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THE PLANKTONIC COPEPOD COMMUNITY AT MAHAHUAL REEF, WESTERN CARIBBEAN

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ABSTRACT

The species composition, distribution, and abundance of the copepods collected during a 4-d zooplankton survey across a Mahahual coral reef system of the Mexican Caribbean Sea were studied. Highest mean copepod abundance and diversity were observed in the fore-reef in daytime samples. Lowest abundances occurred in the reef lagoon and channel at daytime. Forty-five species were identified, with *Temora turbinata*, *Undinula vulgaris*, *Subeucalanus subcrassus*, and *Calanopia americana* as the most abundant. They belong to a group of planktonic copepods dominant in the Caribbean reefs. Cluster analysis revealed a primary (fore-reef) and secondary (reef lagoon, channel) oceanic group, showing the strong oceanic influence across the reef system which was attributed to the narrowness of the shelf and the effect of tidal currents and other hydrological features. Overall day-night differences were related to the influence of near-benthic migrating forms. *Acartia spinata*, an abundant reef lagoon species in the Caribbean, was scarce at Mahahual due to its breeding cycle. Its scarcity may be correlated with the relatively high diversity in the reef lagoon, an oceanic predominance in the reef system, and relatively low overall copepod densities. The main features of the copepod community at Mahahual are similar to those found in other regional reef systems.

The copepod fauna of coastal-neritic and oceanic waters of the Caribbean Sea has been investigated by several workers (Owre and Foyo, 1964, 1967; Michel and Foyo, 1976; Suárez-Morales and Gasca, 1996; Campos and Suárez-Morales, 1994). However, relatively little emphasis has been placed on reef environments, which is a community featured by a particular combination of oligotrophic, shallow water with relatively high temperatures (Emery, 1968; Alldredge and King, 1977; Alvarez-Cadena et al., 1998). Copepods play a relevant role in the reef-related zooplankton community (Raymont, 1983; Renon, 1977, 1993; McKinnon, 1991). The world's second largest barrier reef system runs along the westernmost coast of the Caribbean, including the Mexican Caribbean Sea (Jordán, 1993). On the northern portion of this system, near Cancun, Alvarez-Cadena et al. (1998) studied the distribution of reef copepods on a monthly basis. However, there are no previous works dealing with short-term variations of the copepod fauna in the reef system of the western Caribbean Sea.

The present survey comprised a 4-d period (30 December 1990–2 January 1991), and describes the AM and PM space and time variation of the local copepod community in the three reef environments. Previous works on the zooplankton of this reef area are by Vásquez-Yeomans et al. (1998), by Castellanos and Suárez-Morales (1997), Suárez-Morales and Gasca (1998), and by Suárez-Morales et al. (1999).

The Mahahual reef area lies between 18°43′and 18°46′N and 87°42′00″ and 87°42′27″W, on the southern portion of the Mexican coast of the Caribbean Sea (Fig. 1). The shelf is narrow and depth increases rapidly offshore. A large barrier reef runs along this coast, from Isla Contoy in the north, down through the Belizean coast (Jordán, 1993). The reef lagoon of Mahahual, a small fishing village, is shallow (1.5 m) and narrow (30–180 m) with abundant beds of *Thalassia testudinum* Banks ex König. Surface-water temperature is highest in July–August (32°C), and lowest in December–January (21°C). Average sa-

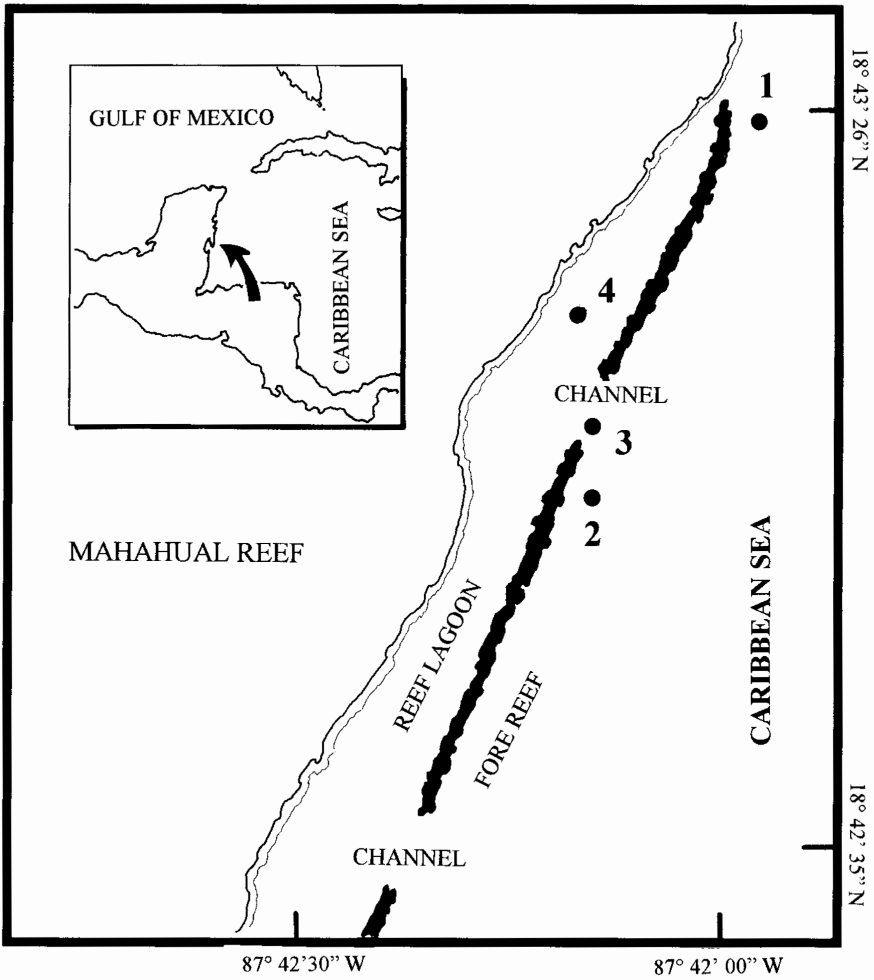

Figure 1. Surveyed area with zooplankton sampling stations, Mahahual reef zone, Mexican coast of the Caribbean Sea.

linity along this coast varies throughout the year within the 32–36‰ range. Oceanographic conditions over this zone are influenced by the northward flow of the Yucatan Current, and by a southward flow of a coastal counter-current. Interaction of both currents produces inshorewards trajectories of drifting objects (Merino, 1986). This flow, coupled with tidal currents and turbulence, seems to affect the reef plankton distribution (Suárez-Morales and Rivera-Arriaga, 1998).

METHODS

A 4-d zooplankton sampling program was carried out from 30 December 1990 to 2 January 1991, during the full of the moon. Stations were located to investigate the three main reef-related zones: fore-reef (FR) (sta. 1 and 2), channel (CH) (sta. 3), and reef lagoon (RL) (sta. 4) (Fig. 1). Daytime sampling was made in bright light between 07:00 and 12:00, evening (dusk) samples were collected between 17:30 and 19:30. No evening collections were made on day 4. Zooplankton was collected by horizontal surface hauls (0–50 m) using a square-mouthed (0.45 m per side) standard plankton net (0.3 mm mesh-size). At least one replicate tow was performed at each sampling station. A digital flowmeter was attached to the net mouth to estimate the species density (org 100 m^{-3}). The mean amount of water filtered during each trawl was 160 m^{3}. Zooplankton samples were fixed and preserved in a buffered 4% formaldehyde solution (Smith and Richardson, 1979). Adult planktonic copepods were sorted from the entire sample. Samples, replicates and zooplankton density data were tested by Vásquez-Yeomans et al. (1998) and found to be statistically valid. An ANOVA was used to test differences expected due to the reef zones (FR, RL, CH), and day-night sampling. Shannon-Wiener's Diversity Index was estimated (bits/individual), and the Bray-Curtis Similarity Index (Ludwig and Reynolds, 1988) was used to cluster the stations. Calculations were performed using the ANACOM software (De la Cruz, 1994).

RESULTS

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

Variations of total copepod densities throughout the survey period are presented in Figure 2. Highest total average densities were recorded during the afternoon of the second day (61,360 org 100 m^{-3}) at the FR zone. Density at the other localities ranged from 10 to 4800 org 100 m^{-3}. Highest mean copepod density occurred in day 1 over the FR (88,250 org 100 m^{-3}).

Overall data for the three reef zones considered herein showed that copepods were most abundant over the FR (mean density 28,025 org 100 m^{-3}), followed by the CH (4618 org 100 m^{-3}) and by the RL (3461 org 100 m^{-3}). Up to 79.7% of the total copepod num-

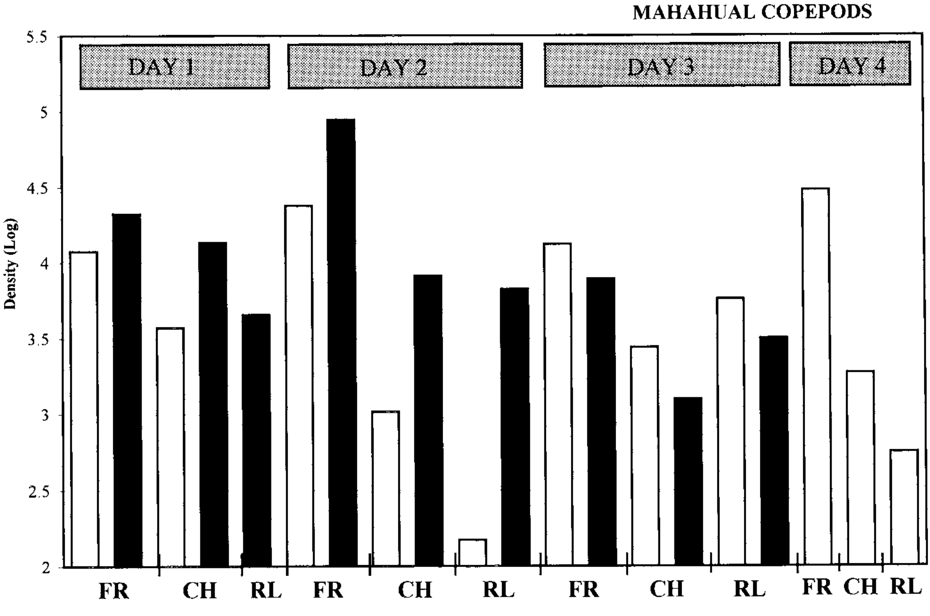

Figure 2. Overall densities of copepods in the three reef-related environments during sampling days 1–4. Scale in Log of density (org. 100 m^{3}). Dark columns indicate dusk samples.

Table 1A. Density (org. 100 m^{-3}) of copepod species at Mahahual by time of day and reef environment for 30 and 31 December 1990 (summary totals in Table 1B).

Date	30 December 1990					31 December 1990					
Station	FR	FR	OH	CH	RL	FR	FR	OH	OH	RL	RL
Time/Species	AM	PM	AM	PM	PM	AM	PM	AM	PM	AM	PM
Acartia lilljborgii Giesbrecht, 1889	0	0	0	0	0	0	0	0	0	0	0
A. spinata Esterly, 1911	3,069	5,259	245	1,101	159	1,106	174	0	0	8	506
Acrocalanus longicornis Giesbrecht, 1888	0	i57	0	78	0	0	0	18	0	4	84
Calocalanus pavo (Dana, 1849)	26	43	0	0	0	0	5	0	0	0	42
Calanopia americana F. DahI, 1894	352	1,876	7	6,956	3,278	1,061	5,269	343	3,366	4	758
Candacia curta (Dana, 1852)	0	0	0	0	0	0	32	0	0	0	0
C. pachydactyla (Dana, 1849)	0	0	7	14	0	0	0	0	0	0	0
C. varicans (Giesbrecht, 1892)	0	0	0	0	5	0	0	0	0	0	0
Clausocalanus furcatus Brady, 1883	663	780	0	0	0	1,113	0	0	555	0	0
Centropages velificatus (De Oliveira, 1947)	712	176	20	317	175	1,346	4,680	0	444	0	0
Copilia mirabilis Dana, 1852	7	22	0	5	0	0	33	0	0	0	0
Corycaeus flaccus Giesbrecht, 1891	0	0	0	0	0	0	0	0	0	0	0
C. speciosus Dana, 1849	358	801	113	119	0	1,793	1,126	89	222	16	0
C. latus Dana, 1849	0	35	0	0	0	0	0	0	0	0	0
C. clausi F.Dahl, 1894	247	0	0	0	0	277	0	0	0	0	0
C. amazonicus F. DahI, 1894	13	0	0	0	0	0	0	0	0	0	0
Farranula gracilis (Dana, 1849)	486	4,701	801	211	0	4,340	0	37	296	0	379
Labidocera aestiva Wheeler, 1901	1,351	1,408	947	1,262	695	509	710	146	148	69	1,096
L. scotti Giesbrecht, 1897	7	94	0	32	0	100	37	0	111	0	0
L. mirabilis Fleminger, 1957	0	22	0	0	0	0	11	0	0	0	0
L. nerii (Kroyer, 1849)	13	147	0	0	21	0	0	0	0	0	0
L. wilsoni Feminger and Engchow, 1968	0	6	0	0	0	16	0	27	0	0	0
Labidocera sp.	0	6	0	0	0	0	0	0	0	0	0
Lubbockia squillimana Claus, 1863	0	0	0	5	0	0	0	0	0	0	0
Lucicutia flavicornis (Claus, 1863)	196	260	0	0	0	203	462	0	0	0	0
Calanus minor (Claus, 1883)	105	0	0	0	0	0	0	0	0	0	0

Table 1A. Continued.

Date	30 December 1990					31 December 1990					
Station	FR	FR	OH	CH	RL	FR	FR	OH	OH	RL	RL
Time/Species	AM	PM	AM	PM	PM	AM	PM	AM	PM	AM	PM
Oncaea media Giesbrecht, 1891	0	0	0	0	0	98	0	0	0	0	0
O. ornata Giesbrecht, 1891	0	0	0	0	0	0	0	0	0	20	0
Oithona setigera Dana, 1849	642	0	0	0	0	0	0	0	37	0	0
Paracandacia simplex (Giesbrecht, 1889)	0	0	0	0	0	0	33	0	0	0	0
Parapeltidium sp.	0	0	0	9	0	0	0	0	0	0	0
Peltidium sp.	0	0	0	37	0	0	0	0	0	0	0
Phaenna spinifera Claus, 1883	0	6	0	0	0	0	0	0	0	0	0
Pontella securifer Brady, 1883	0	0	0	0	9	0	0	0	0	0	0
P. mimocerami Fleminger, 1957	0	0	0	5	0	0	0	0	0	0	0
Pontellina plumata (Dana, 1849)	0	0	0	0	0	0	16	0	0	0	0
Pontellopsis villosa Brady, 1883	0	65	0	0	0	0	98	0	0	4	0
Rhincalanus cornutus (Dana, 1849)	0	0	0	5	0	0	0	0	0	0	0
Saphirella tropica Wolfenden, 1906	8	0	0	0	0	0	0	0	0	0	0
Sapphirina metallina Dana, 1849	0	0	0	9	0	0	0	0	0	0	0
Scolecithrix danae (Lubbock, 1856)	0	0	0	0	0	82	281	0	0	0	0
Subeucalanus subcrassus (Giesbr.,1888)	294	1,830	0	289	0	884	8,624	0	351	0	1,306
S. pileatus Giesbrecht, 1888	0	0	0	0	0	0	84	0	0	0	0
Temora stylifera (Dana, 1849)	15	346	99	584	0	1,664	1,791	0	592	0	84
T. turbinata (Dana, 1849)	633	1,009	278	340	0	6,809	61,355	0	1,757	12	1,517
Undinula vulgaris (Dana, 1849)	2,755	2,093	1,206	1,918	109	2,437	3,350	393	222	0	0
Harpacticoids	0	0	7	284	64	0	79	0	37	12	885
TOTAL	11,849	21,141	3,729	13,558	4,513	23,840	88,248	1,033	8,137	149	6,657

Table 1B. Density (org. 100 m^{-3}) of copepod species at Mahahual by time of day and reef environment for 1 and 2 January 1990 (includes summary totals).

Date	1 January 1990						2 January 1990				
Station	FR	FR	CH	CH	RL	RL	FR	CH	RL	TOTAL	%
Time/species	AM	PM	AM	PM	AM	PM	AM	AM	AM		
Acartia lilljborgii Giesbrecht, 1889	0	6	0	0	0	0	0	0	0	6	0.00
A. spinata Esterly, 1911	881	2,103	0	0	0	0	0	59	0	14,676	5.89
Acrocalanus longicornis Giesbrecht, 1888	0	0	0	0	0	0	126	5	0	472	0.19
Calocalanus pavo (Dana, 1849)	0	0	0	0	0	24	148	0	0	288	0.12
Calanopia americana F. Dahl, 1894	0	1,053	0	0	158	1,034	13	59	0	25,580	10.26
Candacia curta (Dana, 1852)	0	0	0	0	0	0	0	0	0	32	0.01
C. pachydactyla (Dana, 1849)	0	0	0	0	0	0	63	0	0	83	0.03
C. varicans (Giesbrecht, 1892)	0	0	0	0	0	0	0	0	0	5	0.00
Clausocalanus furcatus Brady, 1883	641	74	90	35	607	0	239	574	46	5,418	2.17
Centropages velificatus (De Oliveira, 1947)	478	724	74	0	322	71	2,292	113	0	11,942	4.79
Copilia mirabilis Dana, 1852	0	0	0	0	0	0	0	0	0	66	0.03
Corycaeus flaccus Giesbrecht, 1891	0	0	0	0	0	0	314	0	0	314	0.13
C. speciosus Dana, 1849	709	301	32	112	0	95	271	83	87	6,305	2.53
C. latus Dana, 1849	218	0	0	0	99	0	0	0	12	364	0.15
C. clausi F.Dahl, 1894	0	0	37	0	42	0	327	0	0	930	0.37
C. amazonicus F. Dahl, 1894	0	0	0	0	0	0	0	0	0	13	0.01
Farranula gracilis (Dana, 1849)	0	25	754	77	1,558	0	516	304	12	14,495	5.81
Labidocera aestiva Wheeler, 1901	0	197	117	899	0	166	0	162	208	10,089	4.05
L. scotti Giesbrecht, 1897	0	37	0	0	0	0	158	0	0	575	0.23
L. mirabilis Fleminger, 1957	0	0	0	0	0	0	0	0	0	32	0.01
L. nerii (Kroyer, 1849)	0	0	0	14	0	0	13	10	0	218	0.09
L. wilsoni Feminger and Engchow, 1968	0	0	0	0	0	0	0	0	0	50	0.02
Labidocera sp.	0	0	0	0	0	0	0	0	0	6	0.00
Lubbockia squillimana Claus, 1863	0	0	0	0	0	0	0	0	0	5	0.00
Lucicutia flavicornis (Claus, 1863)	0	441	0	0	83	0	0	0	0	1,646	0.66
Calanus minor (Claus, 1883)	0	0	0	0	0	0	0	0	0	105	0.04

Table 1B. Continued.

Date	1 January 1990						2 January 1990				
Station	FR	FR	CH	CH	RL	RL	FR	CH	RL	TOTAL	%
Time/species	AM	PM	AM	PM	AM	PM	AM	AM	AM		
Oncaea media Giesbrecht, 1891	0	0	0	0	0	0	0	0	35	133	0.05
O. ornata Giesbrecht, 1891	0	0	48	0	0	0	38	265	0	370	0.15
Oithona setigera Dana, 1849	0	0	0	0	0	0	0	0	0	579	0.23
Paracandacia simplex (Giesbrecht, 1889)	0	0	0	0	0	0	0	0	0	33	0.01
Parapeltidium sp.	0	0	0	0	0	1,295	0	0	0	1,304	0.52
Peltidium sp.	0	0	0	0	0	36	0	0	0	72	0.03
Phaenna spinifera Claus, 1883	0	0	0	0	0	0	0	0	0	6	0.00
Pontella securifer Brady, 1883	27	0	0	0	0	0	0	0	0	36	0.01
P. mimocerami Fleminger, 1957	82	0	0	0	0	0	0	0	0	86	0.03
Pontellina plumata (Dana, 1849)	0	0	0	0	0	0	0	0	0	16	0.01
Pontellopsis villosa Brady, 1883	0	24	5	0	0	0	0	15	0	210	0.08
Rhincalanus cornutus (Dana, 1849)	0	0	0	0	0	0	0	0	0	5	0.00
Saphirella tropica Wolfenden, 1906	0	24	0	0	0	0	0	5	0	36	0.01
Sapphirina metallina Dana, 1849	0	48	0	0	0	0	0	0	0	57	0.02
Scolecithrix danae Lubbock, 1856)	0	0	0	0	0	0	0	0	0	362	0.15
Subeucalanus subcrassus (Giesbr.,1888)	4,686	833	1,131	42	1,839	0	7,115	0	0	29,005	11.64
S. pileatus Giesbrecht, 1888	0	0	0	0	0	0	790	0	0	874	0.35
Temora stylifera (Dana, 1849	450	0	0	0	0	0	0	0	0	5,807	2.25
T. turbinata (Dana, 1849)	0	1,473	27	0	0	190	1,317	10	17	76,846	30.83
Undinula vulgaris (Dana, 1849)	5,075	408	340	14	1,224	0	16,358	206	139	36,248	15.34
Harpacticoids	0	0	0	58	0	250	0	0	6	1,679	0.67
TOTAL	13,234	7,769	2,755	1,250	5,727	3,161	30,097	1,868	580	249,278	100

bers occurred over the FR, and only 7% in the RL. Differences among the three zones were statistically significant (Fs = 42.14, $P < 0.0001$). Total density was two times higher at dusk (17,250 org 100 m^{-3}), than in the morning (8622.9 org 100 m^{-3}); day-night differences were also significant (Fs = 9.28, P = 0.0022). About 62% of the individuals were collected during dusk samplings. Over the FR, average density values at daytime (30,140 org 100 m^{-3}) were lower than at dusk (39,050 org 100 m^{-3}). At the RL, values were: 2140 org 100 m^{-3} (AM) and 2830 org 100 m^{-3} (PM); at the CH zone values were 234 and 765, respectively (Fig. 2).

Overall mean density varied day-to-day. Values recorded were as follows: day 1, 10,950 org 100 m^{-3} (23% of total copepod numbers) day 2: 20,370 org 100 m^{-3} (42%); day 3: 5650 org 100 m^{-3} (12%); day 4: 10,840 org 100 m^{-3} (23%, only AM). The day-to-day variation of copepod density in Mahahual reef is presented in Figure 2.

A total of 45 copepod species were identified. The most abundant, *Temora turbinata*, accounted for 31% of the total copepod numbers, with a mean density of 3780 org 100 m^{-3}. It was followed by *Undinula vulgaris* (15.7%; 1910 org 100 m^{-3}), *Subeucalanus subcrassus* (11.4%; 1400 org 100 m^{-3}), *Calanopia americana* (10.2%; 1250 org 100 m^{-3}), *Farranula gracilis* (5.8%; 710 org 100 m m^{-3}), and *Acartia spinata* (5.85%; 710 org 100 m^{-3}). This group comprised about 80% of the total overall planktonic copepod catch. The relative abundance, estimated density, and frequency of all the copepod species recorded in the area are presented in Table 1.

T. turbinata showed an overall mean density in daytime samples of 870 org 100 m^{-3}, the value in dusk samples being much higher (7370 org 100 m^{-3}), mainly due to a very high density value recorded at fore-reef sta.1. Disregarding this value, the figure is lower at night (550 org 100 m^{-3}). The same tendency was observed for *U. vulgaris* (daytime, 2750 org 100 m^{-3}; dusk, 900 org 100 m^{-3}), *S. subcrassus* (1430 vs 1340), *F. gracilis* (800 vs 590). The contrary was determined for *C. americana* (180 vs 2540) and *A. spinata* (490 vs 980). The ANOVA results showed significant differences due to the combined efect of species composition and both, reef zone (Fs = 2.15, $P < 0.0001$) and day-night sampling (Fs = 1.89, $P < 0.0001$).

T. turbinata was most abundant at the FR, nearly 96% of the total numbers of this species occurred in this environment. Only 3% occurred in the CH, and only 1% reached the RL. The figures for *U. vulgaris* were: 85% at the FR, 10% at the CH, and only 5% in RF. The same tendency was shown by *S. subcrassus* (87% in the FR), *F. gracilis* (73% in the FR), and *A. spinata* (88% in the FR). *C. americana* was almost equally abundant in the FR (38%) and in the CH (43%). Several species occurred only at the FR (*Copilia mirabilis*, *Candacia curta*, *Corycaeus amazonicus*, *Labidocera mirabilis*, *Lucicutia flavicornis*, *Phaenna spinifera*, *Pontellina plumata*, and *Pontellopsis villosa*).

Overall diversity (Shannon-Wiener) was highest at the FR (1.84 bits ind^{-1}). In this environment daytime and dusk samples were equally diverse (1.84 bits ind^{-1}). The RL (1.5 bits ind^{-1}) and the CH (1.6 bits ind^{-1}) zones showed lower overall diversity values, with dusk values being lowest.

Clustering with the Bray-Curtis Index produced a dendrogram (Fig. 3) in which two large groups of stations were defined. The one comprised stations with medium and high densities, it included all the fore-reef and some reef-lagoon stations, and in the other were clustered the low density stations (all CH and some RL stations).

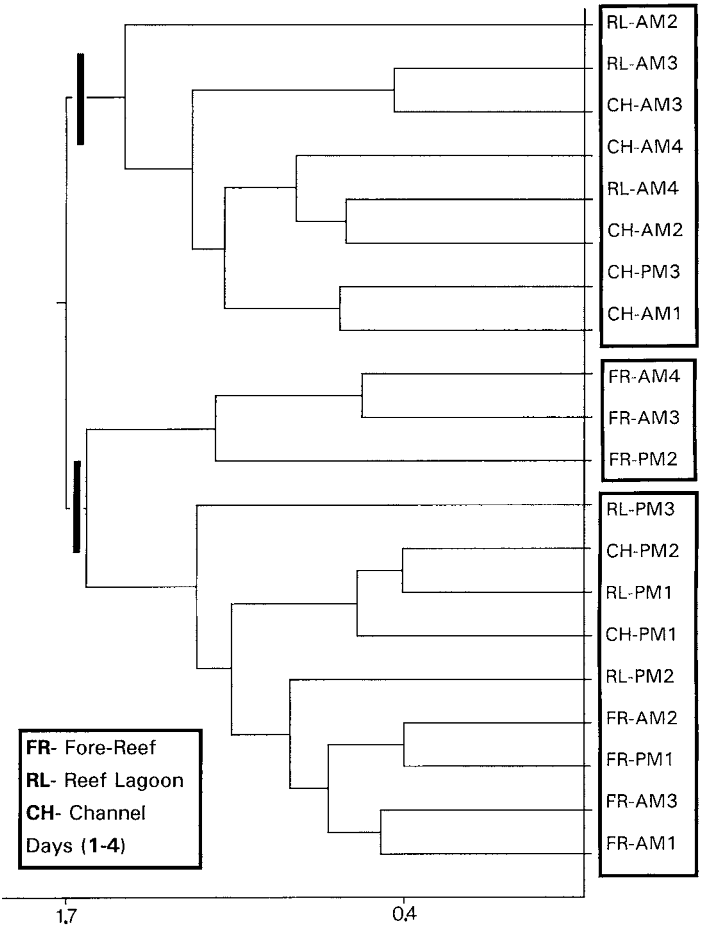

Figure 3. Dendrogram from clustering by Bray-Curtis Index showing distribution of clusters in the three reef-related environments during the surveyed period.

Discussion

All the copepod species recorded at Mahahual have been previously reported from adjacent coastal and reef areas of the Mexican Caribbean (Suárez-Morales and Gasca, 1996; Alvarez-Cadena et al. 1998) and most of them from other Caribbean reef areas (Moore and Sander, 1976). The number of species recorded in this survey (45) is relatively low when compared with the copepod richness found in adjacent zones. More than 120 species have been recorded from the oceanic waters of the Mexican Caribbean (Campos and Suárez-Morales, 1994; Suárez-Morales and Gasca, 1997), and more than 80 in other Caribbean reef zones, including the Mexican Caribbean (Alvarez-Cadena et al. 1998), Jamaica, and Barbados (Moore and Sander, 1976). Only 35 species were found in a large embayment of the Mexican Caribbean coast, with reef fauna influence (Suárez-Morales and Gasca, 1996).

The reef-related copepod fauna recorded off Puerto Morelos by Alvarez-Cadena et al. (1998) is compared herein with that recorded over Mahahual reef. Both faunal groups belong to the same barrier-reef system. Alvarez-Cadena et al. (1998) recorded 80% of their species in the FR and only 20% in the RL. The corresponding values for Mahahual were 65% at the FR and the CH zone, and 35% at the RL. It is difficult to explain the differences in species richness and its distribution with respect to Alvarez-Cadena et al. (1998) results. They sampled with a 0.33 mm mesh net, filtered an average of 200 m^3, and made surface tows. Up to this point, their methods are similar to those used by us at Mahahual. The main differences were probably on (1) the larger period covered by that work, including samples collected during several months, a sampling effort during which rare species are more likely to be captured, and (2) the fact that all of their samples were made at midnight, when a major portion of the demersal zooplankton tends to migrate surfacewards (Alldredge and King, 1977, 1980; Suárez-Morales and Gasca, 1990); our samples were made at daytime and dusk, when most demersal zooplankters are still near the bottom (Alldredge and King, 1980). The harpacticoid copepods, *C. americana*, and other migrating forms (Gonzalez and Bowman, 1965; Villiers and Bodiou, 1996), clearly more abundant at dusk hours in Mahahual, probably restructure the reef plankton community during the night. Significant day-night differences could be attributed to the occurrence and distribution of this kind of species.

Although the number of species is higher at Puerto Morelos reef (Alvarez-Cadena et al., 1998), the measure of species richness, the overall abundance of copepods, and the relative abundance of the dominant species is similar in the three reef areas. In Puerto Morelos differences in composition and a higher density within the RL than in the FR was recorded (Alvarez-Cadena et al., 1998) whereas it was the contrary in Mahahual, probably due to the low densities of *A. spinata*, the most representative reef-lagoon zooplankter in the Caribbean.

Copepod densities are commonly high in reef environments (Sanmarco and Greenshaw, 1984; Morales and Murillo, 1996). The overall mean density recorded at Mahahual during December-January is about three-fold lower (12,170 org 100 m^{-3}) than that recorded by Alvarez-Cadena et al. (1998) off Puerto Morelos during the same season (December): 31,432 org 100 m^{-3}. It is also lower than the overall average density found by Morales and Murillo (1996) during January (52,700 org 100 m^{-3}), and to the figures presented by Ferraris (1982) in a Belizean reef zone (21,287 org 100 m^{-3} in the RL, 52,280 in the FR). *A. spinata* is the most common RL species in the Caribbean (Moore and Sander, 1976); it represented between 60–75% of the total copepod numbers in Puerto Morelos RL (Alvarez-Cadena et al., 1998). It occurred with very low densities in Mahahual. This seems to be related to the strong seasonality of the species, which has its lowest breeding and density levels during the December–March period in the Caribbean (Moore and Sander, 1976); it was absent during some winter months in the Barbados reef. In Puerto Morelos this species had its lowest density during December (Alvarez-Cadena et al., 1998). It is probably quite abundant in Mahahual during summer (August–September) as recorded in adjacent systems by Suárez-Morales and Gasca (1996) and Alvarez-Cadena et al. (1998). The extreme scarcity of *A. spinata* is the main factor related to the Mahahual overall low total copepod densities. Subsampling is not considered a factor since the density of other zooplankton groups surveyed in Mahahual (Vásquez-Yeomans et al., 1998; Suárez-Morales et al., 1999) is similar to that recorded in adjacent areas.

Alvarez-Cadena et al. (1998) recognized *A. spinata*, *C. americana*, *T. turbinata*, *F. gracilis*, *Calanus minor*, *U. vulgaris* and *Clausocalanus furcatus* as the most abundant in all the reef environments. In the Mahahual community and in other Caribbean localities (Moore and Sander, 1976) the same group of species is dominant in the three reef environments but their relative abundance is variable. Communities of planktic copepods in near-shore and coastal systems are frequently dominated by a few of the commonest species (Suárez-Morales and Gasca, 1996). The most dominant copepods were distributed throughout the surveyed area regardless the type of environment (FR, RL, CH).

It is noteworthy also that *T. turbinata* has been previously reported as widespread or moderately abundant in the Caribbean reef zones (Moore and Sander, 1976; Alvarez-Cadena et al., 1998), but not as a dominant form as it was at Mahahual during the surveyed period. It has been recorded as abundant by Suárez-Morales and Gasca (1996) during November-February in adjacent coastal zones, when *A. spinata* numbers are lowest. Local coincidence of unexpectedly high numbers of *T. turbinata* numbers and lowest densities of *A. spinata* suggest an ecological replacement of *A. spinata*.

The near-shore hydrographic structure along the Caribbean coast of Mexico is effected by the flow of a coastal countercurrent moving southwards (Merino, 1986) from the northernmost edge of the Caribbean coast. Its influence would favor uniformity of hydrological conditions and of faunistic features along the entire coast (Suárez-Morales and Rivera-Arriaga, 1998).

It is generally accepted that most zooplankton drifting across the reef is of oceanic origin (Alldredge and King, 1977). In the Mexican Caribbean, a number of planktonic oceanic forms reach even estuarine waters (Suárez-Morales and Gasca, 1996; Suárez-Morales et al., 1999). Plankton transported northwards by the western edge of the Yucatan Current tends to drift inshore (Merino, 1986; Suárez-Morales and Rivera-Arriaga, 1998) giving the oceanic character to the reef community. The mesoscale distribution of zooplankton along the western Caribbean is strongly affected by tidal currents (Greer and Kjerfve, 1982; Kjerfve, 1982; Kjerfve et al., 1982) which favors the inflow of oceanic water to the reef lagoon through the channels and over the reef crests. This has been reported also for Mahahual (Castellanos and Suárez-Morales, 1997; Suárez-Morales et al., 1999). The low densities consistently recorded in the CH at Mahahual seem to be related to the effect of the tidal currents, one of the main dynamic factors of in and out water exchange of the reef system. 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 along the FR. This would explain the occurrence of oceanic copepods (Candacidae, Pontellidae) over the innermost portions of the narrow shelf. Some of the most abundant species across the Mahahual reef zone, such as *C. furcatus*, *F. gracilis*, and *U. vulgaris*, are considered as oceanic forms which penetrate well inside the reef system; this has been documented by Moore and Sander (1976) in Jamaica and Barbados. The same effect has been mentioned also for the reef zooplankton community at Belizean (Ferraris 1982) and Costarrican (Morales and Murillo, 1996) reefs. Particularly, *U. vulgaris* has been described as indicating the extent of the oceanic influence in reef environments (Renon, 1993). It was distributed even within the reef lagoon, confirming the strong across-reef intrusion of oceanic water in Mahahual, favored by the narrow shelf.

The arrival of oceanic forms effects a local enrichment of species and a higher FR diversity. However, a relatively high RL diversity was favored by the low dominance of *A. spinata*, commonly a dominant form in this environment (Moore and Sander, 1976;

Alvarez-Cadena et al., 1998). Mahahual FR ichthyoplankton is also more diverse (Vásquez-Yeomans et al., 1998).

The assemblages defined by the Bray-Curtis Index showed a coast-ocean gradient in the surveyed area. The first and second clusters comprised all the high density FR stations, and only some PM samples of RL and CH. It represents the primary influence of the oceanic fauna over the reef front. The second group, which included most of the CH and RL stations, showed the lowest densities, and a secondary oceanic influence. Therefore, density is the main difference between the local FR and RL copepod communities, the ANOVA results seem to support zonal differences between RL and FR. Alvarez-Cadena et al. (1998) reported a clearly defined RL community, featured by *A. spinata*. The local absence of *A. spinata* could not mask the RL-FR zonation of the community at Mahahual. Variations from this pattern could occur in the summer months, during which *A. spinata* populations are expected to peak.

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