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Distribución de pterópodos (Mollusca: Gastropoda: Thecosomata) en aguas superficiales (0-100 m) del Mar Caribe Occidental (invierno, 2007)

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Resumen.- El principal objetivo de este estudio fue conocer la distribución vertical y horizontal de los pterópodos tecosomados en la capa superior de los 100 m del Mar Caribe occidental. El zooplancton fue recolectado en 60 estaciones durante enero 2007 en intervalos de profundidad de 25 m desde la superficie a 100 m. La comunidad fue analizada en términos de diversidad, equidad, riqueza y similitud. Encontramos 36 taxa de los que 12 son nuevos registros para el Caribe occidental. Los taxa más abundantes fueron *Limacina inflata*, *L. trochiformis, Creseis acicula* f. *clava, Cuvierina columnella atlantica* y *Hyalocylis striata*. En general, mostraron un mismo patrón, sus mayores abundancias ocurrieron consistentemente en el estrato 0-25 m de día y noche; la abundancia decrece con la profundidad. Se encontraron diferencias significativas día/noche en composición y abundancia, no así entre estratos. El estrato de 0-25 m contiene los mayores valores de riqueza, diversidad y abundancia de pterópodos, lo que representa un hallazgo sin precedente respecto a estudios previos. La estructura de la comunidad local está determinada en gran medida por las migraciones verticales día/noche. Los pterópodos tendieron a ser más abundantes en los sectores norte y sur del área, pero su mayor diversidad y riqueza se registró en el sector central. La baja variabilidad de las condiciones hidrográficas y la mezcla horizontal de los grupos generados por el análisis de similitud sugieren que los patrones migratorios día/noche explican la variabilidad observada en la comunidad de pterópodos.

Palabras clave: Moluscos tecosomados, zooplancton marino, migración vertical, abundancia, diversidad

Abstract.- The main goal of this survey was to study the vertical and horizontal distribution of the thecosome pteropods in the upper 100 m of the western Caribbean Sea. Zooplankton was collected at 60 stations in January 2007 at stratified depth intervals of 25 m from the surface to 100 m. The community was analyzed for diversity, evenness, species richness, and similarity. We recorded 36 taxa 12 of which are new records for the western Caribbean. The most abundant taxa were *Limacina inflata*, *L. trochiformis*, *Creseis acicula* f. *clava*, *Cuvierina columnella atlantica*, and *Hyalocylis striata*. In general, these taxa showed a similar pattern, their highest abundances occurred consistently in 0-25 m layer in both night and day samples; abundance decreased with depth. Significant day/night differences were found in the composition and abundance of pteropods, differences among depth intervals were non-significant. Our results showed that the upper 25 m harbored the highest species richness, diversity, and vertical abundance of pteropods, thus providing unprecedented detail with respect to previous surveys. The local community structure of the pteropods is determined largely by vertical day/night migrations. Pteropods tended to be most abundant in the southern and northern sectors of the area, but highest diversity and species richness were recorded in the central sector. Overall, the low variability of the hydrographic conditions and the mixed horizontal distribution of the clusters from the similarity analysis suggest that day/night migratory patterns of the most abundant taxa are determinant of the observed variability of the pteropod community.

Key words: Thecosome molluscs, marine zooplankton, vertical migration, abundance, diversity

Introduction

Pteropods represent a lineage of the Mollusca that have successfully colonized the water column. They are among the most frequent and abundant groups in the oceanic zooplankton communities (Van der Spoel 1967, 1996, Van der Spoel & Dadón 1999). This relatively small group of holoplanktic molluscs includes two orders of the Gastropoda. In this study we deal only with those belonging to the order Thecosomata, which includes the suborders Euthecosomata and Pseudothecosomata (Van der Spoel & Boltovskoy 1981, Van der Spoel & Dadón 1999).

As a group, the thecosome pteropods are widely distributed in the world ocean, including cold, temperate, and tropical latitudes. Their vertical distribution is broad, stretching from the surface layers to the bathypelagic zone. Many euthecosomatous forms are restricted to the upper 200 m but members of the Pseudothecosomata dwell mainly in deeper layers (Van der Spoel 1996). Most thecosome pteropods exhibit relatively short diurnal vertical migrations along the 0-100 m depth range; during the day they tend to move to deeper layers and then migrate to the surface at night (Angel & Pugh 2000). The different species have variable patterns of vertical distribution and day/night migrations (Hays 2003); in many geographical regions, but particularly in the tropics, these patterns remain unknown for most of these species.

In the Caribbean Sea, previous research on this group has focused on its general species composition, horizontal distribution, and abundance (Gasca & Suárez-Morales 1992, Suárez-Morales & Gasca 1998). Only the early work by Haagensen (1976) included information about the vertical distribution of the pteropods from the central and eastern Caribbean. There are no previous studies involving stratified samplings to describe the vertical distribution of this group in the western sector of the Caribbean Sea. Furthermore, this survey provides an unprecedented vertical stratification (each 25 m) of the 0-100 m layer. Based on a set of stratified samples from the upper 100 m of the water column, we describe the composition, abundance, and vertical and horizontal distributional patterns of the thecosome pteropods from oceanic waters of the westernmost sector of the Caribbean Sea during January 2007.

Study area

The surveyed area lies between 16º14' and 21º30'N and 86º59' and 88º22'W off the eastern coast of the Yucatan peninsula (Fig. 1). The area is influenced by the northward flow of the Yucatan Current on its way to the Gulf of Mexico through the Yucatan Channel (Merino 1986). Water circulation is part of the North Atlantic Subtropical Gyre, forced by wind stress over the North Atlantic, this process sheds eddies into the Caribbean Sea Basin. In addition to large-scale processes, local small and mesoscale features change the hydrographical profile of the western Caribbean. Advective processes transport oceanic water onto the coastline; hence, the oceanic influence is detectable very near the coast and tends to favor a generalized oceanic profile in the area (Merino 1986). The northeast portion of the Yucatan peninsula is characterized by a large upwelling system (Merino 1997). The water masses in the area have been described from T-S profiles and correspond to surface tropical Atlantic Ocean water (28ºC, 36 psu), subtropical subsurface water (22ºC, 36.7 psu), the Western North Atlantic Central Water mass below 500 m (20ºC, 34.8 psu), and the uniform deep waters of the Atlantic below 1000 m depth (4ºC, 35 psu). Salinity varies little throughout the year, between 35.8 and 36.2 psu. The sea-surface temperature

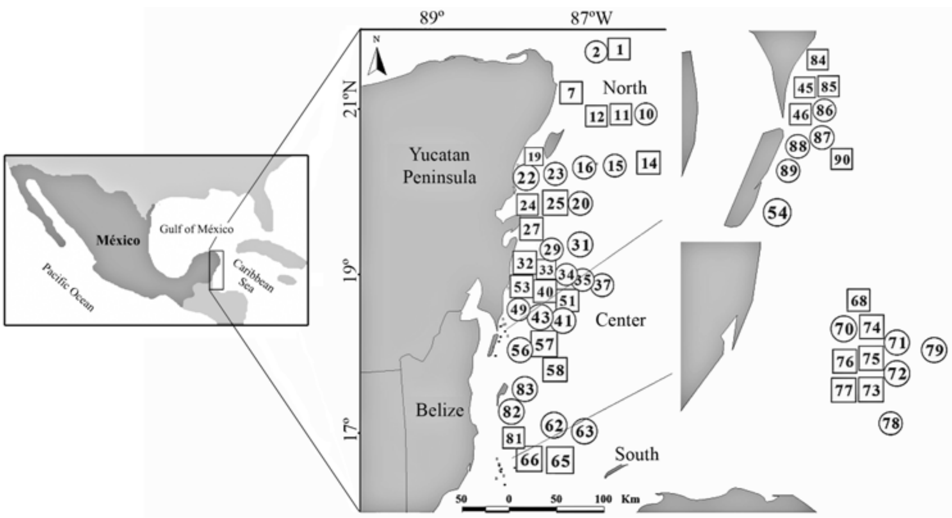

Figure 1

Sampling stations in the western Caribbean Sea off Mexico and Belize visited during January 2007. Circled stations were sampled at night; stations within a square represent daytime samplings

Estaciones de muestreo en el Mar Caribe Occidental de México y Belice visitadas durante enero 2007. Las estaciones encerradas en un círculo fueron muestreadas en la noche; las que están en cuadros representan muestreos diurnos varies seasonally between 26ºC in the winter and 31ºC in the summer (Mooers & Maul 1998). A general description of the oceanographic conditions of the Caribbean Sea was provided by Gallegos & Czitrom (1997).

Material and methods

Samples were collected during a joint project of the National Oceanic and Atmospheric Administration (NOAA) and El Colegio de la Frontera Sur (ECOSUR) to survey the plankton and the physical oceanography of the western Caribbean. A total of 240 zooplankton samples were obtained at 60 stations visited during January 2007 on board the R/V Gordon-Gunter (GU0701, NOAA). Samples were collected using a MOCNESS-1 net system, with 1 m^2 mouth, 335-µm mesh nets, and equipped with a digital flowmeter. The amount of water filtered by the net was 593 ± 115 m^3. Sampling stations were visited at daytime (6:00 a.m.-18:00 p.m.) or nighttime (after 18:00 p.m.), approximately 1 h after dawn and after sunset. Samples were collected at four different depth intervals: 0-25, 25-50, 50-75, and 75-100 m. Temperature and salinity were measured simultaneously at each station/depth layer with a SeaBird CTD. Samples were fixed and preserved in 70% ethanol. The thecosome pteropods were sorted from the original samples and then identified following Van der Spoel & Boltovskoy (1981), Van der Spoel (1996), Van der Spoel *et al.* (1997), and Van der Spoel & Dadón (1999).

Diversity (Shannon index), evenness (Pielou´s evenness index), and species richness (Margalef index) were estimated. Log-transformed [log (x+1)] abundance data and similarity percentages (SIMPER) were used to estimate the relative contribution of each species to the average dissimilarity between day and night samples and depth strata paired combinations. A one-way analysis of

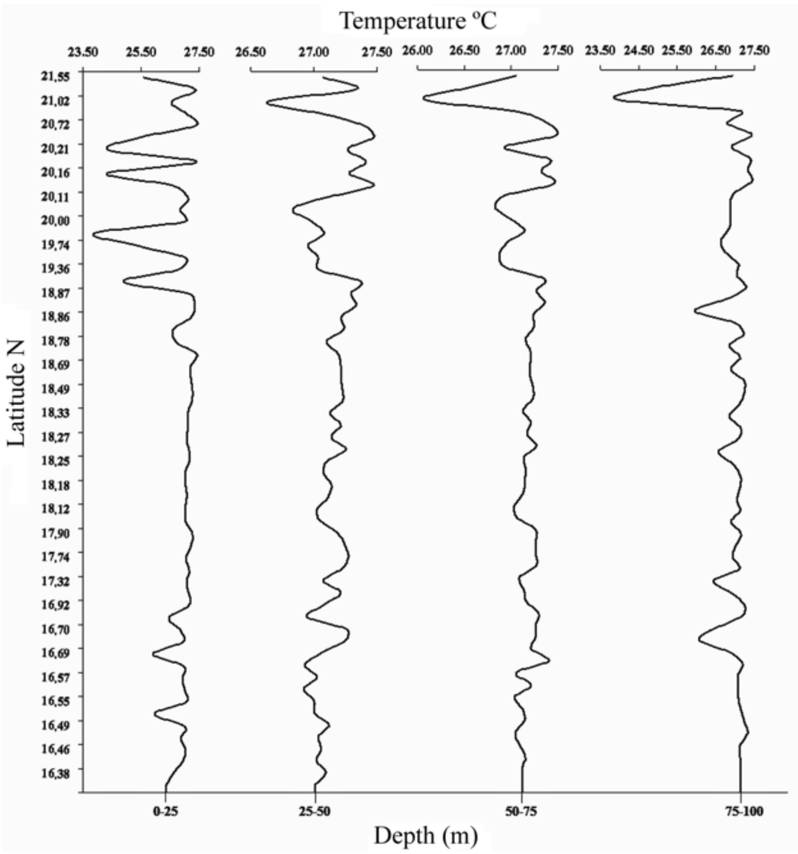

Figure 2

Latitudinal variation of temperature (°C) in the study area including all 60 sampling sites at each of the four interval depths sampled

Variación latitudinal de temperatura (°C) en el área de estudio incluyendo los 60 sitios de muestreo en cada uno de los cuatro intervalos de profundidad

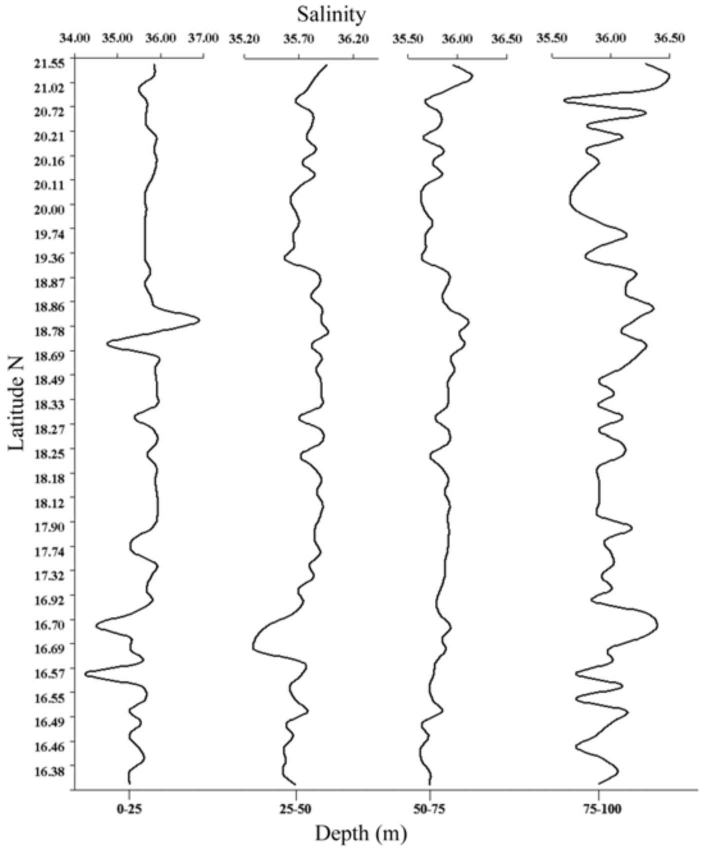

Figure 3

Latitudinal variation of salinity (PSU) in the study area including all 60 sampling sites at each of the four interval depths sampled

Variación latitudinal de salinidad (PSU) en el área de estudio incluyendo los 60 sitios de muestreo en cada uno de los cuatro intervalos de profundidad

similarity (ANOSIM) was used to estimate the significance of the variability among the vertical distributional patterns of the species. Based on a Bray-Curtis rank similarity matrix as a distance measure with a group average linkage, clustering was performed to explore the similarities among sample groups using (1) the entire set of samples with the vertical stratification and (2) the integrated abundance data of nighttime samples, the latter in order to reveal patterns of the horizontal distribution of pteropods in the area. These analyses were performed using the software PRIMER (Clarke & Warwick 2001).

Results

Temperature and salinity showed a generalized uniform pattern at all four depth intervals surveyed in the sampling area (Figs. 2 and 3). The surface (0-25 m) and the deepest (75-100 m) layers showed a similar temperature range (23.8-27.4ºC and 23.9-27.4 ºC, respectively) (Fig. 2). The maximum temperature occurred at 25-50 m (27.4ºC) on the southernmost sector of the surveyed area; lowest values (23.9ºC) were recorded at the maximum depth sampled (75-100 m), off the northern sector of the surveyed area. Salinity ranged from 34.2 and 36.9 psu in the surveyed area, mainly in the surface layer; among the other three layers sampled, the variation range was very low (35.5-36.3) (Fig. 3). Highest values were recorded at the 75-100 m layer south of Belize and the minimum in the surface layer (0-25 m) north of the Yucatan peninsula.

A total of 87,472 thecosome pteropods collected from the studied area were taxonomically examined. This group was represented by 12 genera and 36 species including six subspecies and seven forms. The number of taxa found in day samples was 26, whereas 34 were recorded from nighttime samples; only two species occurred exclusively in day samples and eight at night (Table 1).

Ten species were the most abundant in the surveyed area. *Limacina inflata* (52.5%) and *L. trochiformis* (18.1%) together constituted almost 71% of the total thecosome numerical abundance, both species occurred at 90% of the stations. Several other taxa had overall relative abundances over 0.25% and were considered as common in the area: *C. acicula* f. *clava* (14.9%), *Hyalocylis striata* (1.12%), *Creseis acicula* f. *acicula* (0.78%), *Diacavolinia constricta* (0.70%), *C. inflexa* f. *inflexa* (0.39%), *Cuvierina columnella atlantica* (0.35%), and *L. helicina* (0.50%), and *Cavolinia uncinata* f. *uncinata* (0.28%). The remaining species were considered rare (Table 2).

Table 1

Thecosome pteropod species recorded in the surveyed area during January 2007. The asterisk (*) indicates species that have not been previously recorded in the Western Caribbean

Especies de pterópodos tecosomados registradas en el área de estudio durante enero 2007. El asterisco (*) indica especies que no han sido encontradas previamente en el Caribe occidental

Class GASTROPODA	
Subclass OPISTHOBRANCHIA	
Order THECOSOMATA	
Suborder EUTHECOSOMATA	Suborder PSEUDOTHECOSOMATA
Family LIMACINIDAE	Family PERACLIDIDAE
**Limacina helicina* (Phipps, 1774)	*Peraclis apicifulva* Meisenheimer, 1906
Limacina helicoides (Jeffreys, 1877)	*Peraclis reticulata* (d' Orbigny, 1836)
Limacina inflata (d´Orbigny, 1836)	
Limacina lesueuri (d´Orbigny, 1836)	Family CYMBULIIDAE
Limacina trochiformis (d´Orbigny, 1836)	*Corolla ovata* (Quoy & Gaimard, 1832)
Limacina bulimoides (d´Orbigny, 1836)	*Gleba cordata* Niebuhr, 1776
Family CAVOLINIIDAE	Family DESMOPTERIDAE
Cavolinia inflexa f. *inflexa* (Lesueur, 1813)	*Desmopterus papilio* Chun, 1889
Cavolinia uncinata f. *uncinata* (Rang, 1829)	
Clio pyramidata lanceolata (Lesueur, 1767)	
Clio pyramidata sulcata (Pfeffer, 1879)	
Creseis acicula f. *acicula* (Rang, 1828)	
Creseis acicula f. *clava* (Rang, 1828)	
Creseis virgula f. *conica* (Eschscholtz, 1829)	
Cuvierina columnella atlantica (van der Spoel, 1970)	
**Cuvierina columnella urceolaris* (Mörch, 1850)	
**Diacavolinia aspina* van der Spoel, Bleeker & Kobayasi 1993	
**Diacavolinia atlantica* van der Spoel, Bleeker & Kobayasi, 1993	
**Diacavolinia constricta* van der Spoel, Bleeker & Kobayasi, 1993	
**Diacavolinia deshayesi* van der Spoel, Bleeker & Kobayasi, 1993	
**Diacavolinia elegans* van der Spoel, Bleeker & Kobayasi, 1993	
**Diacavolinia limbata* forma *limbata* (d´Orbigny, 1836)	
**Diacavolinia longirostris* (de Blainville, 1821)	
**Diacavolinia strangulata* (Deshayes, 1823)	
Diacria major (Boas, 1886)	
Diacria quadridentata (de Blainville, 1821)	
Diacria rampali Dupony, 1979	
Diacria trispinosa forma *atlantica* (de Blainville, 1821)	
Diacria trispinosa trispinosa (de Blainville, 1821)	
Hyalocylis striata (Rang, 1828)	
Styliola subula (Quoy & Gaimard, 1827)	

Day/Night abundance

The overall average abundance of thecosome pteropods showed a significant day/night variation; the day average (340 ± 35 org. 1000 m^{-3}) was almost three-times lower than at night (961 ± 112 org. 1000 m^{-3}). The highest night (2,381 org. 1000 m^{-3}) and daytime (697 org. 1000 m^{-3}) abundances were recorded at the surface layer (0-25 m). In general, the overall thecosome abundance was consistently higher at night and decreased with depth (Fig. 4).

Diversity and species richness

The highest number of species was recorded in the 50-75 m layer at night (29 species), followed by 21 species

Table 2

Relative abundance (RA) and average abundance (AA) of pteropods recorded during January 2007 in the study area. (*) Dominant species

Abundancia relativa (RA) y promedio (AA) de los pterópodos registrados durante enero 2007 en el área de estudio. (*) Especies dominantes

Species	RA %	Diurnal AA org. 1000 m^{-3}	Diurnal SD	Diurnal % of positive stations	Nocturnal AA org. 1000 m^{-3}	Nocturnal SD	Nocturnal % of positive stations
Cavolinia inflexa f. *inflexa**	0.39	0.22	0.88	8.33	1.39	2.79	35.83
Cavolinia uncinata f. *uncinata**	0.28	0.59	1.51	20.83	0.92	1.68	30.83
Clio pyramidata lanceolata	0.27				0.58	1.27	21.67
Clio pyramidata sulcata	0.15				0.05	0.27	3.33
Corolla ovata	0.22	0.01	0.15	0.83	0.08	0.44	3.33
Creseis acicula f. *acicula**	0.78	1.21	3.54	15.83	1.52	4.08	20.00
Creseis acicula f. *clava**	14.92	71.40	206.38	54.17	82.26	249.05	50.00
Creseis virgula f. *conica*	0.45	0.40	1.50	9.17	0.35	1.46	7.50
*Cuvierina columnella atlantica**	0.35	0.13	0.61	5.83	2.10	2.38	58.33
Cuvierina columnella urceolaris	0.16				0.01	0.15	0.83
Desmopterus papilio	0.84	0.07	0.77	0.83			
Diacavolina vanutrechti	0.54	0.79	2.45	14.17	0.59	2.12	11.67
Diacavolinia aspina	0.90	0.55	3.50	5.00	0.42	1.77	6.67
Diacavolinia atlantica	0.52	0.51	1.80	10.83	0.57	2.23	10.83
*Diacavolinia constricta**	0.70	1.95	4.14	33.33	2.10	5.32	26.67
Diacavolinia deshayesi	0.71	1.09	2.93	15.83	0.98	3.11	13.33
Diacavolinia elegans	0.61	0.78	2.82	1.67	0.49	1.75	2.50
Diacavolinia limbata f. *limbata*	0.62	0.05	0.39	1.67	0.21	1.95	2.50
Diacavolinia longirostris	0.44	0.20	1.59	2.50	0.09	0.48	4.17
Diacavolinia strangulata	0.59	0.76	2.60	15.00	0.66	2.56	10.00
Diacria quadridentata	0.16				0.04	0.25	2.50
Diacria major	0.18	0.04	0.26	2.50	0.06	0.33	3.33
Diacria trispinosa f. *atlantica*	0.16				0.01	0.15	0.83
Diacria rampali	0.24				0.12	0.55	5.00
Diacria trispinosa trispinosa	0.19	0.07	0.34	4.17	0.24	0.69	11.67
Gleba cordata	0.17	0.01	0.16	0.83			
*Hyalocylis striata**	1.12	0.40	1.55	9.17	29.95	268.14	45.00
*Limacina trochiformis**	18.16	135.01	253.00	91.67	201.83	582.59	91.67
*Limacina inflata**	52.52	120.04	465.72	50.83	626.77	1173.45	90.00
Limacina bulimoides	0.29	0.04	0.35	0.83	0.13	0.68	4.17
Limacina helicina *	0.50	1.51	2.36	40.83	2.67	4.21	44.17
Limacina helicoides	0.18	0.05	0.27	3.33	0.13	0.51	6.67
Limacina lesueuri	0.18				0.01	0.16	0.83
Peraclis apicifulva	0.64				0.21	1.58	3.33
Peraclis reticulata	0.56	0.30	1.54	5.83	0.44	1.91	7.50
Styliola subula	0.32	0.01	0.14	0.83	0.76	1.70	23.33

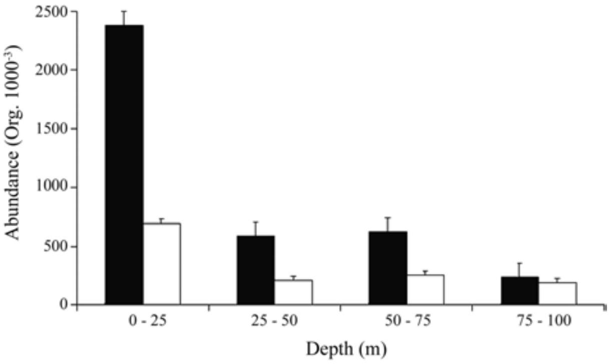

Figure 4

Total abundance (org. 1000 m^{-3}) of pteropods collected during this survey at the different depth ranges sampled. Black bars represent nighttime samples, white bars indicate daytime samples

Abundancia total (org. 1000 m^{-3}) de pterópodos recolectados durante este estudio en los diferentes intervalos de profundidad muestreados. Las barras negras representan muestras nocturnas, las blancas son muestras diurnas

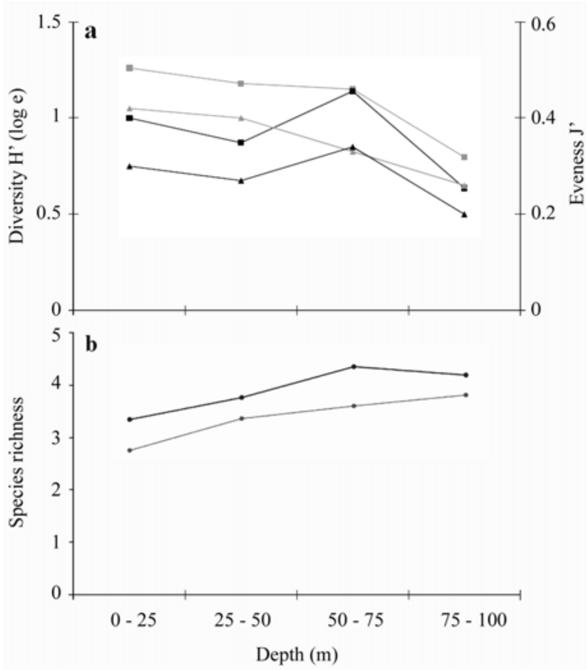

Figure 5

(A) Variation of Shannon-Wiener Diversity (H') (squares) and evenness (J') (triangles) of pteropods collected at different depth ranges during this survey. (B) Variation of species richness at the different depth ranges sampled. Black lines represent nighttime samples and light gray lines daytime samples

(A) Variación de la diversidad de Shannon (H') (cuadros) y equidad (J') (triángulos) de los pterópodos recolectados en diferentes intervalos de profundidad durante este estudio. (B) Variación de la riqueza de especies en los diferentes intervalos de profundidad. Las líneas negras representan muestras nocturnas, las líneas grises muestras diurnas

found at the deeper (75-100 m) and intermediate (50-75 m) layers during the day. Species richness increased gradually with depth in both nighttime and daytime samples; the maximum value (4.35) was observed at the 50-75 m layer at night (Fig. 5A). The highest vertical diversity was recorded at the surface layer (0-25 m) in the three sectors; the same pattern was observed for the species richness except for a relatively high value at 50-75 m in the northern sector. The highest integrated (0-100 m) diversity and species richness were recorded at the central sector of the surveyed area (roughly between 18 and 20°N), with average values of 0.83 and 0.93, respectively; the southern sector (16°30'-18°) showed the lowest species richness (0.65) and diversity (0.69).

Shannon Diversity (H') ranged from 0.63 to 1.26 and Pielou's evenness varied between 0.20 and 0.42; the maximum occurred at daytime at 0-25 m and the minimum during the night at 75-100 m. In daytime samples the H' value decreased and the number of species increased with depth, from 0-25 m (19 species, H' = 1.26) to 75-100 m (21 species, H' = 0.79) (Fig. 5B).

Vertical and horizontal distribution of species

The most abundant pteropod species showed similar patterns in their vertical and horizontal distribution, whereas the rare species had irregular patterns in both nocturnal and diurnal samples. The highest numerical abundance of the 10 commonest species were consistently recorded in the surface layer (0-25 m) in both night and day samples; exceptions of this pattern were *Hyalocylis striata*, *Limacina helicina*, *Cavolinia inflexa* forma *inflexa*, and *C. uncinata* forma *uncinata*, whose maximum abundance occurred at 50-75 m at night and in the 75-100 m during the day.

Limacina inflata was the most abundant species at all depth intervals in night samples, its highest density (1,504 org. 1000 m^{-3}) occurred at 0-25 m and the lowest (199 org. 1000 m^{-3}) was recorded at 75-100 m. A similar

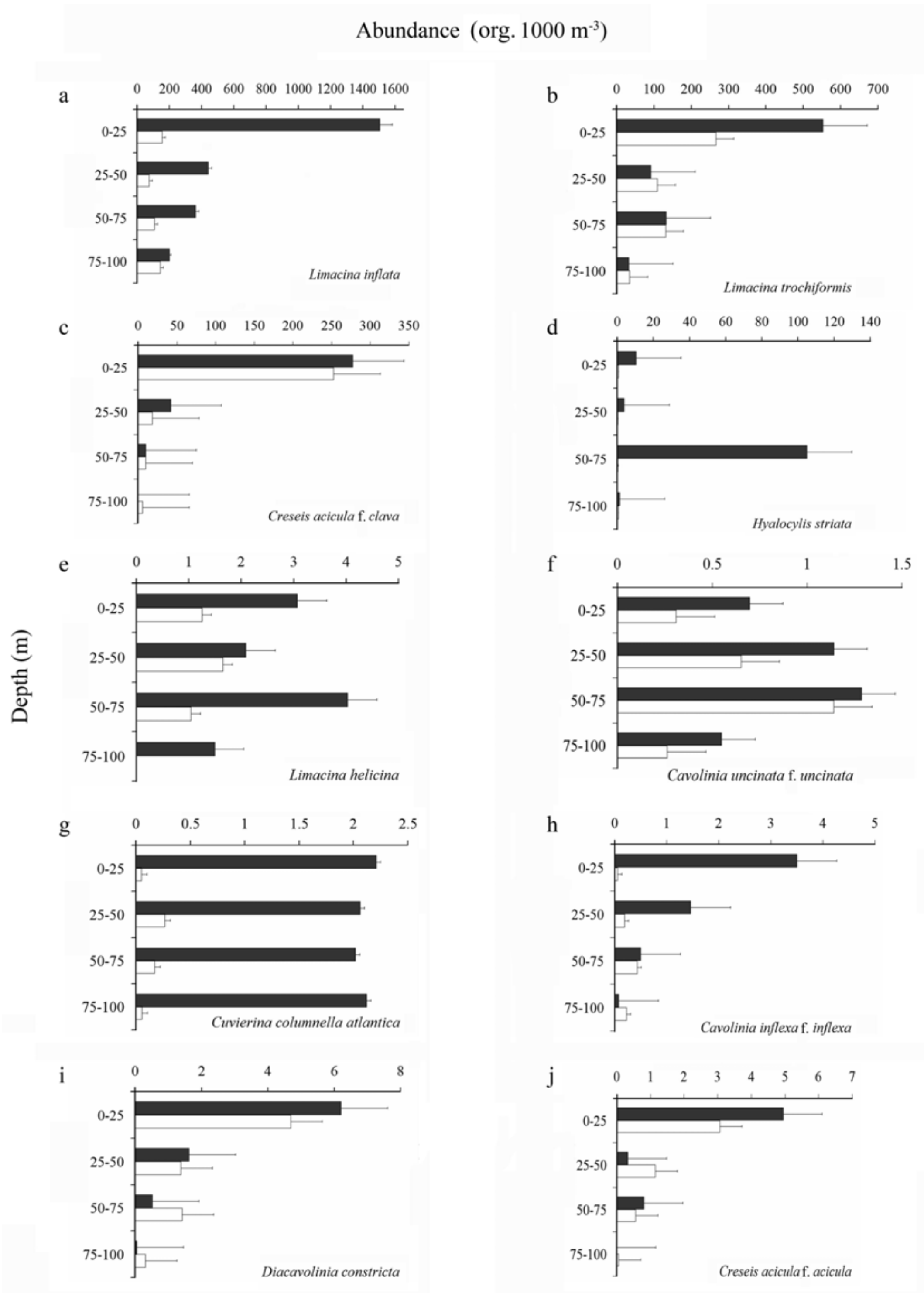

Figure 6

Vertical distribution of the abundance (org. 1000 m^{-3}) of the 10 dominant species of pteropods in the surveyed area during daytime (white bars) and nighttime (black bars)

Distribución vertical de la abundancia (org. 1000 m^{-3}) de las 10 especies de pterópodos dominantes en el área de estudio durante el día (barras blancas) y la noche (barras negras) pattern was observed during daytime, but with lower numerical abundances; the maximum was recorded at 0-25 m (155 org. 1000 m^{-3}) and the minimum at 25-50 m (74 org. 1000 m^{-3}) (Fig. 6A).

Limacina trochiformis occurred at all depth intervals. This species was more abundant at night (552 org. 1000 m^{-3}) than during the day (265 org. 1000 m^{-3}) in the surface layer (0-25 m); during daytime *L. trochiformis* was the most abundant species (Fig. 6B).

Creseis acicula forma *clava* was most abundant at the 0-25 m layer at night (278 org. 1000 m^{-3}) and it was slightly less abundant during the day at the same depth interval (252 org. 1000 m^{-3}). Its density decreased at higher depths (Fig. 6C).

Hyalocylis striata was common, but it had low abundances; its highest density (104 org. 1000 m^{-3}) was recorded at night in the 50-75 m layer. Overall, this species showed an irregular vertical distribution (Fig. 6D). The same pattern was observed for *L. helicina* and *Cavolinia uncinata* f. *uncinata*; their maximum abundances (4 org. 1000 m^{-3} and 1 org. 1000 m^{-3}, respectively), occurred at the same depth interval (Figs. 6E, F).

Cuvierina columnella atlantica showed a uniform pattern of vertical distribution, it was particularly abundant at night; during daytime it was distributed mostly within the 25-75 m range (Fig. 6G). The maximum abundance of *Cavolinia inflexa* f. *inflexa* (4 org. 1000 m^{-3}) was recorded at night in the 0-25 m layer and decreased with depth; during the day it was distributed mainly at the 50-75 m layer (Fig. 6H).

Both *Diacavolinia constricta* and *Creseis acicula* f. *acicula* had similar distributional patterns, their highest abundance was observed at the surface layer both during the nighttime and during the day, but daytime abundance decreased with depth (Figs. 6I, J).

The integrated (0-100 m) numerical abundance of pteropods was highest in the southern sector of the surveyed area, up to 41.2% (average 826 org. 1000 m^{-3}) of the total catch of pteropods occurred in this area, whereas 36.3 (average: 730 org. 1000 m^{-3}) and 22.5% (average: 450 org. 1000 m^{-3}) were collected in the northern and central sectors, respectively.

The distribution of the integrated horizontal abundances of the dominant species is shown in Fig. 7 following a division of the surveyed area into three sectors: northern, central, and southern. Most of the commonest thecosome species recorded in this survey showed a dominant pattern on their horizontal distribution. In general, the highest abundances of these species were recorded in the northern sector of the peninsula and off the Belizean coast, in the southern sector. Hence, the central part showed intermediate values of numerical abundance during day and nighttime samplings (Fig. 7).

Statistical analysis

The similarity analysis (SIMPER) indicated which species contributed most to the differences detected between samples (day/night and depth intervals) (Table 3). These species were: *Limacina inflata* at nighttime at all depth intervals, particularly at the deepest layer 75-100 m (50.7%); *L. trochiformis* at daytime, mostly in the 50-75 m layer, followed by *Creseis acicula* f. *clava* at 0-25 m.

The general cluster analysis revealed four groups. These are characterized by the species composition and abundance, depth intervals, and day/night variation. There is no consistent relation with the location of the sampling stations (Fig. 8). Group I clustered daytime samples from the 0-75 m depth range, with the highest abundance of *Limacina trochiformis* and *Creseis acicula* f. *clava*. Group II included night samples from the same depth layers as in Group I, but with the highest abundances of *L. inflata*. Group III comprised nighttime samples in which *L. inflata*, *L. trochiformis*, and *Cuvierina columnella atlantica* occurred as the most abundant species. Group IV clustered daytime samples from the deepest layers (50-75, 75-100 m), also with *L. inflata*, *L. trochiformis*, and *C. acicula* f. *clava* as the most abundant species. The horizontal distribution of these groups in the surveyed area is presented in Fig. 8. The cluster analysis of the integrated nighttime abundance in the three sectors of the surveyed area (northern, central, southern) revealed three groups (Fig. 9). Group 1 clustered samples with the highest abundance of *Limacina trochiformis*. Group 2 with the highest abundances of *L. inflata*, *L. trochiformis*, and *Creseis acicula* f. *clava*. In Group 3 *L. inflata* and *L. trochiformis* occurred as the most abundant species. No consistent pattern was detected in the horizontal distribution of these clusters

The ANOSIM test showed that the day/night species composition differed significantly (global R = 0.32; $P <$ 0.01%). The major difference was found between night and daytime groups of samples at the extreme depth intervals sampled: 75-100 and 0-25 m. No significant differences were found between intermediate depth intervals of the same type of samples (day or night), except between 50-75 m and the surface (0-25 m) (Table 4).

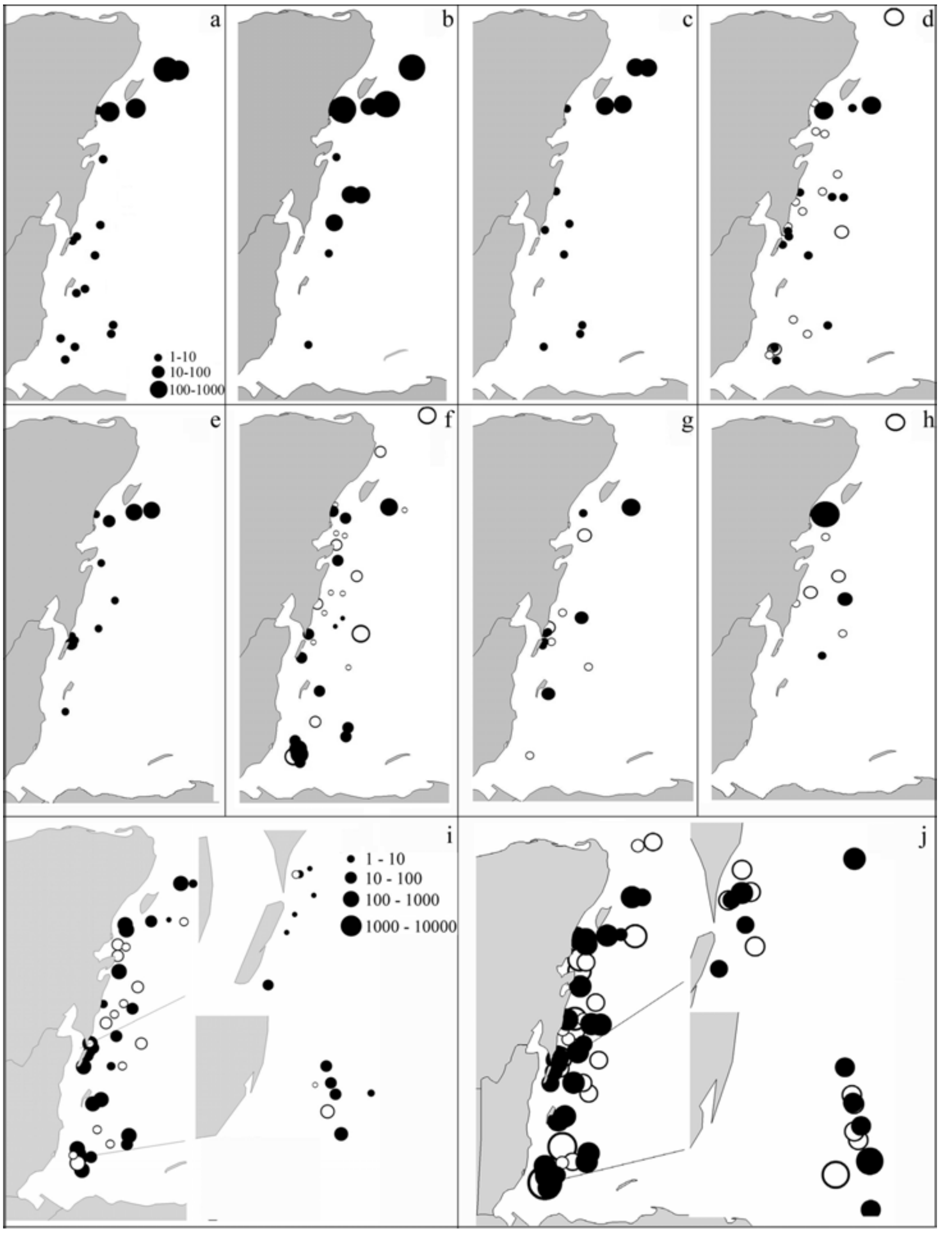

Figure 7

Horizontal distribution of the abundance (org. 1000 m^{-3}) of the dominant species of thecosome pteropods at 0-50, 25-75 and 0-75 m depth ranges; empty circles are daytime samples, black circles are nighttime samples. A) *Cuvierina columnella atlantica*; B) *Hyalocylis striata*; C) *Cavolinia uncinata* f. *uncinata* D) *Limacina helicina*; E) *Cavolinia inflexa* f. *inflexa*; F) *Creseis acicula* f. *clava*; G) *Diacavolinia constricta*; H) *Creseis acicula* f. *acicula*; I) *Limacina inflata*; J) *Limacina trochiformis*. In figures I and J the group of stations on the southern sector of the surveyed area was enlarged to show the abundance of these species with more detail

Distribución horizontal de la abundancia (org. 1000 m^{-3}) de las especies dominantes de petrópodos tecosomados a intervalos de 0-50, 25-75 y 0-75 m de profundidad; los círculos vacíos son muestras diurnas, los círculos negros son muestras nocturnas. A) *Cuvierina columnella atlantica*; B) *Hyalocylis striata*; C) *Cavolinia uncinata* f. *uncinata*; D) *Limacina helicina*; E) *Cavolinia inflexa* f. *inflexa*; F) *Creseis acicula* f. *clava;* G) *Diacavolinia constricta*; H) *Creseis acicula* f. *acicula*; I) *Limacina inflata*; J) *Limacina trochiformis*. En las figuras I y J, el grupo de estaciones en el sector sur del área de estudio fue ampliado para mostrar la abundancia de estas especies con mayor detalle

Table 3

SIMPER analysis between groups in day and night time samples at each depth interval. Only the species that contribute significantly to the community structure are shown

Análisis SIMPER entre grupos en muestras diurnas y nocturnas en cada intervalo de profundidad. Sólo se muestran las especies que contribuyen de manera significativa a la estructura de la comunidad

	Day				Night			
Depth interval (m)	100-75	75-50	50-25	25-surface	100-75	75-50	50-25	25-surface
Similarity average (%)	44.07	41.63	49.34	53.86	51.2	55.68	59.48	62.66
	Contribution (%)							
Limacina trochiformis	63.95	67.01	61.17	42.26	34.53	31.06	35.34	26.56
Limacina inflata	23.00	16.12	11.81	5.03	50.72	47.81	42.94	30.26
Limacina helicina	8.02					5.55		
Hyalocylis striata							4.76	6.12
Diacavolinia constricta				3.18				3.49
Cuvierina columnella atlantica					7.69	4.6	3.11	2.34
Creseis acicula f. *clava*		4.85	17.86	39.59		3.54	6.04	18.51
Creseis acicula f. *acicula*								3.00
Cavolinia uncinata f. *uncinata*		5.17						
Total	94.97	93.15	90.84	90.06	92.94	92.56	92.19	90.28

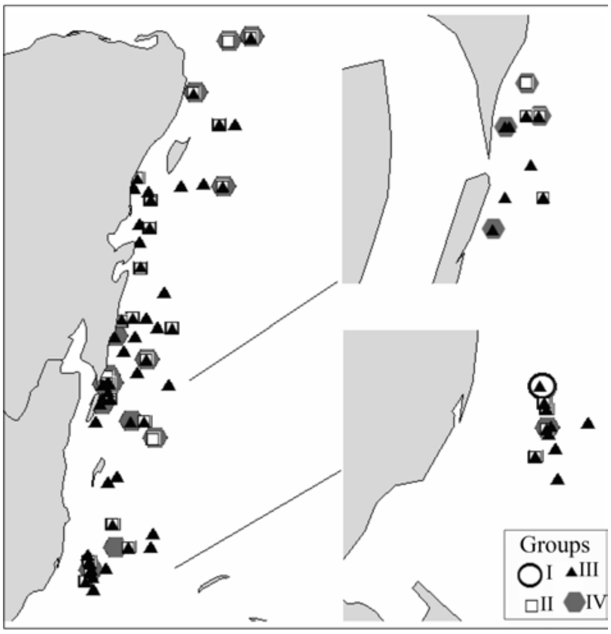

Figure 8

Horizontal distribution of clusters (I-IV) resulting from the ANOSIM (Bray-Curtis). The groups of stations on the central and southern sectors of the surveyed area were enlarged to show these data with more detail. Group I: daytime and nithttime samples in 50-75 and 75-100 m. Group II: daytime samples in 25-50 and 50-75 m. Group III: Nighttime and daytime samples in the four depth intervals, and Group IV, daytime samples at 50-75 and 75-100 m

Distribución horizontal de los grupos (I-IV) resultantes del ANOSIM (Bray-Curtis). El grupo de estaciones de los sectores central y sur se ampliaron para mostrar estos datos con mayor detalle. Grupo I: muestras diurnas y nocturnas a 50-75 y 75-100 m. Grupo II: muestras diurnas a 25-50 y 50-75 m. Grupo III: muestras diurnas y nocturnas de los cuatro intervalos de profundidad, y Grupo IV, muestras diurnas a 50-75 y 75-100 m

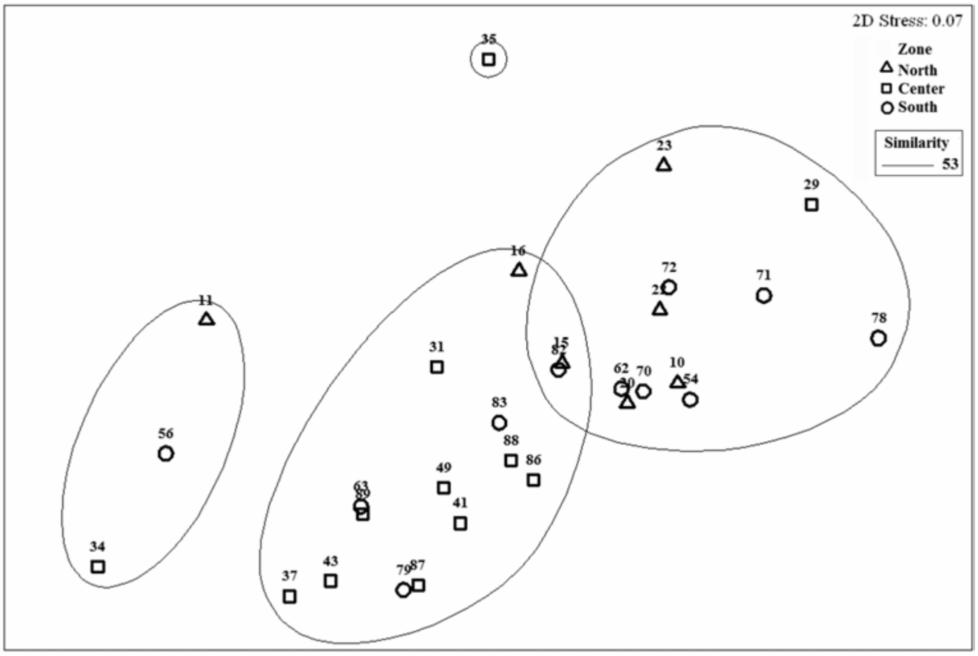

Figure 9

NMDS showing horizontal distribution of clusters (northern, central, southern sectors) resulting from the ANOSIM (Bray-Curtis) analysis using the integrated vertical abundance data of nighttime samples

NMDS que muestra la distribución horizontal de los grupos (sectores norte, central y sur) a partir del análisis de ANOSIM (Bray-Curtis) usando los datos integrados de abundancia vertical en muestras nocturnas

Discussion

The number of taxa of thecosome pteropods hitherto recorded from the entire Northwestern Atlantic is close to 52 (Suárez-Morales 1994, Suárez-Morales & Gasca 1998 and references therein). In the two largest basins of this region, the Gulf of Mexico and the Caribbean, Suárez-Morales (1994) listed 40 species. Haagensen (1976) recorded 46 taxa from the central and eastern sectors of the Caribbean Basin and Suárez-Morales & Gasca (1998) recorded 17 in surface waters of the western Caribbean. The 36 taxa recorded in this survey represent an important addition to the knowledge of the group in this zone of the Caribbean Basin. Several species represent new records in the western Caribbean (Table 1); some species of *Diacavolinia* listed in Table 1 were previously reported generically as *Cavolinia longirostris* (Van der Spoel *et al.* 1993, Van der Spoel *et al.* 1997). Overall, these new records increase from 17 to 36 the number of species of pteropods recorded in the western Caribbean.

The group of the most abundant pteropod taxa in the area included *Limacina inflata, L. trochiformis, Creseis acicula* f. *clava, Hyalocylis striata, Cuvierina columnella atlantica*, and *Cavolinia uncinata* f. *uncinata*; these results largely agree with those by Haagensen (1976) from other areas of the Caribbean Sea. During February 1991, Suárez-Morales & Gasca (1998) recorded both species of *Limacina* as the most abundant in the same area, followed by *C. longirostris* and *C. acicula* f. *acicula*. In the Gulf of Mexico Suárez-Morales & Gasca (1992) found *C. acicula* f. *acicula*, *L. inflata*, and *L. trochiformis* as the commonest species. These data confirm the general affinity between the zooplankton of the Gulf of Mexico and the Caribbean Sea, but the abundance and dominance of these species is different in each basin, as reported also in other zooplankton taxa (Gasca 1997).

Creseis acicula, *L. trochiformis*, and *L. inflata* have been recorded also with high winter densities in other geographic areas; local increases of their abundance have been related to tropical conditions (Chen & Hillman 1970, Suárez-Morales & Gasca 1998, Mohan *et al.* 2006, Zhaoli & Chunju 2006). Most of the pteropod taxa locally recorded as abundant are warm water forms (McGowan 1960, Van der Spoel & Boltovskoy 1981, Resgalia & Montú 1994, Batistic 2004). *Limacina helicina* is regarded as a temperate-cold water species (Chen & Bé 1964), it probably occurs in deeper waters of the tropics.

Table 4

The ANOSIM one-way results and SIMPER similarity average among depth intervals. Global R = 0.32 *P*<0.01%; N = night; D = day, * = significant difference

Resultados del ANOSIM de una vía y Similitud promedio SIMPER entre intervalos de profundidad. R global = 0,32 *P*<0,01%; N = noche; D = día; * = diferencia significativa

Groups	ANOSIM R	SIMPER Similarity Average (%)
Day *vs.* night		
0-25 *vs.* 0-25	**0.452***	51.91
25-50 *vs.* 25-50	**0.302***	53.46
50-75 *vs.* 50-75	**0.269***	59.07
75-100 *vs.* 75-100	0.153	58.15
Day *vs.* day		
0-25 *vs.* 25-50	0.127	52.23
0-25 *vs.* 50-75	**0.294***	61.43
0-25 *vs.* 75-100	**0.488***	66.43
25-50 *vs.* 50-75	0.033	55.66
25-50 *vs.* 75-100	0.165	58.27
50-75 *vs.* 75-100	0.033	58.06
Night *vs.* night		
0-25 *vs.* 25-50	**0.326***	53.46
0-25 *vs.* 50-75	**0.415***	49.98
0-25 *vs.* 75-100	**0.626***	61.48
25-50 *vs.* 50-75	0.033	43.11
25-50 *vs.* 75-100	0.200	50.21
50-75 *vs.* 75-100	0.064	48.76

It was recorded in 44% of our samples, mostly at the northern sector. Its occurrence probably results from the influence of colder waters shed by a local upwelling system on the northeast coast of the peninsula (Merino 1997).

The total abundance of thecosome pteropods was about three-times higher at night than during the daytime at all depth intervals sampled. This pattern was reported also by Wormelle (1962), Haagensen (1976), and Suárez-Morales & Gasca (1998) in the Caribbean and by Larrazábal & Oliveira (2003) off the Brazilian coasts. In these previous works the highest densities of the most abundant species were recorded in night samples at depth intervals of 0-50 and 0-100 m, a pattern that largely agrees with our results. Pteropods tend to concentrate in the upper layers at night to avoid predators and to feed (Hays 2003). Wormuth (1981) suggested that most species probably occur within the upper 150 m, with a night maximum at 60 m. Furthermore, our results provide more detail to previous patterns; the upper 25 m concentrate most of the vertical abundance of pteropods.

There are very few studies on the species vertical distribution and diel migration patterns. Most previous suveys do not have the resolution provided by our 4-layer stratified sampling, which allowed a more detailed view of the upper 100 m. The local overall thecosome abundance, with highest values at 0-25 m, decreased at 25-50 m and then at 75-100 m in both day and night samples. This pattern is attributed to that of the most abundant taxa; some species of *Limacina* have migrations between the surface and down to about 75 m, where they tend to settle. Larrázabal & Oliveira (2003) and Wormuth (1981) suggested that most thecosome pteropods aggregate below 100 m during daytime, but most of them migrate upwards during the night and remain in the upper 75 m, showing a gradual decrease in abundance from the surface to 125 m. Locally, this pattern is clear in *Cavolinia inflexa* f. *inflexa* and *Hyalocylis striata*, both were found to migrate down to 75 m.

There are clear day/night differences in species composition and diversity. The occurence and abundance of the species in the depth intervals shifts during the day/night cycle; this is observed in *Limacina inflata* and *L. trochiformis*. When *L. inflata* is abundant, *L. trochiformis* shows low abundances and viceversa. This pattern is observed in other species, but not as remarkably as in *Limacina* (Fig. 6).

The highest densities of the most abundant species were recorded during the night in the upper layer (0-25 m). There is evidence sustaining that these species vertically migrate and live predominantly within the 0-75 m range at night (Rottman 1978). Surface species such as *L. inflata*, *Creseis acicula* f. *clava*, *C. acicula* f. *acicula*, and *Diacavolinia constricta* have short vertical migrations (Van der Spoel & Boltovskoy 1981). Thus, most of the local community of thecosome pteropods is concentrated between the surface and 75 m; this pattern is largely attributed to the most abundant species in the area.

Three taxa, *Hyalocylis striata*, *L. helicina*, and *Cavolinia uncinata* f. *uncinata* showed the same pattern of vertical distribution, *i.e.* they were most abundant in the uppermost layer (0-25 m) and also in the 50-75 m layer; both were scarce in the deepest stratum sampled (75-100 m). These species were not particularly abundant but they were frequent. Similar results were reported by Haagensen (1976).

Limacina inflata, the most abundant species in our samples was also recorded by Suárez-Morales & Gasca (1998) as the most abundant species of the western Caribbean during winter (41% of total pteropod abundance). The same was reported from other geographic areas of the Tropical Atlantic, with similar relative abundances (Bé & Gilmer 1977, Wormuth 1981). In a Caribbean embayment, *L. inflata* is regarded as rare (Gasca & Suárez-Morales 1992), showing that it can dwell in inner coastal environments.

Van der Spoel & Boltovskoy (1981) reported *Cuvierina columnella atlantica* as rare; in this study it has a moderate frequency. It was most abundant at night and its vertical distribution was homogeneous, thus agreeing with the results by Chen and Bé (1964) in the North Atlantic. Both *Creseis acicula* f. *clava* and *C. acicula* f. *acicula* are regarded as dominant in the Caribbean Sea in the 0-100 m layer. Haagensen (1976) recorded up to 90% of the adults of these species above 65 m in the Caribbean. In this study 90% of the specimens of these species occurred above 75 m. Tesh (1946), Wormelle (1962), and Chan & Hsueh (2005) reported similar observations from other geographical areas. Locally, *Creseis virgula* f. *conica* showed the same pattern.

A contrasting general pattern was found in species of the Pseudothecosomata, in general larger, stronger swimmers, such as *Gleba cordata*, *Desmopterus papilio*, and *Corolla ovata*. These forms are known to dwell in deeper layers (> 200 m) during the day and migrate to the surface at night. In our samples these species were consistently recorded with a higher frequency and abundance at nighttime. Data in reference to pseudothecosome pteropods could be incomplete in some instances because they can evade the plankton nets; thus, their abundance may be underestimated by conventional sampling (Lalli & Gilmer 1989, Cummings & Seapy 2003).

Multivariate analysis detected day/night differences in the local community of thecosome pteropods. Groups were sorted mainly on diversity, depth, and day/night sampling. The results from this analysis is consistent with the values from the R dissimilarity (ANOSIM), which indicated a significant difference between the samples collected during the day at 75-100 m with respect to the surface samples (0-25 m), these stations correspond to clusters I and III, respectively. The largest R difference was detected between night samples at 75-100 m (group I and III) and night samples at 0-25 m (group III). These results suggest that the abundance of species varies depending on day or night and might be related to the vertical migration that characterized this group of zooplankton.

The failure to find significant differences among the depth intervals is probably an effect of many pteropod species migrating to depths below 100 m. It is likely that samples from deeper layers will bring up species whose lowest migratory range ends below the 100 m and also those dwelling in mesopelagic depths. The results of migration studies are difficult to compare because of the use of different types of collecting gear in different localities and seasons. However, some species show a reduced vertical range over a 24-hour period, whereas others, such as *L. inflata*, may migrate several hundred meters each day (Haagensen 1976).

According to Wormuth (1981), the variability in the vertical structure of the thecosome pteropods is probably related to environmental conditions. In this survey we found little structure in both the temperature and salinity vertical profiles, thus suggesting that this hydrographic factor is not the most important in determining the vertical distribution of the pteropod species. Also, the mixed pattern shown by the horizontal distribution of the different clusters resulting from our analysis (Fig. 8) suggests that the local community of thecosome pteropods is largely homogeneous. We found no evidence of hydrographic variation that suggests a consistent horizontal distribution pattern.

Distributional studies had recognized that certain species are restricted to a narrow range of environmental conditions that can be defined in terms of combinations of temperature salinity, depth, or biotic factors. Our results show the influence of both the vertical migration and day/night cycles in the structure of the local pteropod community; however, a detailed hydrographic analysis of the water column at greater depths is needed to fully explain these processes. Also, other environmental parameters such as chlorophyll, nutrients, oxygen concentration, and phytoplankton cell counts could provide additional data to explain the processes involved in the patterns of vertical and horizontal distribution of the pteropods in this tropical area.

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Literature cited

Angel MV & PR Pugh. 2000. Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic. Hydrobiologia 440: 161-179.

Batistic M, F Krsinic, N Jasprica, M Caric, D Vilicic & D Lucic. 2004. Gelatinous invertebrate zooplankton of the South Adriatic: species composition and vertical distribution. Journal of Plankton Research 26: 459-474.

Bé AW & WA Gilmer. 1977. A zoogeographic and taxonomic review of Euthecosomatous Pteropoda. En: Ramsay AT (ed). Oceanic micropaleontology, pp. 733-808. Academic Press, London.

Chan CY & PW Hsueh. 2005. Species composition and seasonal abundance of pteropods (Mollusca: Gastropoda) in nearshore shallow waters of Northwestern Taiwan. Journal of the Fisheries Society of Taiwan 32: 311-316.

Chen C & AW Bé. 1964. A seasonal distribution of thecosomatous pteropods in the surface water of five stations in western north Atlantic. Bulletin of Marine Science of the Gulf and Caribbean 14: 185-220.

Chen C & N Hillman. 1970. Shell-bearing pteropods as indicators of water masses off cape Hatteras, North Carolina. Bulletin of Marine Science of the Gulf and Caribbean 20: 350-367.

Clarke KR & RM Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 141 pp. PRIMER-E, Plymouth.

Cummings FA & RR Seapy. 2003. Seasonal abundances of euthecosomatous pteropods and heteropods from waters overlying San Pedro Basin, California. The Veliger 46: 305-313.

Gallegos A & S Czitrom. 1997. Aspectos de la oceanografía regional del Mar Caribe. In: Lavín M (ed). Contribuciones a la Oceanografía Física en México, Monografía 3, pp. 225-242. Unión Geofísica Mexicana, México.

Gasca R. 1997. Sifonóforos (Cnidaria: Hydrozoa) del Mar Caribe mexicano. Hidrobiológica 7: 51-57.

Gasca R & E Suárez-Morales. 1992. Pterópodos (Mollusca: Gastropoda; Thecosomata) de la Bahía de la Ascensión, Reserva de la Biosfera de Sian Ka'an, Quintana Roo, México. En: Navarro D & E Suárez-Morales (eds). Diversidad biológica en la Reserva de la Biosfera de Sian Ka'an Quintana Roo, pp. 115-121. CIQRO/ SEDESOL, México.

Haagensen DA. 1976. Part II. The Thecosomata. In: Michel HB & M Foyo (eds). Caribbean zooplankton, pp. 551-712. Office of Naval Research, Department of the Navy, Washington.

Hays GC. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503: 163-170.

Lalli MC & RW Gilmer. 1989. Pelagic snails: The biology of holoplanktonic gastropod mollusks, 259 pp. Stanford University Press, California.

Larrazábal ME & VS Oliveira. 2003. Thecosomata e Gymnosomata (Mollusca, Gastropoda) da cadeina Fernando de Noronha, Brasil. Revista Brasileira de Zoología 20: 351-360.

Merino M. 1986. Aspectos de la circulación costera superficial del Caribe Mexicano con base en observaciones utilizando tarjetas de deriva. Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 13: 31-46.

Merino M. 1997. Upwelling on the Yucatan Shelf: hydrographic evidence. Journal of Marine Systems 13: 101-121.

Mohan R, K Verma, LP Mergulhao, DK Sinha, S Shanvas & MV Guptha. 2006. Seasonal variation of pteropods from the Western Arabian Sea sediment trap. Geo-Mar 26: 265-273.

Mooers CNK & G Maul. 1998. Intra-Americas sea circulation. In: Robinson AR & KH Brink (eds). The Sea 11: 183-208, John Wiley & Sons, New York.

Resgalia C & M Montú. 1994. Distribuçao espacial e temporal de Pteropoda Euthecosomata (Mollusca, Gastropoda) na plataforma do Sul do Brasil. Atlântica 16: 99-123.

Rottman ML. 1978. Ecology of recurrent groups of pteropods, euphausiids, and chaetognaths in the Gulf of Thailand and the South China Sea. Marine Biology 48: 63-78.

Suárez-Morales E. 1994. Distribución de los pterópodos (Gastropoda: Thecosomata y Pseudothecosomata) en el Golfo de México y zonas adyacentes. Revista de Biología Tropical 42: 523-530.

Suárez-Morales E & R Gasca. 1992. Pterópodos (Gastropoda: Thecosomata y Pseudothecosomata) de aguas superficiales (0-50m) del sur del Golfo de México. Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 19: 201-209.

Suárez-Morales E & R Gasca. 1998. Thecosome pteropod (Gastropoda) assemblages of the Mexican Caribbean Sea (1991). Nautilus 112: 43-51.

Tesh JJ. 1946. The Thecosomatous Pteropods: I. The Atlantic. Dana Report 28: 1-82.

Van der Spoel S. 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda), 375 pp. J. Noorduijn.en Zoon NV, Gorinchem. [Ph.D. Thesis, University of Amsterdam]

Van der Spoel S. 1996. Pteropoda. In: Gasca R & E Suárez-Morales (eds). Introducción al estudio del zooplancton marino, pp. 459-528. ECOSUR/CONACYT, México.

Van der Spoel S & D Boltovskoy. 1981. Pteropoda. In: Boltovskoy D (ed). Atlas del zooplancton del Atlántico sudoccidental y métodos de trabajo con el zooplancton marino, pp. 493-531. Publicación Especial, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata.

Van der Spoel S & JR Dadon. 1999. Pteropoda. In: Boltovskoy D (ed). South Atlantic zooplankton, pp. 649-706. Backhuys Publishers, Leiden.

Van der Spoel S, J Bleeker & H Kobayashi. 1993. From *Cavolinia longirostris* to twenty-four *Diacavolinia* taxa, with a phylogenetic discussion (Mollusca, Gastropoda). Bijdragen tot de Dierkunde 62: 127-166.

Van der Spoel S, L Newman & KW Estep. 1997. Pelagic molluscs of the world. World Biodiversity Database, CD-ROM Series. Amsterdam: Expert Center for Taxonornic Identification (ETI). [CD-ROM].

Wormelle RL 1962. A study of distribution of the pteropods of the Florida Current. Bulletin of Marine Science of the Gulf and Caribbean 12: 95-136.

Wormuth JH. 1981. Vertical distributions and diel migrations of Euthecosomata in the northwest Sargasso Sea. Deep-Sea Research A 28: 1493-1515.

Zhaoli X & L Chunju. 2006. Study on abundance variation of pteropods in the East China Sea. Acta Oceanologica Sinica 25: 100-107.

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