.7	0.1	33.3
Clytia folleata (McCrady, 1859)	1.6	1.6		1.8	1.6					6.6	0.0	44.4
Clytia hemisphaerica (Linné, 1767)						8.5				8.5	0.0	11.1
Cubaia aphrodite Mayer, 1894		1.6	1.6	11.0	3.3	1.7		1.5		20.6	0.1	66.6
Vallentinia gabriellae (Mendes, 1948)									1.6	1.6	0.0	11.1
Liriope tetraphylla (Chamisso and Eysenhardt, 1821)							3.1			3.1	0.0	11.1
Aglaura hemistoma Péron and Lesueur, 1810							1.6			1.6	0.0	11.1
Linuche unguiculata (Swartz, 1788)		1.6	17672.9	5.5		1.7	1.6	1.5	1.6	17686.3	84.2	77.7
TOTAL	**4.8**	**10.9**	**17687.1**	**316.9**	**31.1**	**15.3**	**15.5**	**2433.0**	**487.9**	**21002.6**	**100.0**	

TABLE 2

Density (ind/100 m^3), relative abundance (RA), and relative frequency (RF) of the species of medusae collected monthly at station B in the Puerto Morelos reef lagoon in 1994. *First record for the Mexican Caribbean Sea.

Species	F	M	A	M	J	J	S	TOTAL	RA	RF
Hydractinia carnea (M.Sars, 1846)			3.4				4.7	8.1	0.1	28.6
Hydractinia minuta (Mayer, 1900)			8.6			1.6		10.1	0.1	28.6
Amphinema dinema (Péron and Lesueur, 1809)		1.4			1.5	1.6	1.6	6.0	0.1	57.1
Amphinema rugosum (Mayer, 1900)						1.6		1.6	0.0	14.3
Dipurena halterata (Forbes, 1846)							1.6	1.6	0.0	14.3
**Dipurena ophiogaster* Haeckel, 1879			3.4					3.4	0.0	14.3
Sarsia angulata (Mayer, 1900)	1.5	5.7	1.7	4.6			6.2	19.8	0.2	71.4
**Sarsia eximia* (Allman, 1859)	6.0	2.8	15.4				12.4	36.7	0.4	57.1
Sarsia prolifera Forbes, 1848			1.7					1.7	0.0	14.3
Vannuccia forbesii (Mayer, 1894)	1.5							1.5	0.0	14.3
Zanclea costata (Kramp, 1959)	3.0							3.0	0.0	14.3
Pachycordyle sp. Weismann, 1883							3.1	3.1	0.0	14.3
Eirene lactea (Mayer, 1900)			5.1				17.1	22.2	0.2	28.6
Laodicea undulata (Forbes and Goodsir, 1851)						1.6	3.1	4.7	0.0	28.6
Eucheilota paradoxica Mayer, 1900		1.4	6.8				15.5	23.8	0.2	42.8
Clytia discoida (Mayer, 1900)	1.5	7.1		1.5	1.5		4.7	16.0	0.2	71.4
Clytia folleata (McCrady, 1859)			5.1		3.0			8.1	0.1	28.6
Obelia sp. Péron and Lesueur, 1810		1.4	6.8					8.3	0.1	28.6
Vallentinia gabriellae (Mendes, 1948)					1.5			1.5	0.0	14.3
Liriope tetraphylla (Chamisso and Eysenhardt, 1821)		1.4				10.9		12.3	0.1	28.6
Linuche unguiculata (Swartz, 1788)	18.1	9456.5			1.5	3.1		9479.0	97.9	57.1
TOTAL	**39.1**	**9477.9**	**58.2**	**7.7**	**10.5**	**21.8**	**69.9**	**9685.1**	**100.0**	

of *Dipurena ophiogaster* Haeckel and *Sarsia eximia* (Allman) in the area represent new Mexican Caribbean records for these hydroidomedusae.

Fifteen species were common to both the coastal and near-reef stations. Four species (*Euphysa* sp., *C. hemisphaerica*, *Cubaia aphrodite* Mayer, and *A. hemistoma*) were restricted to the coastal station and 6 species (*A. rugosum*, *D. halterata*, *Z. costata*, *Pachycordyle* sp., *Laodicea undulata* (Forbes and Goodsir), and *Obelia* sp.) occurred only at the near-reef station. Most of the species recorded are neritic forms, with only 2 oceanic species collected—*A. hemistoma* and *Liriope tetraphylla* (Chamisso and Eysenhardt).

Species richness was highest at the near-reef station where 21 of the 25 species were collected. The lowest number of species (2) was recorded in May and the highest number of species (10) was recorded in April and September. Nineteen species were collected at the coastal station with the lowest number (3) being observed in January and the highest number (11) in April (Table 3). In the near-reef station, the values of the Shannon-Wiener diversity were high, varying from 0.03 to 3.04 (March and April, respectively). The coastal station had lower diversity values of 0.01 to 2.90 in March and May, respectively.

DISCUSSION

Density of medusae recorded in this study ranged from a minimum of 5 to a maximum of 17,687 ind/100 m^3. Araneda (unpubl. data), in a study of medusan fauna in the Puerto Morelos reef lagoon, found densities ranging from 76 to 28,000 ind/100 m^3. The densities recorded at Mahahual reef by Suárez-Morales et al. (1999a) ranged between 1 and 195 ind/100 m^3, whereas Gasca et al. (2003), studying the medusae at Banco Chinchorro, reported mean densities ranging between 12 and 182 ind/100 m^3. In the waters from Carrie Bow Cay, Belize, Larson (1982) reported mean densities of medusae ranging between 1 and

TABLE 3

Species of medusae collected monthly at stations A and B in the Puerto Morelos reef lagoon in 1994.

(MONTH/STATION)	J	F		M		A		M		J		J		A	S	
SPECIES	**A**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**A**	**B**
Hydractinia carnea							+	+								+
Hydractinia minuta						+	+	+					+			
Amphinema dinema					+						+		+	+		+
Amphinema rugosum													+			
Dipurena halterata																+
Dipurena ophiogaster						+	+									
Sarsia angulata			+	+	+	+	+	+	+					+	+	+
Sarsia eximia	+	+	+	+	+	+	+	+		+				+	+	+
Sarsia prolifera	+	+				+	+									
Vannuccia forbesi			+					+								
Euphysa sp.		+														
Zanclea costata			+													
Pachycordyle sp.																+
Eirene lactea						+	+	+				+		+	+	+
Laodicea undulata													+			+
Eucheilota paradoxica					+	+	+	+								+
Clytia discoida			+		+	+			+		+			+	+	+
Clytia folleata	+					+	+	+			+					
Clytia hemisphaerica										+						
Obelia sp.					+		+									
Cubaia aphrodite		+		+		+		+		+				+	+	
Vallentinia gabriellae											+					
Liriope tetraphylla			+		+							+	+			
Aglaura hemistoma												+				
Linuche unguiculata		+	+	+	+	+				+	+	+	+	+	+	
TOTAL	**3**	**5**	**7**	**4**	**8**	**11**	**10**	**9**	**2**	**4**	**5**	**4**	**6**	**7**	**6**	**10**

831 ind/100 m^3. The differences in density recorded in these studies may be the result of hydrographic and ecological features of each of the sampled areas. Differences in density may also reflect local high aggregations of particular species and may be linked to different sampling efforts over different temporal and spatial scales.

The overall density of the medusan fauna showed seasonal variability throughout the studied period and were dominated by *L. unguiculata*. This small coronate scyphomedusa occurs in dense aggregations during the spring. Recently, the whole life cycle of *L. unguiculata* under natural and experimental conditions, has been studied in relation to outbreaks of “seabather's eruption” in the Mexican Caribbean (Segura-Puertas et al. 2001). In late January the scyphistomae (polyps) release huge numbers of ephyrae which grow and mature into adults between March and May. In May and early June, the planktonic planulae of the next generation appear in abundance. The phases of the life cycle can be observed sequentially, overlapping from late winter until late spring (Segura-Puertas et al. 2001). The seasonal occurrence of this species seems to be a distinctive and dominant feature of the neritic and near-ocean environments along the western Caribbean Sea (Larson 1982, Suárez-Morales et al. 1999b) and is influenced by an increase in the water temperature (Segura, in prep.). Larson (1992), studying aggregations of *L. unguiculata* along the Belizean reef barrier, found that physical factors, especially Langmuir circulation and the circular swimming behavior of the medusae, are the primary mechanisms responsible for such aggregations. According to this author, swarms of this scyphomedusa probably improve fertilization by minimizing sperm dilution. Larson (1992) also found that wind patterns (direction and speed) play an important role in the variation of both the shape and the density of the aggregations. The highest numbers of *L. unguiculata* recorded in the survey area may be partially determined by the wind regime. When the east and southeast trade winds are dominant, dense aggregations of this species accumulate in the reef lagoon and along the shore line. In contrast, when northerlies are dominant, the aggregations are observed in the open sea.

Eirene lactea was the second most dense species of hydroidomedusa recorded. The highest density value was observed in August. Similar results were obtained by Araneda (unpubl. data), who recorded *E. lactea* as a dominant species with the highest density in September and October. Differences in time suggest an interannual variability between the pulses of maximum density of this neritic species. In contrast, the communities of medusae recorded off Mahahual, Banco Chinchorro, and Carrie Bow Cay, Belize were numerically dominated by 2 oceanic species, *L. tetraphylla* and *A. hemistoma* (Larson 1982, Suárez-Morales et al. 1999a, Gasca et al. 2003). The difference in composition indicates distinct community structures and may be due to local hydrology interactions with topography.

No significant correlations between temperature or salinity and density of medusae were found. These results suggest that the community of medusae may be controlled by other factors such as hydrographic conditions, food availability, and in the case of hydroidomedusae, the complexity of their life cycles.

The medusan fauna is particularly diverse in reef environments. The number of species recorded in the present study was 25. This is lower than that recorded in Carrie Bow Cay, Belize (71 species) by Larson (1982) but higher than those found in Mahahual (17 species) by Suárez-Morales et al. (1999a) and in Banco Chinchorro (16 species) by Gasca et al. (2003). The differences in diversity observed among the locations may result partially from the different sampling efforts and may also reflect the heterogeneity of methods used in the collection. For example, in the study by Larson (1982) medusae were captured using a plankton net, by beach seine, night light, dip net, and while diving.

The Shannon-Wiener species diversity indices obtained in our study can be considered as high, especially at the near-reef station (3.04). This increase the local species richness clearly reveals the influence of oceanic water in the reef lagoon system. The occurrence of *L. tetraphylla* and *A. hemistoma*, although in low numbers, can be considered an indication of oceanic influence. This effect has been observed by other authors in adjacent reef areas (Larson 1982, Suárez-Morales et al. 1999a, Gasca et al. 2003) and may be a consequence of the narrowness of the continental shelf in the region.

Only 50% of the species recorded in this work have been reported previously from the Campeche Bank and part of the Mexican Caribbean (Segura-Puertas 1992, Segura-Puertas and Ordóñez-López 1994), whereas 61% are known from coastal environments along the Mexican Caribbean (Zamponi et al. 1990, Suárez-Morales et al. 1997, 1999a, b). Only 2 species collected in the surveyed area, *D. ophiogaster* and *S. eximia*, have not been recorded previously in the Mexican Caribbean Sea.

Dipurena ophiogaster is a small hydroidomedusa that has been recorded on the south coast of Britain (Haeckel 1879), in the Mediterranean (Chun 1896), in Ceylon (Mayer 1910), in the south of Japan (Yamazi 1958), in the Bay of Valencia, Ireland (Russell 1938), in the Palau Islands, Central Pacific (Uchida 1947), and in the Gulf of Mexico (Phillips 1972).

Sarsia eximia is a small neritic species. The distribution of this species includes northwestern Europe, the western region of the Mediterranean, the west coast of North America (Kramp 1958), the Adriatic Sea (Mayer 1910), the British Isles (Russell 1953) and the western tropical Pacific, Peru, and Chile (Vannucci 1957). The collection of *D. ophiogaster* and *S. eximia* in the Mexican Caribbean extends their geographical distribution limit to the western tropical Atlantic.

In summary, the surveyed area contains a relatively homogeneous medusan fauna characterized by the co-occurrence of neritic and oceanic forms regulated by the local hydrographic conditions. This community shows seasonal changes in abundance and composition with 2 important pulses—one in spring dominated by the scyphozoa *L. unguiculata* and the second during late summer characterized by the hydroidomedusa *E. lactea*. Most of the species collected have previously been recorded from the region (Segura-Puertas 1992, Segura-Puertas and Ordópez-López 1994, Suárez-Morales et al. 1999a), but there are 2 new records for the Mexican Caribbean, *D. ophiogaster* and *S. eximia*. Although this survey focused on the medusa stage only, it is important to emphasize the relevance of studying both planktonic (medusa) and benthic (polyp) phases of their life cycle to understand the dynamics of this important group.

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