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A SURVEY OF THE REEF-RELATED MEDUSA (CNIDARIA) COMMUNITY IN THE WESTERN CARIBBEAN SEA

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ABSTRACT The species composition, distribution, and abundance of medusae collected during a 4-day plankton survey in a reef system of the Mexican Caribbean were studied. Highest mean medusae abundance was observed over the fore-reef zone and in daytime samples. Lowest abundances occurred in the reef lagoon and at dusk. Seventeen species were identified, with *Liriope tetraphylla*, *Aglaura hemistoma*, *Cubaia aphrodite*, and *Sarsia prolifera* being the most abundant. They belong to a group of medusae dominant along the world's second largest barrier reef. Cluster analysis revealed primary (fore-reef) and secondary (reef lagoon, channel) oceanic groups, showing the strong oceanic influence along and across the reef system. Day-to-day variation in the reef medusan community seemed relatively unimportant. The community structure of the reef medusa fauna appeared to be quite uniform despite the expected migratory behavior of these predators, tidal exchange across the reef, introduction of oceanic species, and time of day. The species composition was most closely related to that of the Campeche Bank and oceanic Caribbean waters. Dominance of oceanic medusae within the reef lagoon was attributed to the narrowness of the continental shelf and the mesoscale hydrological features of the zone.

Introduction

The medusa fauna of coastal, neritic and oceanic waters of the Northwestern Tropical Atlantic has been investigated by several surveys (Phillips 1972, Burke 1975, Segura-Puertas 1991, 1992, Segura-Puertas and Ordóñez-López 1994, Suárez-Morales et al. 1997, Suarez-Morales et al. 1998). However, relatively little emphasis has been placed on coastal environments, where medusae can play a relevant role as predators in the zooplankton food webs (Raymont 1983). Studies dealing with these cnidarians have been developed in estuarine and littoral systems of the Mexican Caribbean (Collado et al. 1988, Zamponi et al. 1990, Zamponi and Suárez-Morales 1991, Suárez-Morales et al. 1998). Along this coast runs the world's second largest barrier reef system (Jordán 1993). Coral reef zooplankton has been surveyed mainly for the most abundant groups such as copepods (Renon 1977, 1993, McKinnon 1991), but not for the less numerous zooplankters of a higher trophic level, such as medusae. There are no previous works dealing with the medusa fauna dwelling in this Mexican reef system. The closest regional antecedent for reef-related medusae is the qualitative survey of Larson (1982) from samples collected in the Carrie Bow Cay reef area off Belize.

This study describes changes in the numerical abundance, composition and diversity of the reef-related medusa fauna of the Mahahual reef system, Mexican Caribbean Sea. The survey comprised a 4-day period, (30 December 1990-2 January 1991), and describes the small-scale space and time variation of the medusan community. Previous works on the plankton of this reef area refer to zooplankton groups (Castellanos and Suárez-Morales 1997) and to ichthyoplankton (Vásquez-Yeomans et al. 1998).

Study Area

The Mahahual reef area lies between 18°43' and 18°46'N and 87° 42' and 87°42'27"W, on the southern portion of the Mexican coast of the Caribbean Sea (Figure 1). The entire coast receives the influence of Caribbean waters before flowing into the Gulf of Mexico through the Yucatan Channel. The shelf is narrow along this coast and depth increases rapidly offshore (Merino and Otero 1991). A large barrier reef runs along the Mexican Caribbean, from Isla Contoy in the north down through the Belizean coast (Jordán 1993). Mahahual is a small fishing village located on the southern portion of the Yucatan eastern coast. In this area the reef barrier forms a shallow (1.5 m) and narrow (30-180 m) reef lagoon. Benthic vegetation within the lagoon is dominated by beds of *Thalassia testudinum*. Coral cover is minimal along the shallow portions of the lagoon, but increases towards the fore-reef. 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‰ range. Oceanographic conditions over this zone are influenced by the Yucatan Current, which flows northward and by a coastal counter current which flows southward. Interaction of both currents produces inshoreward, semi-circular trajectories of drifting objects (Merino 1986). This flow, coupled with tidal currents and turbulence, seems to be the most relevant hydrological phenomenon affecting the reef zooplankton (Suárez-Morales and Rivera-Arriaga 1998).

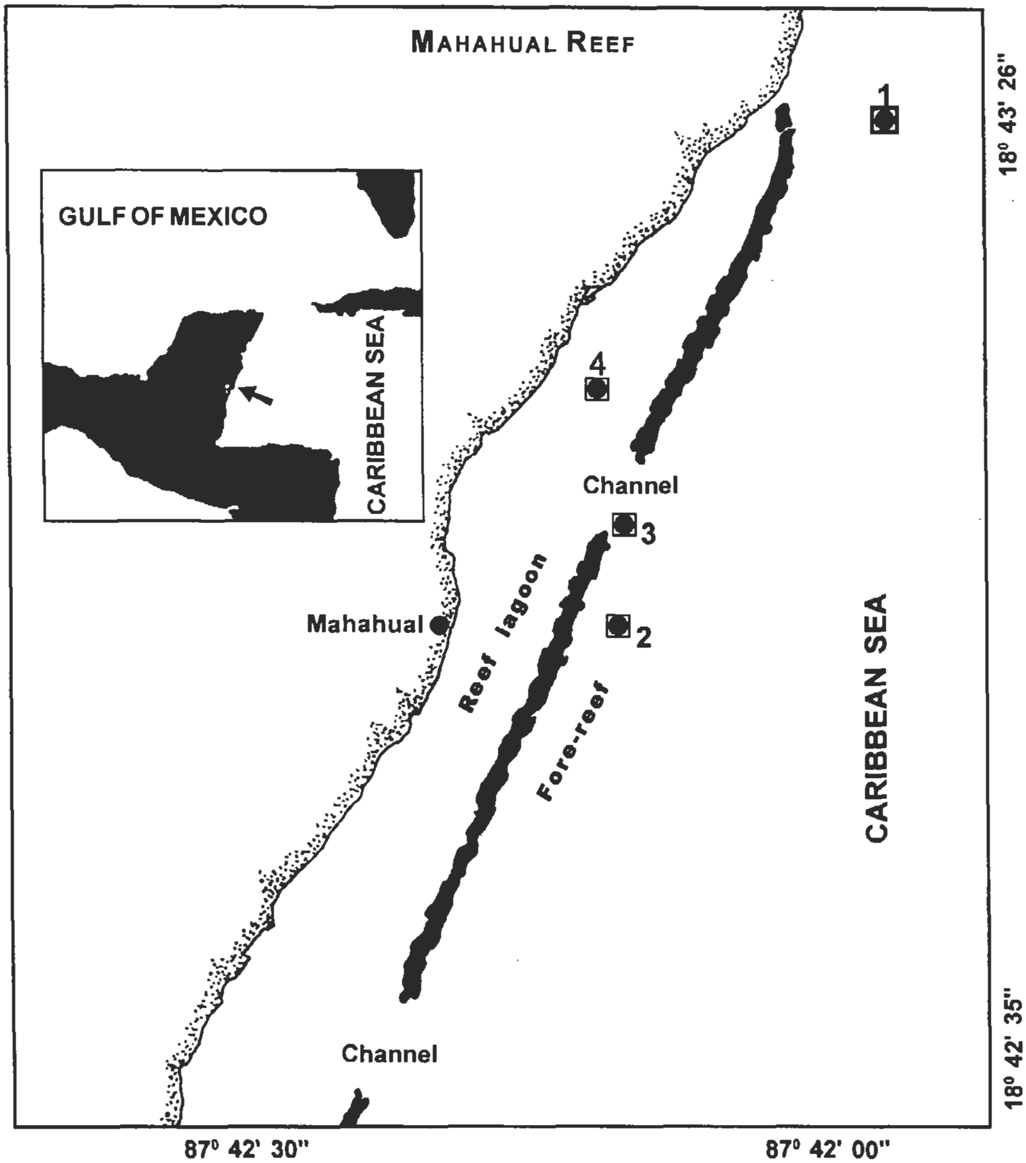

Figure 1. Surveyed area with zooplankton sampling stations, Mahahual reef zone, Mexican coast of the Caribbean Sea.

MATERIALS AND METHODS

A 4-day zooplankton sampling program was carried out from 30 December 1990 to 2 January 1991, during the full moon. Stations were located to investigate the three main reef-related zones: fore-reef (FR), Stations 1 and 2; channel (CH), Station 3; and reef lagoon (RL), Station 4 (Figure 1). Daytime sampling was made hourly between 0700 and 1200; evening (dusk) samples were collected between 1730 and 1930. No night collections were made on Day 4. Zooplankton was collected by surface hauls (0-50 m) using a square-mouthed (0.45 m per side) standard plankton net (0.3 mm mesh). This gear 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 during each trawl was 160 m^3. At least one replicate tow was performed at each sampling station. Zooplankton samples were fixed and preserved in buffered 4% formaldehyde solution (Smith and Richardson 1979). Medusae were sorted from the entire sample and then identified and counted to obtain the species density (org./100 m^3). Zooplankton density data were not significantly different among collections (Vásquez-Yeomans et al. 1997). Shannon-Wiener's Diversity Index (bits/individual, which represents the degree of uncertainty about the identity of a given species) and the Index of Importance Value (IIV, a dominance measurement) were estimated for each collection. The Bray-Curtis Similarity Index (Ludwig and Reynolds 1988) was used in the construction of a dendrogram clustering the stations. These calculations were performed with the aid of the ANACOM software computer program (De la Cruz 1994).

RESULTS

Conditions throughout the surveyed period were quite uniform. Mean surface temperature during the surveyed period ranged from 26° to 28°C. Salinity averaged 36‰, and ranged from 34 to 38‰.

Total medusa densities showed temporal variation through the survey period. Highest total mean densities were recorded during the morning of the first day, the highest two being at Station 2 (578 org./100 m^3), and at Station 1 (469 org./100 m^3), both representing the fore-reef zone. Values at the other localities ranged from 7 to 280 org./100 m^3. Highest mean medusae density occurred in Day 1 over the fore-reef (Station 2,421 org./100 m^3).

Overall data for the three reef zones considered herein showed that medusae were most abundant over the fore-reef (mean density 185 org./100 m^3), followed by the channel (18 org./100 m^3) and by the reef lagoon (16.7 org./100 m^3). Up to 87% of the total medusae numbers occurred over the fore-reef, and only 4% in the reef lagoon. Total density was 1.4 times higher in the morning (91 org./100 m^3) than at dusk (67 org./100 m^3), with 64% of the individuals being collected during daytime samplings. Over the fore-reef, density values at daytime (190 org./100 m^3) and at dusk (176 org./100 m^3) were similar. At the reef lagoon, values were 28 org./100 m^3 (AM) and 6 org./100 m^3 (PM); at the channel zone values were 18.4 and 15.2, respectively (Figure 2). Overall mean density varied day to day. Values recorded were as follows: Day 1, 135 org./100 m^3; Day 2, 54.35 org./100 m^3; Day 3, 45.1 org./100 m^3; Day 4, 97.6 org./100 m^3. Up to 40% of the total medusan numbers were collected during Day 1, 13% in Day 2, 19% in Day 3, and 28% in Day 4 (only AM).

A total of 17 medusan species were identified (Table 1). The most abundant, *Liriope tetraphylla* (Chamisso and Eysenhardt 1821), accounted for 41% of the medusae, with a mean density of 33.3 org./100 m^3. Also abundant were *Aglaura hemistoma* Péron and Lesueur 1810 (22%; 17.8 org./100 m^3), *Cubaia aphrodite* Mayer 1894 (11.6%; 9.4 org./100 m^3), *Sarsia prolifera* Forbes 1848 (8.2%; 6.6 org./100 m^3), and *Obelia* sp. (7.11%; 5.7 org./100 m^3). These five comprised about 90% of the total overall medusan catch. The relative abundance, estimated density, and frequency of all the medusan species recorded in the area are presented in Table 1.

Liriope tetraphylla showed an overall mean density in daytime samples of 48 org./100 m^3, with lower values in dusk samples (40 org./100 m^3). The same tendency in day vs dusk samples was observed for *Obelia* sp., 12 org./100 m^3 vs 4 org./100 m^3; *Clytia folleata* (McCrady 1859), 5.7 org./100 m^3 vs 1.5 org./100 m^3; and *S. prolifera*, 7.8 org./100 m^3 vs 1.8 org./100 m^3. Values for *A. hemistoma* were equal in day (17.25 org./100 m^3) and night samples (18.5 org./100 m^3).

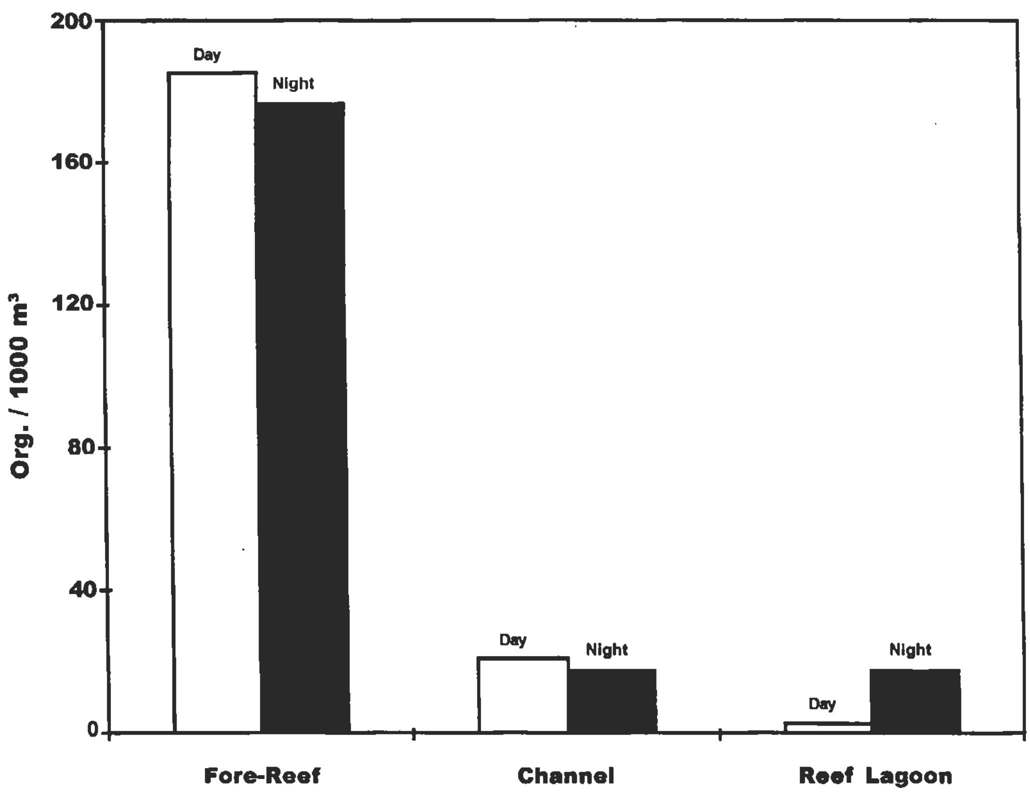

Figure 2. Mean day/night densities (org./100m^3) of medusae in the three reef-related environments.

Liriope tetraphylla was most abundant at the fore-reef. More than 90% of the total numbers of this species occurred in this environment. Only 8.3% occurred in the channel, and the remaining 1.4% reached the lagoon. *Aglaura hemistoma* was collected only at the fore-reef. *Cubaia aphrodite* was most abundant at the fore-reef (57%), and was more abundant at the channel zone (27%) than at the reef lagoon (15%). *Sarsia prolifera* occurred mostly over the fore-reef (80.6%), and was scarce at the channel zone (15%) and the reef lagoon (4.3%).

Several species occurred in either day or dusk samples, and in a specific environment. Occuring only in fore-reef samples at dusk were *Podocoryne minima* (Trinci 1903), *Amphinema dinema* (Péron and Lesueur 1809) and *Halitiara formosa* Fewkes 1882. *Amphinema rugosum* (Mayer 1900) and *Cunina octonaria* (McCrady 1852) were recorded only in fore-reef day time samples. *Halocordyle disticha* (Goldfuss 1820) was observed only in the reef lagoon at dusk.

The species richness was highest at the fore-reef, where 16 out of the 17 medusa species were recorded. Only three species (*L. tetraphylla*, *S. prolifera*, and *C. aphrodite*) were recorded in the channel zone, and only five were observed in the reef lagoon (*L. tetraphylla*, *C. aphrodite*, *H. disticha*, *Zanclea costata*, and *S. prolifera*). Overall diversity (Shannon-Wiener) was highest at the fore-reef (1.66 bits/ind.). In this environment, day samples were more diverse (1.84 bits/ind.) than those collected at dusk (1.38 bits/ind.). The reef lagoon (0.4 bits/ind.) and the channel zones (0.6 bits/ind.) showed lower overall diversity values.

Clustering with the Bray-Curtis Index produced a dendrogram (Figure 3) in which two large groups of stations were defined. One group included all the fore-reef stations, and in the other group the remaining stations (reef lagoon and channel) were clustered and mixed.

Discussion

Only 44% of the species recorded at Mahahual have been previously reported from the reef area off Belize (Larson 1982), while 50% are known from neritic and oceanic waters of the Gulf of Mexico (Phillips 1972, Burke 1975), and 72% from the Campeche Bank and the Mexican Caribbean (Phillips 1972, Zamponi et al. 1990, Zamponi and Suárez-Morales 1991, Segura-Puertas 1992, Segura-Puertas and Ordóñez-López

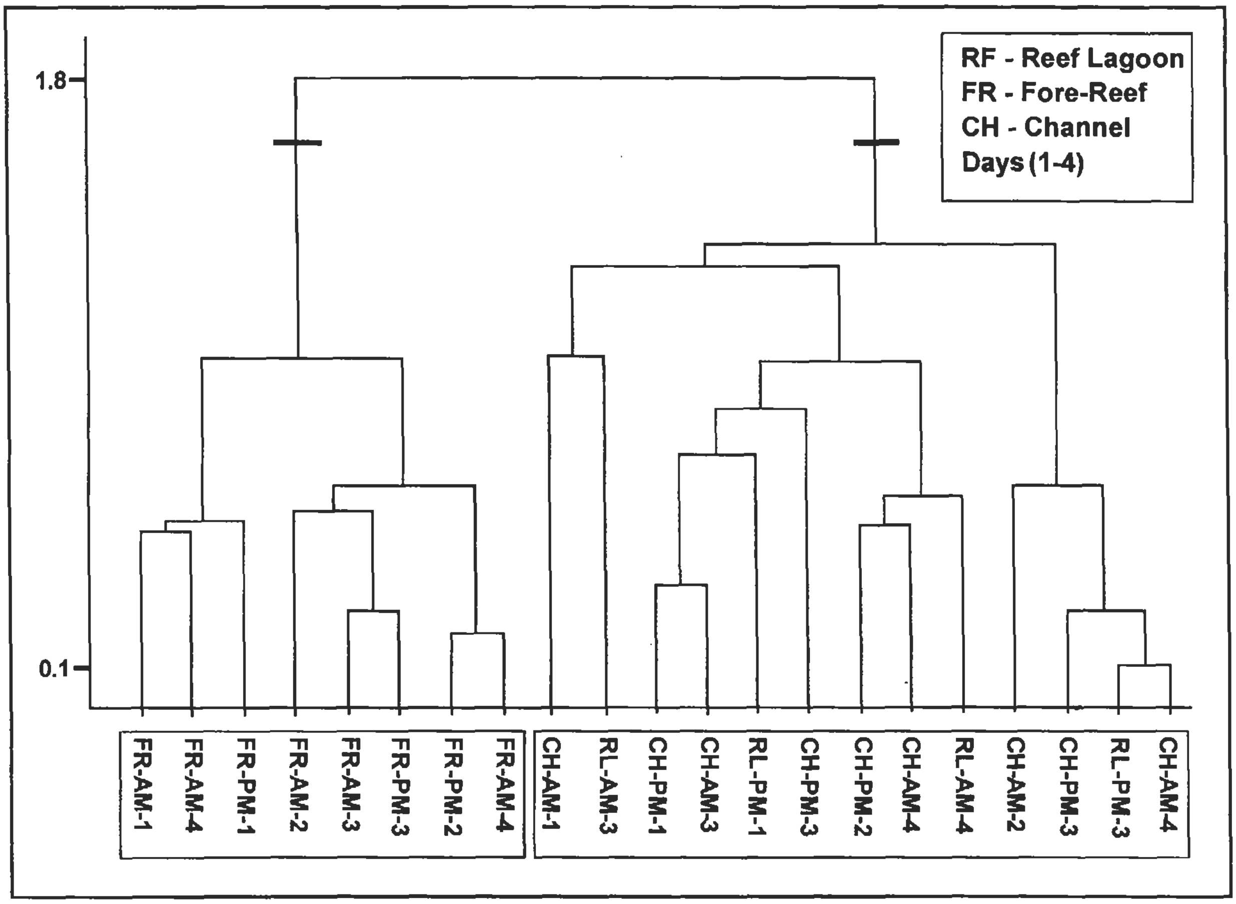

Figure 3. Dendrogram from clustering by Bray-Curtis Index showing distribution of the clusters in the three reef-related environments during the surveyed period.

TABLE 1

Medusan species density (org./100m^3) by environment, sampling day, and time of day at Mahahual

	30 December 1990					31 December 1990				1 January 1991						2 January 1990			
Station/Time/Species	FR AM	FR PM	CH AM	CH PM	RL PM	FR AM	FR PM	CH AM	CH PM	FR AM	FR PM	CH AM	CH PM	RL AM	RL PM	CH AM	FR AM	RL AM	Total
Liriope tetraphylla	88	195	0	18	5	15	20	0	5	87	55	35	6	0	0	0	0	0	615
Aglaura hemistoma	14	25	0	0	0	28	111	0	0	49	31	0	0	0	0	0	56	0	314
Obelia sp.	90	25	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	119
Clytia folleata	42	8	0	0	0	2	1	0	0	0	0	0	0	0	0	0	3	0	56
Clytia mccrady	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0	0	0	12
Carybdea marsupialis	4	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	10
Podocoryne minima	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Sarsia prolifera	52	3	7	6	0	8	3	0	5	4	0	0	0	0	0	5	24	6	123
Amphinema dinema	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Amphinema rugosum	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2
Halitiara formosa	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Cubaia aprhrodite	0	0	0	9	17	2	0	3	5	0	0	12	7	0	12	13	52	0	132
Halocordyle disticha	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	19
Solmundella bitentaculata	0	19	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	22
Zanclea costata	0	0	0	0	3	1	2	2	0	2	0	0	0	0	0	0	3	0	11
Cunina octonaria	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Rhopalonema velatum	0	0	0	0	0	2	0	0	0	0	0	0	0	5	0	0	0	0	7
Total	290	298	7	33	44	61	140	3	15	154	92	47	13	5	12	18	226	6	1,464

1994, Suárez-Morales et al. 1995, Suárez-Morales et al. 1998). Only one species collected at Mahahual (*S. prolifera*) has not been recorded previously in the region. It has been reported from the northeastern Atlantic (Ranson 1925, Sanderson 1930, Russell 1938), and even from the Black Sea (Thiel 1935). This is the first record of this species in the northwestern Atlantic.

The number of species collected in this survey (17) is relatively low when compared with the medusa richness recorded in adjacent zones. Sixty-two species have been recorded from the Campeche Bank and the Mexican Caribbean (Phillips 1972, Segura-Puertas 1992, Segura-Puertas and Ordóñez-López 1994, Suárez-Morales et al. 1998). More than 20 species were found in a large embayment on the central portion of the Mexican Caribbean coast (Suárez-Morales et al. 1997).

The reef-related medusa fauna recorded off Belize by Larson (1982) can be compared with that recorded over Mahahual reef. Both belong to the same barrier reef system. Larson recorded 71 species in reef-related areas of Carrie Bow Cay, of which 80% were recorded in the fore-reef and 64% in the reef lagoon. The corresponding values for Mahahual were 88% at the fore-reef, 27% at the channel zone, and only 20% at the reef lagoon. It is difficult to explain the differences in species richness with respect to Larson's (1982) results in a reef environment. To obtain most of the samples, he used a net with a 0.56 mm mesh opening, filtered an average of 250 m^3, and made surface tows; his collections were made between 1730 and 1830. Up to this point, Larson's methods are similar to those we used at Mahahual. The main difference was probably related to material analyzed by Larson resulting from qualitative collections performed while diving, using light traps at night, and sampling with a beach seine and with dip nets. Medusa densities are commonly low in reef environments (Sammarco and Greenshaw 1984, Morales and Murillo 1996). The overall mean density recorded at Mahahual is similar (83 org./100 m^3) to that recorded by Larson (1982) in plankton trawls from Carrie Bow (92.5 org./100 m^3). However, there is no estimate on the species richness from plankton net collections. Larson (1982) recognized only 13 species as dominant; of this group, 8 are shared with the Mahahual community. In both cases, *L. tetraphylla*, *A. hemistoma*, *Solmundella bitentaculata*, and *C. aphrodite* were among the most abundant medusae. However, abundance of the dominant species in both systems showed several differences (Table 2). This suggests that although the number of species is almost

TABLE 2

The medusae collected in this survey at Mahahual and previously from the Campeche Bank, the Mexican Caribbean, and Belize. Key for citations in this table: 1. Larson (1982), 2. Phillips (1972), 3. Segura-Puertas (1992), 4. Segura-Puertas and Ordóñez-López (1994), 5. Zamponi et al. (1990), 6. Zamponi and Suárez-Morales (1991), 7. Suárez-Morales et al. (1995), and Suárez-Morales et al. (1997). [a]Not previously recorded in the Caribbean Sea or Gulf of Mexico.

	Mahahual (this survey)	Campeche Bank (3, 4)	Mexican Caribbean (2, 5, 6, 7)	Belize (1)
Amphinema dinema	X	X		
Amphinema rugosum	X	X		X
Zanclea costata	X	X		
Obelia sp.	X	X		
Clytia mccradyi	X	X		
Clytia folleata	X		X	
Solmundella bitentaculata	X	X		X
Liriope tetraphylla	X	X	X	X
Aglaura hemistoma	X	X	X	X
Rhopalonema velatum	X	X		X
Carybdea marsupialis	X		X	X
Podocoryne minima	X	X		
Sarsia prolifera [a]	X			
Halitiara formosa	X	X		
Cubaia aphrodite	X			X
Halocordyle disticha	X			X
Cunina octonaria	X	X		X

TABLE 3

Density of the five dominant medusa species at two Caribbean reef environments.

	Mahahual (this survey)		Carrie Bow Cay (Larson 1982)	
	Relative density (%)	Density (org./100m³)	Relative density (%)	Density (org/100m³)
Clytia mccradyi + *C. folleata* (as *Phialucium* in Larson 1982)	4.1	35.5	32.0	28.0
Solmundella bitentaculata	1.3	1.04	1.5	1.2
Liriope tetraphylla	41.0	33.3	57.0	48.6
Aglaura hemistoma	22.0	18.0	3.3	2.9
Cubaia aphrodite	11.6	9.4	0.4	0.3

four times higher at Belize, the distribution of the species richness, the overall density, and the abundance of the dominant species are similar in the two surveys. This probably relates to the local abundance of *C. aphrodite* and of *A. hemistoma* at Mahahual; both were relatively scarce at Carrie Bow. *Aglaura hemistoma* is probably even more abundant in Mahahual during summer as recorded off the Caribbean (Suárez-Morales et al. 1998). Differences between the medusa fauna of Carrie Bow and Mahahual could be related to the physiographic features of each particular reef section.

In both areas, most of the remaining medusan species occurred in low numbers, which is a common feature of the medusa communities (Gili and Pagés 1987). The arrival of these oceanic species effects a local enrichment of species, but does not produce a major increase in the overall number of individuals. This pattern agrees with parallel results of Gili et al. (1988) from studies of cnidarian zooplankton in the western Mediterranean.

The nearshore hydrographic structure along the Caribbean coast of Mexico is related to the flow of a coastal countercurrent moving southward (Merino 1986) from the northernmost edge of the Caribbean coast. Its influence would explain, at least partially, the high affinity of the local medusa fauna with that of the Campeche Bank and the southern Gulf of Mexico (Phillips 1972, Segura-Puertas and Ordóñez-López 1994), and the relatively low affinity with the adjacent Belizean reef, which lies to the south (Larson 1982).

Segura-Puertas and Ordóñez-López (1994) reported 6 species (*A. hemistoma*, *L. tetraphylla*, *Nausithoe punctata*, *Rhopalonema velatum*, *Eutima gracilis* and *Z. costata*) as being the most common in the Campeche Bank and the oceanic Mexican Caribbean Sea. Our results and those of Larson (1982) show that *L. tetraphylla* and *A. hemistoma* are also successful over reef environments (Table 3). *Aglaura hemistoma* has been reported as highly abundant in other tropical and subtropical environments (Gili and Pagés 1987, Gili et al. 1988). The seasonal (March-May) occurrence of the aggregating scyphozoan *Linuche unguiculata* seems to be a distinctive and dominant feature of the western Caribbean neritic and near oceanic environments (Larson 1982, Suárez-Morales et al. 1998). Reflecting its well-known seasonal behavior, this species was absent from our samples.

Communities of planktonic cnidarians are frequently dominated by a few of the most common species (Pugh and Boxshall 1984, Gili and Pagés 1987). Our results are similar. The most dominant medusae were distributed throughout the surveyed area; *L. tetraphylla*, *C. aphrodite*, and *A. hemistoma* were dominant in the three environments sampled. Uniformity in the distribution of planktonic cnidarian species is related to their high adaptability (Gili et al. 1988). This would explain, at least partially, the wide distribution of these medusae in the Mahahual reef area, and probably along the western Caribbean coasts. However, other groups, such as copepods, show a sharp difference in composition and a higher density within the reef lagoon than outside (Alvarez-Cadena et al. 1998).

In the Mexican Caribbean, a number of oceanic medusae reach neritic and even estuarine waters (Suárez-Morales et al. 1997, Suárez-Morales et al. 1998). This has been shown also for other zooplankton groups (Suárez-Morales and Gasca 1996). According to the results of Merino (1986) with drifting bottles, planktonic organisms transported northward by the western edge of the Yucatan Current tend to drift inshore. This would explain the presence of oceanic medusae over the innermost portions of the narrow shelf. A relevant factor in the mesoscale distribution of zooplankton along the western Caribbean is the strong effect of tidal currents (Greer and Kjerfve 1982, Kjerfve 1982, Kjerfve et al. 1982) which bring an inflow of oceanic water to the lagoon through the channels and over the reef crests. This has been reported also for Mahahual (Castellanos and Suárez-Morales 1997). There is a strong import of oceanic fauna into the Mahahual reef area, as reflected in the dominance of oceanic forms and the high species richness over the fore-reef. This effect has been described also in the general reef zooplankton community at Carrie Bow Cay (Ferraris 1982).

The two assemblages defined by the Bray-Curtis Index showed a clear separation of the sampling stations in the surveyed area. The first, which comprised all the fore-reef stations, represents the primary influence of the oceanic fauna over the reef front. At this point, separation between the fore-reef and the reef lagoon seems to be sharp. However, the second group, which included the channel and reef lagoon stations, showed a secondary oceanic influence. This was represented mainly by the occurrence of the most common oceanic species in the area, a much lower species richness, and the occurrence of coastal species. Therefore, the main difference between the fore-reef and the reef lagoon medusa communities is the species richness, all areas being dominated by a few oceanic species. Migration and exchange of water into and out of the reef lagoon are seen to be relatively unimportant in determining the across-reef medusa community structure. This pattern is useful to describe the small-scale distribution of the medusae across the reef from day to day. Due to the expected uniformity of the zooplankton community along this reef system (Suárez-Morales and Rivera-Arriaga 1998), this pattern is probably valid along the entire reef system.

Apparently, the effect of the coastal countercurrent prevents the formation of a distinct seaward gradient of medusae, which is common in some other shelf-related areas studied (Pagés and Gili 1992). The occurrence of euryhaline medusae mixed with the oceanic ones has been reported also by Arai and Mason (1982) in the Strait of Georgia, and by Gili et al. (1988) in the Mediterranean.

From the known ecological affinities of the medusae recorded at Mahahual reef, three general groups can be recognized: 1) oceanic species (*L. tetraphylla*, *S. bitentaculata*, *A. hemistoma*, *R. velatum*, *N. punctata*, *Cytaeis tetrastyla*, and *Carybdea marsupialis*), which represented 60% of the medusa population; 2) neritic/coastal species (*A. dinema*, *A. rugosum*, *Obelia* sp., *C. folleata* and *Clytia mccradyi*), which accounted for 30% of the medusae, and 3) coastal species (*P. minima*, *Zanclea costata*). The groups showed an overlapping distribution through the surveyed area.

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