

Mesoscale distribution of *Oikopleura* and *Fritillaria* (Appendicularia) in the Southern Gulf of Mexico: spatial segregation

Distribución a mesoescala de *Oikopleura* y *Fritillaria* (Appendicularia) en el sur del Golfo de México: segregación espacial

César Flores-Coto¹, Laura Sanvicente Añorve¹, Felipe Vázquez-Gutiérrez¹ and Marina Sánchez-Ramírez²

¹Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Apdo. Postal 70-305, 04510 México D.F., México. cotoce@unam.mx

²Instituto Politécnico Nacional, Escuela Nacional de Ciencias Biológicas, Laboratorio de Ecología, Col. Santo Tomas C.P. 11340, Delegación Miguel Hidalgo, México, D.F. México

Resumen. - Se analizó la existencia de segregación espacial a meso-escala en la distribución de *Oikopleura* y *Fritillaria* en el sur del Golfo de México. Se obtuvieron 97 muestras en la capa superficial de 50 m. Se midió la salinidad, temperatura y turbidez. A las densidades de *Oikopleura* y *Fritillaria* se aplicó el índice de Segregación Espacial 'D', y el nivel de significancia del resultado se probó con el método de Monte Carlo. El análisis de regresión de árbol (RT) se empleó para identificar los principales factores del medio ambiente que afectan la distribución de los géneros. El valor del índice de segregación fue de 0,67 y es considerado un valor alto. El análisis RT mostró a la turbidez como el principal factor influyendo en la distribución espacial de ambos géneros. *Fritillaria* fue encontrada en aguas turbias frente a los principales sistemas fluvio-lagunares y *Oikopleura* fue más abundante en aguas de surgencia sobre la plataforma de Yucatán. La distribución segregada de las apendicularias en el área de estudio parece fuertemente influenciada por las surgencias y corrientes asociadas y por la turbidez generada por la descarga de aguas continentales. Puede asumirse a las cadenas tróficas como un importante factor asociado. Se plantea la hipótesis que *Oikopleura* tiene una amplia dieta y una mayor eficiencia de filtración para grandes partículas (microfitoplancton) que le permiten explotar la producción en áreas de surgencia, en tanto las especies de *Fritillaria* no pueden. Esto permite explicar la segregación de estos géneros.

Palabras clave: Apendicularias, distribución a mesoescala, segregación espacial, turbidez

Abstract. - The mesoscale spatial distribution of *Oikopleura* and *Fritillaria* in the southern Gulf of Mexico was analyzed to know the existence of segregation between them. Samples were taken on 97 stations in the 50 m upper layer. Temperature, salinity and turbidity were measured. The spatial segregation index 'D' was applied to *Oikopleura* and *Fritillaria* densities and its significance was tested with Monte Carlo method. Regression Tree (RT) analyses were performed to identify the main environmental factors affecting the distribution of genera. The D index value was 0.67, considered as a high value. RT analyses showed the water turbidity was the main factor affecting the spatial distribution of both genera. *Fritillaria* was found in turbid waters off the main fluvio-lagoon systems and *Oikopleura* was most abundant in the up welling waters over Yucatan Shelf. The segregation distribution of appendicularians in the study area appear to be strongly influenced by up welling and associated currents, and turbidity generated by continental water discharges. It could be assumed that food webs are an important associated factor. We hypothesize that a broad diet and higher filtration efficiency for larger particles (microfitoplankton) allows *Oikopleura* species to exploit the production in up welling areas, whereas *Fritillaria* species can not. It may explain its spatial segregation of these genera.

Key words: Appendicularians, mesoscale distribution, spatial segregation, turbidity

INTRODUCTION

Appendicularians are among the most common zooplankton organisms and are widely distributed in all the oceans. In the pelagic environment, the ecological relevance of larvaceans is that they mobilize microbial

production to higher trophic levels in marine food webs (Gorsky & Fenaux 1998, Capitanio *et al.* 2005). These animals are major consumers of small phytoplankton, bacteria, as well as particulate and colloidal organic matter

suspended in the water column (Flood *et al.* 1992). Appendicularians feed using a mucous structure called 'house' to filter and concentrate small particles ranging from colloids to large diatoms (Deibel 1998, Lambert 2005). The houses are rejected when the particles clog the filters (Esnal 1999). The houses in Oikopleuridae are discarded and renewed up to 16 times a day (Fenaux 1985). Living appendicularians and discarded houses are eaten by larger pelagic carnivores, including copepods, medusae, fish larvae, chaetognaths, and foraminifera (Lambert 2005, Purcell *et al.* 2005), as well as some fishes (Capitanio *et al.* 2005). Most species inhabit the 200 m surface layer however, permanent populations of appendicularians occur at meso- and bathypelagic zones indicating that a constant source of foods exists at those depths since larvaceans are incapable to store food energy (Lambert 2005).

One interesting aspect of the appendicularians biology, is the ability of some species to form large aggregations in seasons and areas where others species are very scarce or do not appear at all (Björnberg & Forneris 1956a,b, Fenaux 1963, Alldredge 1982, Uye & Ichino 1995). At a temporal scale, a seasonal segregation occurs among several species in a local station of the Mediterranean Sea (Fenaux 1963). At a spatially fine-scale *Oikopleura* and *Fritillaria* species co-occurred, however, at a spatial mesoscale where the areas are affected by the main circulation pattern, continental water discharges, mixing processes and oceanic gyres, some segregation among Oikopleuridae and Fritillariidae has been observed in Brazilian waters (Björnberg & Forneris 1956a), California coast in USA (Alldredge 1982), or Rio de la Plata estuary, in Argentina (Capitanio & Esnal 1997).

Particularly in coastal areas the appendicularians distribution is strongly affected by continental water discharges. Capitanio & Esnal (1998) considered that appendicularians distribution off the Rio de la Plata estuary is influenced by turbidity front. Generally the fronts of the rivers are zones of high concentration of appendicularians (Dagg *et al.* 1996; Dagg & Brown 2005).

In the Gulf of Mexico practically there are not studies on the distribution and abundance of appendicularian, except those of Flores-Coto (1974) in a small area around the La Blanquillia reef off Veracruz coasts and Tokioka & Suarez-Caabro (1956) around Cuba Island.

There is little quantitative information on appendicularian abundance to analyze the co-occurrence or segregation of species at a spatial mesoscale.

Nevertheless, based on some studies (Fernández *et al.* 2004, Choe & Deibel 2008) it could be assumed that food webs are an important factor in segregation distribution of *Oikopleura* and *Fritillaria* species in the southern Gulf of Mexico. Considering two different food webs in the study area we hypothesize that the size of available food plays a determining role in the segregation distribution of appendicularians.

MATERIAL AND METHODS

The study area is located in the southern Gulf of Mexico, between 18° and 22°N and 18° and 20°W (Fig. 1). The continental shelf in the study area is highly contrasting, as wide as 150 km in the northeastern region and no rivers; whereas in the southern region, is 50 km wide and with a strong influence of continental water discharges.

Water discharges from the Grijalva-Usumacinta River are $7\text{--}10 \times 10^9 \text{ m}^3 \text{ month}^{-1}$ from July to November, and $1.6\text{--}4 \times 10^9 \text{ m}^3 \text{ month}^{-1}$ from December to June (Czitrom *et al.* 1986). During the autumn-winter period, a down-coast current reaches the southern Bay of Campeche and meets an opposite west-current, generating an offshore transport (Zavala-Hidalgo *et al.* 2003). In the adjacent oceanic water the circulation is predominantly cyclonic (Salas *et al.* 1992).

Samples were collected mainly over the shelf on a grid of 97 oceanographic stations, at the end of summer from September 3 to October 8, 2003. Temperature and salinity data were measurement *in situ* with calibrate CTD sonde (Marc III/Woce). Turbidity (Nephelometric Turbidity Units) was measured on board with a nephelometer Hach Model 0220 (APHA 2005). Zooplankton was sampled from the upper 50 m of the water column using a conical net of 30 cm mouth diameter, 200 μm mesh size, equipped with a flow meter (General Oceanic, model 2030R). Samples were fixed in 4% formaldehyde solution. All appendicularian were sorted and identified using mainly the Tokioka & Suarez Caabro (1956) and Esnal (1999) studies.

Spatial segregation of *Oikopleura* and *Fritillaria* genera was tested by means of the dissimilarity index D (White 1983): which ranges from 0 to 1, indicating no segregation to perfect segregation respectively.

$$D = \frac{1}{2} \sum_{i=1}^{97} \left| \frac{N_{1i}}{N_1} - \frac{N_{2i}}{N_2} \right|$$

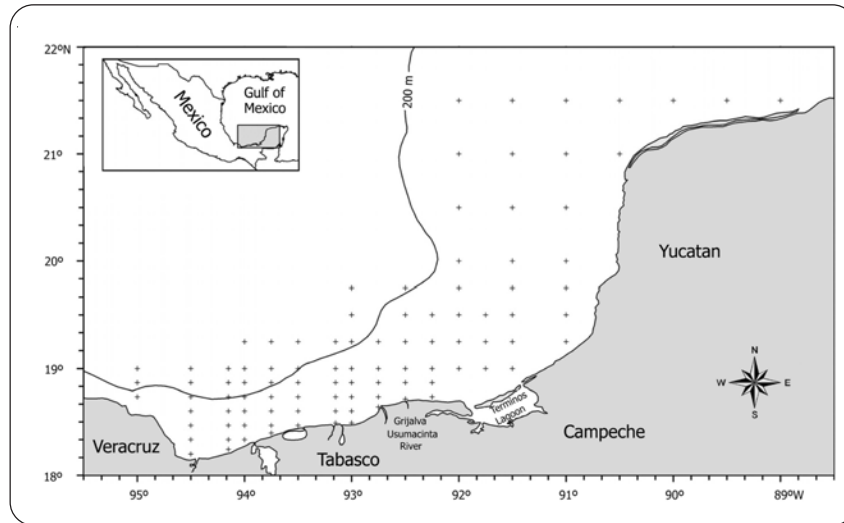


Figure 1. Study area and location of sampling stations indicated with '+' / Área de estudio y localización de estaciones de muestreo indicadas con '+'

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 significance level of the D statistic was evaluated by means of Monte Carlo simulations of the contingency table using the algorithm proposed by Roff & Bentzen (1989). In this algorithm, a large number of randomizations (1000 in this study) of the original data set must be generated, subject to the constraint that the original row (Both genera) and column totals (sampling stations) remain equal to the original data matrix. A MATLAB program was developed for this purpose.

Regression Tree Analyses (Breiman *et al.* 1984, Urban 2002) were also employed to look for the environmental variables determining the spatial distribution of *Oikopleura* and *Fritillaria* genera in the southern Gulf of Mexico. SPLUS 2000 software was used. Data matrices included the temperature, the salinity, the turbidity, and the bottom depth as explanatory variables, and the log-transformed *Fritillaria* and *Oikopleura* densities as response variables. Regression Tree Analysis (RTA) explains the variation of a single numeric response variable using explanatory variables. RTA proceeds by a recursive binary splitting of the data into mutually exclusive groups, each of which has similar values of the response variable. Splits are generally chosen to minimize the total sum of squared residuals of the regression models fitted to data of resulting

two nodes. The terminal nodes represent the groups of data formed by the tree (De'ath & Fabricius 2000).

RESULTS

Temperature distribution as average of first 50 m of the water column, fluctuate between 27 to 30°C (Fig. 2A). Low temperatures were recorder in two zones, one in Tabasco neritic waters by the influence of continental water discharges of the Grijalva-Usumacinta River and the second one in the eastern portion of Yucatán shelf under the influence of Yucatán upwelling waters. Highest temperatures were recorded in coastal shallow waters around Terminos Lagoon. Average salinity of surface water down to 50 m fluctuated between 35.75 to 36.50 (Fig. 2B). Over the Campeche and Yucatan shelf salinity was very homogeneous and the largest variation occurred on the Tabasco shelf as consequence of the continental water discharges (Fig. 2B). Turbidity fluctuated between 0.2 and 0.8 NTU, with lower values (0.2 a 0.3 NTU) over the Campeche and Yucatán shelf, and higher values (0.4 a 0.8 NTU) on the Tabasco shelf (Fig. 2C).

Twenty species of appendicularians were identified in the study area during September 2003. The most abundant species were *Oikopleura longicauda* (70.30%), *O. fusiformis* (13.62%) and *Fritillaria haplostoma* (10.10%). By genera, *Oikopleura* accounted for 85.93% of the total abundance, while *Fritillaria* 13.83% (Table 1). *Oikopleura* (especially *O. longicauda* and *O. fusiformis*) was widely distributed in the study area, and was more abundant over

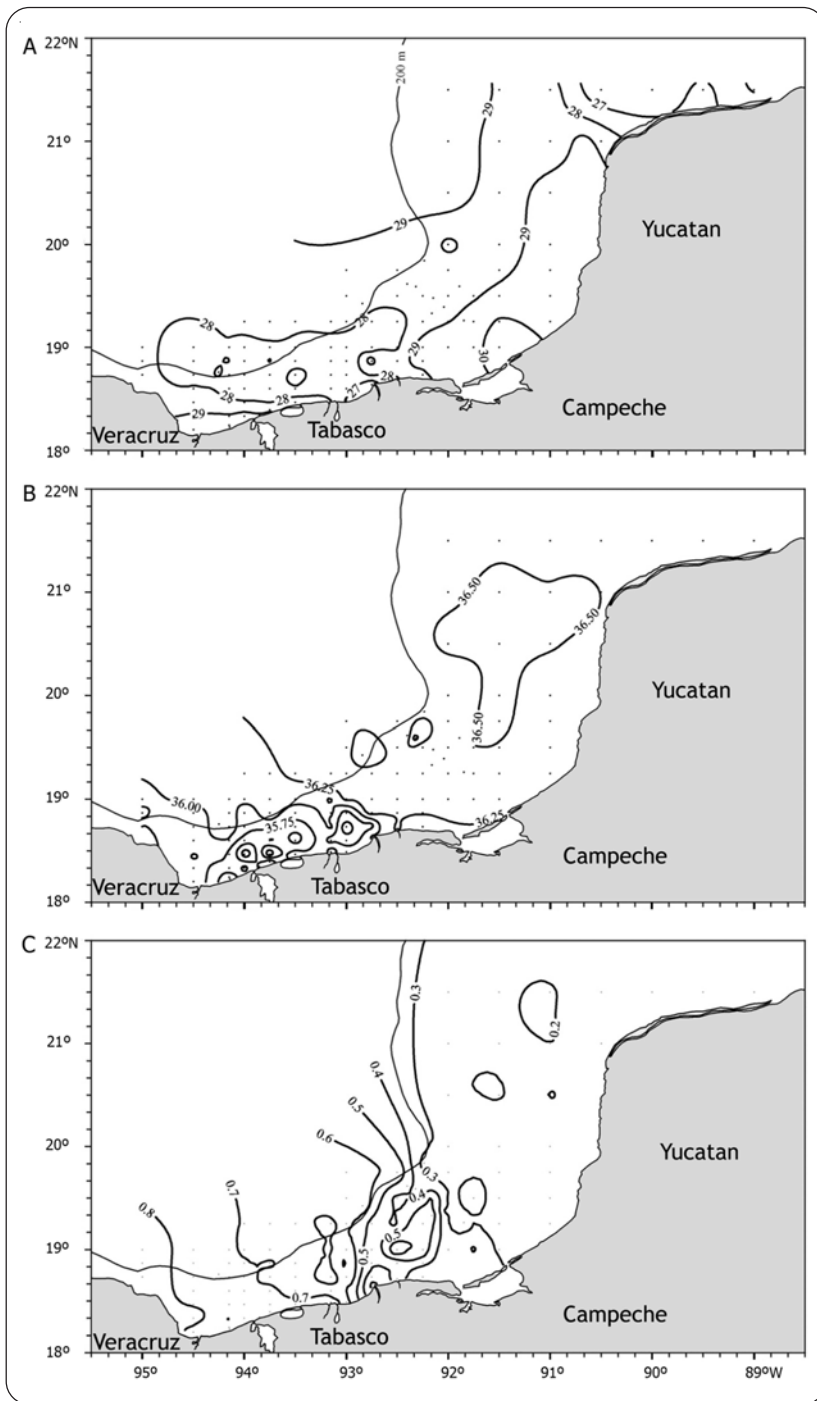


Figure 2. Isopleths of temperature (A), salinity (B) and turbidity (C), in the southern Gulf of Mexico, during September 2003 / Isoplethas de temperatura (A), salinidad (B) y turbidez (C), en el sur del Golfo de México, durante septiembre de 2003

the wide Yucatán shelf (Fig. 3A). *Fritillaria* (especially *F. haplostoma*, *F. borealis*, and *F. formica*) was mainly found over Tabasco shelf, off of the main fluvial systems of the southern Gulf (Fig. 3B).

The spatial segregation index (D) was 0.67, estimated from *Fritillaria* and *Oikopleura* densities. None of the

1000 Monte Carlo simulations of the original data matrix produced a D value higher than that obtained from the original data set (0.67). Thus, the null hypothesis of no significant variation between the observed D value and those randomly generated was rejected ($P < 0.001$).

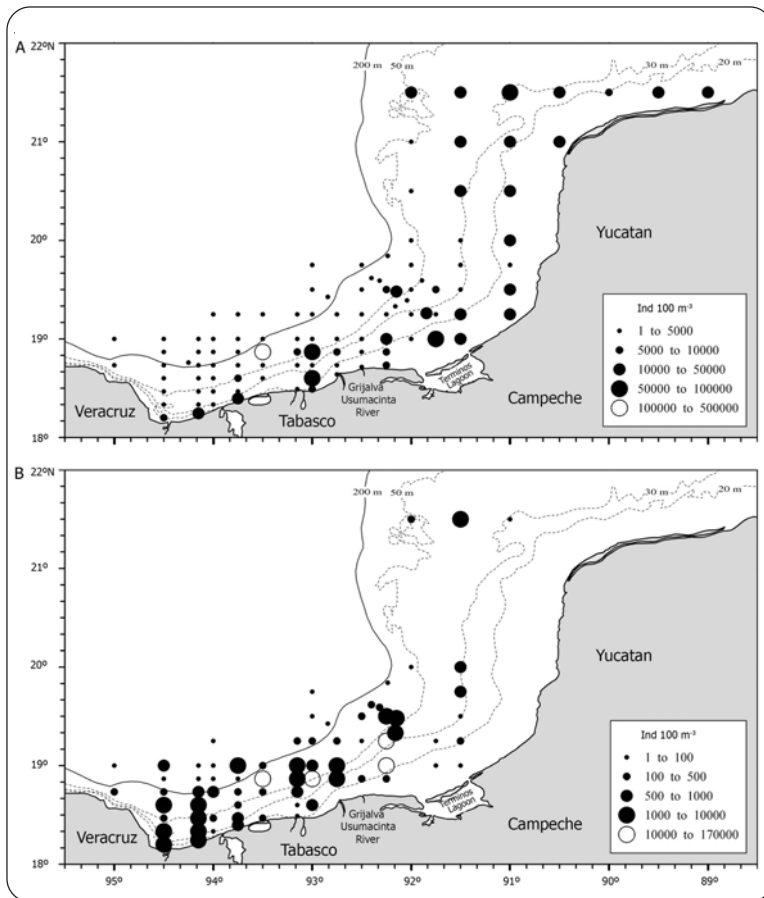


Figure 3. Distribution of *Oikopleura* (A) and *Fritillaria* (B) genera in the southern Gulf of Mexico, during September 2003 / Distribución de los géneros *Oikopleura* (A) y *Fritillaria* (B) en el sur del Golfo de México, durante septiembre de 2003

Table 1. Appendicularians collected in the southern Gulf of Mexico during September 2003. MA = Mean abundance (ind 100 m⁻³) and its SD = standard deviation, %MA = percentage of species, and FO = Frequency of Occurrence (total stations 97) / Apendicularias colectadas en el sur del Golfo de México en septiembre 2003. MA = Media de la abundancia (ind 100 m⁻³) y su DE = desviación estándar, %MA = porcentaje de las especies, y FO = Frecuencia de ocurrencia (total de estaciones 97)

Species	MA	SD	% MA	% FO
<i>Oikopleura longicauda</i>	8488.12	18293.2	70.759	95.88
<i>Oikopleura fusiformis</i>	1528.21	4050.3	12.740	70.10
<i>Oikopleura gracilis</i>	22.12	85.5	0.184	15.46
<i>Oikopleura intermedia</i>	14.22	110.9	0.119	4.12
<i>Oikopleura dioca</i>	57.65	299.8	0.481	13.40
<i>Oikopleura rufescens</i>	135.06	636.7	1.126	28.87
<i>Oikopleura parva</i>	6.50	21.0	0.054	11.34
<i>Oikopleura cophocerca</i>	9.52	25.8	0.079	18.56
<i>Fritillaria haplostoma</i>	1243.38	4992.7	10.365	51.55
<i>Fritillaria formica</i>	91.48	440.8	0.763	28.87
<i>Fritillaria pellucida</i>	9.83	43.5	0.082	11.34
<i>Fritillaria borealis</i>	291.49	937.1	2.430	34.02
<i>Fritillaria magachile</i>	0.19	1.3	0.002	2.06
<i>Fritillaria fraudax</i>	64.83	539.3	0.540	15.46
<i>Fritillaria venusta</i>	4.11	40.5	0.034	1.03
<i>Tectillaria fertilis</i>	1.42	6.9	0.012	5.15
<i>Appendicularia sicula</i>	26.34	248.6	0.220	4.12
<i>Pelagopleura oppressa</i>	0.60	3.6	0.005	3.09
<i>Stegosoma magnum</i>	0.49	3.4	0.004	2.06
<i>Folia gracilis</i>	0.24	2.4	0.002	1.03

Regression Tree Analyses showed the turbidity as the major factor affecting the spatial distribution of *Oikopleura* and *Fritillaria*. Turbidity values lower than 0.49 NTU determine the highest densities of *Oikopleura* (Fig. 4A), whereas values higher than 0.356 NTU did the same for the *Fritillaria* species (Fig. 4B). At lower hierarchical levels of the trees, the temperature appears to have a secondary influence on the distribution of both genera, as well as the salinity and the bottom depth on *Oikopleura* and *Fritillaria*, respectively. In fact, RTA indicated that the highest densities of *Oikopleura* are found in low turbid and low temperature waters, whereas for *Fritillaria* the highest densities are found in highly turbid, shallow and high temperature waters (Fig. 4A, B).

DISCUSSION

SPATIAL SEGREGATION

The spatial segregation index *D* estimated from *Fritillaria* (mainly represented by *F. haplostoma* and *F. borealis*) and *Oikopleura* (mainly *O. longicauda* and *O. fusiformis*)

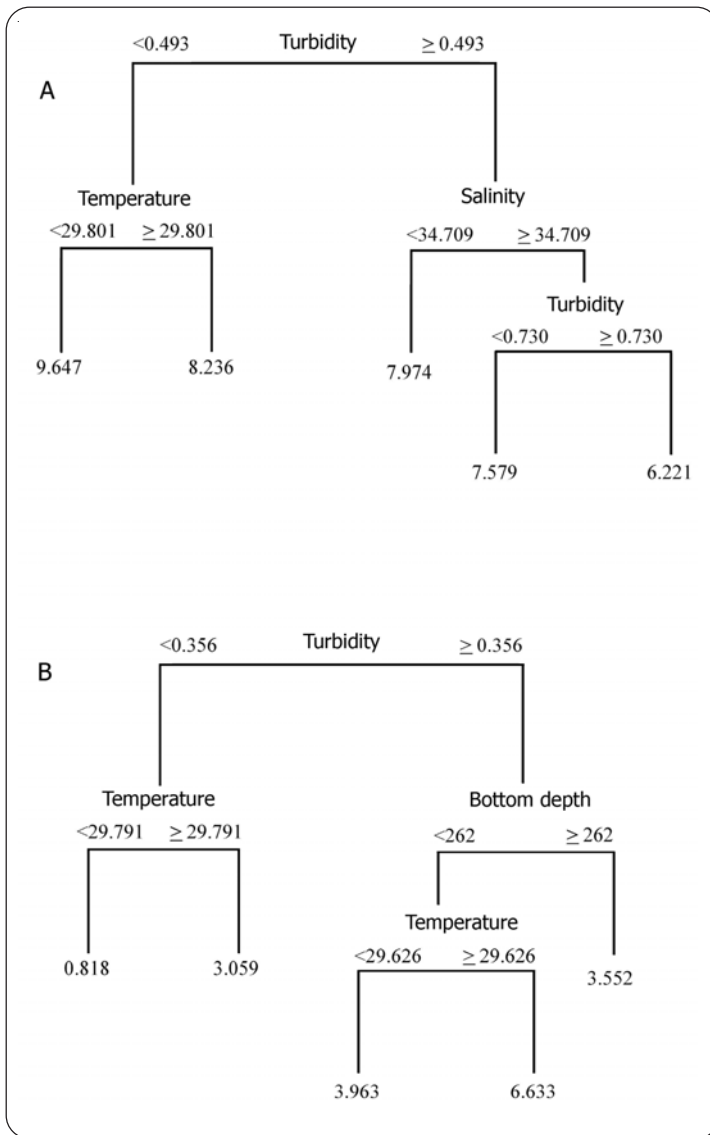


Figure 4. Regression Tree Analysis applied to the log-transformed A) *Oikopleura*, and B) *Fritillaria* density as response variable, and temperature, salinity, turbidity and bottom depth as explanatory variables. Values at the end of branches represent the appendicularian mean density (ind 100 m⁻³) / Análisis de regresión de árbol aplicado al logaritmo de la densidad de A) *Oikopleura*, and B) *Fritillaria* como variable de respuesta y temperatura, salinidad, turbidez y profundidad, como variables explicativas. Los valores al final de la rama representan la densidad media de apendicularias (ind 100 m⁻³)

densities was relatively high (0.67) and the Monte Carlo simulations proved its statistical significance. This result indicated that there is a clear mesoscale spatial segregation of both genera in the Southern Gulf of Mexico. The studies regarding to spatial segregation of appendicularians are scarce. Björnberg & Forneris (1956a, b) described uneven distribution of appendicularians in Brazilian waters. Acuña (1994) and Fenaux *et al.* (1998) showed a vertical gradient of appendicularian species abundance in the epipelagic layer.

There are more documented examples about temporal segregation in nature rather than spatial. Fenaux (1963) in the French Mediterranean, recorded that *Oikopleura* species were dominant in summer and *Fritillaria* species were dominant in winter. López-Urrutia *et al.* (2005) also mentioned a seasonal segregation of appendicularians in some European seas, with oikopleurids dominating in summer and fritillarids in winter. Choe & Deibel (2008) showed that the seasonal peak of abundance of tree species did not overlap on time.

DIFFERENT HYDRODYNAMIC AREAS

The temperature, salinity and turbidity analysis showed that there are at least two areas with different hydrodynamic properties in the study zone; the eastern area, corresponding to the continental shelf of Yucatán and Campeche, and the western area, corresponding to the Tabasco shelf and adjacent oceanic area.

Yucatán-Campeche area, where oikopleurids were dominant and fritillarids almost absent, is characterized by no rivers discharges, low turbidity, relatively homogenous temperature and salinity. The hydrodynamic is determined by a branch of Yucatán Current, with high nutrient waters from the upwelling and associate flora (Hulburt & Corwing 1972, Merino 1997, Zavala-Hidalgo *et al.* 2003). The western area where a high fritillarids density was recorded is characterized by low salinity and high turbidity waters, the hydrodynamic is determined by the continental water discharges and a cyclonic gyre in the oceanic adjacent area (Salas *et al.* 1992, Signoret *et al.* 2006), and associate flora (Licea & Santoyo 1991, Licea *et al.* 2004). The characteristics of these two areas have been described in the study of the Campeche Bank by Besonov *et al.* (1971). Differences in oikopleurids and fritillarids abundances between these two areas must be related to the differences en hidrodinamics and associated food weeb.

The boundary between these two zones is variable through the seasons, nevertheless, the sediment on the shelf, which reflects long term phenomena, let us locate this on the continental shelf between the inlet of Grijalva-Usumacinta system and western inlet of Terminos Lagoon; with a carbonate sediments on the east and terrigenous sediments on the west of such boundary (Ayala-Castañares & Gutiérrez Estrada 1990).

TURBIDITY

RT analyses revealed the turbidity as the main environmental factor affecting the spatial distribution of *Oikopleura* and *Fritillaria* genera (Fig. 3A, B). We consider that turbidity is mainly generated by the input of organic and inorganic matter coming from the continental water discharges. Capitanio & Esnal (1997) considered that distribution limits of the recorded species in the Rio de la Plata estuary might be influenced by turbidity front. Turbid water are also rich in nutrients and usually associated with phytoplankton blooms (Dagg 1995) which mean food availability for appendicularians.

TEMPERATURE AND SALINITY

Temperature and salinity had a small role on the distribution of both *Oikopleura* and *Fritillaria* genera (Fig. 3A, B). Studies (Acuña & Anadón 1992, Acuña 1994) suggested that appendicularians are highly sensitive to water temperature and that species abundance exhibit an optimal unimodal response to temperature variations. However, different populations of the same species are adapted to different ranges depending on the localities (Fenaux *et al.* 1998). López-Urrutia *et al.* (2005) considered that temperature and in some degree salinity explain a considerable extent of seasonal and geographical distribution pattern, but also found a positive correlation between appendicularians abundance and chlorophyll concentration.

Choe & Deibel (2008) base on vertical distribution found that some species are eurythermal and euryhaline (*Fritillaria borealis*) other mesothermal and mesohaline (*Oikopleura labradorensis*), and other stenothermal and stenohaline (*Oikopleura vanhoeffeni*), and also referred a positive correlation between temporal variation of last species and chlorophyll concentration suggesting that physical parameters alone do not adequately explain the temporal distribution of appendicularians species.

Oikopleura longicauda is a eurythermic, warm water species even reaching the 60° parallel (Aravena & Palma 2002). In contrast, *Fritillaria haplostoma* is a more thermophilic form, mainly found in a temperature range of 21.1 to 28.2°C in a bay of Japan (Uye & Ichino 1995). In accordance, highest densities of this species were here found at temperatures higher than 29°C (Fig. 3B). Temperature effects are more conspicuous in cold and temperate regions than in tropical ones (Fenaux *et al.* 1998). Results of this study showed that both temperature and salinity have minor effect on the distribution of both genera, as shown in the tree analysis.

SIZES FOOD

We assume that trophic chains are different in those two previously mentioned areas. In the upwelling waters on the Yucatan shelf, the primary production starts with large chains of diatoms, while in waters like those of Tabasco shelf generally start with nano and microphytoplankton (Ryther 1969, Urban *et al.* 1992). Besonov *et al.* (1971) indicated that in the eastern zone production of organic mater results only from primary producers and in the western zone organic matter is also added by the continental water discharges.

Differences in the sizes food availability among these two areas must have an important role in the segregation of appendicularians. Oikopleurids species can retain besides of very small (0.2 to 6 µm) (Fernández *et al.* 2004), large particles which fritillarids can not. *Oikopleura longicauda* in particular can feed in a wide size spectrum of particles because it house lacks of incurrent filters which pre-filter the incoming water and remove large particles from the current, allowing feed in a wide spectrum of particles (Alldredge 1976) and exploits a variety of habitats, as observed in this study. In general *Oikopleura* species had a broad diet (Deibel 1998).

The size food for the appendicularias related with their distribution come to be more relevant every day. Choe & Deibel (2008) related the seasonal abundance peaks of *Fritillaria borealis* in summer, *Oikopleura labradorensis* in fall and *O. vanhoeffeni* in spring with picoplankton, nanoplankton and large diatoms respectively as predominant preys species.

There are no comparative works on the types of primary producers between eastern (Yucatán) and westerns (Tabasco) areas. Nevertheless, Licea *et al.* (2004) found a pronounced difference between both areas, in the composition of the dominant species of dinoflagellates. Licea & Santoyo (1991) indicated that primary production in the Tabasco shelf is mainly generated by nanoplankton and microplankton. On the other hand phytoplankton floras indicative of upwelling zones have been described on the Campeche Bank (Hulburt & Corwing 1972). Consequently, over the Yucatán shelf with microplankton, characteristic of upwelling waters (Hulburt & Corwing 1972, Cushing 1975), it must be an important food source for oikopleurids, but not for fritillarids. Knowledge on the diet of most of fritillarids is limited, but Brena *et al.* (2003) emphasized that cytological characters of the gut of fritillarids are different from those of the oikopleurids, indicating the possibility of different nutritional requirements. In the Artic polynyas during the spring upwelling Deibel *et al.* (2005) found a high production of oikopleurids. On the contrary, on the Tabasco shelf, primary production is mainly generated by nanoplankton and microplankton (Licea & Santoyo 1991), and we assumed also picoplankton as result of microbial loop. Because the small size it must be an important food source for fritillarids and also for oikopleurids. Considering two different food webs we hypothesize that the size of available food plays a determining role in the segregation distribution of appendicularians.

In summary the mesoscale examination of *Oikopleura* and *Fritillaria* distribution indicate spatial segregation rather than a niche overlap. Aside of physical environmental features like, salinity, temperature, currents, gyres, continental waters discharges, turbidity, the causes of this spatial segregation obey to eco-physiological differences of oikopleurids and fritillarids: *Oikopleura* species had a broad diet, higher filtration efficiency for large particles than *Fritillaria* species. These ecological characteristics also explain the ecological success of *Oikopleura* in the Campeche Bank and other tropical areas.

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