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# Vertical segregation of holoplanktonic molluscs in the epipelagic layer, southern Gulf of Mexico

**L. Sanvicente-Añorve · E. Lemus-Santana ·
C. Flores-Coto · M. Alatorre-Mendieta**

**Abstract** The small-scale vertical distribution of five genera of holoplanktonic molluscs inhabiting the upper oceanic layer (0–105 m) was analysed to test whether evident distribution patterns could be attributed to habitat partitioning. Zooplankton samples were taken over neritic waters during the day and night using a 505-µm multiple closing net at five levels (0–6, 6–12, 12–18, 45–55 and 95–105 m) of the water column. Flowmeters were placed in each net to estimate the amount of filtered water. From the 55,654 identifiable specimens of holoplanktonic molluscs, only 6.2 % were in juvenile stage, and *Cavolinia*, *Diacavolinia*, *Diacria*, *Oxygyrus* and *Clio* were the most abundant genera. Adults of these genera comprised 3 % of the total abundance. The abundance data were examined using a spatial segregation index, and its significance was tested with null model methods based on Monte Carlo randomizations. Results indicated that adults showed a much more overlapped distribution in the water column than the in the earlier stages. Indeed, juveniles of *Cavolinia*, *Diacavolinia* and *Oxygyrus* were mainly found in the 0–18-m layer, whereas *Diacria* and *Clio* were recorded in the 45–105-m stratum. Null model arguments revealed a significant vertical segregation among them. Potential ecological factors involve preferential spawning areas of adults, avoidance of competition for feeding and spatial resources, use of visual capabilities in searching prey,
brood protection and avoidance of strong turbulence conditions.

## Introduction

The oceanic plankton distribution is subject to many spatiotemporal scales of variability nested in a hierarchic cascade pattern (Haury et al. 1978; Allen and Starr 1982). From meso- to large scales, the distribution of planktonic organisms is influenced mostly by physical factors, whereas at fine scale, ecological and biological processes become more important (Wiens 1989; Sanvicente-Añorve et al. 2006). In the horizontal plane, planktonic organisms have a limited capability to define their position in space; however, in the vertical axis, many species are well capable of vertical migrations related to their response to light, the availability of food and/or avoidance of predation (Basedow et al. 2008; Cohen and Forward 2009).

The zooplankton distribution throughout the water column displays different patterns of vertical structure for a variety of groups (Criales-Hernández et al. 2008). Field and theoretical studies suggested that this heterogeneous use of space can be mainly attributed to physical processes, seasonal, ontogenetic or diel vertical migrations, body size, morphologies, feeding resources, reproductive success, predation risk and/or competitive abilities (Jeffries and Lawton 1984; Fossheim and Primicerio 2008; Marrari et al. 2011; Sato et al. 2011). The vertical movements of zooplankters exhibit high variability in amplitude, which increases with the developmental stage of the organisms

L. Sanvicente-Añorve (✉) · E. Lemus-Santana ·
C. Flores-Coto · M. Alatorre-Mendieta
Instituto de Ciencias del Mar y Limnología,
Universidad Nacional Autónoma de México,
Circuito Exterior S/N, Ciudad Universitaria,
04510 México, DF, Mexico
e-mail: lesa@unam.mx

(Dale and Kaartvedt 2000; Cohen and Forward 2009). For instance, in Norwegian waters, the youngest stages of a copepod species were generally confined to the upper 30-m layer, whereas the older specimens were distributed progressively deeper according to their increasing developmental stage (Dale and Kaartvedt 2000).

In the pelagic environment, molluscs represent only a small fraction of the zooplankton biomass. Nevertheless, these animals may have a significant impact on the ecology of epipelagic marine communities and on the global cycle of carbon dioxide. Although many of the planktonic molluscs are rare, they are nonetheless of interest in illustrating the evolution of morphological adaptations to the pelagic environment and unique lifestyles in the ocean (Lalli and Gilmer 1989). Compared to crustaceans or fishes, studies dealing with the vertical distribution or behavioural migration of molluscs are very scarce (Solis and von Westernhagen 1978; Seapy 1990, 2008) and have seldom dealt with their earlier developmental stages. In the Arctic Ocean, Kobayashi (1974) has evidenced several developmental stages of *Limacina helicina* at different depths of the water column, but the causes remain poorly understood. Based on the assumption that the youngest stages of pelagic molluscs have a limited vertical motility in the water column, we propose that their position in the upper oceanic layer is therefore related to their ecological requirements and/or life history characteristics.

## Materials and methods

### Field survey and laboratory analyses

The study area comprised neritic waters of the southern Gulf of Mexico, between 18°–22°N and 91°–95°W.

Zooplankton sampling was carried out during two periods, May and November 1995, over a sampling grid including 28 oceanographic stations (Fig. 1). Five vertical strata were sampled (0–6, 6–12, 12–18, 45–55 and 95–105 m), and a total of 187 samples were collected during the day and night using a multiple opening–closing net equipped with 75-cm-diameter and 505-μm-mesh-size nets. Day (night) period ranged from 7 am to 6 pm (7 pm to 6 am). A flowmeter was placed on the mouth of each net to estimate the amount of water filtered by nets. Samples were preserved in a 4 % formaldehyde seawater solution neutralized with sodium borate. Salinity and temperature measurements were also taken with a CTD probe at each sampling station. In the laboratory, zooplankton biomass, taken as a measure of food availability, was estimated as displaced volume and standardized to 100 $m^3$ of water (ml 100 $m^{-3}$). All pelagic molluscs were separated from samples and identified to the genus level. Abundance values of the five genera considered in this study were expressed as ind 100 $m^{-3}$.

### Data analysis

Mean monthly wind speeds (3.8 m $s^{-1}$ for May and 6.1 m $s^{-1}$ for November; Anonymous 1999) were used to estimate the turbulent kinetic energy ($k$), the dissipation rate of kinetic energy ($\varepsilon$) and the length ($\eta$) and velocity ($v_t$) Kolmogorov scales. Wind speed values were used for the calculations of the significant wave height ($H_{1/3}$) and the period ($T$) of waves, as the JONSWAP Spectrum stated (Hasselmann et al. 1973):

$$H_{1/3} = 4\left[1.67 \times 10^{-7} \frac{F}{g}\right]^{1/2} \tag{1}$$

**Fig. 1** Location of sampling stations in neritic waters of the southern Gulf of Mexico
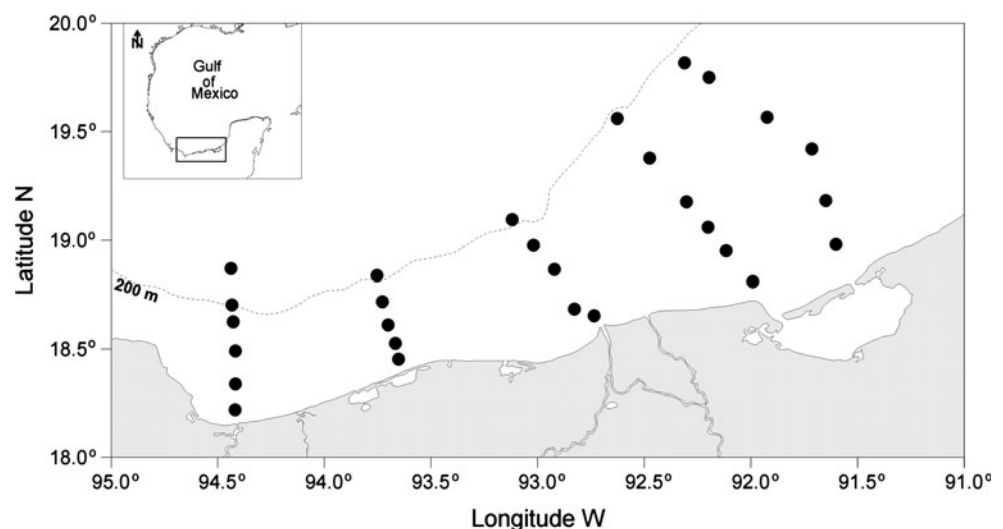
$$\omega = \frac{2\pi}{T} = 22\left(\frac{g^2}{U_{10}F}\right)^{1/3} \qquad (2)$$

where $F$ = fetch length, here taken as 300 km; $g$ = acceleration of gravity; $U_{10}$ = wind speed at a height of 10 m; $\omega$ = wave frequency.

The values of $H_{1/3}$ and $T$ were used to estimate the wave length ($L$) and the horizontal and vertical velocities ($u$ and $w$) of the water particles (SPM 1977):

$$L = \frac{gT^2}{2\pi}\tanh\left(\frac{2\pi d}{L}\right) \qquad (3)$$

$$u = \frac{H_{1/3}gT}{2L}\frac{\cosh(2\pi(z+d)/L)}{\cosh\left(2\pi/L\right)}\cos(\omega t) \qquad (4)$$

$$w = \frac{H_{1/3}gT}{2L}\frac{\sinh(2\pi(z+d)/L)}{\cosh\left(2\pi/L\right)}\sin(\omega t) \qquad (5)$$

where $H_{1/3}$ = significant wave height (the average height of the largest one-third of the waves); $t$ = time (varying from 0 to $T$); $z$ = water column depth (negative); and $d$ = bottom depth (positive, here equal to 100 m).

Based on the previous calculations, the fluctuations from the horizontal and vertical mean velocities were computed:

$$\tilde{u}^2 = \frac{4}{T}\int_0^{T/4}(\bar{u}-u)^2\mathrm{d}t \quad \tilde{w}^2 = \frac{4}{T}\int_0^{T/4}(\bar{w}-w)^2\mathrm{d}t$$

The mean values ($\bar{u}$ and $\bar{w}$) of these velocities were estimated, taken $\sin(\omega t)$ and $\cos(\omega t)$ equal to $\frac{2}{\pi}$, since $\frac{4}{T}\int_0^{T/4}\sin\omega t\,\mathrm{d}t = \frac{4}{T}\int_0^{T/4}\cos\omega t\mathrm{d}t = \frac{2}{\pi}$ in Eqs. 4 and 5.

The turbulent kinetic energy ($k$) is a measure of the turbulence intensity. It is defined as the kinetic energy per unit mass (J kg$^{-1}$) of the horizontal ($\tilde{u}^2$) and vertical ($\tilde{w}^2$) velocity variances (Burchard 2002):

$$k = \frac{1}{2}\left(\tilde{u}^2 + \tilde{w}^2\right)$$

Kolmogorov theory states that a turbulent flow is formed by eddies that decrease in diameter with depth. The dissipation rate of the turbulent kinetic energy through the spectrum of eddies in the water column is related to the turbulent velocities $\left(\sqrt{k}\right)$ and the diameter of eddies ($\ell$), with units of velocity squared per second (m$^2$ s$^{-3}$) (Tennekes and Lumley 1972):

$$\varepsilon = \frac{AU}{\ell}$$

where $A$ = constant near to one; $U$ = root-mean-square velocity fluctuations, equal to $\sqrt{k}$; $\ell$ = diameter of the gyre.

At the superficial waters, $\ell$ is equal to $H_{1/3}$; at deeper waters, $\ell$ is twice the amplitude ($\zeta$) of the waves, defined as:

$$\zeta = \frac{H_{1/3}}{2}\frac{\sinh\left[2\pi(z+d)/L\right]}{\sinh\left(2\pi d/L\right)}$$

The dissipation of energy mainly occurs at the smallest turbulence scales, that is, at the so-called Kolmogorov microscales. At this point, the driving energy is finally overcome by the viscosity $\left(v \approx 10^{-6}\,\text{m}^2\,\text{s}^{-1}\right)$, and the size of the smallest eddy ($\eta$) and its characteristic velocity ($v_t$) are defined as (Tennekes and Lumley 1972) follows:

$$\eta \equiv \left(v^3/\varepsilon\right)^{1/4}$$

$$v_t \equiv (v\varepsilon)^{1/4}$$

These Kolmogorov microscales are crucial to understanding the interactions of planktonic organisms with their microdistribution patterns in the water column (Rothschild and Osborn 1988).

A spatial segregation index ($D$) was also calculated between all possible pairs formed by the most abundant genera. This index is (White 1983):

$$D = \frac{1}{2}\sum_{i=1}^n\left|\frac{N_{1i}}{N_1} - \frac{N_{2i}}{N_2}\right|$$

where $N_{1i}$ = number of individuals of genus 1 at station $i$; $N_{2i}$ = number of individuals of genus 2 at station $i$; $N_1$ = total number of individuals of genus 1; $N_2$ = total number of individuals of genus 2.

The values of $D$ range from 0, in the case of the maximum spatial co-occurrence between the two genera, to 1, which indicates a perfect spatial segregation. The level of significance of an observed index value was estimated through the use of null models (Manly 1991). This procedure consists of the following: (1) estimation of the observed index Do from two vectors, (2) random reallocation of one vector (genera 1 or 2), (3) the repetition of the second step a large number of times (1,000 in this case) to estimate new random values (Dr) in order to find the null distribution of $D$ and (4) the comparison of the Do value within the null distribution: If Do represents a typical value within the $D$ distribution, then the spatial pattern of the two genera seems to be random. In contrast, if Do is on one of the extremes of the distribution, the conclusion is that the two genera are spatially associated (lower tail) or segregated (upper tail). In this study we tested the level of spatial segregation among the genera, and the $P$ value was considered to be the proportion of the Dr values higher than or equal to Do. A MATLAB procedure was developed for these calculations.

## Results

### Environmental conditions

The hydrological data indicated that surface temperature conditions were warmer in May (~28 °C) than in November (24–26 °C); in deeper strata (45–105 m), the temperature varied from 18.5 to 24 °C in May, and from 21 to 26 °C in November due to a deeper thermocline. Surface salinity values were more variable in November (30–33.5) than in May (35.9–36.8), due to higher continental water discharges in November; in deeper waters (45–105 m), the salinity values were more stable than in surface waters, with values around 36.1 in both seasons.

The turbulence parameter profiles in the southern Gulf of Mexico were different in the two studied periods, especially in the 0–40-m stratum. During May, when calm meteorological conditions prevailed, winds of 3.1 m s$^{-1}$ induced turbulent kinetic energy ($k$) values ranging from $1.51 \times 10^{-2}$ to $4.42 \times 10^{-10}$ J kg$^{-1}$, and the associated dissipation rate of energy ($\varepsilon$) ranged from $2.26 \times 10^{-3}$ to $1.14 \times 10^{-10}$ m$^2$ s$^{-3}$ (Table 1). Moreover, the size of the smallest eddy was less than 1 mm at surface waters. During November, winds of 6.1 m s$^{-1}$ induced $k$ values that varied from $3.27 \times 10^{-2}$ to $1.18 \times 10^{-7}$ J kg$^{-1}$ and $\varepsilon$ values from $4.19 \times 10^{-3}$ to $3.32 \times 10^{-8}$ m$^2$ s$^{-3}$. The values of the Kolmogorov microscales were on the same order of magnitude as those observed in May (Table 1).

### Vertical distribution of zooplankton biomass and holoplanktonic molluscs

The values of zooplankton biomass (ml 100 m$^{-3}$) were highest in the upper three levels (0–18 m) during both

seasons with no significant differences ($t$ test, $P > 0.05$) between the comparable strata. In turn, pelagic molluscs' densities were highest in May, especially in the upper three strata, where significant differences ($t$ test, $P < 0.05$) were observed between months.

The pelagic mollusc community was mainly composed (92.5 %) of organisms belonging to the Thecosomata order. From the 55,654 identifiable specimens of holoplanktonic molluscs collected in the two seasons, only 6.2 % were in juvenile stage, with *Cavolinia*, *Diacavolinia*, *Diacria*, *Oxygyrus* and *Clio* being the most abundant genera; juveniles of *Oxygyrus* were only collected in May. Adults of these genera represented 3 % of the total abundance.

The patterns of vertical distribution revealed that juveniles of *Cavolinia*, *Diacavolinia* and *Oxygyrus* mainly inhabit the upper layer (0–18 m), while those of *Diacria* and *Clio* are more abundant in the deeper stratum (45–105 m) (Table 2), at both noon and midnight (Table 3). The highest spatial segregation values were found between the pairs formed by combinations of genera from the upper (*Cavolinia*, *Diacavolinia* and *Oxygyrus*) and lower strata (*Diacria* and *Clio*). Moreover, null models revealed significant $P$ values in the pairs formed by *Cavolinia* or *Diacavolinia* with *Diacria* or *Clio* (Table 4). The distribution of *Diacavolinia* and *Diacria* in the five horizontal planes (Figs. 2, 3) illustrates well the genera inhabiting the upper and lower layers. Adults of the same genera exhibited less marked differences between the upper and deeper strata of the water column (Table 5).

## Discussion

The mean density values of pelagic molluscs in the warmer period, May, almost doubled those recorded in November

**Table 1** Values of turbulent kinetic energy ($k$), dissipation rate of energy ($\varepsilon$) and length ($\eta$) and velocity ($v_t$) Kolmogorov scales at different discrete depths under different wind conditions ($U_{10}$) in the southern Gulf of Mexico

| Stratum (m) | Depth (m) | $k$ (J kg$^{-1}$) | $\varepsilon$ (m$^2$ s$^{-3}$) | $\eta$ (mm) | $v_t$ (cm s$^{-1}$) | Zooplankton (ml 100 m$^{-3}$) | Molluscs (ind 100 m$^{-3}$) |
|---|---|---|---|---|---|---|---|
| May ($U_{10}$ = 3.8 m s$^{-1}$) | | | | | | | |
| 0–6 | 3 | $1.51 \times 10^{-2}$ | $2.26 \times 10^{-3}$ | 0.14 | $6.89 \times 10^{-1}$ | $31.8 \pm 23.8$ | $281.0 \pm 368.1$ |
| 6–12 | 6 | $8.54 \times 10^{-3}$ | $1.28 \times 10^{-3}$ | 0.17 | $5.98 \times 10^{-1}$ | $41.8 \pm 37.2$ | $421.3 \pm 591.5$ |
| 12–18 | 12 | $2.73 \times 10^{-3}$ | $4.09 \times 10^{-3}$ | 0.22 | $4.49 \times 10^{-1}$ | $33.5 \pm 28.9$ | $221.8 \pm 217.2$ |
| 45–55 | 45 | $5.17 \times 10^{-6}$ | $7.75 \times 10^{-7}$ | 1.06 | $9.38 \times 10^{-2}$ | $14.2 \pm 6.2$ | $43.4 \pm 37.6$ |
| 95–105 | 95 | $4.42 \times 10^{-10}$ | $1.14 \times 10^{-10}$ | 9.66 | $1.03 \times 10^{-2}$ | $13.6 \pm 16.0$ | $28.3 \pm 18.1$ |
| November ($U_{10}$ = 6.1 m s$^{-1}$) | | | | | | | |
| 0–6 | 3 | $3.27 \times 10^{-2}$ | $4.19 \times 10^{-3}$ | 0.12 | $8.04 \times 10^{-1}$ | $37.7 \pm 24.5$ | $134.6 \pm 159.3$ |
| 6–12 | 6 | $2.16 \times 10^{-2}$ | $2.76 \times 10^{-3}$ | 0.14 | $7.25 \times 10^{-1}$ | $31.4 \pm 25.7$ | $218.4 \pm 354.1$ |
| 12–18 | 12 | $9.40 \times 10^{-3}$ | $1.20 \times 10^{-3}$ | 0.17 | $5.89 \times 10^{-1}$ | $21.0 \pm 15.8$ | $192.4 \pm 283.5$ |
| 45–55 | 45 | $9.70 \times 10^{-5}$ | $1.24 \times 10^{-5}$ | 0.53 | $1.87 \times 10^{-1}$ | $10.3 \pm 6.3$ | $54.1 \pm 62.9$ |
| 95–105 | 95 | $1.18 \times 10^{-7}$ | $3.32 \times 10^{-8}$ | 2.34 | $4.27 \times 10^{-2}$ | $8.4 \pm 5.6$ | $86.6 \pm 148.2$ |

Mean zooplankton biomass ($\overline{X} \pm$ SD) and density of the holoplanktonic molluscs ($\overline{X} \pm$ SD) of each stratum are also shown

**Table 2** Mean abundance (ind 100 m$^{-3}$ ± SD) of five genera of juvenile holoplanktonic molluscs in five strata (m) of the water column during two sampling periods

| Stratum | Cavolinia | Diacavolinia | Oxygyrus | Diacria | Clio |
|---|---|---|---|---|---|
| May |
| 0–6 | 114.1 ± 34.7 | 8.8 ± 3.0 | 2.1 ± 0.5 | 0.0 | 0.0 |
| 6–12 | 118.5 ± 22.5 | 11.9 ± 2.1 | 3.8 ± 0.9 | 0.2 ± 0.1 | 0.0 |
| 12–18 | 175.1 ± 19.3 | 45.2 ± 10.5 | 4.4 ± 0.9 | 3.4 ± 1.0 | 0.4 ± 0.1 |
| 45–55 | 83.5 ± 14.5 | 2.8 ± 0.5 | 1.2 ± 0.2 | 6.7 ± 1.1 | 0.0 |
| 95–105 | 20.1 ± 2.1 | 3.6 ± 0.8 | 0.2 ± 0.1 | 16.4 ± 2.3 | 10.0 ± 1.4 |
| November |
| 0–6 | 19.4 ± 3.3 | 9.2 ± 2.0 | – | 0.0 | 0.0 |
| 6–12 | 59.2 ± 15.2 | 32.6 ± 11.7 | – | 0.0 | 0.0 |
| 12–18 | 107.4 ± 12.3 | 50.5 ± 11.2 | – | 1.1 ± 0.4 | 0.0 |
| 45–55 | 21.1 ± 2.3 | 2.9 ± 0.4 | – | 3.3 ± 0.3 | 4.5 ± 1.3 |
| 95–105 | 10.4 ± 1.4 | 0.6 ± 0.1 | – | 9.6 ± 2.6 | 7.2 ± 2.0 |

Mean values are multiplied by 10

**Table 3** Day (D) and night (N) mean abundance (ind 100 m$^{-3}$) of five genera of juvenile holoplanktonic molluscs in five strata (m) of the water column during two sampling periods

| Stratum | Cavolinia | | Diacavolinia | | Oxygyrus | | Diacria | | Clio | |
|---|---|---|---|---|---|---|---|---|---|---|
| | D | N | D | N | D | N | D | N | D | N |
| May |
| 0–6 | 22.4 | 2.4 | 1.0 | 0.9 | 0.2 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| 6–12 | 22.5 | 2.1 | 1.4 | 1.2 | 0.3 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 |
| 12–18 | 24.3 | 2.7 | 6.8 | 1.1 | 0.0 | 1.2 | 0.5 | 0.1 | 0.0 | 0.0 |
| 45–55 | 8.4 | 0.5 | 0.4 | 0.0 | 0.0 | 0.4 | 0.9 | 0.4 | 0.0 | 0.0 |
| 95–105 | 2.3 | 1.1 | 0.6 | 0.0 | 0.0 | 0.1 | 1.4 | 2.7 | 1.4 | 0.5 |
| November |
| 0–6 | 1.1 | 3.7 | 0.4 | 1.8 | – | – | 0.0 | 0.0 | 0.0 | 0.0 |
| 6–12 | 2.1 | 13.1 | 0.8 | 7.5 | – | – | 0.0 | 0.0 | 0.0 | 0.0 |
| 12–18 | 4.4 | 13.2 | 0.9 | 8.7 | – | – | 0.0 | 0.3 | 0.0 | 0.0 |
| 45–55 | 2.3 | 1.7 | 0.4 | 0.2 | – | – | 0.3 | 0.4 | 0.1 | 1.1 |
| 95–105 | 1.6 | 0.3 | 0.1 | 0.1 | – | – | 1.6 | 0.1 | 1.2 | 0.0 |

Dawn and dusk (6–7 am/pm) values were eliminated for calculations

**Table 4** Values of spatial segregation index (Do) estimated from combinations of five genera of juvenile holoplanktonic molluscs collected in five strata of the water column during May (upper matrix) and November (lower matrix)

| | Cavolinia | Diacavolinia | Oxygyrus | Diacria | Clio |
|---|---|---|---|---|---|
| Cavolinia | 0.00 | 0.29 | 0.13 | 0.67** | 0.93** |
| Diacavolinia | 0.11 | 0.00 | 0.28 | 0.78** | 0.92** |
| Oxygyrus | – | – | 0.00 | 0.75 | 0.95 |
| Diacria | 0.78** | 0.89** | – | 0.00 | 0.35 |
| Clio | 0.86** | 0.96** | – | 0.15 | 0.00 |

** Significant P values at α = 0.10, as revealed by null model arguments

in the 0–18-m layer. Accordingly, Xu and Li (2005) stated that temperature is a major factor determining the seasonal changes in the molluscs' total abundance. In the southern Gulf of Mexico, higher temperatures seem to induce reproductive processes of pelagic molluscs, as the total density values showed (Table 1).

The vertical distribution of the holoplanktonic molluscs was closely related to the distribution of the zooplankton biomass (Table 1), suggesting that food availability plays an important role in the position of these organisms in the water column. Pelagic molluscs have a wide variety of feeding mechanisms; they feed upon an ample spectrum of microplankton particles and may also exhibit a certain degree of dietary specialization (Lalli and Gilmer 1989). The thecosomatous pteropods, like most of the specimens encountered here, catch their prey using a mucous web which can be swallowed by such predators in less than 3 min (Gilmer and Harbison 1986). In this study, the lowest observed density of molluscs in the 0–18-m layer occurred at the first level (0–6 m) in November, when the highest turbulence values (k and ε) were registered (Table 1). In accordance with this finding, the in situ Arctic explorations performed by Gilmer and Harbison (1991) revealed that the pteropods avoid the ∼4-m upper layer because the strong turbulence could disrupt their fragile

**Fig. 2** Vertical distribution of juveniles of *Diacavolinia* in the southern Gulf of Mexico during two seasons
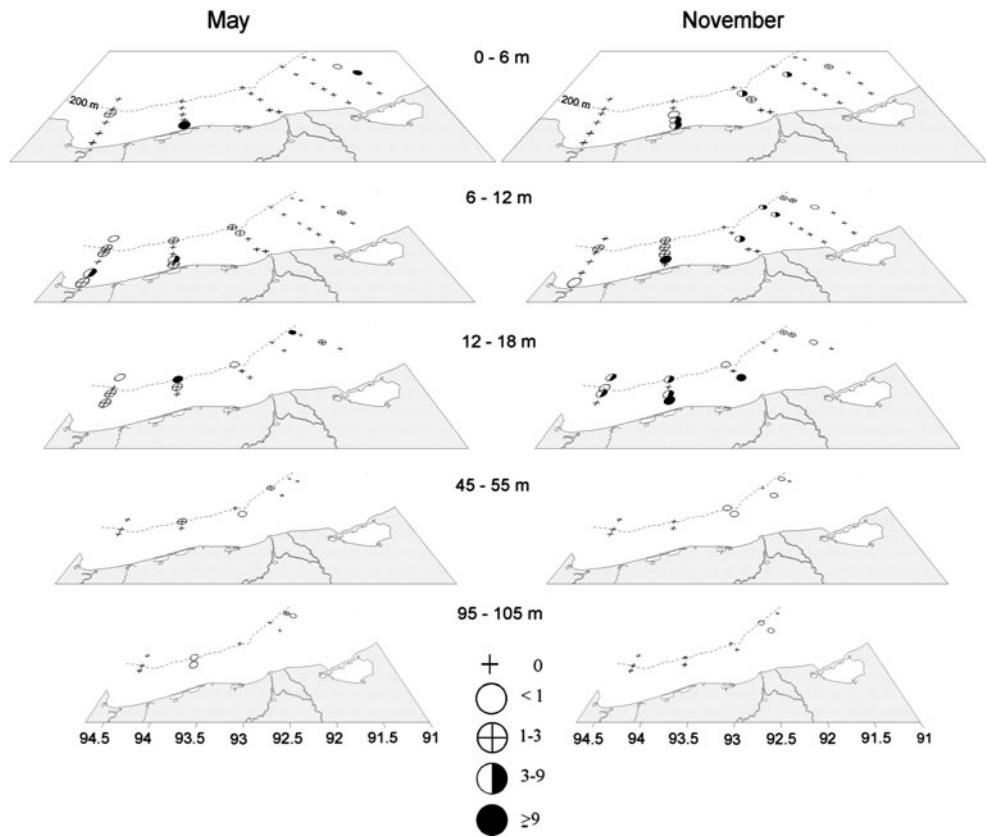


**Fig. 3** Vertical distribution of juveniles of *Diacria* in the southern Gulf of Mexico during two seasons
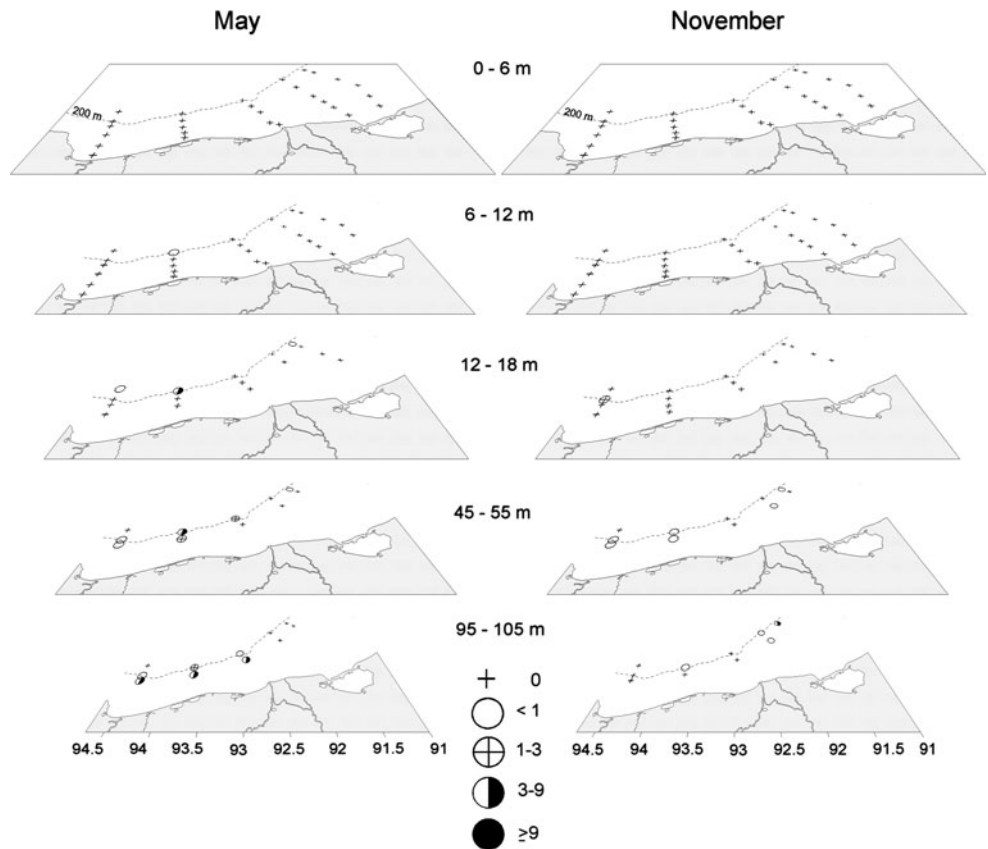
**Table 5** Values of spatial segregation index (Do) estimated from combinations of five genera of adult holoplanktonic molluscs collected in five strata of the water column during May (upper matrix) and November (lower matrix)

|  | *Cavolinia* | *Diacavolinia* | *Oxygyrus* | *Diacria* | *Clio* |
|---|---|---|---|---|---|
| *Cavolinia* | 0.00 | 0.29 | 0.27 | 0.12 | 0.75 |
| *Diacavolinia* | 0.11 | 0.00 | 0.17 | 0.24 | 0.96** |
| *Oxygyrus* | 0.47 | 0.43 | 0.00 | 0.21 | 0.92 |
| *Diacria* | 0.14 | 0.25 | 0.61 | 0.00 | 0.83 |
| *Clio* | 0.69 | 0.74 | 0.96 | 0.63 | 0.00 |

** Significant $P$ values at $\alpha = 0.10$, as revealed by null model arguments

mucous web. Trophic and other ecological interactions take place in the so-called Kolmogorov microscales. According to Rothschild and Osborn (1988), the ecological processes of plankton are coupled with physical phenomena of the same scales of space and time. For instance, the size of the microparticles (15–800 μm) ingested by the molluscs (Gilmer and Harbison 1991) has the same magnitude as the length Kolmogorov scales here calculated (Table 1). Furthermore, the swimming ($\sim 4$–$14$ cm s$^{-1}$), escape ($\sim 10$–$30$ cm s$^{-1}$) and sinking ($\sim 0.5$ cm s$^{-1}$) speeds of the pelagic molluscs (Gilmer and Harbison 1986; Harbison and Gilmer 1992) are within the range of the turbulence velocities ($\sqrt{k}$ and $v_t$) estimated in this study (Table 1).

The vertical distribution of both adults and juveniles of targeted genera was quite different. While juveniles showed a significant vertical segregation, adults exhibited a much more vertical overlapped distribution (Tables 4, 5). In the upper 100-m layer of Philippine waters, Solis and von Westernhagen (1978) reported different patterns in the vertical distribution of adults and juveniles of *Cavolinia*, *Diacria* and *Clio*. Indeed, no adults of *Clio* were caught in their samples, because juveniles seemed to be distributed shallower in the water column (Furnestin 1961).

The vertical partitioning of *Cavolinia*/*Diacavolinia*/*Oxygyrus* and *Diacria*/*Clio* does not match the vertical conditions of temperature and salinity. Also, the differences in the day/night abundance data of *Cavolinia* and *Diacavolinia* were not consistent in the two sampling periods (Table 3). Hence, we believe that the effects of hydrological conditions and diel movements of organisms have a negligible role in explaining the observed vertical segregation. Therefore, we propose that ecological interactions and/or life history characteristics of species can explain this result:

### Suitable areas for eggs deposition

Taking into account that the earlier stages of planktonic organisms have a limited motility in the water column, we think that the selection of suitable areas for adults'

oviposition is the main cause and the first step for juvenile habitat partitioning. In accordance with Resetarits (1996), the choice of proper sites for eggs deposition affects hatching success, larval performance and parental fitness. This author stressed that the choice of an area for oviposition must optimize locally survivorship of phenotypes. Thus, this life history strategy might avoid competition among organisms having similar ecological requirements, as we show below.

### Competition avoidance

In niche theory, the importance of competition for limited feeding or space resources has been widely recognized in the spatial structure of communities. In ecologically similar taxa, such as the cavoliniids here encountered, interspecific competition may account for mutual exclusion. When feeding, the cavoliniids produce a spherical mucous web which can attain 200 mm diameter in *Cavolinia*, 40 mm in *Diacavolinia* (as *Cavolinia longirostris*), 100 mm in *Diacria* and 40 mm in *Clio* (Gilmer and Harbison 1986). Then, considering a one-dimensional, 1-m-diameter plankton patch, this means that only five individuals deploying a 200-mm-diameter web can coexist. Unfortunately, the spatial relationships among neighbouring individuals in pelagic communities are practically unknown. However, interspecific competition for food and space seems to be a strong reason for habitat partitioning between *Cavolinia*/*Diavolinia* and *Diacria*/*Clio* groups.

### Visual predation

Within the gastropods, the eyes of heteropod molluscs are unusually large and complex (Land 1982). In *Oxygyrus*, a small epipelagic carnivorous heteropod, the eyes make smooth scanning movements to detect their prey in the surrounding waters, allowing a wide field of view (Land 1982). Blumer (1999), who examined the photoreceptor organs of different growth stages of a heteropod species, indicated that while the larvae have only two sensory cells, the eyes of both juvenile and adults are well adapted to be visual predators. This fact explains the presence of *Oxygyrus* juveniles in the upper layer (0–18 m), where light intensity magnifies visual abilities for searching prey.

### Brood protection

In the epipelagic layer, visual or tactile predators can be common, while physical refuges are rare (Hamner 1995). A way to protect progeny from predation is providing parental cares. Most pelagic opisthobranch molluscs are protandrous hermaphrodites, laying free-floating mucous egg masses and releasing free-swimming veliger larvae

(Lalli and Wells 1973; Lalli and Gilmer 1989), vulnerable to predation. However, some mesopelagic molluscs have developed particular reproductive strategies to guarantee the survival of their offspring. For instance, *Clio* retains embryos and larvae within the mantle cavity, enhancing the offspring success (Tesch 1946). Brood protection is more effective in the darkest part of the water column studied, where *Clio* was mainly found (Table 2).

### Turbulence conditions

Wind-induced turbulence can strongly impact the vertical distribution of planktonic organisms with either beneficial or detrimental consequences for their populations (Margalef 1997). While turbulence promotes encounters between predator and prey, a relatively high velocity would make catching the prey more difficult (Lewis and Pedley 2001). In the case of *Oxygyrus*, the only visual predator here studied, turbulence may enhance encounters with its prey. In the cavoliniids *Cavolinia* and *Diacavolinia*, which deploy and suspend beneath themselves a fragile mucous feeding web, turbulence may induce more suspended particles to be trapped in the web. There are very few in situ observations of pteropod feeding webs (Gilmer and Harbison 1986; Gilmer 1990; Harbison and Gilmer 1992), and no quantifiable relationships between turbulence intensity and mucous webs resistance have been observed. Empirical studies suggest that turbulence might be a major factor in determining the position of molluscs and other zooplankters in the water column, and sometimes the main responsible of vertical partitioning of co-generic species (Mackas et al. 1993; Tsurumi et al. 2005). It seems that suitable turbulence conditions for *Cavolinia* and *Diacavolinia* correspond to the third level (12–18 m), as revealed by their abundance data (Table 2). Even when *Diacria* and *Clio* could also obtain a beneficial effect from turbulent levels similar to those in the upper layer, their presence in the lower stratum suggests that other ecological or biological phenomena have more influence on their vertical distribution.

### Conclusion

This study provides a major contribution to niche requirements of five pelagic mollusc genera (*Cavolinia*, *Diacavolinia*, *Diacria*, *Oxygyrus* and *Clio*) inhabiting the ocean epipelagic layer. An examination of their vertical position in the water column, based on null model arguments, evidenced a small-scale spatial segregation among them. Several ecological mechanisms are involved in the observed spatial segregation, each of them having differential importance upon the distribution of each genus. Habitat partitioning of

ecologically related genera, such as cavoliniids, suggests an avoidance competition. Thus, position in the water column of juvenile pelagic molluscs represents an equilibrium between the need to minimize the detrimental consequences of competition, the risk of predation and/or the effects of strong turbulence against the necessity of inhabiting suitable areas for feeding and growth.

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