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Article

Spatial and seasonal variability of *Acartia* (Copepoda) in a tropical coastal lagoon of the southern Gulf of Mexico

Variabilidad espacial y estacional de *Acartia* (Copepoda) en una laguna costera del sur del Golfo de México

Benigno J. Escamilla[1], Uriel Ordóñez-López[2] and Eduardo Suárez-Morales[3]

[1]Instituto Tecnológico de Mérida, Av. Tecnológico s/n, Mérida, Yucatán 97118, México
[2]Centro de Investigación y de Estudios Avanzados (CINVESTAV), Unidad Mérida, Km 6 carretera a Progreso, A.P. 73, Mérida, Yucatán 97310, México
[3]El Colegio de la Frontera Sur (ECOSUR), Av. Centenario Km 5.5, Chetumal, Quintana Roo 77014, México. esuarez@ecosur.mx

Resumen.- En este estudio se analizó la variabilidad estacional de la distribución y abundancia de especies de copépodos del género *Acartia* en una laguna costera de la costa norte de la Península de Yucatán, México, durante meses representativos de las tres épocas climáticas (secas, lluvias y nortes) de un ciclo anual. Se caracterizaron dos áreas distintas (interna y externa) de la laguna, basadas en su salinidad y biomasa de copépodos. *Acartia lilljeborgii* y *A. tonsa* fueron las especies más abundantes, y juntas representaron cerca del 95,5% del número total del género; la fracción remanente estuvo representada por *A. spinata*. Más de la mitad (52.3%) de la abundancia total de *A. tonsa* ocurrió en la época de lluvias, 30.6% durante nortes y 17.1% en la época seca. Los valores estacionales correspondientes de *A. lilljeborgii* fueron 57% en secas, 21.3% en lluvias y 20.4% en nortes. El 85% de los individuos de *A. spinata* ocurrieron en nortes. En épocas secas sólo *A. tonsa* fue más abundante en la zona interna mientras que *A. lilljeborgii* dominó la zona externa en la misma época. El análisis de correlación reveló cambios estacionales en la manera en que las especies de *Acartia* se relacionan con diferentes factores bióticos y abióticos. *Acartia tonsa* y *A. spinata* mostraron diferencias significativas relacionadas con la época y esta última a la combinación de zona (interna-externa) y la época. La variación espacial y temporal de la abundancia de las especies de *Acartia* estuvo relacionada con las condiciones hidro-biológicas de la laguna de cada estación. Por lo tanto, los cambios locales y de pequeña escala, y la respuesta de las especies según las condiciones estacionales, favorecen la coexistencia de los copépodos en este sistema lagunar.

Palabras clave: Zooplancton costero, ecología del plancton, copépodos, abundancia estacional, Atlántico Tropical Noroccidental

Abstract.- In this study, the seasonal variability of the distribution and abundance of the copepod *Acartia* spp. in a coastal lagoon on the northern coast of the Yucatan Peninsula, Mexico, was analyzed during representative months of the three main seasons (dry, rainy, and northerlies=nortes) of an annual cycle. Also, two distinct areas of the lagoon (inner and outer) were revealed according to salinities and zooplankton biomass. *Acartia lilljeborgii* and *A. tonsa* were the most abundant species, representing together up to 95.5% of the overall abundance of the genus. More than half (52.3%) of the total abundance of *A. tonsa* occurred in the rainy season, 30.6% during nortes, and 17.1% in the dry season. Corresponding seasonal values for *A. lilljeborgii* were 57% in the dry season, 21.3% in the rainy season, and 20.4 in nortes. Up to 85% of the individuals of *A. spinata* occurred during nortes. Only in the dry season *A. tonsa* was most abundant species at the inner zone, whereas *A. lilljeborgii* was dominant in the outer zone during the same season. The correlation analysis revealed seasonal changes in the way that species of *Acartia* relate to different biotic and abiotic factors: *Acartia tonsa* and *A. spinata* showed significant differences related to the season and the former species to the combination of zone (inner-outer) and season. The spatial and temporal variation of *Acartia* species abundance was related to seasonal changes of the hydro-biological conditions of the lagoon. Hence, the local and small scale changes, together with the seasonal conditions and the response of these species to them, favor their coexistence in this lagoon system.

Key words: Coastal zooplankton, plankton ecology, copepods, seasonal abundance, Northwestern Tropical Atlantic

Introduction

The aquatic biota of coastal systems such as lagoons, estuaries, and bays is affected by continuous, cyclical changes of environmental conditions both temporally and spatially as a result of the influence of tides, coastal currents, freshwater runoff, atmospheric processes, and human activities (Elliott & McLusky 2002). The zooplankton community is also affected by the variability of physical and chemical parameters and by the nutrient input from adjacent ecosystems (Malone *et al.* 1996, Waniek 2003).

Copepods compose the most relevant groups of coastal zooplankton; they usually represent 60 to 95% of the total biomass in coastal lagoons (Suárez-Morales 1994b, Lopes *et al.* 1998). Species of the genus *Acartia* are consistently present in these environments. *Acartia tonsa* Dana, 1852, *A. lilljeborgii* Giesbrecht, 1889, and *A. spinata* Esterly, 1911 have been previously reported as abundant and common in different coastal systems of the Northwestern Tropical Atlantic (Suárez-Morales 1994a, Suárez-Morales & Gasca 1996, Álvarez-Cadena & Segura-Puertas 1997, Escamilla & Suárez-Morales 1999, Escamilla *et al*. 2001, Ordóñez-López & Ornelas-Roa 2003, Álvarez-Cadena *et al*. 2007).

Distributional patterns of lagoonal planktonic copepods are influenced by environmental factors (Hwang *et al.* 2006). Salinity gradients resulting from varying intensities of marine influence and freshwater runoff often represent the main parameter in defining the local distributional patterns and succession of species of *Acartia* (Suárez-Morales 1994a). In some tropical estuarine systems seasonal variations have been described as weak despite the variability of hydrographic conditions and in other cases seasonal changes do not correspond to the expected pattern based on their known ecological affinities (Hwang *et al*. 2010). Therefore, in order to understand the dynamics of the planktonic biota, the study of the distribution and abundance of copepods and its variability represents a basic step. In this study we analyzed the seasonal abundance and distributional patterns of copepods of the genus *Acartia* in relation to the variation of zooplankton biomass and physical and chemical parameters in a coastal lagoon of the southern Gulf of Mexico.

Chelem lagoon is a coastal karstic shallow system partially protected by a sand barrier; it is located on the northern coast of the Yucatan Peninsula, Mexico (21º17'N; 89º40'W). The lagoon is approximately 25 km long, 800 m wide, and it has an average depth of 1.3 m; it has a north-south and east-west slope causing a weak runoff to the north and west (Zizumbo 1989). Since 1968 it has a permanent connection to the sea; it is influenced by waters from the Gulf of Mexico and the Caribbean Sea and during the dry season it becomes hyper-saline, but in some conditions it can become oligohaline (Valdés-Lozano 1995, Herrera-Silveira *et al.* 1999, Herrera-Silveira 2006). The inner flows of water in the lagoon are influenced mainly by tidal currents; tides in Chelem are mixed semidiurnal.

Materials and Methods

Zooplankton samples were collected in February, June, and October, 2000 by performing surface tows at eight sampling stations (Fig. 1). These months were selected as the most representative of the three main seasons that characterize the climate in this region: northerlies or nortes (February), dry (June), and rainy (October). A conical net of 30 cm mouth diameter, 120 cm long, and 0.33 mm mesh size was used in all cases (Harris *et al*. 2000). A General Oceanics 2030 digital flowmeter was adapted to the net mouth in order to estimate the amount of water filtered by the net. Sampling was conducted during the day between 08:00 and 14:00 h by trawling the net for 5 min. The biological material was fixed in a 4% formalin solution in seawater buffered with sodium borate.

Hydrological parameters including temperature (± 0.5°C), salinity (± 0.1), and dissolved oxygen were measured at each sampling site with the aid of a YSI85-50FT field multisensor; pH values were obtained with a Corning field potentiometer. All measurements were obtained at mid-water depth. Zooplankton biomass was obtained by the method of wet weight (mg m^{-3}) (Beers 1981) using an Ohaus analytical scale (± 0.1 mg). The species of *Acartia* were identified following Campos-Hernández & Suárez-Morales (1994). The numerical abundance of copepods was standardized to organisms 100 m^{-3}. Hydrographic data (depth, temperature, salinity, pH) were analyzed by the Ward Agglomerative Method with Euclidean distances linkage in order to identify affinities among groups of stations and then processed by a one-way ANOVA ($P < 0.05$, Zar 1988) to detect differences related to a single variable. A two-way ANOVA was performed with both the biotic and abiotic data to evaluate the space and time variability. Using the abundance data of the species of *Acartia* we performed a canonical correspondence analysis (CCA) (CONOCO 4.5) with log+1-transformed data to determine the relationships

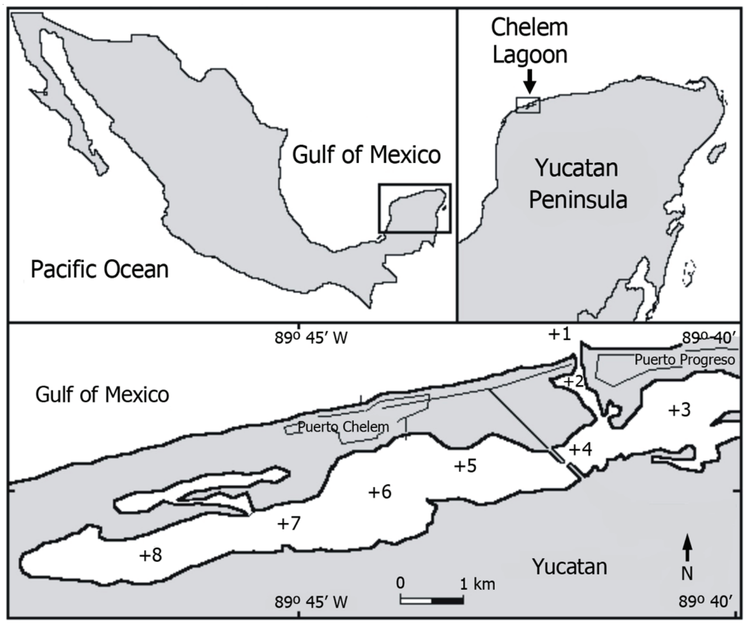

Figure 1. Location of the surveyed area and zooplankton sampling sites in Chelem lagoon system, Yucatan Peninsula, Mexico / Localización del área de estudio y de los sitios de muestreo de zooplancton en la laguna de Chelem, Península de Yucatán, México

between copepod species and the parameters recorded during each of the three seasonal periods included in this survey (Braak & Verdonschot 1995).

Results

Hydrological features

The cluster analysis of the sampling stations, based on the average values of the main environmental variables measured, allowed the detection of two distinctive areas, each containing four sampling stations: internal (sta. 1-4) and external (sta. 5-8). Each zone was significantly different (*P* > 0.05) with respect to the other in terms of the physical and chemical variables evaluated (Fig. 2, Table 1).

The average depth was 2.1 ± 1.1 m for the outer and 0.8 ± 0.01 m for the inner sector. The lowest average was recorded during the nortes season within the inner zone; the highest average was observed in the outer zone during the rainy season (Table 1).

The overall average temperature for the inner sector (25.9°C) was 1.2°C higher than in the outer sector. The highest seasonal value was recorded during the dry season (28.1 ± 1.2ºC), whereas the lowest occurred during nortes (21.0 ± 0.8ºC).

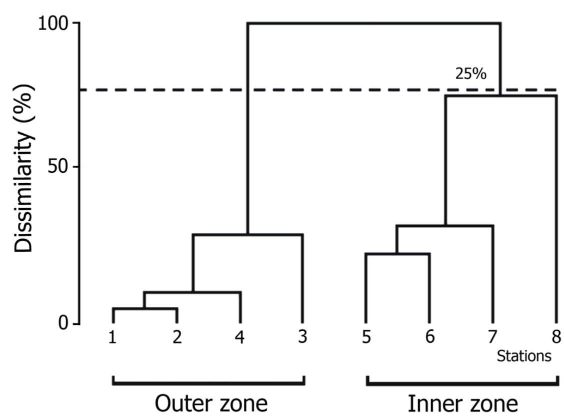

Figure 2. Dendrogram showing hydrographic affinities of sampling stations in Chelem lagoon dividing the system into two distinct zones (inner and outer). Data were log_{10} transformed before comparing stations by using the Bray-Curtis index / Dendrograma que muestra las afinidades hidrográficas entre las estaciones de muestreo en la laguna de Chelem dividiendo el sistema en dos zonas distintas (interna y externa). Datos transformados (log_{10}) antes de comparar las estaciones mediante el Indice de Bray-Curtis

Table 1. Spatial (inner/outer hydrographic zones) and seasonal (nortes, dry, rainy) variation of the hydro-biological parameters evaluated in Chelem lagoon, Mexico during the surveyed period. Std: Standard deviation / Variación espacial (zonas interna/externa) y estacional (nortes, secas, lluvias) de los parámetros hidro-biológicos evaluados en la laguna de Chelem, México durante el periodo estudiado. Std: Desviación estándar

Season	Nortes		Dry		Rainy		
Variable / Zone	Inner	Outer	Inner	Outer	Inner	Outer	Average
Abiotic							
Depth (m)	0.80	1.87	0.84	2.42	0.89	2.29	1.33
(Std)	0.14	0.97	0.05	1.36	0.09	2.29	0.87
Temperature (°C)	21.42	20.92	28.96	27.46	27.92	26.21	25.48
(Std)	0.90	0.90	0.96	0.89	0.51	0.26	3.27
Salinity (psu)	25.17	32.21	28.29	31.21	24.16	28.13	28.19
(Std)	2.87	2.62	0.26	2.62	1.96	2.52	3.68
Oxygen (mg l^{-1})	8.09	6.72	6.56	6.39	7.31	5.86	6.82
(Std)	0.40	0.57	2.13	0.32	1.07	0.61	1.24
pH	8.40	8.00	8.41	8.14	8.48	8.34	8.29
(Std)	0.10	0.12	0.10	0.03	0.05	0.11	0.19
Biotic							
Biomass (mg m^{-3})	134.8	137.5	106.7	425.4	62.4	51.1	114.7
(Std)	26.3	29.8	26.5	88.5	9.2	7.9	92.9
Zooplankton Density (org. 100 m^{-3})	168037.0	99934.0	77587.0	443348.0	77587.0	117877.0	123046.3
(Std)	36734.5	11886.6	6330.1	153491.7	6330.1	25646.1	112996.2
Copepod density (Copep. 100 m^{-3})	37125.0	55766.0	30741.0	50928.0	35024.0	72085.0	35208.6
(Std)	7046.0	11162.9	4122.2	9677.0	3507.0	17291.2	18282.0

Table 2. Values of F and *P* from the two-way ANOVA of the biotic and abiotic factors (log+1 transformed data) in Chelem during the surveyed period. Significant values in boldface / Valores de F y *P* obtenidos del ANDEVA de dos vías de los factores bióticos y abióticos (datos transformados a log+1) en Chelem durante el periodo estudiado. Valores significativos en negritas

	Effects								
	Zone (2)			Season (3)			Zone x Season		
	F	g.l.	*P*	F	g.l.	*P*	F	g.l.	*P*
Abiotic									
Depth	41.25	1	**<0.001**	0.78	2	0.464	0.18	5	0.839
Temperature	43.46	1	**<0.001**	567.34	2	**<0.001**	3.69	5	**0.030**
Salinity	67.30	1	**<0.001**	14.59	2	**<0.001**	4.85	5	**0.010**
Oxygen	11.91	1	**<0.001**	6.59	2	**<0.001**	3.91	5	**0.024**
pH	96.81	1	**<0.001**	27.92	2	**<0.001**	8.46	5	**<0.001**
Biotic									
Biomass	1.13	1	0.302	2.73	2	0.092	1.17	5	0.332
Zooplankton density	1.10	1	0.308	0.67	2	0.522	2.03	5	0.160
Copepod density	1.91	1	0.183	0.24	2	0.787	0.01	5	0.990

Salinity showed a higher overall average in the outer sector of the lagoon (28.1 ± 1.0 psu); salinity was lower (25.8 psu) within the inner sector. The highest salinity average occurred during the dry period (28.3 ± 0.8 psu) and the lowest in the rainy season (24.1 ± 2.3 psu). Dissolved oxygen showed the highest average value during the northerlies season (8.0 ± 2.3 mg L^{-1}), lower values were observed both in dry and wet seasons (see Table 1).

Overall, recorded pH values were slightly alkaline in the lagoon; the highest average was observed for the inner sector (8.5 ± 0.08), 0.3 units higher than in the outer area; the highest seasonal average was recorded in the rainy season (8.48 ± 0.1) (Table 1). The two-way ANOVA of the hydrological data confirmed these zonal differences (Table 2).

Biomass, zooplankton and copepod abundance

Overall, the average zooplankton biomass of the surveyed lagoon was 114.7 ± 92.9 mg m^{-3}. Considering the two main hydrologic areas defined, the average zooplankton biomass recorded in the outer sector during the year cycle was 204.5 ± 61.6 mg m^{-3}, almost two times higher than the inner sector (103.5 ± 20.6 mg m^{-3}). During the dry season, this biomass value was highly variable (see Table 1); the average (265.5 ± 92 mg m^{-3}) was almost twice that recorded during nortes (136 ± 21.4 mg m^{-3}) and up to 4.5 times of that observed in the rainy season (56.7 ± 8.3 mg m^{-3}). The total zooplankton abundance average was 123,046 ± 112,996 org.100 m^{-3} (see Table 1). Highest averages were recorded during the dry season in the outer sector, about two times higher than that for the inner zone. During this period zooplankton abundance was between 1.9 and 2.5 times higher than in northerlies and the rainy seasons, respectively (Table 1). The total average abundance of copepods followed a different pattern where highest values were recorded during the rainy season for the outer sector (72,085 ± 17,291 org. 100 m^{-3}), about twice the figure recorded from the internal part of the lagoon in the same season. During the other two seasons, copepod abundance values were lower but the same pattern prevailed, with higher values shown for the outer zone (Table 1).

Abundance and distribution of *Acartia*

Copepods represented up to 55% of the total numerical abundance of the zooplankton in the surveyed area. Species of *Acartia* represented more than 84% of the local copepod fauna. Three species of this genus were present in our samples: *A. lilljeborgii*, accounting for 49.8% of the total number of acartiids, followed by *A. tonsa* (45.6%), and *A. spinata* (4.6%). The seasonal relative abundance of *A. tonsa* was variable; 52.3% of the total number of this species occurred during the rainy season, 30.6% in the nortes, and 17.1% in the dry season. The seasonal values of *A. lilljeborgii* were 57.0% in the dry season, 21.8% in the rainy season, and 20.4% during the nortes. *Acartia spinata* was the less abundant and less frequent, up to 85.6% of its abundance was observed during northerlies, 13.6% in the rainy season, and 0.8% during the dry season (Table 3).

Table 3. Spatial (inner/outer hydrographic zones) and seasonal (nortes, dry, rainy) variation of the total numerical abundance (org. 100 m^{-3}) for species of *Acartia* in Chelem lagoon, Mexico during the surveyed period. Std: Standard deviation / Variación espacial (zonas interna/externa) y estacional (nortes, secas, lluvias) de las abundancias totales (org. 100 m^{-3}) de las especies de *Acartia* en la laguna de Chelem, México durante el periodo estudiado. Std: Desviación estándar

Season	Nortes		Dry		Rainy		Total	
Species / Zone	Inner	Outer	Inner	Outer	Inner	Outer	Inner	Outer
A. tonsa	7420.0	18721.0	11422.0	3208.0	18388.0	26334.0	37230.0	48263.0
(Std)	1537.6	3206.0	1534.3	572.1	2689.4	5258.0	5550.3	11785.7
A. lilljeborgii	12630.0	6373.0	17809.0	36190.0	7806.0	12488.0	38245.0	55051.0
(Std)	2917.8	2323.1	3361.0	7693.9	628.5	1831.3	5002.5	15749.2
A. spinata	1302.0	6035.0	13.0	47.0	632.0	586.0	1947.0	6668.0
(Std)	325.7	1485.0	6.5	9.4	164.3	174.0	644.7	3312.6
Total	21352.0	31129.0	29244.0	39445.0	26826.0	39408.0	77422.0	109982.0
(Std)	5670.1	7228.7	9015.3	20017.2	8932.3	12886.2	4043.4	4790.6

The highest mean abundances of *Acartia* were recorded for the outer zone of the lagoon system, up to 58.7% of the individuals occurred in this sector (Table 3). *Acartia tonsa* and *A. lilljeborgii* were, in general, more abundant in the outer sector than within the inner zone, but *A. spinata* showed an opposite pattern, it was about four times more abundant in the outer sector (Table 3). These patterns showed seasonal variations; *A. tonsa* was more abundant in the outer zone during the nortes and rainy periods but a reverse pattern occurred in the dry season, when its abundance was three-fold higher within the inner zone (see Table 2). In the same season (dry), *A. lilljeborgii* showed the opposite tendency, it was twice as abundant in the outer zone (Table 3); it was also more abundant in the outer zone during the rainy season. *Acartia spinata* was clearly more abundant in the outer zone except for the rainy season, during which it was equally abundant in both areas of the lagoon (Table 3).

In terms of seasonal variation, *A. tonsa* was mostly abundant in the rainy season, followed by nortes and the dry season. *Acartia lilljeborgii* had its highest abundance during the dry period, which was between 2.5 and 3 times higher than in the rainy and northerlies periods, respectively. *Acartia spinata*, though relatively scarce, showed its highest abundance during nortes, clearly higher than that in the other two seasonal periods (see Table 3). Significant differences in the abundances of *A. tonsa* and *A. spinata* were found among seasons (Table 4).

Environmental parameters and *Acartia*

The canonical correlation analysis (CCA) between measured environmental variables and the abundance of species of *Acartia* in the surveyed area, yielded values over 85% of the variance explained by relating component one and two during the three seasons, thus indicating a high correlation between both components. During the nortes season the variance explained was 99%, axis 1= 85.9, axis 2= 13.1%. The relation of *A. spinata* with deeper and more saline sites can be clearly observed, but the graphic also reflects the high density of *A. tonsa* in the same conditions, particularly in the outer zone of Chelem, where it had its highest densities. *Acartia lilljeborgii* was associated with relatively warmer water and with higher pH values and oxygen. Biomass was more correlated with depth than with salinity (Fig. 3). During

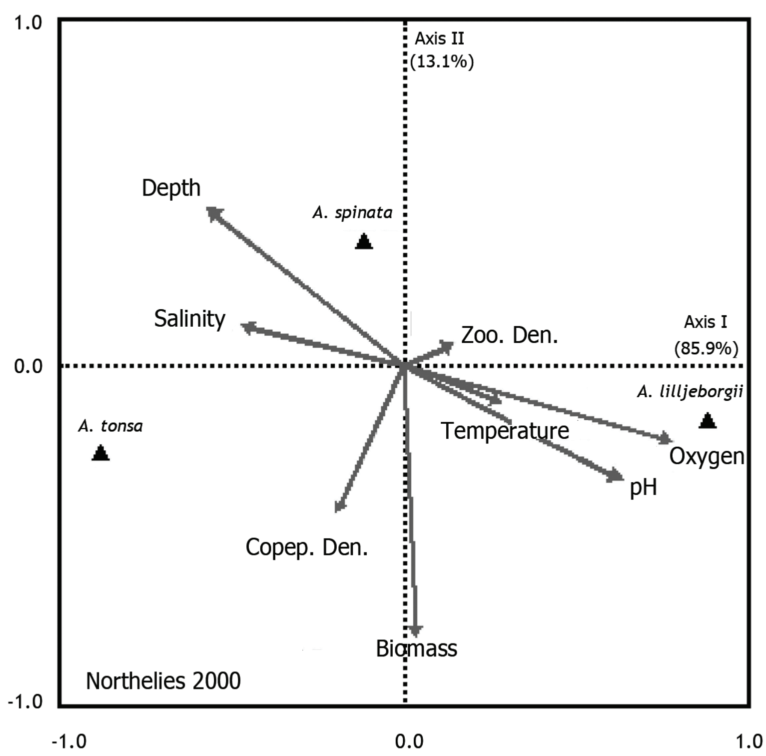

Figure 3. Canonical Correspondence Analysis (CCA) of hydrographic and biological data for species of *Acartia* during the nortes season. Data were $\log_{10}$ transformed / Análisis de Correspondencia Canónica (CCA) de los datos hidrográficos y biológicos con respecto a las especies de *Acartia* durante la época de nortes. Datos transformados ($\log_{10}$)

the dry season the variance explained was 99% (axis 1= 92%, axis 2= 7.0%), *A. tonsa* showed low correlation with most variables but a high correlation with pH values and temperature; the position of *A. spinata*, close to the axes origin (0,0), suggests an overall low correlation with the parameters measured during this season. *Acartia lilljeborgii* was associated with relatively higher values of oxygen and biomass and low values of pH and temperature (Fig. 4). Finally, during the rainy period, the variance explained was 99% (axis 1= 98.4%, axis 2= 0.6%). Both *A. tonsa* and *A. lilljeborgii* were correlated with high values of zooplankton biomass, temperature, zooplankton density, pH, and dissolved oxygen, whereas *A. spinata* was related to the deeper and more saline sites, as observed during nortes (Fig. 5). *Acartia tonsa* and *A. spinata* showed significant differences when related to the season and the former species to the combination of zone (inner-outer) and season. The results of the ANOVA for the abundance of *Acartia* species in the surveyed area is presented in Table 4.

Table 4. Results of two-way ANOVAs to compare the abundance of species of *Acartia* (log+1-transformed data) in Chelem according to zone and season during the surveyed period. Significant values in boldface / Resultados de ANDEVAs de dos vías que comparan la abundancia de las especies de *Acartia* (datos transformados a log+1) en Chelem según zona y estación durante el periodo estudiado. Valores significativos en negritas

	Effects								
	Zone (2)			Season (3)			Zone x Season		
Species	F	g.l.	*P*	F	g.l.	*P*	F	g.l.	*P*
A. tonsa	0.05	1	0.831	3.89	2	**0.039**	3.86	5	**0.040**
A. lilljeborgii	0.63	1	0.871	3.04	2	0.072	1.50	5	0.249
A. spinata	2.72	1	0.116	9.54	2	**0.001**	0.95	5	0.405

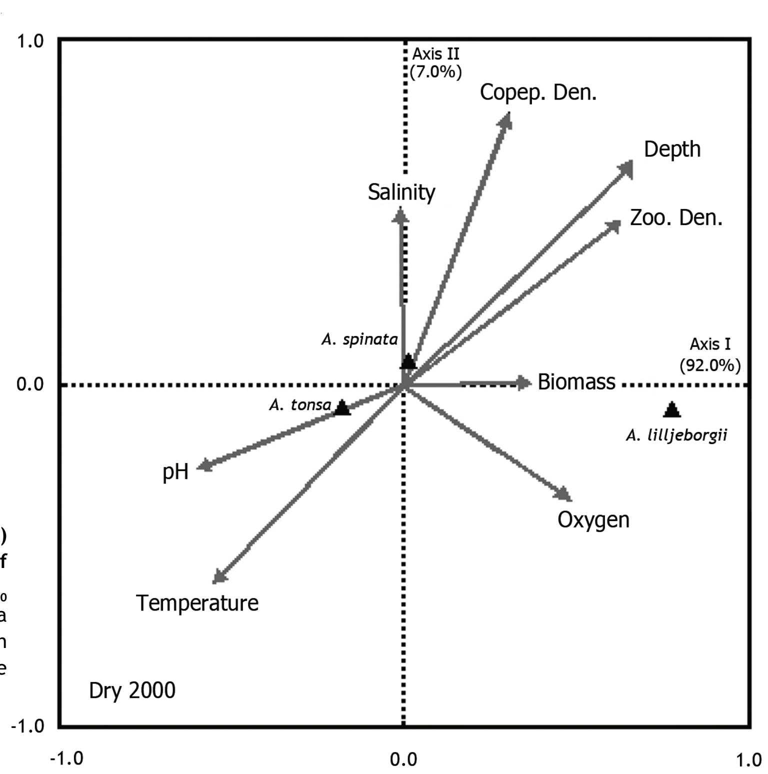

Figure 4. Canonical Correspondence Analysis (CCA) of hydrographic and biological data for species of *Acartia* during the dry season. Data were log_{10} transformed / Análisis de Correspondencia Canónica (CCA) de los datos hidrográficos y biológicos con respecto a las especies de *Acartia* durante la época de secas. Datos transformados (log_{10})

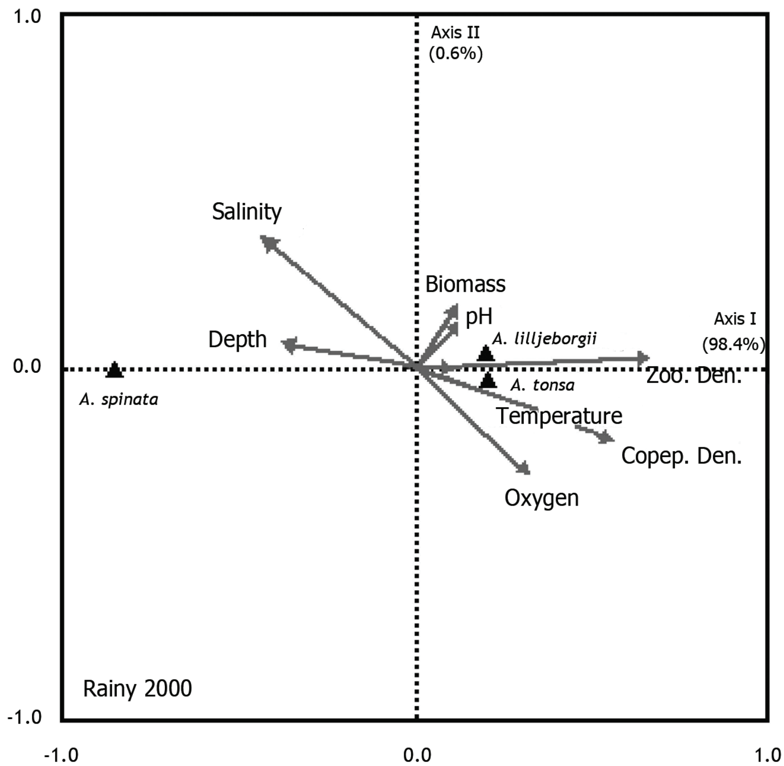

Figure 5. Canonical Correspondence Analysis (CCA) of hydrographic and biological data for species of *Acartia* during the rainy season. Data were $\log_{10}$ transformed / Análisis de Correspondencia Canónica (CCA) de los datos hidrográficos y biológicos con respecto a las especies de *Acartia* durante la época de lluvias. Datos transformados ($\log_{10}$)

Discussion

The analysis of the hydrographic data recorded in Chelem revealed a spatial zonation of the system but also a seasonal pattern involving distinctive changes of general conditions during each of the three seasons surveyed. According to the results by Valdés-Lozano (1995) and Herrera-Silveira *et al.* (1999) in this coastal system, such variations result from the confluence of different factors including the intensity of winds, patterns of advective processes, residence time of water, and intensity of land effluents (springs).

Considering the variability of the biomass average in Chelem (114.7 ± 92.9 mg m^{-3}), the wet weight zooplankton biomass is within the range reported for other coastal lagoons with similar physiographic features (Batllori-Sampedro 1988, Ordóñez-López & Ornelas-Roa 2003). These values are higher than those recorded from other semi-enclosed coastal systems of the western Caribbean coast such as Chetumal Bay (1-25 mg m^{-3}) (Gasca *et al*. 1994) but lower than those recorded for systems with an open oceanic front (25-125 mg m^{-3}) (Suárez-Morales & Gasca 1994). However, according to Escamilla *et al*. (2001), the high residence time of water in Chelem favors relatively homogeneous local biomass values and thus relatively high food availability for copepod populations.

The three species of *Acartia* recorded in this system are commonly found in other coastal areas of the Western Tropical Atlantic (Suárez-Morales 1994a, Álvarez-Cadena & Segura-Puertas 1997, Lopes *et al*. 1998, Ornelas-Roa & Ordóñez-López 2000). Their abundance in Chelem is also comparable to that recorded for other coastal water bodies in the region (Suárez-Morales & Gasca 1996, Ornelas-Roa & Ordóñez-López 2000). The dominance of *Acartia* populations over other copepods has been commonly reported in reference to coastal lagoons and estuaries (Miller 1983, Suárez-Morales 1994 a, b, Sterza & Loureiro-Fernandes 2006); however, in some other tropical estuarine systems *Acartia* is not dominant (Hwang *et al.* 2010).

The highest overall abundances of *Acartia* (nearly 60% of the total) were recorded at the outer zone of Chelem, related to an average salinity of 30.5 psu and a temperature of 24.8°C. This pattern agrees with the known affinity of these estuarine-coastal species of *Acartia* in tropical inshore environments (Lopes *et al*. 1998, Ornelas-Roa & Ordóñez-López 2000, Suárez-Morales *et al*. 2009).

Overall, the presence of abundant populations of *Acartia* in the same area, suggests both sustained food availability and continuous competition; being a shallow system it is presumed that phytoplankton and small zooplankters are highly available along the water column. Many species of *Acartia*, including *A. tonsa*, feed on heterotrophic and autotrophic prey (Rollwagen-Bollens & Penry 2003). The evaluation of the trophic relations within the system should include an analysis of all the developmental stages of these copepods. The abundances reported here are in reference to adult populations only; future surveys should take into account juvenile (copepodite) numbers in order to determine the seasonal population dynamics of each species in the area (Hoffmeyer *et al*. 2009).

Acartia lilljeborgii is widely distributed in estuaries with salinities ranging from 20 to 30 psu, with no detectable variations in abundance along the gradient (Sterza & Loureiro-Fernandes 2006). *Acartia tonsa* can occur in oligohaline systems like the bay of Chetumal (Suárez-Morales 1994a) and also in hyper-saline lagoons of the Gulf of Mexico like Laguna Madre and Corpus Christi bay (Britton & Morton 1989), basically due to a wide tolerance to varying salinities (Cervetto *et al.* 1999), but it is usually dominant within the innermost reaches of the coastal systems (Sabatini 1989), a pattern observed in Chelem only during the dry season.

Both species of *Acartia* appear to feed on the same resources when they are present in the same system (Kennish 1986), but they can coexist because of the space and time segregation effected by the local restrictions imposed by the small scale changes of saline conditions and tidal patterns (Suárez-Morales 1994a, Escamilla *et al*. 2001). So, in order to coexist in the same system with a similar spatial distribution for long periods, a shift in the seasonal succession would then become a strategy to avoid continuous competition. According to our results, such a pattern could be occurring in Chelem, where the highest overall abundances of *A. tonsa* occurred in the outer zone and during the rainy season, whereas *A. lilljeborgii* reached its maximum abundance in the same area, but during the dry season. The distribution of *A. tonsa* and *A. lilljeborgii* within the inner or outer zones (Table 3), was different during seasons, *i.e., A. tonsa* was more abundant in the outer zone while *A. lilljeborgii* was abundant in the inner zone during nortes, however, the abundances of these two copepods were opposite during the dry season. During the rainy season, both species were more abundant in the outer zone, probably avoiding lower salinity conditions at the inner zone. Seasonal conditions modify the structure and distribution of local populations of *Acartia*. This is also supported by the results of the two-way ANOVA and the CCA, as discussed below. In this regard, Miller (1983) noted the existence of a temporal and spatial succession between species of *Acartia* in estuaries at higher latitudes, where *A. clausi* Giesbrecht, 1892 often replaces *A. tonsa*. Similar results were previously reported by Jeffries (1962). Similarly, Sullivan *et al*. (2007) described the succession of *A. tonsa* and *A. hudsonica* in the North Atlantic Ocean, but in this case, this process is clearly related to temperature; the former is replaced during the winter. Suárez-Morales (1994b) mentioned that in warm coastal waters it is likely that *A. lilljeborgii* replaces *A. tonsa*, which is dominant in coastal lagoons of the Gulf of Mexico and the Mexican Pacific.

On the other hand, *A. spinata*, with a well-known marine affinity (Suárez-Morales *et al*. 2009), is among the predominant species in an adjacent reef lagoon (Suárez-Morales & Gasca 2000). However, it was the least abundant species of *Acartia* in Chelem. Its affinity for more saline waters would explain its greater abundance in the deeper area with the strongest marine influence in Chelem (outer zone) during at least two seasons (nortes and dry). In relatively stable estuarine systems with persisting zonal conditions, up to four species of *Acartia* have been known to coexist (Alcaraz 1983). The relatively high residence time of water in Chelem (Escamilla *et al*. 2001) together with the salinity gradients and also other factors (as suggested by the CCA) appear to be relevant in allowing the coexistence of three congeneric species of copepods.

Aside from temperature and salinity, there are other unexplored environmental factors that might be important to understand these patterns. There are no previous data about the tolerance of dominant species of *Acartia* to changes in pH; our results of the overall abundance of *Acartia* in Chelem suggest that they tend to become less abundant in waters with pH values greater than 8.2 (inner zone) during the three seasonal periods (see Tables 1, 3). However, the CCA indicated that *A. tonsa* and *A. lilljeborgii* appear to be differently correlated with pH in the nortes and dry seasons (Figs. 3, 4). During the rainy season, when the pH is more homogeneous, both species have nearly the same correlation with this factor. In a temperate coastal system of South America, differential responses to certain parameters have been described as relevant in allowing the coexistence between two species with similar characteristics. The developmental stages of *A. tonsa* were most positively correlated with temperature and photoperiod whereas the estuarine *Eurytemora americana*, showed positive correlations with chlorophyll-*a* and salinity (Hoffmeyer *et al*. 2009). Hence, the gradients of more than one environmental factor provide a niche separation facilitating the coexistence of two competitive copepods. The tidal pattern could be yet another additional factor contributing in shaping the abundance of some species in Chelem, as suggested by Escamilla *et al.* (2001) from data obtained during nortes, but the results of Ali *et al.* (2011) indicated that copepod abundance could be related to other parameters rather than tides.

The different seasonal configurations of the CCA (Figs. 3-5) suggest that there are detectable variations in the local community and also in regards to the effects of the variability of the parameters measured on the distribution and abundance of the species of *Acartia*. During nortes, when *A. tonsa* was more than 2.5 times more abundant in the outer zone than in the inner sector, its distribution coincided with that of *A. spinata*, clearly related to deeper, more saline waters. In the same season, *A. lilljeborgii* was correlated with warmer waters, high pH and oxygen values, that were also kept during the other two seasons. During the dry season the community of *Acartia* changed; *A. lilljeborgii* had the highest overall density, which explains its high correlation with the biomass; its abundance tended to be correlated with lower pH values (Fig. 4). During this season *A. tonsa* was more abundant within the inner zone of Chelem. This is in contrast to *A. lilljeborgii*, which was clearly related to high pH values. The undefined correlations of *A. spinata* in this season are probably obscured by its very low abundance. In the rainy season the pH values were more homogeneous and thus both *A. tonsa* and *A. lilljeborgii* were correlated with this parameter. Both species were also found in relation to high values of temperature, zooplankton density, and dissolved oxygen, whereas *A. spinata* was related to the deeper and more saline sites, as observed during nortes.

Conservation strategies are based on a previous knowledge of the communities; these kind of surveys allow for the detection of non-indigenous planktonic species invading these tropical coastal environments and impacting the ecosystems. Through a monitoring program, these measurements will also help in revealing changes to the structural and functional parameters of the local plankton communities derived from different kinds of alterations. At larger scales, long term changes regarding seasonality of succession for species of *Acartia* in a coastal system have been studied in relation to global warming (Sullivan *et al*. 2007); hence, the interannual variability of these patterns should be monitored for this and other coastal systems of the region. Variations of salinity, temperature, and biomass were not the only factors that determined the local distribution patterns of *Acartia*. It is likely that biological factors such as reproductive cycles, competition and predation have an important role the variation of the abundance of copepod populations in coastal systems (Costello *et al*. 2006).

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