



Appendicularian distribution and diversity in the southern Gulf of Mexico

Distribución y diversidad de apendicularias en el sur del golfo de México

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Abstract. The diversity and distribution of appendicularians on the continental shelf and upper part of the oceanic sea in the southern Gulf of Mexico is analyzed here for the first time. Samples were collected in September 2003 using a fine mesh net. Twenty species were identified, of which *Fritillaria venusta* and *Pelagopleura oppressa* are first records for the Gulf of Mexico. *Oikopleura* species occur throughout the area, with greatest abundances in the upwelling waters of the inner shelf off Yucatán and Campeche. The greatest abundances of *Fritillaria* species and of the other genera were recorded in the mid, outer shelf, and oceanic areas of Campeche and Tabasco that are influenced by continental water discharges and an oceanic gyre. Diversity and abundance varied in differing directions, with high abundance and low diversity characterizing the costal areas and low abundance and high diversity in the mid, outer shelf, and oceanic areas. The distribution of appendicularian species appears to be influenced by upwelling currents, gyres, water column depth, continental water discharges, salinity, and temperature. However, it could be assumed that the reasons behind these physical environmental factors include the food supply, a short life cycle, and high reproductive efficiency, factors that are commonly associated with distribution.

Key words: pelagic tunicates, upwelling, continental shelf, ecology.

Resumen. Se analiza por primera vez la diversidad y distribución de las apendicularias en la capa superficial de la columna de agua de la plataforma continental del sur del Golfo de México. Las muestra se recolectaron en septiembre de 2003 usando una malla fina- Se identificaron 22 especies de las cuales *Fritillaria venusta* y *Pelagopleura opresa* tienen aquí su primer registro para el Golfo de México. Las especies de *Oikopleura* ocurrieron en toda el área con sus mayores abundancias en aguas de surgencia que corren sobre la plataforma de Yucatán y Campeche. La mayor abundancia de las especies de *Fritillaria* y de los otros géneros se registro en la plataforma media, externa y área oceánica de Campeche y Tabasco que están influenciadas por las descargas de aguas continentales y un giro oceánico. La diversidad y abundancia varían en sentido contrario una de otra; alta abundancia y baja diversidad caracterizan a las áreas costeras, en tanto baja abundancia y alta diversidad ocurren en la plataforma media, externa y área oceánica. La distribución de las especies parece estar influenciada por las corrientes de la surgencia, giros, profundidad del área, descargas de aguas continentales, salinidad y temperatura. Sin embargo, puede asumirse que detrás de estos factores físicos están la disponibilidad de alimento, el corto ciclo de vida y la alta eficiencia reproductiva, como los factores mas comúnmente asociados a su distribución

Palabras clave: tunicados pelágicos, surgencia, plataforma continental, ecología

Introduction

Appendicularians constitute one of the small zooplankton groups that have received little attention, in spite of their relative abundance and ecological importance. Factors that make this group important include the part that it plays in the rapid transfer of energy toward higher trophic levels through filtering of nanoplankton and picoplankton particles and of dissolved organic matter (Flood et al.,

1992; Deibel, 1998; Gorsky and Fenaux, 1998), and the high reproductive rates of the species (Hopcroft and Roof, 1995; Hopcroft et al., 1998).

Most of the studies that have been carried out during the past 15 years on this group have focused on population and physiological aspects (Flood et al., 1992; Hopcroft and Roff, 1995, 1998; Nakamura et al., 1997; Cima et al., 2002; Brena et al., 2003), and few have dealt with its distribution.

Basic studies on the composition, distribution, and seasonality of appendicularians in the Gulf of Mexico are scarce. In fact, only 5 papers are related to these topics, and

include those of Brooks and Kelner (1908) for the Tortugas, Florida, a study which also includes the description of a new species; Tokioka and Suarez-Caabro (1956) for Cuba, which reported 13 species; Flores-Coto (1965, 1974) for the reef system off Veracruz, which reported 20 species; and Lohmann (1916; *vide* Tokioka and Suarez-Caabro, 1956) who mentioned 8 species.

Thus, many aspects of the diversity, distribution, seasonal abundance and environmental factors that influence these matters are yet to be investigated.

This study analyzes the diversity and species distribution of appendicularians in the southern Gulf of Mexico, mainly on the continental shelf, in relation to the environmental parameters.

Materials and methods

The study area is located at 18–22°N and 88–95°W, and includes the continental shelf off the coasts of Tabasco, Campeche and Yucatán (Fig. 1).

The shelf north of the Yucatán Peninsula is very wide (about 150 km). The hydrodynamics on the shelf are regulated by a branch of the Yucatán Current with upwelling off Cabo Catoche (Besonov et al., 1971; Furnas and Smayda, 1987; Merino, 1997; Zavala-Hidalgo et al., 2003). The Tabasco shelf is only 50 km wide and is

influenced by a variety of continental water outflows (Shirasago-German, 1991, Rivera-Arriaga and Borges-Souza, 2006). Water circulation in Campeche Bay is predominantly cyclonic (Monreal-Gómez and Salas de Leon, 1990).

Samples were collected at 107 stations during the SGM8 cruise from September 3rd to October 8th. A Neil Brown Mark III CTD was used to record conductivity, temperature and pressure throughout the water column. Biological samples were obtained by vertical sampling along the first 50 m of the water column, using a 30 cm diameter and 200 µm mesh size conical net with a flow meter to calculate the volume of filtered water. The samples were fixed with 4% formalin and were processed in the laboratory to separate the appendicularians.

Correlations between species abundance and the environmental parameters were determined by means of a multiple regression and a canonical correspondence analysis, in order to evaluate the influence of environmental factors on the distribution of the species. The Shannon-Wiener diversity index was also obtained.

Results

The highest temperatures were recorded on the inner and mid shelf of Campeche, and the lowest in 2 areas,

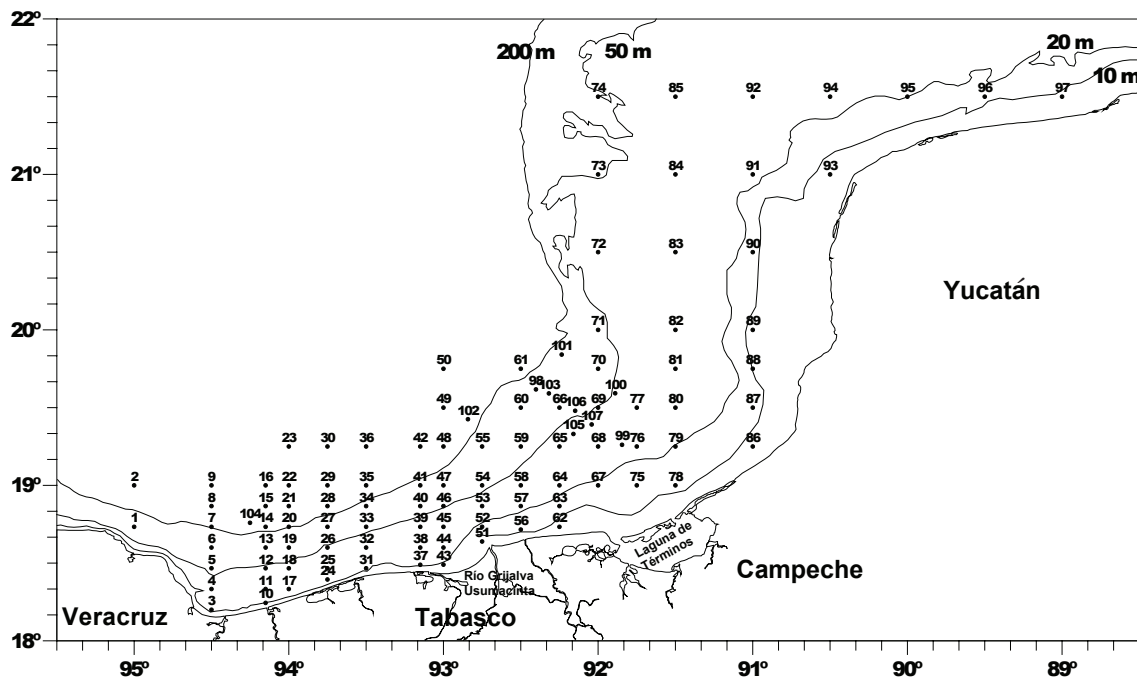


Figure 1. Study area and location of sampling stations.

one off the eastern Yucatán shelf that is influenced by upwelling and the other in the coastal area of Tabasco that receives freshwater discharges (Fig. 2a).

The highest salinities were recorded on the wide shelf off Yucatán and the lowest on the Tabasco shelf off the main freshwater discharge areas (Fig. 2b).

Twenty species were collected, of which *Oikopleura longicauda* (70.3%), *O. fusiformis* (13.6%), *Fritillaria haplostoma* (10.1%), *F. borealis* (2.3%), and *O. rufescens* (1.0%) represented >97% of the total abundance. The other 15 species were very scarce, each representing <1%. Eight of these were present in 5 or less sampling stations (Table 1).

The 2 most abundant species, *Oikopleura longicauda* (Fig. 3A) and *O. fusiformis* (Fig. 3B), were widely distributed throughout the study area and occurred in 95.3% and 71.9% of the stations respectively.

Other species including *O. rufescens* (Fig. 3C), *O. dioica* (Fig. 3D), *O. cophocerca* (Fig. 4A) and *O. parva* (Fig. 4B) were much less abundant but had relatively wide distributions. *Oikopleura gracilis* (Fig. 4C) was collected only on the Tabasco-Campeche shelf, in contrast with *O.*

intermedia (Fig. 4D) that was restricted to the Yucatán shelf.

The remaining species were less widely distributed. *Fritillaria venusta* was collected at only 1 station but was more abundant than *Tectillaria fertilis*, *F. megachile*, *Pelagopleura oppressa*, *Stegosoma magnum*, and *Folia gracilis* (Table 1).

Fritillaria species were practically absent on the Yucatán shelf, and their greatest densities were recorded on the Tabasco shelf. The species *F. haplostoma* (Fig. 5A), *F. borealis* (Fig. 5B), and *F. formica* (Fig. 5C) were collected at 1 or 2 stations on the Yucatán shelf with very low abundances. *Fritillaria haplostoma*, the most abundant species of the genus, was relatively abundant on the Campeche shelf, while *F. fraudax* (Fig. 5D) and the other species of this genus (Fig. 6) were present in low numbers in this area, and were found mainly on the narrow Tabasco shelf. *Fritillaria venusta* was found at only 1 station on the Tabasco shelf (Figs. 6). The species of the other genera had low abundances and frequencies of occurrence, and were collected at the oceanic and outer shelf stations off Tabasco (Fig. 6).

The diversity index (Shannon-Wiener) fluctuated from zero at some stations to 3.4 bits/individual at those where 10 species were recorded. The lowest values were at the coastal stations at depths of 30 m, mainly in the Yucatán and Campeche areas, with other notably low values occurring at depths between 30 and 75 m (Fig. 7). One to 3 species were recorded at these stations. One species only, *O. longicauda*, was found in 9 stations. The low diversity is a reflection of the high density and wide distribution of the *Oikopleura* genus.

The greatest diversity values (>2.75 bits/individual) were recorded for the stations located off Tabasco, particularly the outer shelf and oceanic stations where very low densities were recorded, as well as for a few stations in the adjacent areas of the Campeche shelf. These values are related to the presence of species of genera different from *Oikopleura* and *Fritillaria*.

The results of the multiple regression analysis between species abundance and the parameters indicate a significant negative correlation ($p < 0.05$) between depth and *O. longicauda*, *O. parva* and *F. haplostoma*, between salinity and *F. borealis*, *F. formica* and *O. dioica*, and between temperature and *F. fraudax*. The very uncommon species were not included in the analysis.

Similarly, the canonical correspondence analysis indicated that *F. formica*, *F. borealis*, *A. sicula* and *O. dioica* occurred in areas of lower salinity, whereas *F. megachile* was present in areas of higher salinity. *Oikopleura longicauda* tended to be found in shallow low temperature areas, while *S. magnum*, *F. pellucida*, *O. gracilis* and *Folia*

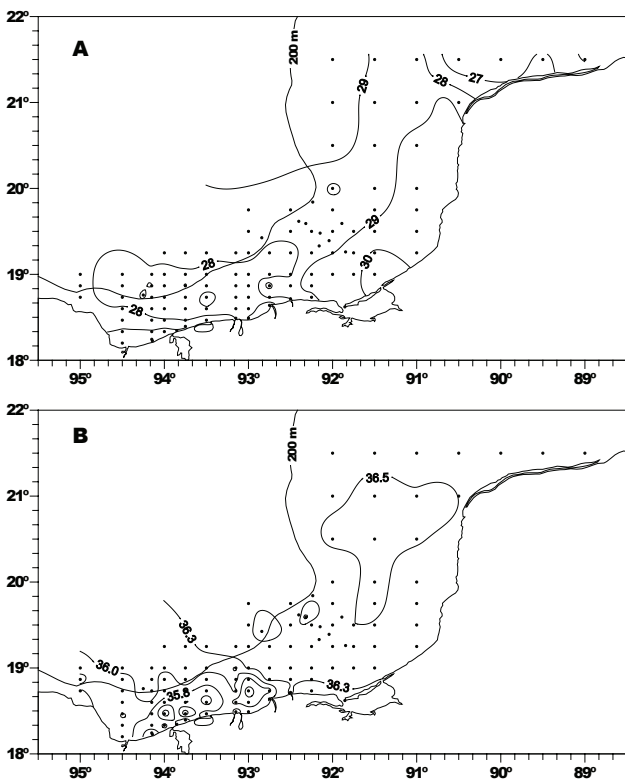


Figure 2. Isolines of average temperature (a) and salinity (b) of the top 50 m of the water column.

Table 1. Average abundance (org/100 m³), frequency and percentages of appendicularians species. September 2003, southern Gulf of Mexico

Species	average	percent	frequency	percent
<i>Oikopleura longicauda</i>	7988.95	70.307	102	95.33
<i>Oikopleura fusiformis</i>	1547.07	13.615	77	71.96
<i>Fritillaria haplostoma</i>	1147.99	10.103	53	49.53
<i>Fritillaria borealis</i>	264.99	2.332	36	33.64
<i>Oikopleura rufescens</i>	123.98	1.091	31	28.97
<i>Fritillaria formica</i>	85.64	0.754	32	29.91
<i>Fritillaria fraudax</i>	59.15	0.521	16	14.95
<i>Oikopleura dioca</i>	52.67	0.464	14	13.08
<i>Appendicularia sicula</i>	24.28	0.214	5	4.67
<i>Oikopleura gracilis</i>	22.07	0.194	16	14.95
<i>Oikopleura intermedia</i>	12.89	0.113	4	3.74
<i>Oikopleura cophocerca</i>	9.95	0.088	21	19.63
<i>Fritillaria pellucida</i>	9.49	0.084	13	12.15
<i>Oikopleura parva</i>	6.60	0.058	13	12.15
<i>Fritillaria venusta</i>	3.73	0.033	1	0.93
<i>Tectillaria fertilis</i>	1.89	0.017	6	5.61
<i>Fritillaria magachile</i>	0.78	0.007	3	2.80
<i>Pelagopleura oppressa</i>	0.54	0.005	3	2.80
<i>Stegosoma magnum</i>	0.04	0.004	2	1.87
<i>Folia gracilis</i>	0.03	0.003	2	1.87

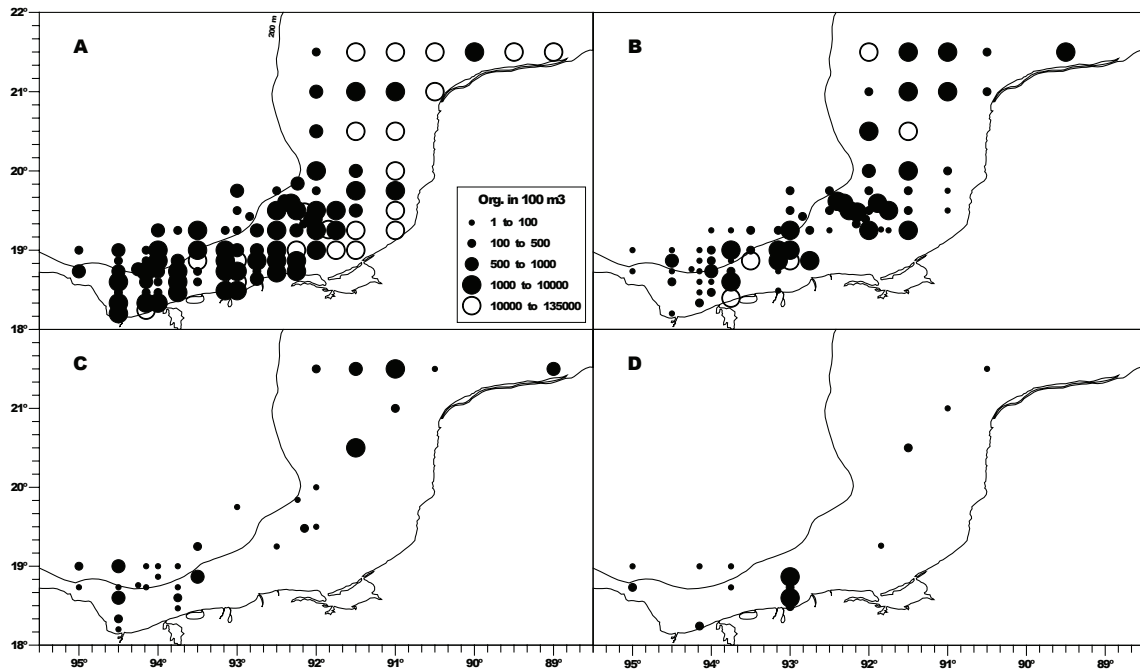


Figure 3. Abundance of *O. longicauda* (A), *O. fusiformis* (B), *O. rufescens* (C) and *O. dioca* (D).

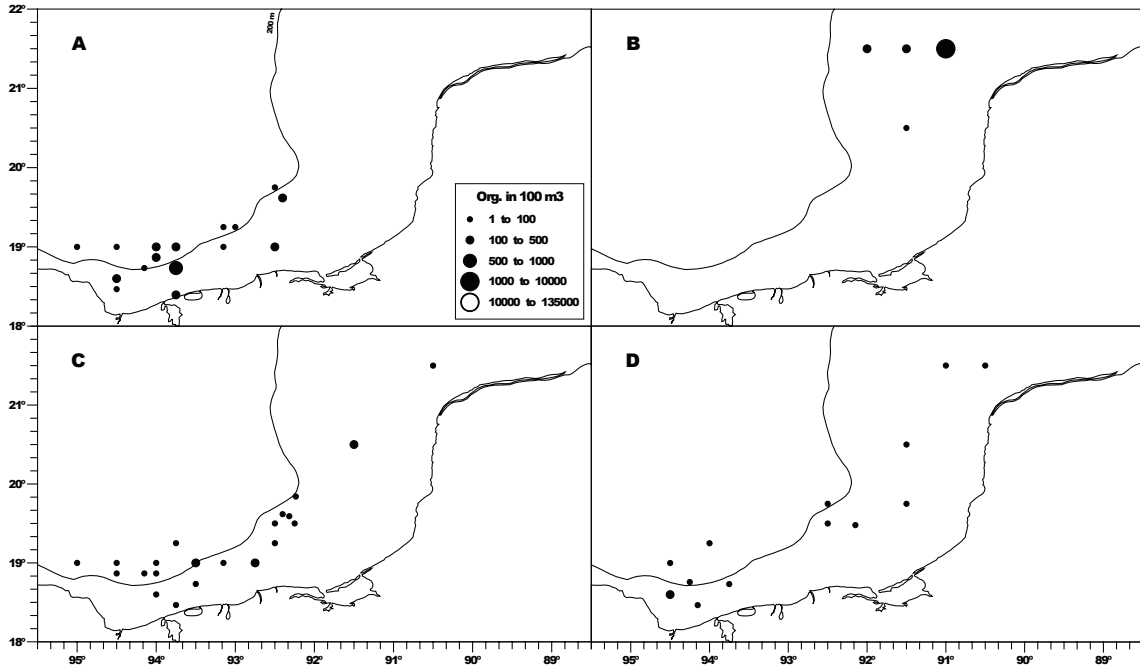


Figure 4. Abundance of *O. cophocerca* (A), *O. parva* (B), *O. gracilis* (C) and *O. intermedia* (D).

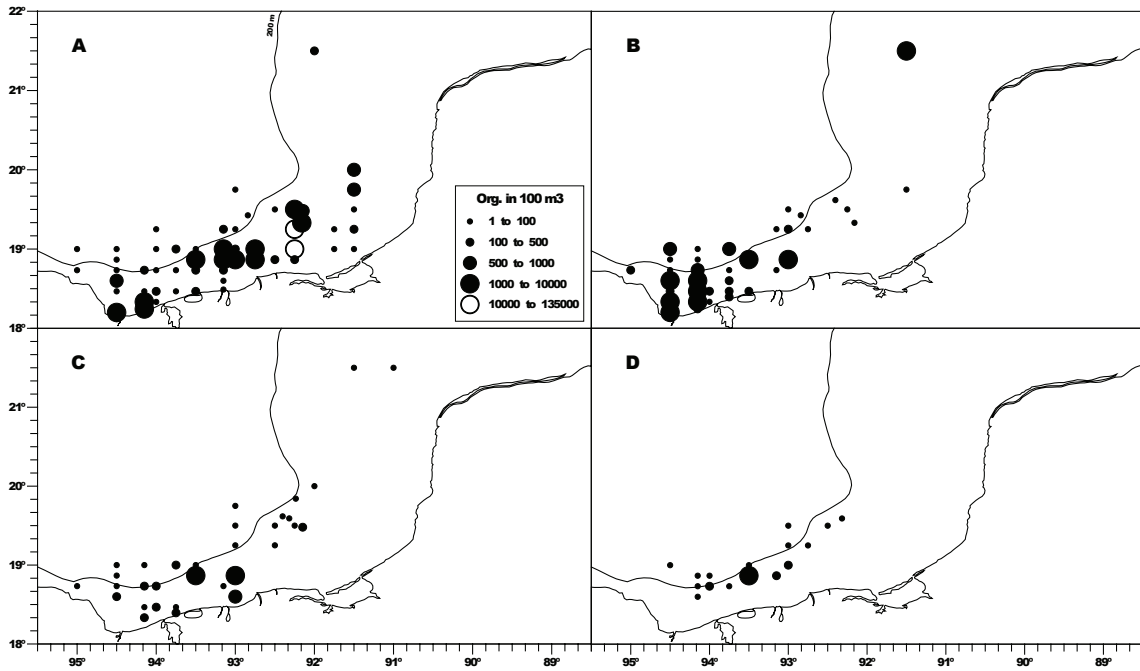


Figure 5. Abundance of *F. haplostoma* (A), *F. borealis* (B), *F. formica* (C) and *F. fruadax* (D).

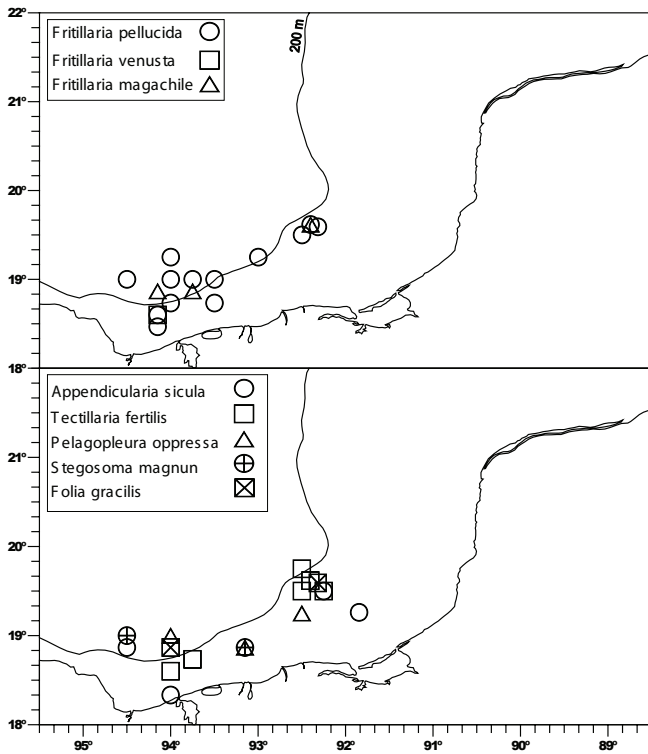


Figure 6. Distribution of some species of *Fritillaria* (A) and other genera (B).

gracilis occurred in the outer shelf and oceanic stations at higher temperatures (Fig. 8).

Discussion

Of the 20 identified species, *Fritillaria venusta* and *Pelagopleura oppressa* are first records for the Gulf of Mexico. Apart from these 20 species, Flores-Coto (1971) had previously recorded the species *O. albicans*, *Althofia tumida*, *F. aequatorialis*, *K. oceánica* and *T. veracruzana* for the Veracruz reefs, which provide a total of 25 species recorded for the Gulf of Mexico.

The recording of *O. longicauda* as a dominant species is added to the list of studies that have found it to be the dominant species in tropical and subtropical waters around the world (Tokioka and Suarez-Cabro, 1956; Flores-Coto, 1974; Esnal, 1979, 1999; Hopcroft and Roof, 1998; Aravena and Palma, 2002).

The oceanic versus neritic nature for most species has not been definitively established, but *P. oppressa*, *S. magnun*, *T. fertilis*, *A. sicula* and *F. gracilis* have most frequently been found in oceanic as opposed to neritic waters, whereas *O. dioca* has been found more frequently in coastal areas (Tokioka and Suarez-Cabro, 1956; Fenaux, 1963; Zoppi de Roa, 1971; Esnal, 1972; Castellanos et al.,

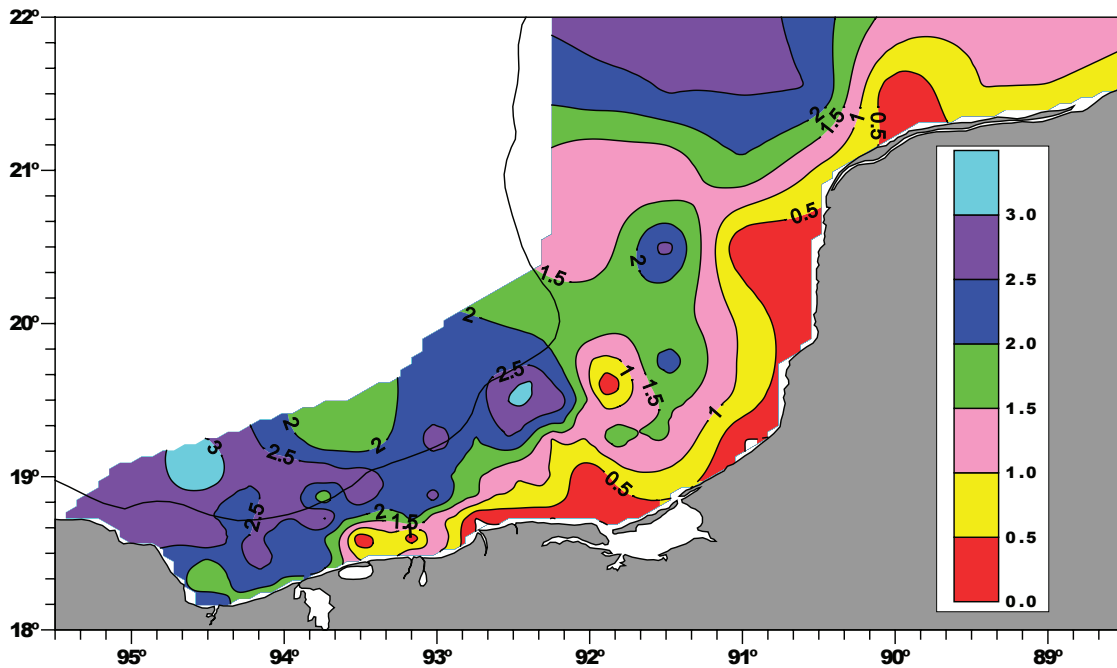


Figure 7. Schematic presentation of the diversity of appendicularians in the southern Gulf of Mexico based on the Shannon-Wiener Index.

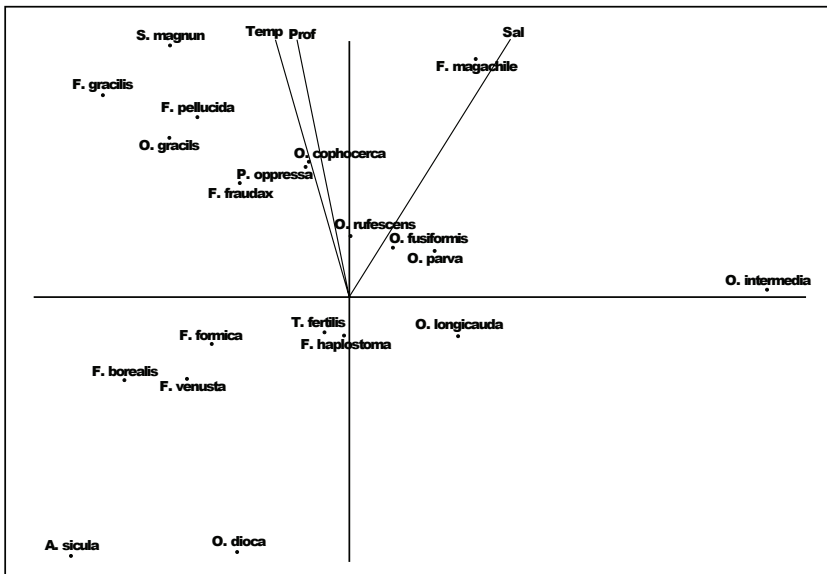


Figure 8. Ordination diagram, represented by vectors, of appendicularians and environmental factors in the southern Gulf of Mexico. X= axis 1, Y= axis 2.

1994; Esnal and Castro, 1977; Capitano and Esnal, 1997), in agreement with our findings.

It should be noted that, with respect to the distribution of this group, diversity and abundance presented opposite trends and divided the study area into 2 regions. Whereas the greatest diversity and lowest abundance occurred in the outer shelf and oceanic stations off Tabasco, the lowest diversity and greatest abundance was observed at the shallow stations off Campeche and Yucatán. The latter region, where *Oikopleura* species were abundant and *Fritillaria* species and other genera were practically absent, lies under the influence of a branch of the Yucatán current that is formed by clear upwelling waters (Besonov et al., 1971; Merino, 1997) that reach the shallow areas of Campeche and occasionally those of Tabasco (Inoue and Welsh, 1997; Zavala Hidalgo et al., 2003). In contrast, the mid and outer shelf of Tabasco, where most of the *Fritillaria* species and other genera occurred, is subject to continental water discharges, as well as a cyclonic gyre (Besonov et al., 1971; Salas de León et al., 1998).

The results indicate a significant negative relationship between *O. longicauda*, *O. parva* and *F. haplostoma* and depth, between *F. fraudax* and temperature, and between *O. dioca*, *F. borealis* and *F. formica* and salinity. Nevertheless, these relationships did not explain the dissimilar genera and species distribution between the deep and shallow areas, as mentioned above.

All the observed species have been characterised as tropical and subtropical inhabitants of neritic and oceanic waters, throughout wide ranges of salinity and

temperature.

Different populations of the same species may be adapted to different ranges depending on the locality (Fenaux et al., 1998; López-Urrutia et al., 2005). Tomita et al. (2003) suggested that the spatial patterns of appendicularians in Toyama Bay were more likely the result of biological factors than of physical factors.

It is probable that the salinity and temperature in the study area could have a more evident effect on distribution as a consequence of large seasonal variations in continental water discharges, mixing processes, currents, gyres and other climatologically related activities, as previous studies have suggested for meso-scale distribution patterns of ichthyoplankton (Salas de León et al., 1998; Sanvicente et al., 2000).

Although currents, oceanic gyres, continental water discharges, depth, salinity and temperature appear to be the main factors that determined the distributions and abundances recorded in this study, similarly uneven distributions have been observed elsewhere (Bojorber and Forneris 1956a, 1956b; Fenaux, 1963; Nakamura et al., 1977; Aldridge, 1982; Capitano and Esnal, 1998; Brena et al., 2003). These being independent of the local Gulf of Mexico physical factors, other factors must be considered. We assume that the food supply, a short life cycle, and high reproductive efficiency (massive production) are factors commonly associated with distribution (Hopcroft and Roof, 1995, 1998; Capitano and Esnal, 1998; Cima et al., 2002). Food supply could probably be the main factor, as appendicularians do not store energy in lipid deposits (Gorky and Fenaux, 1998). Consequently, the presence and abundance of this group of animals should indicate environments rich in detritus of ingestible size and quality.

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