

# Medusan (Cnidaria) Assemblages off the Caribbean Coast of Mexico

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## ABSTRACT

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The species composition, distribution and abundance of medusae collected off the Mexican coast of the Caribbean Sea was analyzed from samples gathered from oblique plankton tows (0-50 m) during five months (February, March, May, August and November, 1991). The highest mean medusan abundance was observed during March (2,354 org./1000 m<sup>3</sup>) while lowest values occurred in August (102 org./1000 m<sup>3</sup>). Twenty-four species and 4 genera were identified. *Linuche unguiculata*, *Liriope tetraphylla*, *Clytia mcraady* and *Aglaura hemistoma* were the most abundant. They represented more than 96% of the total medusan numbers. Cluster analysis and the known ecological affinities of the species revealed two oceanic (primary and secondary) and one neritic assemblage whose distribution showed month to month variations, apparently related to the prevailing wind regimes. Intergradation of these assemblages and the presence of oceanic and even deep-living species very near the coast was attributed to the narrowness of the continental shelf.

**ADDITIONAL INDEX WORDS:** *Medusae, zooplankton, coast, Caribbean, Mexico.*



## INTRODUCTION

Knowledge of the medusan fauna of coastal-neritic and oceanic waters of the Northwestern Tropical Atlantic is still limited (SEGURA-PUERTAS, 1992). This is especially true for the eastern coast of the Yucatan Peninsula, also known as the Caribbean coast of Mexico, where the species composition and population dynamics of medusae remain largely unknown. There is some recent work on adjacent areas, with much emphasis placed on the highly productive Campeche Bank (SEGURA-PUERTAS, 1991, 1992; SEGURA-PUERTAS and ORDONEZ-LOPEZ, 1994). The work of PHILLIPS (1972) in the Gulf of Mexico included 3 stations within the Mexican Caribbean area. Other studies dealing with medusae have examined estuarine and littoral systems along the same coast (COLLADO *et al.*, 1988; ZAMONI *et al.*, 1990; ZAMONI and SUAREZ-MORALES, 1991; SUAREZ-MORALES *et al.*, 1995) and in reef areas of Belize (LARSON, 1982). However, relatively little effort has been made to study the medusae dwelling offshore (SEGURA-PUERTAS, 1992).

Hydromedusae are the most important group of gelatinous zooplankton in coastal bays of the Mexican Caribbean (GASCA and SUAREZ-MORALES, 1994). However, quantitative information on the medusan community off this coast of Mexico is still limited. This study describes changes in the numerical

abundance, composition and diversity of the medusan fauna during five months of 1991, and analyzes their distributional patterns in Mexican Caribbean waters during this period.

The surveyed area lies between 18° and 21°30'N and 86°30' and 87°50'W, off the Mexican coast of the Caribbean Sea (Figure 1). This area represents the northwesternmost limit of the Caribbean Basin. It receives the flow of Caribbean waters before they enter the Gulf of Mexico through the Yucatan Channel. The shelf is very narrow along this coast and depth drops very quickly after the first 50 or 60 m offshore (MERINO and OTERO, 1991). Along the Mexican Caribbean, from Isla Contoy in the north, down through the Belizean coast, runs the world's second largest barrier reef, with Banco Chinchorro, a large oceanic atoll, off Xcalac (JORDAN, 1993). Surface water temperature is highest in July-August (32°C), and lowest in December-January (21°C). Mean annual salinity along this coast varies within the 32-36 PSU range. Oceanographic conditions over the entire Caribbean coast of Mexico are influenced by the Yucatan Current, which flows northwards before entering the Yucatan Channel; it creates a coastal countercurrent flowing southwards. The strength of the Yucatan Current varies seasonally, with its maximum intensity during spring, and minimum in winter (MERINO, 1992).

## METHODS

Five cruises were carried out during February, March, May, August and November, 1991, on board "Dragaminas" (D1-12)

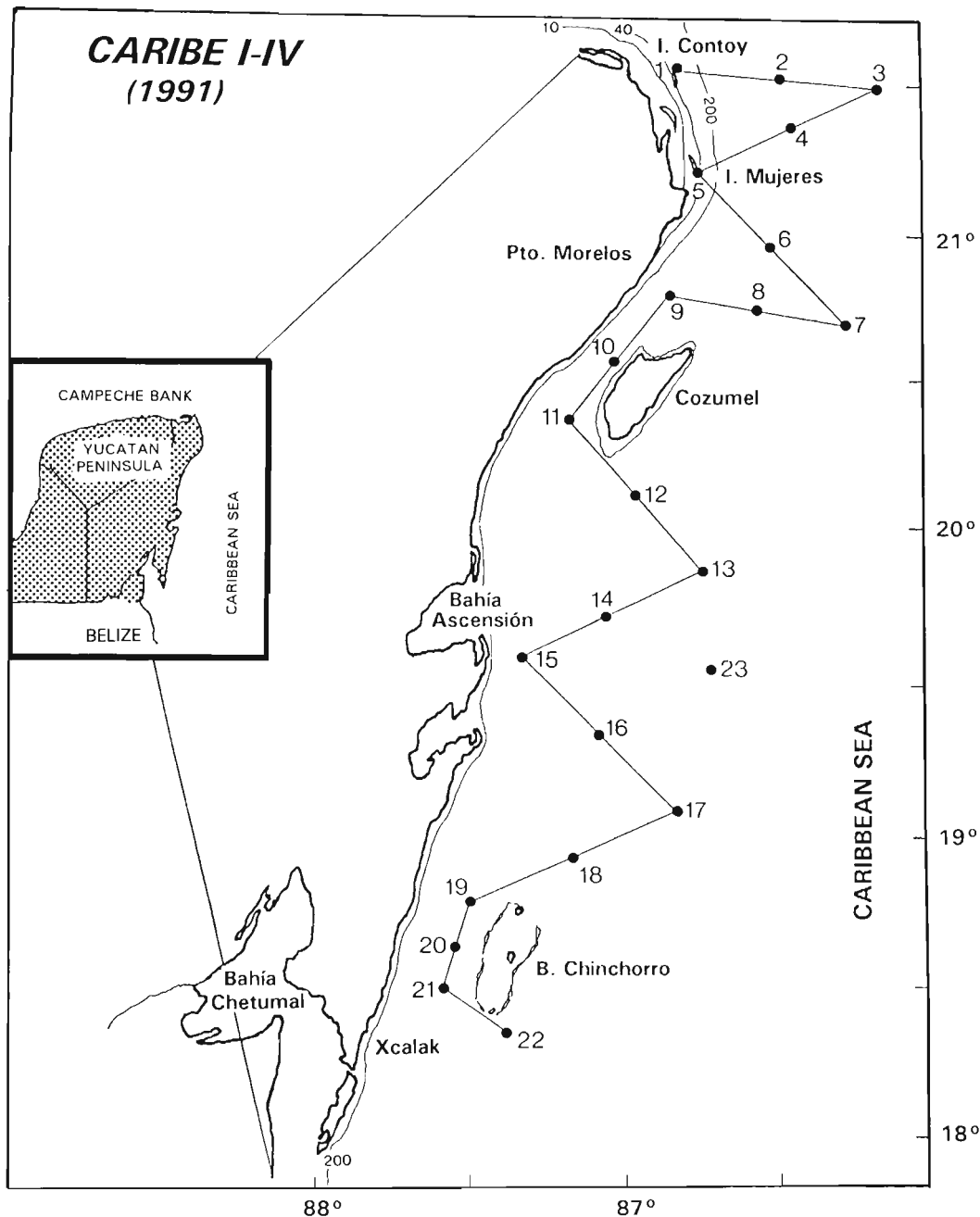


Figure 1. Surveyed area with zooplankton sampling stations off the Mexican coast of the Caribbean Sea (1991).

ships of the Mexican Secretaría de Marina (February: D-12; March: D-04; May, August and November: D-05). The sampling plan included 22 stations (Figure 1); the number of samples obtained during each month was variable (see Table 1). Zooplankton was collected by surface oblique hauls (0–50 m) using a square-mouthed (0.45 m per side) standard plankton net (0.5 mm mesh-size). This net allowed collection of small and medium-sized medusae. A digital flowmeter was attached to the net mouth to estimate the volume of water filtered; the

mean amount of water filtered was about 160 m<sup>3</sup> (16% of 1000 m<sup>3</sup>) per haul. Zooplankton samples were fixed and preserved in a buffered 4% formalin solution (SMITH and RICHARDSON, 1979). Medusae were sorted from the entire sample and then identified. Density data were combined from data sets of the five cruises. Shannon-Wiener's Diversity Index was estimated (bits/individual, which represents the uncertainty degree about the identity of a given species), along with the Index of Importance Value (IIV) as a dominance measurement, and the

Table 1. Mean density (org./1000m<sup>3</sup>), with standard deviation ( $\pm$  s.d.), and relative abundance (%) of medusae species during each of five CARIBE cruises off the Mexican Caribbean Sea (1991). The number of stations visited is indicated next to each month (n). The arrangement of species is phylogenetic.

	CARIBE I February (22)		CARIBE II March (17)		CARIBE III May (20)		CARIBE IV August (22)		CARIBE V November (8)	
	Density	%	Density	%	Density	%	Density	%	Density	%
* <i>Bougainvillia muscus</i> (Allman)				0.27						
<i>Bythotia depressa</i> Naumov	0.5 ( $\pm$ 1.98)	0.31	0.4 ( $\pm$ 1.39)	0.01						
<i>Euphysora gracilis</i> (Brooks)			0.33 ( $\pm$ 1.40)	0.21						
<i>Cyanea tetrastryla</i> Eschscholtz			0.23 ( $\pm$ 0.82)	0.009			0.60 ( $\pm$ 1.88)	0.58		
<i>Amphinema dinema</i> (Péron & Lesueur)									3.19 ( $\pm$ 7.13)	2.2
<i>A. rugosum</i> (Mayer)	0.4 ( $\pm$ 1.64)	0.25								
<i>Stomatoca pterophylla</i> Haeckel			0.25 ( $\pm$ 1.04)	0.16						
<i>Hybocodon forbesi</i> Mayer			0.4 ( $\pm$ 0.82)	0.009						
<i>Zanlea costata</i> Gegenbaur	16.2 ( $\pm$ 43.51)	10.7	2.13 ( $\pm$ 3.30)	0.09	1.7 ( $\pm$ 3.27)	1.16	2.42 ( $\pm$ 5.11)	2.37	0.92 ( $\pm$ 2.07)	0.6
<i>Aequorea aequorea</i> Péron & Lesueur			0.4 ( $\pm$ 1.68)	0.27	0.4 ( $\pm$ 1.68)	0.27	0.93 ( $\pm$ 2.93)	0.90		
<i>Laodicea undulata</i> Forbes & Goodsir			0.4 ( $\pm$ 1.68)	0.27						
* <i>Staurodiscus tetrastaurus</i> Haeckel									3.19 ( $\pm$ 7.13)	2.2
<i>Obelia</i> sp	0.9 ( $\pm$ 3.77)	0.58			0.42 ( $\pm$ 1.78)	0.31				
<i>Phialidium murrayi</i> (Brooks)	4.3 ( $\pm$ 8.81)	2.81	0.31 ( $\pm$ 1.11)	0.013	10.4 ( $\pm$ 31.96)	7.20	4.71 ( $\pm$ 10.21)	4.61	6.38 ( $\pm$ 14.27)	4.4
<i>Aegina citrea</i> Eschscholtz							1.84 ( $\pm$ 4.18)	1.80		
<i>Solmundella bitentaculata</i> (Qy. & Gaim.)	8.9 ( $\pm$ 17.89)	5.9	1.15 ( $\pm$ 2.82)	0.05			7.69 ( $\pm$ 15.95)	7.53		
<i>Pegantha triloba</i> Haeckel	1.84 ( $\pm$ 6.12)	1.2	0.31 ( $\pm$ 1.11)	0.013	0.45 ( $\pm$ 1.91)	0.32	4.44 ( $\pm$ 6.56)	4.34		
<i>Liriope tetraphylla</i> (Cham. & Eysen.)	67.10 ( $\pm$ 99.64)	44.1	5.84 ( $\pm$ 6.88)	0.24	21.0 ( $\pm$ 37.68)	14.5	8.57 ( $\pm$ 11.36)	8.38	112.6 ( $\pm$ 249.25)	77.7
<i>Agaura hemistoma</i> Péron & Lesueur	38.64 ( $\pm$ 98.99)	25.4	1.67 ( $\pm$ 4.02)	0.08	44.9 ( $\pm$ 88.87)	31.0	65.6 ( $\pm$ 81.05)	64.2	15.04 ( $\pm$ 19.54)	10.4
<i>Rhopalomena velatum</i> Gegenbaur	5.87 ( $\pm$ 17.78)	3.9	4.37 ( $\pm$ 5.34)	0.18	0.94 ( $\pm$ 2.76)	0.65	1.70 ( $\pm$ 3.61)	1.66		
<i>Linuche unguiculata</i> Schwartz			2335 ( $\pm$ 8420.90)	99.2	57.6 ( $\pm$ 143.11)	39.7				
<i>Nausithoe punctata</i> Kölliker	7.33 ( $\pm$ 17.85)	4.8	2.54 ( $\pm$ 5.60)	0.11	4.61 ( $\pm$ 8.96)	3.18	3.71 ( $\pm$ 11.74)	3.63		
<i>Carybdea alata</i> Reynaud									1.85 ( $\pm$ 4.14)	1.27
<i>C. marsupialis</i> (Linné)	0.40 ( $\pm$ 1.64)	0.25			0.90 ( $\pm$ 3.82)	0.62			1.85 ( $\pm$ 4.14)	1.27

\* Not previously recorded in the Caribbean Sea or Gulf of Mexico

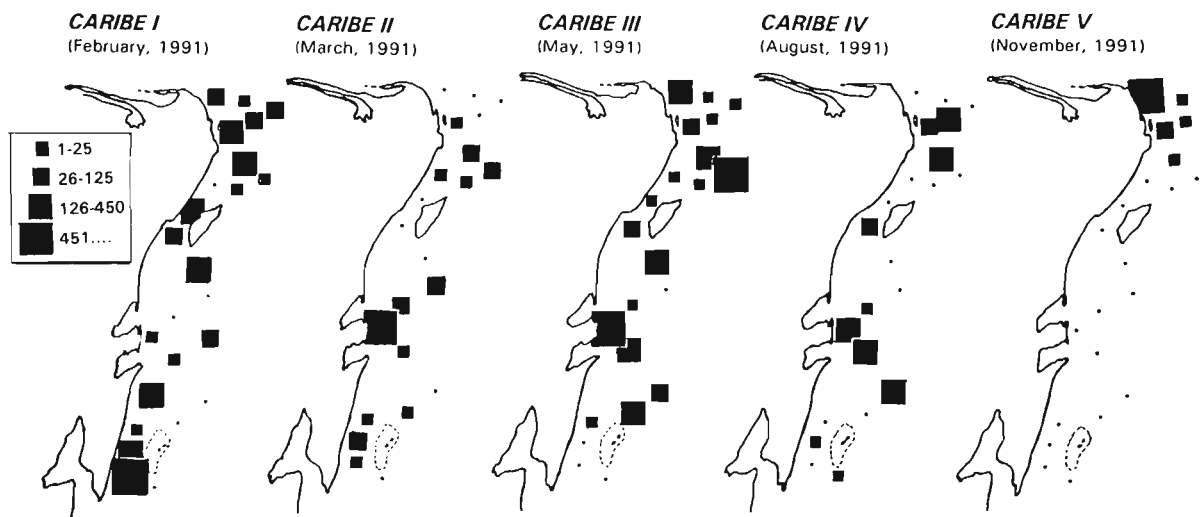


Figure 2a-e. Monthly densities (org./1000 m<sup>3</sup>) of medusae for sampling station during the surveyed period in the Mexican Caribbean Sea.

Bray-Curtis Similarity Index, which allowed the detection of station clusters in each month (LUDWIG and REYNOLDS, 1988).

**RESULTS**

Mean surface temperature during the five cruises was 28°C, with a minimum of 23°C in February. Salinity averaged 35.2 PSU, with a maximum of 35.6 in November, and a minimum of 34.5 in February. Total medusan densities showed temporal variation between cruises. Highest total mean density was recorded during March (x = 2,354 org./1000 m<sup>3</sup>; in this cruise, 99.3% of the medusae were *Linuche unguiculata*, from only one station; without *L. unguiculata*, the mean abundance value drops to 19 org./1000 m<sup>3</sup>). Total mean densities for other months (with *L. unguiculata*) were: February (152 org./1000

m<sup>3</sup>), May and November (145 org./1000 m<sup>3</sup>), and August (102 org./1000 m<sup>3</sup>). The distribution of total densities of medusae at each station during each month is shown in Figure 2.

A total of 24 species (20 hydromedusae and 4 scyphomedusae) belonging to 22 genera, were collected in the surveyed area (Table 1). Only *Liriope tetraphylla*, *Phialidium mccrady*, *Zanclaea costata*, and *Aglaura hemistoma* were recorded during all five cruises (Figure 3). These four species, along with *Linuche unguiculata* were the most representative medusae throughout the five months sampled. Together they constituted about 97% of the total overall medusan catch (83% in February, more than 99% in March; 93.4% during May; 79% in August; 93% in November). The remaining species formed a minor component. The relative abundance and estimated

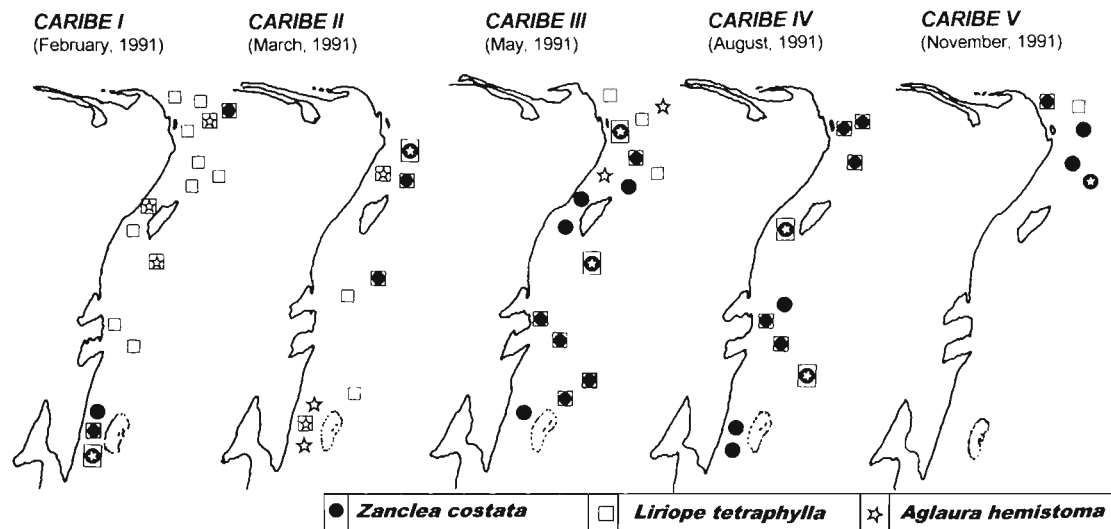


Figure 3. Distribution of the three most abundant species in the Mexican Caribbean Sea during the surveyed period.

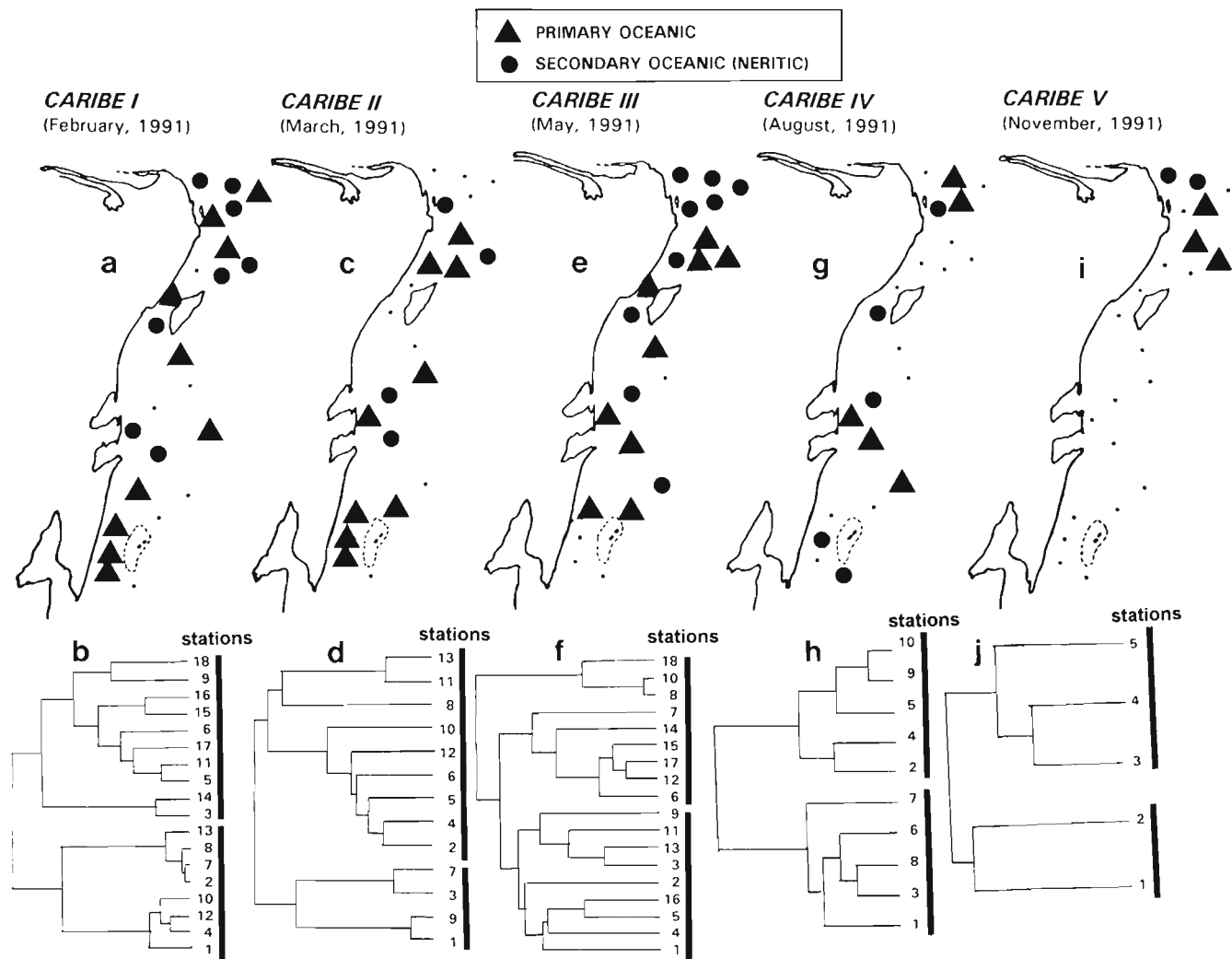


Figure 4. Dendrograms from clustering by Bray-Curtis Index, and distribution of resulting assemblages during the five months.

density of each medusan species during the five cruises is shown in Table 1.

In February the most abundant species was *L. tetraphylla*, representing 44% of the total medusae numbers; it was followed by *A. hemistoma* (25.3%) and by *Z. costata* (10.7%). *Liriope tetraphylla* occurred in 90% of the stations, while both, *A. hemistoma* and *Z. costata*, occurred in 27%. The Index of Importance Value (IIV) showed a high dominance of *L. tetraphylla* (77.36), followed by *A. hemistoma*, *Z. costata* and *Solmundella bitentaculata* (IIV below 40). Mean diversity was low, below 1.0 bits/ind. Clustering revealed two station groups (Figures 4a, b), the first—oceanic—included stations on the fully oceanic zone and in the area close to the shelf border. In this assemblage, very low densities of *L. tetraphylla* (below 4 org./1000 m<sup>3</sup>), and the occurrence of one or two additional species, were observed. The second assemblage (neritic) showed the same distribution as the first one; it included stations with abundant *L. tetraphylla* (over 18 org./1000 m<sup>3</sup>), some oceanic species (*S. bitentaculata*, *N. punc-*

*tata*, *R. velatum*, *P. triloba*), plus two neritic derivatives (*Amphepinema rugosum*, *P. mccrady*). Diversity was high.

In March, the aggregating coastal species *Linuche unguiculata* represented up to 99% of total medusan numbers, followed by *L. tetraphylla* (0.25%) and by *Rhopalonema velatum* (0.18%). Although *L. unguiculata* was the overall most abundant species during this cruise, it occurred in only one station, while both, *L. tetraphylla* and *R. velatum*, occurred in more than 50% of the stations. Of course, IIV values for *L. unguiculata* were extremely high (102.2), followed by *L. tetraphylla* (21.4), *R. velatum* (21.3) and *Z. costata* (15). Diversity was slightly higher than in February. Two station clusters were defined (Figures 4c,d), with a distribution similar to that in February. A first group (oceanic) showed low densities of *L. tetraphylla* with one or two additional species, and low diversity. A contrasting second group (neritic) showed high densities of *L. tetraphylla* with several other oceanic species (*A. hemistoma*, *R. velatum*, *Z. costata*), and with only *L. unguiculata* as the neritic species.

In May the most abundant species was again *L. unguiculata*, (40% of total medusan numbers), followed by *A. hemistoma* (30.9%) and *L. tetraphylla* (15%). *Linuche unguiculata* occurred in 33% of the stations; however, *A. hemistoma* (61%) and *L. tetraphylla* (55%), were more widely distributed. The IIV showed a shared dominance of *A. hemistoma* (51.7) and *L. unguiculata* (51.1), followed by *L. tetraphylla* (33) and *Phialidium mccrady* (16.6). Diversity was low (under 1.5 bits/ind.). Three clusters were defined (Figs. 3e,f). The first one (neritic) included shelf border stations, with very low densities of *L. unguiculata* and of *L. tetraphylla*, and with the relevant occurrence of the neritic *P. mccrady*, *Euphysora gracilis* and *Z. costata*; this group showed a low diversity. The oceanic group showed a more offshore distribution, high densities of *L. unguiculata* (10–73 org./1000 m<sup>3</sup>) and *A. hemistoma* (over 8 org./1000 m<sup>3</sup>), together with other oceanic (*L. tetraphylla*, *N. punctata*, *L. undulata*, *A. aequorea*) and neritic (*H. forbesi*, *B. ramosa*) medusae; diversity was higher. A third group of widespread localities showed the occurrence of the oceanic species *A. hemistoma*, with minimum densities.

In August, *A. hemistoma* was the most abundant species (64% of the total medusae numbers), followed by *L. tetraphylla* (8.3%) and by *S. bitentaculata* (7.5%). *Aglaura hemistoma* occurred in all the stations; *L. tetraphylla* occurred in 70%, while the other species occurred in less than 40% of the sampling stations. *Aglaura hemistoma* showed a high dominance (IIV = 92.7), while *L. tetraphylla* (28.3) and *S. bitentaculata* (16.1) were fairly less dominant. Diversity was low, mostly under 1.5 bits/ind. Again, two clusters appeared (Figs. 4g,h). The oceanic assemblage, with stations on the outermost oceanic areas, showed high densities of *A. hemistoma*, together with the oceanic *S. bitentaculata*, *L. tetraphylla*, *P. triloba*, *N. punctata*, and *R. velatum*. This assemblage showed a high diversity. The neritic group included stations closer to the shelf border, with low diversity, low densities of *A. hemistoma*, and the occurrence of the neritic *Z. costata* and the oceanic *P. triloba* and *A. citrea*.

In November, *L. tetraphylla* represented 77.7% of the total medusae numbers, followed by *A. hemistoma* (10.3%) and by *P. mccrady* (4.4%). *Liriope tetraphylla* occurred in 40% the stations; *A. hemistoma* was more widely distributed (80%), while the remaining species occurred in only one station. *Liriope tetraphylla* was the dominant species (IIV = 94.3), followed by *A. hemistoma* (43.7) and *P. mccrady* (12.7). Diversity was low (below 0.6 bits/ind.). Clustering formed two assemblages (Figs. 4i,j). The neritic group showed low densities of *L. tetraphylla* and *A. hemistoma*, and the occurrence of the neritic *P. mccrady* and *Amphinema dinema*. The oceanic one included stations with *A. hemistoma*, *C. alata*, and *C. marsupialis*.

## DISCUSSION

Previous records of medusae from the Campeche Bank and the northern portions of the Mexican Caribbean include 59 species (PHILLIPS, 1972; SEGURA-PUERTAS, 1992; SEGURA-PUERTAS and ORDÓÑEZ-LOPEZ, 1994). Two new biogeographic records (*Bougainvillia muscus* (Allman) and *Staurodiscus tetrastaurus* Haeckel) can be added to the regional lists (Table 2). A comparison of the species recorded in this survey with those of previous regional works, showed that only 42% of the species recorded here have been reported from coastal Belize

Table 2. Previous Caribbean and southern Gulf of Mexico records of the medusae collected in this survey.

	Gulf of Mexico (2)	Campeche Bank (3, 4)	Mex. Carib. (2, 5, 6, 7)	Belize (1)
* <i>Bougainvillia muscus</i>				
<i>Bythotia depressa</i>	X	X		
<i>Euphysora gracilis</i>	X	X	X	X
<i>Cytaeis tetrastyla</i>	X	X	X	X
<i>Amphinema dinema</i>	X	X		
<i>A. rugosum</i>	X	X		X
<i>Stomotoca pterophylla</i>	X		X	X
<i>Hybocodon forbesi</i>	X	X	X	
<i>Zanclaea costata</i>	X	X		
<i>Aequorea aequorea</i>	X	X		
<i>Laodicea undulata</i>	X	X		
† <i>Staurodiscus tetrastaurus</i>				
<i>Obelia</i> sp.		X		
<i>Phialidium mccrady</i>		X	X	
<i>Aegina citrea</i>	X	X	X	X
<i>Solmundella bitentaculata</i>	X	X	X	X
<i>Pegantia triloba</i>		X		X
<i>Liriope tetraphylla</i>	X	X	X	X
<i>Aglaura hemistoma</i>	X	X		X
<i>Rhopalonema velatum</i>	X	X	X	X
<i>Linuche unguiculata</i>		X		X
<i>Nausithoe punctata</i>	X	X		X
<i>Carybdea alata</i>				X
<i>C. marsupialis</i>				X

‡ Not previously recorded in the Caribbean Sea or Gulf of Mexico  
Key for numeric references in table: 1.—LARSON (1982), 2.—PHILLIPS (1972), 3.—SEGURA-PUERTAS (1992), 4.—SEGURA-PUERTAS & ORDÓÑEZ-LOPEZ (1994), 5.—ZAMPONI *et al.* (1990), 6.—ZAMPONI & SUAREZ-MORALES (1991), 7.—SUAREZ-MORALES *et al.* (1995).

(LARSON, 1982), 70% from neritic waters of the Gulf of Mexico (PHILLIPS, 1972), 79% from the Campeche Bank and part of the Mexican Caribbean (SEGURA-PUERTAS, 1992; SEGURA-PUERTAS and ORDÓÑEZ-LOPEZ, 1994), and only 28% of the species found in our study have been recorded in coastal/estuarine systems along the Mexican Caribbean (PHILLIPS, 1972; ZAMPONI *et al.*, 1990; ZAMPONI and SUAREZ-MORALES, 1991; SUAREZ-MORALES *et al.*, 1995). The fauna of the westernmost portion of the Caribbean Sea seems to be an intermediate complex with mixed Caribbean (*L. unguiculata*, *Carybdea alata*, *C. marsupialis*) and Gulf of Mexico/Campeche Bank (*Zanclaea costata*, *Laodicea undulata*, *Aequorea aequorea*) derivatives, with some additional influence of the adjacent estuarine/coastal and reef systems along the Caribbean zone. The strong faunistic affinity with the Caribbean is related to the primary influence of the Tropical Surface Water from the Equatorial Current System in the area, which has been proved for other zooplankton groups (SUAREZ-MORALES *et al.*, 1991; GASCA and SUAREZ-MORALES, 1991).

The near-shore hydrographic structure along the Caribbean coast of Mexico is related to the strength of a coastal countercurrent moving southwards (MERINO, 1986) from the northernmost edge of the Caribbean coast, which is also the easternmost portion of the Campeche Bank. Its influence would explain—at least partially—the high affinity of the local medusan fauna with that of the Campeche Bank (79%) (SEGURA-PUERTAS and ORDÓÑEZ-LOPEZ, 1994) and the Gulf of Mexico (71%) (PHILLIPS, 1972). The affinity is surprisingly

Table 3. Comparison of the relative abundance (%) of the most common medusae recorded by Segura-Puertas & Ordóñez-López (1994) and by this survey, off the Mexican Caribbean Sea during the warmest (S-P & O-L: July; this survey: August) and coldest (S-P & O-L: January; this survey: February) months surveyed.

	Segura & Ordóñez (1994)		This Survey		Comment
	July	January	August	February	
<i>Aglaura hemistoma</i>	72.7	45.4	64.3	25.4	summer species
<i>Liriope tetraphylla</i>	11.8	13	8.4	44.1	all seasons
<i>Nausithoe punctata</i>	4.5	4.1	3.63	4.8	all seasons
<i>Rhopalonema velatum</i>	7.5	6.7	1.7	3.9	all seasons
<i>Zanclea costata</i>	—	21.3	2.3	10.7	winter species

higher than that estimated with the adjacent Belizean area, southwards (41%) (LARSON, 1982).

The medusan fauna of reef environments in the area has been proved to be particularly diverse (i.e., more than 75% of the 71 medusae species recorded by LARSON (1982) in the coasts of Belize were associated with reef environments). In this work, even at those stations located relatively far from the main reefs, the medusan fauna seemed to be enriched by the reef influence in the neritic environment; some of the most speciose samples throughout this survey were from stations near the large oceanic atoll Banco Chinchorro, or near the coastal reef areas (sta. 21, February; sta. 5, March). However, the arrival of these allochthonous medusan species only effects a local enrichment of species, but does not increase the overall number of individuals. This has been observed by GILI *et al.* (1988) in the western Mediterranean.

SEGURA-PUERTAS and ORDONEZ-LOPEZ (1994) reported 6 species (*A. hemistoma*, *L. tetraphylla*, *N. punctata*, *R. velatum*, *E. gracilis* and *Z. costata*) as being the most representative in the Campeche Bank and part of the Mexican Caribbean Sea. Results of our survey largely agree with this scheme (see Tables 2 and 3); at least three of these species (*A. hemistoma*, *N. punctata*, *Z. costata*) have been reported as highly abundant in other Atlantic areas (GILI and PAGES, 1987; GILI *et al.*, 1988). The relevant seasonal (March–May) occurrence of the aggregating species *L. unguiculata* along the Caribbean coast of Mexico, seems to be a distinctive and dominant feature of the neritic and near-oceanic environments along this coast. Several of the main factors of aggregation of medusae described by ARAI (1992) occur along the coasts of the Mexican Caribbean Sea.

It is normal for planktic cnidarians populations to be dominated by a few of the commonest species which have a large influence on the overall features of the communities (PUGH, 1984; GILI and PAGES, 1987). Our results support this concept; the most abundant species are homogeneously distributed throughout the surveyed area (see Figs. 2 and 3). Uniformity in the distribution of planktonic cnidarian species is related to their high adaptability (GILI *et al.*, 1988); this would explain the wide distribution of the most abundant medusae in our area.

In the Mexican Caribbean, a number of oceanic medusae such as *Liriope tetraphylla*, *S. bitentaculata* and *C. tetrastyla* reach neritic and even estuarine waters. Similarly, oceanic species have been recorded within the Bahía de la Ascensión (SUAREZ-MORALES *et al.*, 1997); *P. mccradyi*, a neritic derivative, has been recorded from the middle portions of Chetumal Bay (SUAREZ-MORALES *et al.*, 1995). The occurrence of oceanic

fauna well inside the coastal systems in the area has been proved also for other zooplanktic groups (SUAREZ-MORALES *et al.*, 1994; SUAREZ-MORALES and GASCA, 1996). According to the results of MERINO (1986) with drifting bottles, planktic organisms carried northwards by the western edge of the Yucatan Current tend to drift inshore describing curved trajectories; this would explain the presence of several oceanic medusae very near the short shelf or even in the embayments along our study area. The two main types of assemblages defined by the Bray-Curtis Index (neritic and oceanic), showed a uniform pattern throughout the five surveyed periods, with an overlapping distribution and irregular zonation patterns along the entire coast. Both assemblages overlapped along the survey area, probably as a result of the mixing processes between oceanic and neritic waters, and favoured by the shelf narrowness. SANCHEZ-VELASCO and FLORES-COTO (1994) described the Mexican Caribbean area as featured by oceanic species, but mixed with coastal forms due to the narrowness of the continental shelf and the closeness of reef environments. Apparently, the effect of the coastal countercurrent prevents the formation of a distinct inshore-offshore gradient of medusae, which is common in other shelf-related areas (PAGES and GILI, 1992). The occurrence of bay-resident or euryhaline medusae mixed with the oceanic fauna has been reported also by ARAI and MASON (1982) in the Strait of Georgia, and by GILI *et al.* (1988) in the Mediterranean.

As a consequence of the narrowness of the shelf in this zone, deep-water oceanic species such as *B. depressa* (st. A, February; st. 15, March) and *Aegina citrea* occur very near the shore. The occurrence of the former species in the northern portion of this Caribbean coast has been previously attributed to upwelling (SEGURA-PUERTAS and ORDONEZ-LOPEZ, 1994); however, our results show that it can also be collected occasionally in coastal non-upwelling areas, probably during the top part of its vertical migration. *Aegina citrea* has been recorded also in shallow bays of British Columbia by ARAI and MASON (1982).

From the known ecological affinities of the recorded medusae, three general groups can be stated: (1) oceanic species (*S. pterophylla*, *Z. costata*, *L. undulata*, *S. tetrastaurus*, *L. tetraphylla*, *S. bitentaculata*, *P. triloba*, *A. hemistoma*, *R. velatum*, *N. punctata*, *C. tetrastyla*, *C. alata* and *C. marsupialis*), which represented 54% of the medusae; (2) neritic/coastal species (*B. ramosa*, *E. gracilis*, *A. aeguorea*, *A. dinema*, *A. rugosum*, *H. forbesi*, *L. unguiculata*, *Obelia* sp. and *P. mccradyi*), which accounted for 38% of the medusae, and (3) deep-living species (*B. depressa*, *A. citrea*). The study area showed an oceanic affinity with a variable degree of neritic influence.

Oceanic species were dominant or subdominant during the five-month survey. The influence of shelf waters in this community was represented by the occurrence—during the five cruises—of *P. maccradyi*, a typical neritic species. Other coastal and neritic medusae, such as *A. aequorea*, *E. gracilis*, *A. dinema*, *A. rugosum* and *H. forbesi* were recorded well outside the shelf border probably as a result of the hydrologic mixing processes between the edges of the main current and of the countercurrent.

The studied area represented a mixing zone in which oceanic, neritic and deep-living species show intergradating distributional patterns during the surveyed period. This fact is related with the presence of different types of environments in a relatively reduced space range, and by the mesoscale dispersion and transport effect of the local hydrographic dynamics. This pattern is probably valid year-round. A similar mixture of oceanic, deep-living and neritic-coastal medusae was described by ARAI and MASON (1982) for an oceanic area with a strong influence of the shelf and adjacent shallow bays.

Medusan highest densities were observed at stations near the coast, where crustacean zooplankton is more abundant (GASCA and SUAREZ-MORALES, 1994; SUAREZ-MORALES *et al.*, 1994). Local herbivorous populations, mainly of decapod larvae and copepods, seem to be the main food source for medusae. However, there is still little quantitative information on the impact of these predators and there are difficulties in making conclusions about the ways cnidarians and their preys are related (PUGH and BOXSHALL, 1984).

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