Seasonal vertical distribution of fish larvae in the southern Gulf of Mexico

Distribución vertical estacional de larvas de peces en el sur del Golfo de México

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ABSTRACT

Changes in the composition and abundance of fish larvae in the water column were analyzed throughout an annual cycle (1994-1995) in the southern Gulf of Mexico, in order to establish the difference between the habitat of the larvae and the effect of oceanographic events on larval vertical distribution. The study area comprised the continental shelf off Tabasco and Campeche in the southern Gulf of Mexico. Samples were collected at five water column levels: 0-6, 6-12, 12-18, 45-55 and 95-105 m. A total of 118 taxa were identified, 52 were dominant species, 33 were larvae of neritic parents and 19 were larvae of mesopelagic parents. The results indicate that the water column presented two layers above the 105 m depth: a surface layer (0-18 m) and a deep layer (45-105 m). The greatest density of larval species that inhabit neritic areas as adults was recorded in the surface layer (0-18 m), while larvae of which the parents inhabit mesopelagic areas were found in the deep layer (45-105 m). The mixing of the water column was the most important physical factor regarding the variation in the vertical distribution of the larvae of both groups, particularly in winter. However, the biology of each species and the habit to occupy a particular depth was the most important factor that determined their distribution in the water column.

Key words: Larval fish, mixing processes, neritic habitat and mesopelagic habitat, vertical distribution.

RESUMEN

Se analizaron los cambios en la composición y abundancia de larvas de peces en la columna de agua a lo largo de un ciclo anual (1994-1995) en el sur del Golfo de México, a fin de establecer diferencias entre el hábitat de las larvas y el efecto de eventos oceanográficos en su distribución vertical. El área de estudio comprendió la plataforma continental de los estados de Tabasco y Campeche en el sur del Golfo de México. Se obtuvieron muestras de cinco niveles de la columna de agua: 0-6, 6-12, 12-18, 45-55 y 95-105 m. Se identificaron un total de 118 taxones, de los cuales 52 fueron especies dominantes, 33 correspondieron a larvas de progenitores neríticos y 19 a larvas de progenitores mesopelágicos. Los resultados indican que por arriba de los 105 m, la columna de agua presenta dos capas: superficial (0-18 m) y profunda (45-105 m). La mayor densidad de las larvas de especies que como adultos habitan en áreas neríticas, se registró en la capa superficial (0-18 m), mientras que las larvas cuyos progenitores habitan áreas oceánicas, se encontraron en la capa profunda (45-105 m). La mezcla de la columna de agua fue el factor físico más importante en la variación de la distribución vertical de las larvas de ambos grupos, especialmente en invierno. Sin embargo, la propia biología de cada especie y el hábito para ocupar una profundidad particular fue el factor más importante que determinó su distribución en la columna de agua.

Palabras clave: Distribución vertical, hábitat nerítico, hábitat mesopelágico, larvas de peces, procesos de mezcla.

INTRODUCTION

Studies on ichthyoplankton have become important since the beginning of last century in view of its close relationship with fisheries. Studies on the early life history of fish have been useful in developing a better understanding of fish population dynamics and determining the causes of major fluctuations in fish stock production (Blaxter, 1974; Smith, 1981; Trippel & Chambers, 1997; Fuiman, 2002).

Studies on larval fish communities necessarily require an analysis of hydrological processes such as currents, eddies and upwellings (John, 1985; Röpke, 1993; Rodríguez *et al.,* 2006; Sánchez-Velasco *et al.*, 2007; Aceves-Medina *et al.,* 2008), particularly in the case of neritic areas that receive freshwater discharges and present river fronts, mixing processes and stratification (Gray, 1996; Reiss & McConaugha, 1999).

These studies generally include meso-scale processes. However, in order to obtain a better understanding of the conformation and variations in the communities, a fine-scale study of dozens of meters along the vertical distribution is required (Espinosa-Fuentes & Flores-Coto, 2004; Okazaki & Nakata, 2007; Sánchez-Velasco *et al.,* 2009; Hsieh *et al.,* 2010).

Previous studies on the vertical distribution of fish larvae in several regions of the world have recorded different groups of species with different distribution patterns. Similarly, larvae of shelf dwelling species generally occur in the surface layer of the ocean, while those of mesopelagic species live in the deeper layers (Loeb, 1979; Röpke, 1993; Cha *et al.,* 1994; Conway *et al.,* 1997; Gray & Kingsford, 2003; Sabatés, 2004).

Species distribution patterns are the result of an evolutionary adjustment of larval habits to the hydrographic processes that guarantee their survival. However, no studies on the yearly seasonal variations of these patterns have been carried out, and it is assumed that they differ according to the geographical area, particularly where strong discharges of freshwater are received.

The southern Gulf of Mexico is a very dynamic area with currents, eddies and wind effects, and continental shelf waters that receive a strong fluvio-lagoon influence. The main freshwater discharge in this area is provided by the Grijalva-Usumacinta river system that generates haline fronts and low salinity and low temperature areas, mostly at surface (~15 m). The greatest salinity variations occur during the rainy months, from June to October (Czitrom *et al.,* 1986; Monreal-Gómez *et al.,* 1992), when the water column is stratified by a thermocline at a depth of 20 to 30 m. Lower temperatures and a deeper mixing layer (70-100 m) have been recorded during the winter, when the presence of cold fronts known as “northers” is common (Alatorre *et al.,* 1989).

The ichthyoplankton of the Gulf of Mexico has been studied during the last four decades, resulting in a general overview of the composition, abundance and distribution of species (Flores-Coto *et al.,* 1988, 2009). However, studies on the vertical distribution of the species are pending. For that reason, the purpose of this study was to define, on a fine-scale, the seasonal variability of the composition and abundance of larval fish species in the water column, and to identify the changes in the distribution caused by the effects of the species behavior and habits and the effects of oceanographic events in the area.

MATERIALS AND METHODS

The study area spans the continental shelf of the southern Gulf of Mexico (18º-20º N, 91º-94º W) (Fig. 1). Twenty two sampling stations distributed along four transects, perpendicular to the coastline, were established off the states of Campeche and Tabasco (Fig. 1). Sampling was carried out in May 21-30 (spring), August 19-29 (summer) and November 17-27 (autumn) of 1994 and in February 7-17 (winter) of 1995.

Samples were collected with a multiple open-closure net plankton system with a 75 cm diameter, a 500 µm mesh size and General Oceanic flowmeters, at five levels in the water column: level 1 (0-6 m), level 2 (6-12 m), level 3 (12-18 m), level 4 (45-55 m) and level 5 (95-105 m). Samples were preserved with 4% formalin neutralized with sodium borate. Larval fish were sorted and identified to the lowest taxonomic level possible according to Richards (2006). The specimens identified to the level of species were included in the seasonal variation analysis. Larvae density (LD) was standardized at 100 m^3:

$$LD = \frac{\text{Num. of larvae}}{\text{filtered volume}}(100)$$

Since the spatial distribution of plankton is not homogeneous, the geometric mean (GM) was calculated from the density of larvae at each sampling level (Zar, 2010).

The Importance Value Index (IVI) was applied in order to define the most important species for each level and season, considering the total percentage of abundance (% A) and the frequency of occurrence (% F). Only the species that reached an IVI value greater than 5% were analyzed. The analysis was carried out using the ANACOM software (De la Cruz-Agüero, 1994).

The continental shelf was divided into inner, middle and outer based on the location and depth of the sampling stations in order to analyze the horizontal distribution of the larvae (Table 1).

An Analysis of Variance (ANOVA) was applied at a significance level of 0.05 for each sampling period in order to identify significant differences on the continental shelf related to the distribution of fish larvae density. A Tukey test was used for *post hoc* comparisons (Zar, 2010).

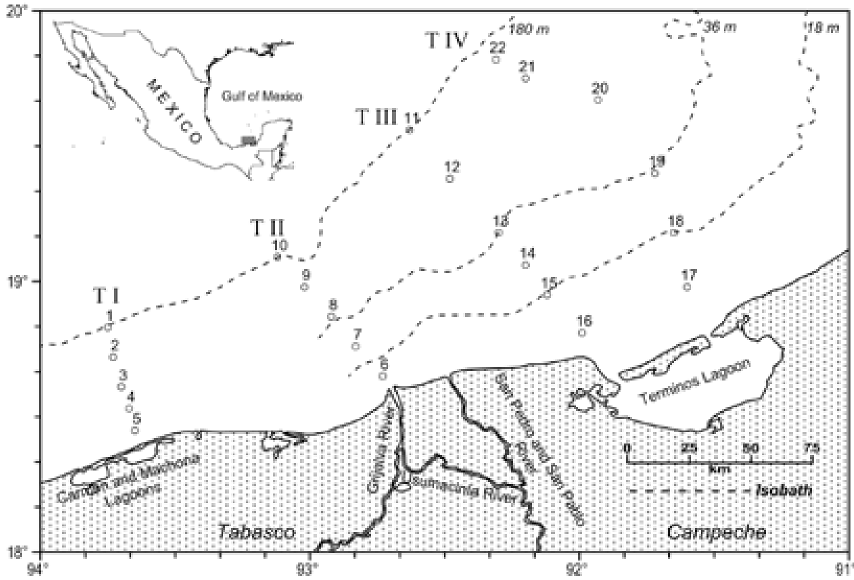

Figure 1. Study area and sampling stations in the southern Gulf of Mexico.

Table 1. Division of the continental shelf based on the location and depth of the sampling stations.

Shelf	Depth (m)	Stations	Levels
Inner	0-30	4, 5, 6, 7, 13, 14, 15, 16, 17, 18	2
Middle	31-100	3, 8, 19, 20	3
Outer	>100	1, 2, 9, 10, 11, 12, 21, 22	5

The analysis of the vertical distribution of the fish larvae throughout the water column was carried out considering only the stations of the outer shelf where samples were obtained at all levels. The dissimilarity in species composition among the five sampling levels was determined for each season by the Bray-Curtis Index (Bray & Curtis, 1957). Clusters were constructed using complete linkage and the data were transformed to ln (x+1).

Salinity and temperature data were obtained with a Neil Mark IV CTD at each sampling period. The degree of stratification of the water column was estimated calculating the potential energy anomaly or ϕ parameter (Simpson *et al.*, 1978).

The influence of the physical parameters, temperature, salinity and potential energy anomaly (stratification or mixing of the water column) on the vertical distribution of fish larvae was established by the Canonical Correspondence Analysis (CCA) using the ANACOM software (De la Cruz-Agüero, 1994).

RESULTS

Water temperature was homogeneous during May, August and November 1994, with a mean of 28 °C from the surface to a depth of 18 m (levels 1, 2 and 3) and 20 °C to 24 °C in the deeper levels (45 and 105 m). In February 1995, the mean temperature was 24 °C from the surface down to 70 m and 18.8 °C at 100 m (Fig. 2).

Salinity at the surface layer (0-18 m) varied from 36.2 to 37.4 in May. It decreased greatly during the rainy season (August to November) with the lowest value of 34.0 near the shore and the highest of 36.4 in offshore waters. In February, salinity and temperature presented a similar vertical distribution with homogeneous values from the surface to 70 m, as well as a coast-ocean gradient with values of 35.2 to 36.8 (Fig. 3).

The mixing layer was present from the surface to a depth of 30 m with ϕ values <40 J m^{-3} during May, August and November. In deeper waters (100 m), the ϕ increased to more than 250 J m^{-3} indicating a marked stratification. In February, the mixing layer reached 70 m with a ϕ <50 J m^{-3} and at 100 m the ϕ was ~150 J m^{-3} (Fig. 4).

A total of 63,655 specimens of 118 taxa of larval fish were identified (Table 2) for the four seasons and five sampling levels in the water column (depths of 0 to 105 m). There were 52 dominant species according to the IVI, 33 were species of neritic parents and 19 were mesopelagic dwellers. Among the dominant species, only nine were observed in all the periods: *Auxis rochei* Risso, 1810, *Benthosema suborbitale* Gilbert, 1913, *Bothus ocellatus* Agassiz, 1831, *Bregmaceros cantori* Milliken & Houde, 1984, *Cynoscion arenarius* Ginsburg, 1930, *Hygophum taaningi* Becker, 1965, *Selar crumenophthalmus* Bloch, 1793, *Syacium gunteri* Ginsburg, 1933 and *Syacium papillosum* Linnaeus, 1758.

The distribution across the continental shelf of larvae of neritic fish presented a coast-ocean gradient in all the sampling periods, with the greatest density values on the inner and middle

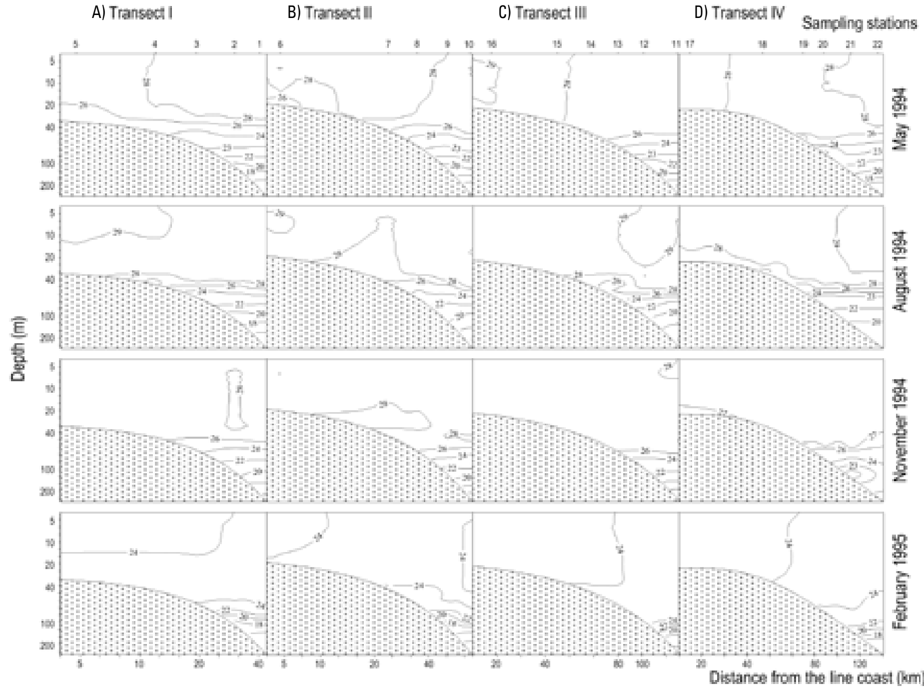

Figure 2A-D. Temperature distribution profiles (°C) at different depths of the four transects. May, August and November 1994 and February 1995 in the southern Gulf of Mexico (modified from Estuarine, Coastal and Shelf Science 59, M. L. Espinosa-Fuentes and C. Flores-Coto, Cross-shelf and vertical structure of ichthyoplankton assemblages in the continental shelf waters of the southern Gulf of México, page 336, Copyright 2004, with permission from Elsevier).

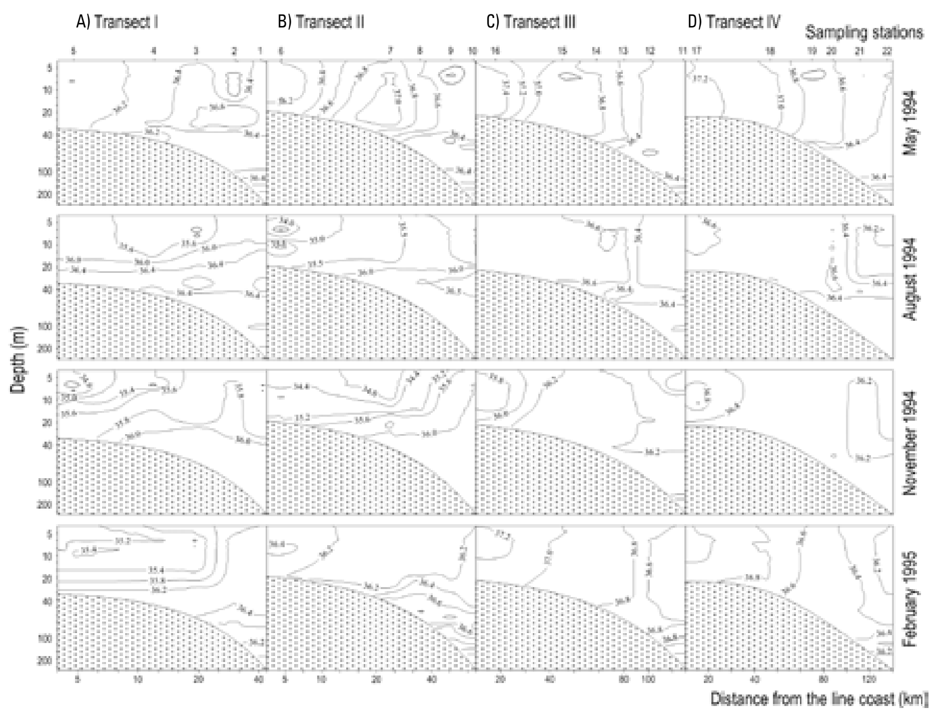

Figure 3A-D. Salinity distribution profiles at different depths of the four transects. May, August and November 1994 and February 1995 in the southern Gulf of Mexico (Reprinted from Estuarine, Coastal and Shelf Science 59, M. L. Espinosa-Fuentes and C. Flores-Coto, Cross-shelf and vertical structure of ichthyoplankton assemblages in the continental shelf waters of the southern Gulf of México, page 337, Copyright 2004, with permission from Elsevier).

Table 2. List of species of larval fish recorded during the four seasons and five sampling levels in the water column (depths of 0 to 105 m).

Anguilliformes
Ophichthidae
Callechelys muraena Jordan & Evermann, 1887
Ophichthus cruentifer (Goode & Bean, 1896)
Stomiiformes
Gonostomatidae
Bonapartia pedaliota Goode & Bean, 1896
Gonostoma atlanticum Norman, 1930
Margrethia obtusirostra Jespersen & Tåning, 1919
Sternoptychidae
Maurolicus muelleri (Gmelin, 1789)
Valenciennellus tripunctulatus (Esmark, 1871)
Phosichthyidae
Ichthyococcus ovatus (Cocco, 1838)
Pollichthys mauli (Poll, 1953)
Vinciguerria attenuata (Cocco, 1838)
Vinciguerria nimbaria (Jordan & Williams, 1895)
Vinciguerria poweriae (Cocco, 1838)
Aulopiformes
Scopelarchidae
Scopelarchus guentheri Alcock, 1896
Synodontidae
Synodus foetens (Linnaeus, 1766)
Trachinocephalus myops (Forster, 1801)
Paralepididae
Lestidiops affinis (Ege, 1930)
Lestidiops jayakari jayakari (Boulenger, 1889)
Macroparalepis brevis Ege, 1933
Paralepis coregonoides Risso, 1820
Myctophiformes
Myctophidae
Benthosema suborbitale (Gilbert, 1913)
Ceratoscopelus maderensis (Lowe, 1839)
Ceratoscopelus warmingii (Lütken, 1892)
Diogenichthys atlanticus (Tåning, 1928)
Diogenichthys atlanticus (Tåning, 1928)
Hygophum hygomii (Lütken, 1892)
Hygophum macrochir (Günther, 1864)
Hygophum reinhardtii (Lütken, 1892)
Hygophum taaningi Becker, 1965

Table 2. Continue.

Lobianchia gemellarii (Cocco, 1838)
Myctophum asperum Richardson, 1845
Myctophum nitidulum Garman, 1899
Myctophum obtusirostre Tåning, 1928
Notolychnus valdiviae (Brauer, 1904)
Notoscopelus resplendens (Richardson, 1845)
Gadiformes
Bregmacerotidae
Bregmaceros atlanticus Goode & Bean, 1886
Bregmaceros cantori Milliken & Houde, 1984
Bregmaceros n. sp.
Ophidiiformes
Ophidiidae
Brotula barbata (Bloch & Schneider, 1801)
Ophidion nocomis Robins & Böhlke, 1959
Otophidium omostigma (Jordan & Gilbert, 1882)
Scorpaeniformes
Triglidae
Prionotus evolans (Linnaeus, 1766)
Perciformes
Serranidae
Hemanthias aureorubens (Longley, 1935)
Hemanthias vivanus (Jordan & Swain, 1885)
Priacanthidae
Heteropriacanthus cruentatus(Lacepède, 1801)
Pristigenys alta (Gill, 1862)
Malacanthidae
Lopholatilus chamaeleonticeps Goode & Bean, 1879
Rachycentridae
Rachycentron canadum (Linnaeus, 1766)
Carangidae
Caranx crysos (Mitchill, 1815)
Chloroscombrus chrysurus (Linnaeus, 1766)
Decapterus punctatus (Cuvier, 1829)
Hemicaranx amblyrhynchus (Cuvier, 1833)
Oligoplites saurus (Bloch & Schneider, 1801)
Selar crumenophthalmus (Bloch, 1793)
Selene setapinnis (Mitchill, 1815)
Selene spixii (Castelnau, 1855)
Selene vomer (Linnaeus, 1758)
Trachurus lathami Nichols, 1920
Lutjanidae

Table 2. Continue.

Lutjanus campechanus (Poey, 1860)
Pristipomoides aquilonaris (Goode & Bean, 1896)
Rhomboplites aurorubens (Cuvier, 1829)
Sparidae
Lagodon rhomboides (Linnaeus, 1766)
Sciaenidae
Bairdiella chrysoura (Lacepède, 1802)
Cynoscion arenarius Ginsburg, 1930
Cynoscion nothus (Holbrook, 1848)
Larimus fasciatus Holbrook, 1855
Menticirrhus americanus (Linnaeus, 1758)
Micropogonias undulatus (Linnaeus, 1766)
Stellifer lanceolatus (Holbrook, 1855)
Polynemidae
Polydactylus octonemus (Girard, 1858)
Mugilidae
Mugil cephalus Linnaeus, 1758
Mugil curema Valenciennes, 1836
Pomacentridae
Microspathodon chrysurus (Cuvier, 1830)
Stegastes partitus (Poey, 1868)
Labridae
Clepticus parrae (Bloch & Schneider, 1801)
Decodon puellaris (Poey, 1860)
Percophidae
Bembrops anatirostris Ginsburg, 1955
Blenniidae
Hypleurochilus geminatus (Wood, 1825)
Microdesmidae
Cerdale floridana Longley, 1934
Microdesmus bahianus Dawson, 1973
Microdesmus lanceolatus Dawson, 1962
Microdesmus longipinnis (Weymouth, 1910)
Sphyraenidae
Sphyraena borealis DeKay, 1842
Sphyraena guachancho Cuvier, 1829
Gempylidae
Diplospinus multistriatus Maul, 1948
Gempylus serpens Cuvier, 1829
Nealotus tripes Johnson, 1865
Neoepinnula orientalis (Gilchrist & von Bonde, 1924)
Ruvettus pretiosus Cocco, 1833

Table 2. Continue.

Trichiuridae
Lepidopus caudatus (Euphrasen, 1788)
Trichiurus lepturus Linnaeus, 1758
Scombridae
Auxis rochei rochei (Risso, 1810)
Auxis thazard thazard (Lacepède, 1800)
Euthynnus affinis (Cantor, 1849)
Euthynnus alletteratus (Rafinesque, 1810)
Katsuwonus pelamis (Linnaeus, 1758)
Scomber japonicus Houttuyn, 1782
Scomberomorus cavalla (Cuvier, 1829)
Scomberomorus maculatus (Mitchill, 1815)
Thunnus alalunga (Bonnaterre, 1788)
Thunnus albacares (Bonnaterre, 1788)
Thunnus obesus (Lowe, 1839)
Nomeidae
Cubiceps pauciradiatus Günther, 1872
Stromateidae
Peprilus paru (Linnaeus, 1758)
Peprilus triacanthus (Peck, 1804)
Pleuronectiformes
Paralichthyidae
Citharichthys cornutus (Günther, 1880)
Citharichthys gymnorhinus Gutherz & Blackman, 1970
Citharichthys spilopterus Günther, 1862
Cyclopsetta fimbriata (Goode & Bean, 1885)
Syacium gunteri Ginsburg, 1933
Syacium papillosum (Linnaeus, 1758)
Bothidae
Bothus ocellatus (Agassiz, 1831)
Trichopsetta ventralis (Goode & Bean, 1885)
Achiridae
Achirus lineatus (Linnaeus, 1758)
Trinectes maculatus (Bloch & Schneider, 1801)
Cynoglossidae
Symphurus plagiusa (Linnaeus, 1766)
Tetraodontiformes
Balistidae
Balistes capriscus Gmelin, 1789
Canthidermis sufflamen (Mitchill, 1815)
Xanthichthys ringens (Linnaeus, 1758)

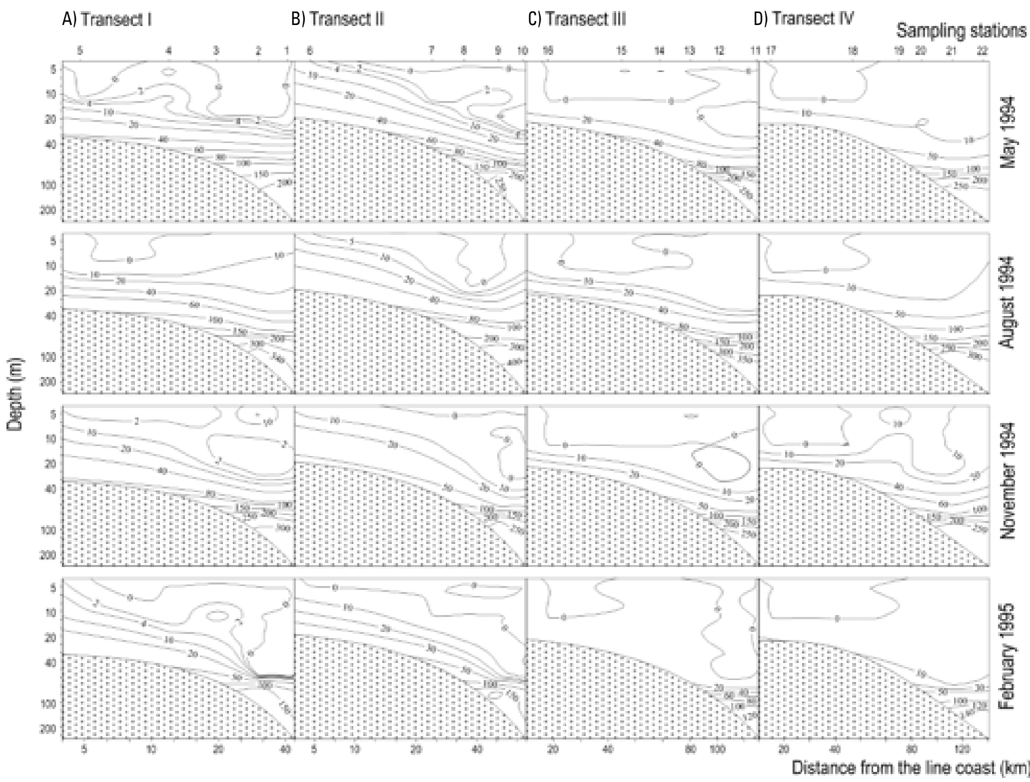

Figure 4A-D. Potential energy anomaly distribution profiles at different depths of the four transects (J m^{-3}). May, August and November 1994 and February 1995 in the southern Gulf of Mexico (Reprinted from Estuarine, Coastal and Shelf Science 59, M. L. Espinosa-Fuentes and C. Flores-Coto, Cross-shelf and vertical structure of ichthyoplankton assemblages in the continental shelf waters of the southern Gulf of México, page 338, Copyright 2004, with permission from Elsevier).

shelves (>62%) and significantly lower values towards the outer shelf (<38%) (Table 3).

The larvae of mesopelagic fish showed an inverse distribution, with the greatest density percentage on the outer shelf (> 95 %), a lower percentage on the middle shelf (< 5%) and none on the inner shelf (Table 3).

This distribution pattern was confirmed through the ANOVA and Tukey multiple range tests which indicated significant differences ($p < 0.05$) between the larval density of the inner and middle shelves, and that of the outer shelf.

The greatest average density on the inner and middle shelves was recorded at level 2 (6-12 m) with species of the Carangidae and Sciaenidae families as the most representative (Tables 4-7).

As the results indicated that the larval distribution of the neritic and mesopelagic species was not homogeneous across the continental shelf, the analysis of the vertical larval distribution was carried out exclusively for the outer shelf stations where specimens were collected from the five sampling levels.

The Bray-Curtis dissimilarity index clearly defined two groups of fish larvae in the water column of these stations. During spring, summer and autumn, the first group was formed by larvae located at the surface (0 to18 m, levels 1, 2 and 3) and the second group consisted of larvae of the deeper layer (45 and 105 m, levels 4 and 5) (Figs. 5A-C). During the winter, the first group was formed by larvae of levels 1, 2, 3 and 4 (0-45 m) and the second group had the larvae of level 5 (105 m) (Fig. 5D).

Table 3. Cross-shelf percentage of the average density of larvae of neritic and mesopelagic species at different sampling periods of 1994 and 1995 in the southern Gulf of Mexico.

		Continental Shelf		
Period	Species	Inner	Middle	Outer
May 1994	Neritic	35.5	40.9	23.6
	Mesopelagic			100.0
August 1994	Neritic	50.0	31.5	18.5
	Mesopelagic			100.0
November 1994	Neritic	41.4	20.8	37.8
	Mesopelagic		2.3	97.7
February 1995	Neritic	16.3	50.4	33.4
	Mesopelagic		4.9	95.1

Table 4. Geometric mean density of dominant species of fish larvae at the different levels in May in the southern Gulf of Mexico.

		Continental shelf									
		Inner		Middle			Outer				
		L 1	L 2	L 1	L 2	L 3	L 1	L 2	L 3	L 4	L 5
Neritic	*Auxis rochei*	0.6 (1)		3.1 (3)	2.8 (5)	1.6 (4)	4.6 (7)	3.5 (7)	1.7 (5)	0.7 (1)	
	Balistes capriscus	1.8 (3)	1.2 (1)	3.8 (6)	5.9 (6)	2.2 (5)	1.6 (6)	1.7 (6)	1.4 (2)	0.9 (1)	0.3 (1)
	Bothus ocellatus	2.1 (1)		0.9 (4)	1.2 (5)	0.9 (3)	1.3 (3)	0.9 (5)	1.9 (6)	0.5 (3)	0.4 (3)
	Bregmaceros atlanticus			0.6 (1)	0.4 (1)					0.7 (1)	0.4 (5)
	Bregmaceros cantori			5.3 (1)	1.7 (3)	6.1 (4)		0.5 (1)	2.6 (4)	4.5 (5)	1.7 (6)
	Bregmaceros n. sp.									0.5 (3)	0.4 (4)
	Brotula barbata										0.3 (1)
	Caranx crysos	27.9 (1)	2.4 (2)	6.7 (5)	10.3 (4)	6.9 (3)	3.4 (7)	3.2 (7)	1.4 (5)	0.6 (3)	
	Chloroscombrus chrysurus	104.6 (4)	154.6 (4)	4.4 (4)	4.8 (6)	4.4 (3)	1.0 (1)				
	Citharichthys spilopterus		3.0 (1)		2.1 (2)						
	Cyclopsetta fimbriata			0.9 (1)	1.5 (4)	9.0 (3)	0.6 (1)		0.5 (1)		0.3 (1)
	Cynoscion arenarius	3.4 (3)	15.9 (3)	4.5 (1)	3.8 (2)						
	Decapterus punctatus		3.0 (3)	0.6 (3)	1.2 (1)	28.0 (1)			1.6 (1)		0.3 (1)
	Euthynnus alletteratus	0.6 (1)		1.1 (4)	1.5 (5)	7.0 (3)	1.7 (3)	2.2 (4)	2.4 (2)		
	Heteropriacanthus cruentatus					0.4 (1)	0.9 (3)	0.9 (3)			0.5 (1)
	Lutjanus campechanus		0.7 (2)	1.6 (3)	7.2 (4)	1.8 (4)	2.6 (3)	1.6 (4)	2.5 (3)	0.4 (1)	1.0 (1)
	Microdesmus bahianus					14.9 (1)	1.2 (2)	1.5 (3)	6.1 (2)	0.5 (2)	
	Mugil cephalus		1.2 (2)	1.1 (1)		0.4 (1)	0.5 (1)	0.6 (2)	0.5 (1)		
	Pristipomoides aquilonaris							0.5 (2)	0.5 (1)	0.4 (1)	
	Rhomboplites aurorubens			1.1 (1)	0.5 (3)	1.0 (4)	1.3 (2)	6.8 (1)	1.6 (2)		0.3 (1)
	Scomberomorus cavalla			1.6 (1)	0.7 (5)	1.4 (4)	0.7 (2)	0.9 (4)	0.6 (3)		
	Selar crumenophthalmus	2.4 (3)	0.8 (2)	1.8 (7)	3.4 (7)	4.6 (4)	3.6 (8)	3.4 (8)	2.2 (7)	0.4 (1)	0.3 (3)
	Selene setapinnis	1.5 (1)	8.9 (1)	6.1 (5)	7.1 (7)	14.0 (5)	2.5 (3)	5.5 (3)	2.2 (4)	0.9 (1)	0.6 (1)
	Sphyraena guachancho			3.3 (7)	4.8 (7)	2.0 (4)	5.5 (3)	2.1 (4)	0.5 (2)		
	Stellifer lanceolatus					0.4 (1)					
	Syacium gunteri			1.8 (1)	2.4 (4)	7.0 (2)	1.3 (1)	1.4 (2)	1.3 (5)		0.4 (2)
	Syacium papillosum				0.8 (2)	4.7 (2)	1.1 (3)	1.0 (3)	9.5 (3)	0.6 (3)	1.2 (1)
	Symphurus plagiusa	0.6 (1)	2.2 (1)	3.2 (1)	4.8 (1)	14.6 (2)					0.3 (1)
	Thunnus albacares			5.3 (1)	6.4 (1)						
	Trachurus lathami	1.4 (3)	1.4 (1)		0.4 (1)	0.3 (1)	8.0 (2)	7.9 (2)			
	Trichiurus lepturus					1.6 (3)			0.5 (1)		
Mesopelagic	*Benthosema suborbitale*									0.9 (1)	1.3 (2)
	Ceratoscopelus warmingii						0.5 (1)	3.7 (2)	1.0 (4)		
	Diogenichthys atlanticus										0.9 (2)
	Hygophum hygomii									0.9 (1)	0.3 (1)
	Hygophum macrochir								0.9 (2)	1.5 (6)	0.7 (3)
	Hygophum reinhardtii						0.6 (1)	0.4 (1)		0.9 (5)	0.7 (2)
	Hygophum taaningi									1.2 (3)	1.5 (1)
	Lestidiops jayakari								0.7 (2)	2.0 (2)	
	Macroparalepis brevis									1.1 (2)	
	Maurolicus muelleri									0.2 (1)	0.3 (3)
	Myctophum asperum									0.8 (2)	0.7 (1)
	Myctophum nitidulum									0.5 (4)	0.4 (2)
	Notolychnus valdiviae								2.7 (1)	0.5 (2)	3.5 (1)
	Scopelarchus guentheri								0.5 (1)	0.7 (1)	
	Vinciguerria nimbaria								0.5 (3)	1.7 (2)	0.5 (1)
	Vinciguerria poweriae									0.4 (1)	0.6 (2)

L = Depth level. L1 = 0-6 m; L2 = 6-12 m; L3 = 12-18 m; L4 = 45-55 m; L5 = 95-105 m. In parenthesis is indicate number of samples where the species was present.

Table 5. Geometric mean density of dominant species of fish larvae at the different levels in August in the southern Gulf of Mexico.

		Continental shelf									
		Inner		Middle			Outer				
		L 1	L 2	L 1	L 2	L 3	L 1	L 2	L 3	L 4	L 5
Neritic	*Auxis rochei*			1.7 (3)	4.9 (2)	0.9 (2)	1.3 (6)	1.1 (4)	0.5 (1)		
	Balistes capriscus	2.7 (3)	5.2 (1)	4.6 (1)	5.5 (3)	4.2 (1)	1.4 (3)	1.7 (4)	0.8 (2)	1.0 (2)	
	Bothus ocellatus	2.7 (2)	1.5 (1)	1.0 (3)	5.4 (2)	2.1 (2)	3.0 (3)	3.1 (5)	1.9 (5)	1.8 (4)	0.3 (3)
	Bregmaceros atlanticus									0.8 (2)	1.2 (4)
	Bregmaceros cantori	0.9 (1)			0.9 (1)	2.9 (1)				8.2 (5)	2.9 (6)
	Bregmaceros n. sp.									0.4 (1)	0.3 (1)
	Caranx crysos										0.3 (1)
	Chloroscombrus chrysurus	21.0 (5)	35.9 (3)	5.6 (2)	9.7 (4)	0.9 (2)		0.5 (1)	0.5 (1)		
	Citharichthys spilopterus	0.3 (1)			1.9 (1)					3.6 (1)	
	Cyclopsetta fimbriata	0.6 (1)	1.5 (1)	1.5 (1)	2.1 (2)	3.6 (2)	0.5 (2)	0.5 (2)	1.0 (3)	1.0 (2)	0.4 (2)
	Cynoscion arenarius	3.0 (4)	3.7 (2)	3.9 (1)		0.6 (1)					
	Decapterus punctatus	0.9 (1)	0.8 (1)					0.5 (1)			
	Euthynnus alletteratus			43.6 (1)	2.8 (3)	0.4 (1)		0.9 (3)	0.6 (1)		
	Heteropriacanthus cruentatus				1.2 (1)	0.4 (1)				0.3 (1)	
	Lutjanus campechanus	1.7 (3)	9.7 (1)	1.4 (2)	2.2 (2)	2.9 (1)	0.5 (1)	1.0 (2)			
	Microdesmus bahianus				1.2 (1)	0.8 (1)		0.5 (2)			
	Mugil cephalus	0.8 (1)					0.5 (1)				
	Pristipomoides aquilonaris			0.5 (2)	0.5 (1)		2.9 (3)	1.5 (3)	8.3 (1)		
	Rhomboplites aurorubens							1.5 (1)			
	Scomberomorus cavalla	1.4 (1)	1.4 (1)	2.0 (3)	3.4 (3)	1.8 (2)	0.7 (2)	0.4 (2)	4.7 (1)		
	Selar crumenophthalmus	2.4 (2)	1.1 (3)	1.7 (3)	2.7 (4)	1.9 (2)	2.3 (5)	3.2 (4)	2.4 (3)		0.3 (2)
	Selene setapinnis		1.1 (2)	5.9 (1)	3.5 (4)	7.6 (2)	3.0 (3)	4.8 (5)	2.0 (5)	0.7 (2)	0.3 (3)
	Sphyraena guachancho	0.7 (1)	3.0 (2)	2.3 (3)	5.9 (4)	1.5 (2)	4.8 (5)	1.5 (5)	2.2 (3)		
	Stellifer lanceolatus	1.2 (2)		2.3 (1)							
	Syacium gunteri	3.2 (3)	10.2 (2)	21.9 (1)	13.8 (2)	11.8 (2)	1.8 (2)	2.2 (5)	4.6 (5)	1.1 (5)	0.5 (3)
	Syacium papillosum	2.7 (1)	3.7 (1)	4.6 (1)	0.7 (1)	2.1 (2)	0.7 (2)	0.7 (3)	0.8 (2)	0.8 (4)	
	Symphurus plagiusa	0.3 (1)			0.7 (1)	2.9 (1)			0.5 (1)	3.0 (1)	0.3 (1)
	Thunnus albacares			0.7 (2)							
	Trichiurus lepturus			0.8 (1)					0.6 (1)		
Mesopelagic	*Benthosema suborbitale*										0.6 (2)
	Diogenichthys atlanticus										0.9 (3)
	Hygophum macrochir									0.6 (2)	0.3 (1)
	Hygophum reinhardtii										0.3 (2)
	Hygophum taaningi									1.1 (3)	
	Lestidiops jayakari									0.4 (2)	0.3 (1)
	Lobianchia gemellarii									3.6 (2)	
	Macroparalepis brevis									0.3 (1)	
	Myctophum asperum										0.4 (2)
	Myctophum nitidulum									1.4 (1)	0.7 (1)
	Myctophum obtusirostre									1.7 (1)	
	Notolychnus valdiviae										0.4 (3)
	Scopelarchus guentheri									0.4 (1)	
	Vinciguerria poweriae										0.3 (1)

L = Depth level. L1 = 0-6 m; L2 = 6-12 m; L3 = 12-18 m; L4 = 45-55 m; L5 = 95-105 m. In parenthesis is indicate number of samples where the species was present.

Table 6. Geometric mean density of dominant species of fish larvae at the different levels in November in the southern Gulf of Mexico.

		Continental shelf									
		Inner		Middle			Outer				
		L 1	L 2	L 1	L 2	L 3	L 1	L 2	L 3	L 4	L 5
Neritic	*Auxis rochei*			1.4 (2)	1.2 (1)		11.8 (1)	0.4 (2)	0.4 (2)		
	Balistes capriscus			0.5 (1)		0.7 (1)	0.7 (3)	0.6 (2)			
	Bothus ocellatus			0.9 (2)	4.3 (3)	1.1 (3)	2.5 (3)	2. (5)	1.7 (5)	1.7 (3)	0.8 (3)
	Bregmaceros atlanticus									1.1 (2)	
	Bregmaceros cantori	2.8 (1)			0.7 (3)	4.3 (3)	0.6 (1)	1.2 (2)	3.3 (1)	9.6 (3)	6.6 (4)
	Brotula barbata							2.6 (1)		2.4 (4)	0.3 (1)
	Caranx crysos							0.4 (1)	0.3 (1)		
	Chloroscombrus chrysurus	2.0 (3)	3.8 (3)	0.9 (3)	2.6 (2)		0.5 (1)	0.4 (1)	0.5 (1)		
	Citharichthys spilopterus		0.4 (1)					4.8 (1)	2.3 (2)	0.8 (2)	0.8 (1)
	Cyclopsetta fimbriata			0.5 (1)	2.0 (2)	0.8 (2)	0.5 (1)	0.4 (2)	1.0 (3)		0.5 (1)
	Cynoscion arenarius	7.1 (1)	4.5 (1)	8.8 (1)	6.6 (2)						
	Decapterus punctatus							0.6 (2)			
	Euthynnus alletteratus								0.4 (1)		
	Heteropriacanthus cruentatus			2.4 (1)	0.7 (1)	0.4 (1)	1.8 (1)	0.6 (4)	0.9 (3)		
	Lutjanus campechanus				1.7 (1)	1.1 (1)		0.4 (1)	2.1 (1)	1.6 (1)	
	Microdesmus bahianus			0.5 (1)	1.1 (3)	5.9 (1)	0.6 (2)	0.7 (2)	0.8 (1)		
	Micropogonias undulatus	17.2 (2)	84.2 (2)		43.1 (1)	8.9 (1)			15.3 (2)		
	Mugil cephalus										0.3 (1)
	Peprilus paru	4.3 (1)	0.9 (1)	1.1 (2)			0.5 (1)	0.9 (1)	0.5 (1)		
	Pristipomoides aquilonaris								0.5 (1)		
	Rhomboplites aurorubens								0.6 (2)		
	Scomberomorus cavalla					0.4 (1)	1.4 (1)	0.9 (1)			
	Selar crumenophthalmus	2.8 (1)	1.0 (1)	3.8 (3)	1.5 (5)	2.4 (2)	2.7 (6)	1.6 (7)	1.0 (4)	0.5 (1)	0.3 (2)
	Selene setapinnis	1.4 (1)	1.9 (1)	2.0 (2)	1.9 (4)	3.9 (1)	2.4 (3)	1.6 (4)	1.5 (2)	0.3 (1)	
	Sphyraena guachancho	0.7 (1)	1.1 (1)	1.6 (5)	1.1 (6)	0.5 (2)	0.9 (5)	1.0 (4)	0.9 (3)	0.7 (3)	0.4 (3)
	Stellifer lanceolatus	24.8 (2)	68.2 (1)	16.7 (1)					8.4 (2)	4.7 (1)	
	Syacium gunteri				0.8 (1)	2.7 (2)		1.6 (2)	1.9 (5)	1.3 (3)	0.8 (2)
	Syacium papillosum			3.3 (1)	0.6 (2)	2.3 (2)		0.4 (1)	1.4 (4)	0.5 (2)	0.7 (2)
	Symphurus plagiusa			2.0 (1)	2.1 (2)	0.8 (2)	1.4 (2)	4.8 (2)	4.4 (2)	2.5 (1)	2.7 (1)
	Trachurus lathami	0.4 (1)					0.8 (2)				
	Trichiurus lepturus	0.4 (1)						0.5 (3)	0.9 (1)	0.6 (3)	
Mesopelagic	*Benthosema suborbitale*									1.9 (1)	5.1 (1)
	Ceratoscopelus warmingii				0.5 (1)		0.4 (2)				
	Diogenichthys atlanticus									1.2 (1)	1.6 (1)
	Hygophum hygomii									0.3 (2)	1.3 (1)
	Hygophum macrochir									1.7 (3)	2.3 (1)
	Hygophum reinhardtii										0.3 (2)
	Hygophum taaningi									0.4 (1)	1.3 (2)
	Lestidiops jayakari									1.8 (1)	
	Macroparalepis brevis						0.4 (1)			0.4 (1)	
	Myctophum asperum								0.5 (1)	0.6 (1)	0.3 (1)
	Myctophum nitidulum									2.5 (1)	0.3 (1)
	Myctophum obtusirostre					0.4 (1)					0.4 (4)
	Pollichthys mauli										0.2 (1)
	Scopelarchus guentheri									1.2 (1)	
	Vinciguerria nimbaria									0.3 (1)	
	Vinciguerria poweriae									0.6 (1)	

L = Depth level. L1 = 0-6 m; L2 = 6-12 m; L3 = 12-18 m; L4 = 45-55 m; L5 = 95-105 m. In parenthesis is indicate number of samples where the species was present.

Table 7. Geometric mean density of dominant species of fish larvae at the different levels in February in the southern Gulf of Mexico.

		Continental shelf									
		Inner		Middle			Outer				
		L 1	L 2	L 1	L 2	L 3	L 1	L 2	L 3	L 4	L 5
Neritic	*Auxis rochei*			0.5 (1)	0.4 (1)	1.2 (1)	2.0 (2)	1.9 (2)	0.8 (2)	1.0 (3)	0.2 (1)
	Bothus ocellatus		0.5 (1)		1.3 (3)	1.5 (3)	1.0 (5)	1.7 (5)	1.3 (5)	1.9 (5)	0.6 (2)
	Bregmaceros atlanticus									0.5 (1)	
	Bregmaceros cantori	4.1 (1)	9.8 (3)	6.6 (4)	12.9 (6)	31.9 (3)	3.5 (3)	2.3 (6)	3.0 (5)	3.7 (6)	1.4 (6)
	Bregmaceros n. sp.									0.5 (1)	
	Brotula barbata					0.4 (1)					
	Caranx crysos						1.8 (1)			0.9 (1)	
	Chloroscombrus chrysurus				0.8 (2)			0.6 (2)	0.7 (1)	0.3 (1)	0.3 (1)
	Citharichthys spilopterus	0.8 (1)		2.3 (1)	1.8 (3)	1.4 (3)	0.6 (1)	1.1 (1)	1.0 (1)	0.9 (1)	
	Cyclopsetta fimbriata				0.6 (1)	0.4 (1)		0.5 (1)	0.8 (1)		
	Cynoscion arenarius	15.9 (2)	6.5 (1)				1.5 (1)	2.6 (1)	1.1 (2)	0.7 (1)	
	Decapterus punctatus			1.3 (1)			0.6 (1)	0.5 (1)	0.4 (1)		
	Heteropriacanthus cruentatus							0.5 (1)		0.3 (1)	
	Microdesmus bahianus			3.5 (2)	1.4 (2)		0.7 (3)	1.1 (2)	1.0 (2)		
	Micropogonias undulatus	2.6 (3)	3.3 (1)	1.5 (1)	2.1 (3)				0.7 (1)	0.7 (2)	
	Mugil cephalus			2.6 (3)	0.6 (1)	0.6 (1)	3.6 (3)	3.2 (5)	1.6 (3)	2.0 (3)	0.3 (2)
	Peprilus paru				0.4 (1)	0.4 (1)		0.3 (1)		0.4 (1)	
	Scomberomorus cavalla									0.4 (1)	
	Selar crumenophthalmus			0.8 (3)	5.2 (1)		0.9 (5)	1.2 (5)	0.9 (3)	0.9 (3)	
	Selene setapinnis			0.4 (1)	0.6 (1)		1.5 (2)	2.3 (3)	0.8 (4)	0.5 (2)	0.2 (1)
	Sphyraena guachancho							0.6 (1)		0.6 (1)	
	Stellifer lanceolatus	0.6 (1)	6.0 (1)	1.2 (1)			1.1 (1)			0.5 (3)	0.2 (1)
	Syacium gunteri			1.3 (1)	1.7 (2)	0.8 (3)	0.8 (2)	1.4 (4)	1.5 (3)	2.1 (2)	0.9 (2)
	Syacium papillosum		0.5 (1)		0.6 (3)	0.5 (2)	0.6 (1)	0.5 (3)	0.9 (2)	0.6 (2)	
	Symphurus plagiusa			0.6 (2)	1.4 (4)	2.0 (3)	0.7 (2)	1.7 (2)	0.9 (4)	1.3 (2)	0.4 (4)
	Trachurus lathami			2.4 (2)	1.6 (2)	19.9 (1)	5.1 (5)	3.4 (7)	3.2 (5)	4.1 (4)	0.5 (2)
	Trichiurus lepturus		4.3 (1)	2.1 (3)	2.9 (4)	2 (4)	0.9 (3)	0.8 (5)	1.0 (3)	1.1 (4)	0.8 (2)
Mesopelagic	*Benthosema suborbitale*					0.4 (1)				0.9 (1)	1.3 (4)
	Ceratoscopelus warmingii						0.5 (2)	1.3 (3)	0.8 (4)		0.3 (2)
	Diogenichthys atlanticus									0.5 (1)	
	Hygophum hygomii										1.2 (2)
	Hygophum macrochir			0.5 (1)	0.5 (1)		0.9 (1)	0.5 (1)	1.6 (1)	1.6 (4)	
	Hygophum taaningi									0.5 (1)	0.3 (2)
	Lestidiops jayakari					0.3 (1)	0.4 (1)	0.3 (1)	0.4 (1)	1.2 (2)	
	Macroparalepis brevis									0.9 (1)	
	Maurolicus muelleri										0.3 (2)
	Myctophum asperum							0.5 (1)			
	Myctophum nitidulum					0.4 (2)			0.4 (1)	1.0 (3)	0.4 (3)
	Notolychnus valdiviae							0.5 (1)			0.4 (1)
	Pollichthys mauli					0.4 (1)				0.4 (1)	0.6 (2)
	Scopelarchus guentheri										2.0 (1)

L = Depth level. L1 = 0-6 m; L2 = 6-12 m; L3 = 12-18 m; L4 = 45-55 m; L5 = 95-105 m. In parenthesis is indicate number of samples where the species was present.

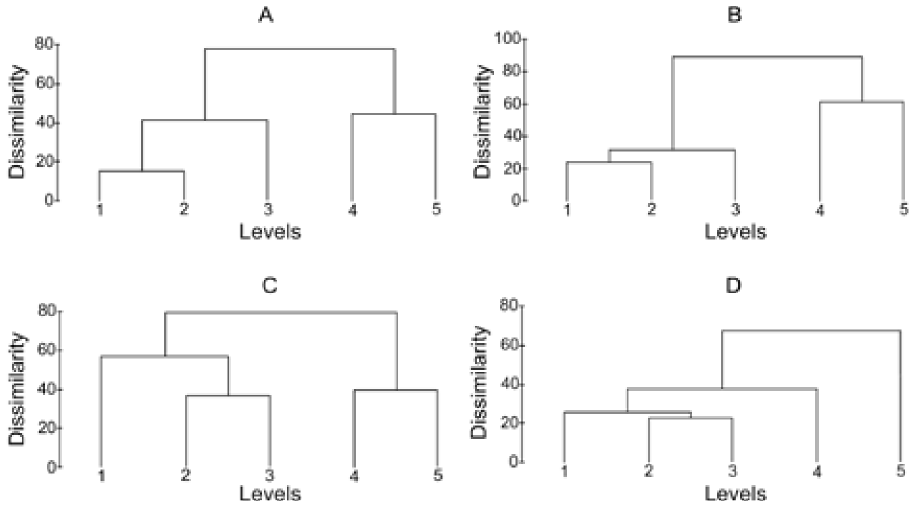

Figure 5A-D. Bray-Curtis cluster analysis based on sampling level affinities of fish larvae in the water column. A) May 1994, B) August 1994, C) November 1994, D) February 1995.

The results indicate that there were two layers in the first 105 m of the water column: a surface and a deep layer.

Larvae of neritic fish presented their greatest abundance in the surface layer (> 85%) at all times, whereas the larvae of mesopelagic parents recorded more than 74% of their total density in the deep layer, except for winter when they represented only 64% (Table 8). The high percentages of neritic and mesopelagic components in the surface and deep layers respectively show that the larvae remain in a particular stratum all the time.

In the spring, 47 species were dominant (IVI > 5%), 31 were neritic and 16 were mesopelagic. Six neritic species, *Chloroscombrus chrysurus* Linnaeus, 1766, *Euthynnus alletteratus* Rafinesque, 1810, *Scomberomorus cavalla* Cuvier, 1829, *Sphyraena guachancho* Cuvier, 1829, *Trachurus lathami* Nichols, 1920 and *Trichiurus lepturus* Linnaeus, 1758 occurred exclusively in the surface layer, while the species *Balistes capriscus* Gmelin, 1789, *Bothus ocellatus*, *Lutjanus campechanus* Poey, 1860, *Selene setapinnis* Mitchill, 1815 and *Syacium papillosum* occurred throughout the water column (Table 4).

In the deep layer, the most abundant mesopelagic species, including *Benthosema suborbitale, Hygophum taaningi* and *Myctophum asperum* Richardson 1845, were recorded exclusively in this depth layer (Table 4, Fig. 6A).

In the summer, the IVI recorded 43 dominant species, 29 in the surface layer and 14 in the deep layer. The most abundant species in the surface layer were *Pristipomoides aquilonaris* Goode & Bean 1896, *Scomberomorus cavalla* and *Sphyraena guachancho.* The larvae of mesopelagic fish were all restricted to the deep layers, with the most representative being *Lobianchia gemellarii* Cocco, 1838, *Hygophum macrochir* Günther, 1864 and *Myctophum nitidulum* Garman, 1899 (Table 5, Fig. 6B). The presence in this depth layer of *Bregmaceros cantori*, with 96% of its abundance, must be mentioned. Species including *Syacium gunteri*, *Bothus ocellatus* and *Selene setapinnis* were found throughout the water column (Fig. 6B).

In the autumn, 47 dominant species were recorded of which 31 were neritic and 16 mesopelagic. The species with the greatest density percentage in the surface layer were *Micropogonias*

Table 8. Percentage of the average density of larvae of neritic and mesopelagic species at the surface (0-18 m) and deep (45-105 m) layers.

Month	Neritic		Mesopelagic	
	Surface layers (L1, L2, L3)	Deep layers (L4, L5)	Surface layers (L1, L2, L3)	Deep layers (L4, L5)
May	98.0	2.0	25.3	74.7
August	96.0	4.0		100.0
November	85.6	14.4	6.6	93.4
February	90.9	9.1	35.2	64.8

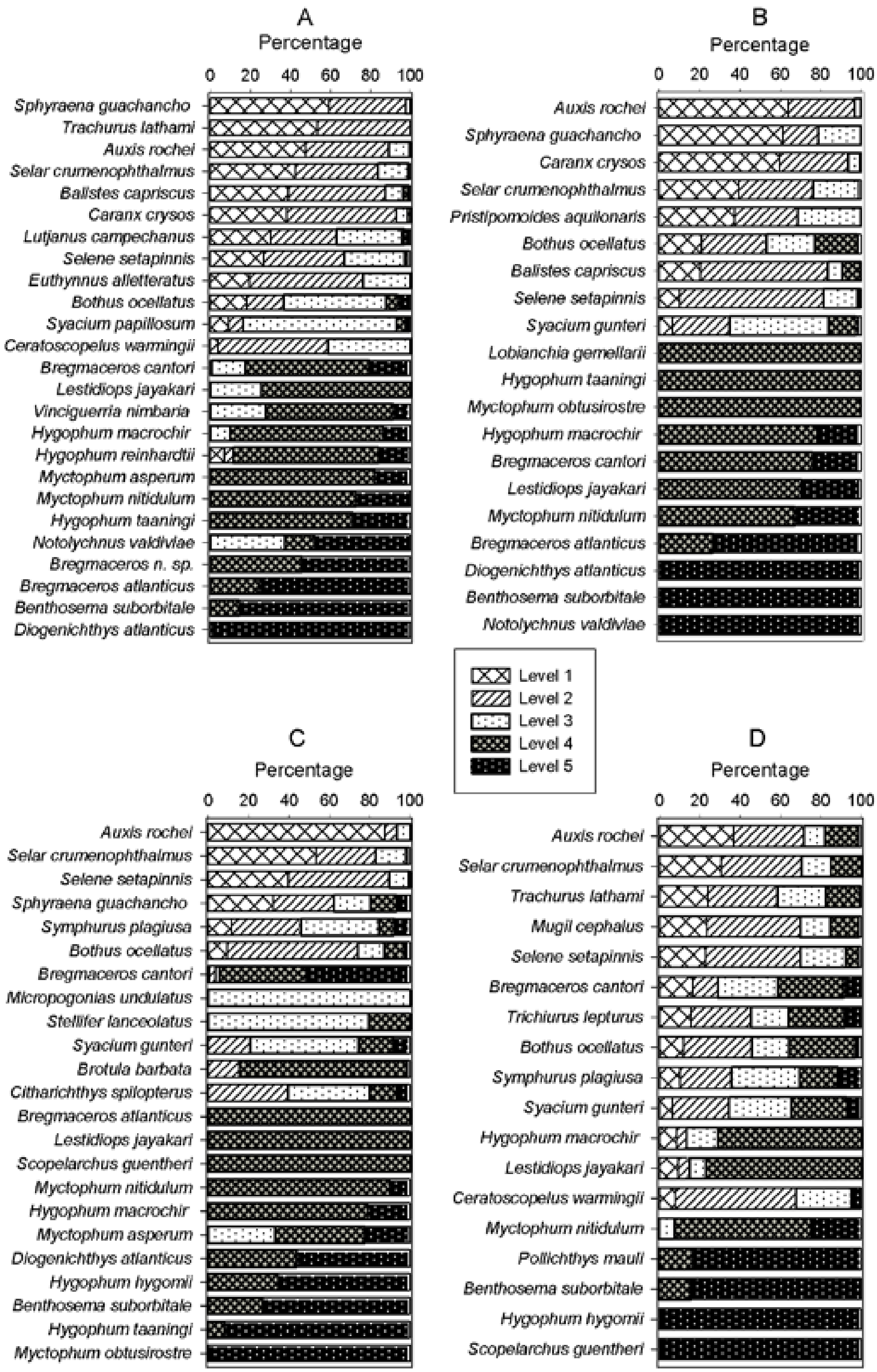

Figure 6A-D. Schematic representation of the percentage distribution of the dominant species of fish larvae in the water column. A) May, B) August, C) November, D) February.

undulatus Linnaeus, 1766 and *Stellifer lanceolatus* Holbrook, 1855. The larvae of mesopelagic fish recorded 93% of their density in the deep layer during this period (Table 8, Fig. 6C). Other species, particularly those of the flatfish families, also occupied the deep layer with relatively high abundance values.

In the winter, the IVI identified 41 dominant species of which 27 were neritic and 14 were mesopelagic. The larval distribution throughout the water column presented a mixture of neritic and mesopelagic species, with these last recording a density of 35% at the surface layer (Table 8).

Hygophum macrochir, Lestidiops jayakari Boulenger, 1889, *Myctophum nitidulum* Garman, 1899 and *Notolychnus valdiviae* Brauer, 1904, which at other times have shown a greater affinity for deeper waters, were observed in the surface layer, with some even reaching level 1. Furthermore, neritic species like *Chloroscombrus chrysurus*, *Auxis rochei*, *Stellifer lanceolatus, Trachurus lathami* and *Trichiurus lepturus* which had occupied the surface levels (6-45 m) in the previous months, were observed in the deeper waters (level 5) (Table 7, Fig. 6D).

Neritic species like *Auxis rochei, Bothus ocellatus, Cyclopsetta fimbriata* Goode & Bean, 1885*, Selene setapinnis, Selar crumenophthalmus, Sphyraena guachancho, Syacium gunteri* and *Syacium papillosum* presented a wide distribution throughout the water column in all the sampling periods, though their greatest abundance was recorded in the surface layers. Other species also occurred in all the depth levels, but not in all the seasons (Tables 4-7).

With respect to the larvae of mesopelagic species, *Diogenichthys atlanticus* Tåning, 1928, *Hygophum hygomii* Lütken, 1892*, Hygophum taaningi, Myctophum nitidulum, Vinciguerria poweriae* Chevrolat, 1863 and *Maurolicus muelleri* Gmelin, 1789 were present in different seasons always in the deep layer (Tables 4-7).

The CCA applied to the data recorded in May yielded a species-environment correlation of 0.99 for the first axis, of 1.00 for the second axis and of 0.96 for the third axis. The potential energy generated the greatest variability in axes I and II. Neritic species like *Auxis rochei, Caranx crysos* Mitchill, 1815*, Balistes capriscus* and *Microdesmus bahianus* Dawson, 1973 presented a direct relationship with temperature and salinity, whereas mesopelagic species like *Bregmaceros cantori, Benthosema suborbitale* and *Notolychnus valdiviae*, among others, did so with the potential energy anomaly (Fig. 7A).

In August, the species-environment correlations were 1.0, 0.99 and 0.83 in axes I, II and III respectively. The species *Bothus ocellatus, Syacium gunteri* and *Balistes capriscus* were directly related to salinity and temperature, whereas the mesopelagic species were related more with the potential energy anomaly (Fig. 7B).

The CCA in November presented a species-environment correlation of 0.99 for axes I and II, and of 0.62 for the third axis. The neritic species were mostly related to the temperature and salinity, particularly the larvae of the families Carangidae, Sciaenidae and the flatfish. The larvae of the mesopelagic *Ceratoscopelus warmingii* Lütken, 1892, presented a direct relationship with salinity in this season, while the neritic *Bregmaceros cantori* did so with the potential energy anomaly (Fig. 7C).

The CCA for February 1995 revealed a species-environment correlation of 0.99 for the first axis, of 0.84 for the second and of 0.96 for the third. Temperature and salinity presented a strong positive relationship with both neritic and mesopelagic species like *Cynoscion arenarius, Bothus ocellatus, Trichiurus lepturus, Lestidiops jayakari* and *Hygophum macrochir*. Species that were generally located in the deeper layer, including *Notolychnus valdiviae, Benthosema suborbitale* and *Hygophum higomii*, presented a direct relationship with the potential energy anomaly (Fig. 7D).

DISCUSSION

The results obtained clearly indicate that fish larvae present a cross-shelf distribution that is directly related to the habitat of the adults. The larval composition on the inner shelf consisted mainly of species of which the adults are estuarine-dependent or are linked to coastal areas that receive a fluvio-lagoon influence, while the larvae of mesopelagic adult fish presented their greatest densities in the oceanic areas. An inshore-offshore gradient of fish larvae has been reported for other places (Leis, 1982; Smith *et al.*, 1999; Gray & Miskiewicz, 2000; Catalán *et al.,* 2006; Alemany *et al.*, 2006, 2010).

The results also showed that the larvae of species that inhabit neritic waters as adults presented their greatest diversity and density at the surface layer (0-18 m), whereas the larvae of species that inhabit oceanic areas as adults occupied the deeper waters (45-105 m), with only a few species occasionally occupying the surface layer. Similar results have been observed in the Mediterranean Sea (Sabatés, 2004), the southeastern coast of Australia (Gray, 1993; Gray & Kingsford, 2003) and the western tropical Atlantic (Cha *et al.*, 1994). The larvae of *Bregmaceros cantori*, a neritic species (Zavala-García & Flores-Coto, 1994), broke the distribution pattern of the neritic species, when its greater abundance was recorded in the deep layer, except for winter when it occurred at all depths.

Differences were observed in the vertical distribution of the larvae of some groups of species. The larvae of the Carangidae, Sciaenidae and Scombridae mainly occupied the surface layer and were very scarce in deeper layers, coinciding with other records on the distribution of these families (Boehlert & Mundy, 1994; Flores-Coto *et al.*, 1999, 2001; Comyns & Lyczkowski-Shultz, 2004; Torres *et al.*, 2011).

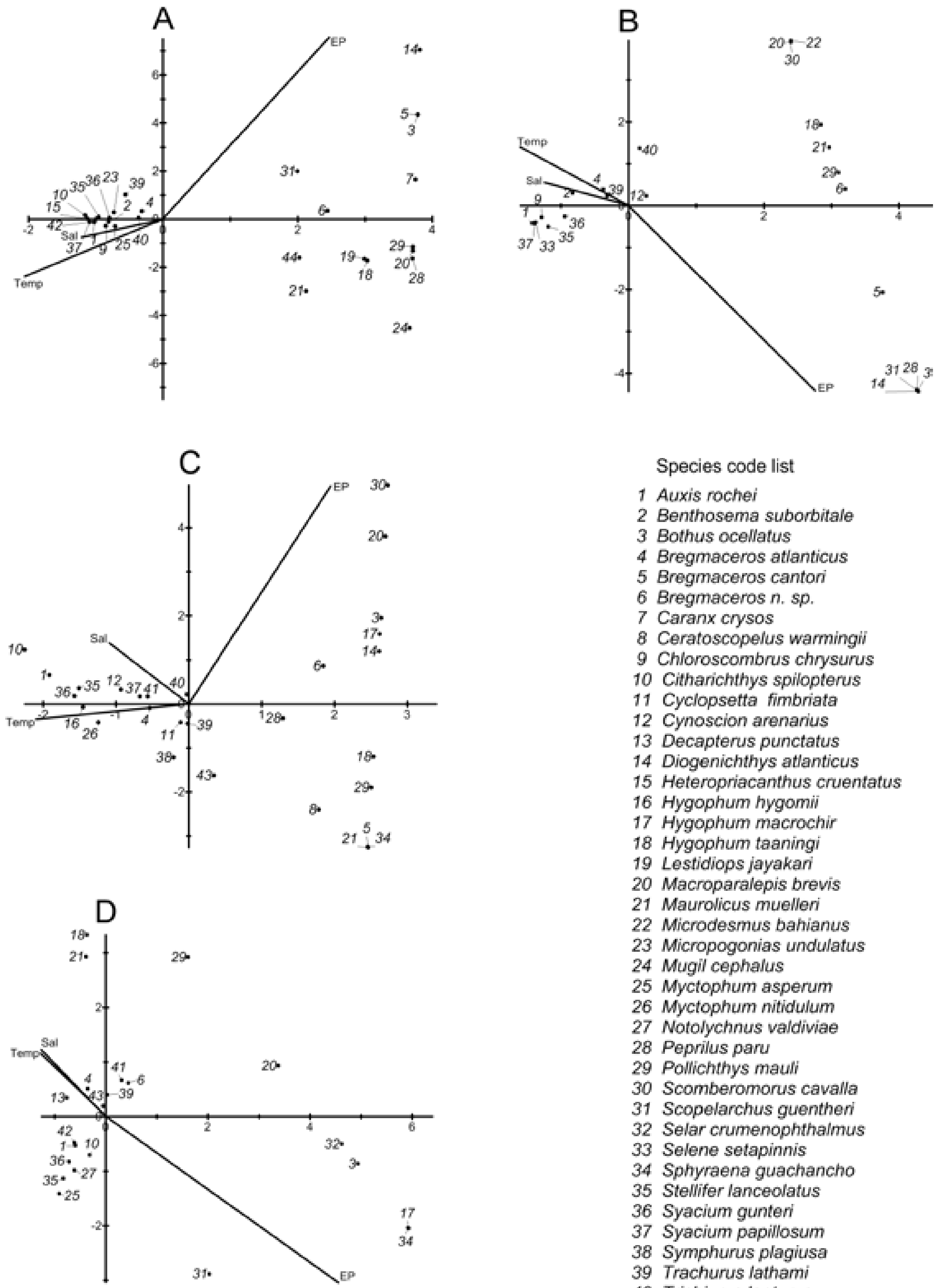

Figure 7A-D. Canonical correspondence analysis (CCA) ordination diagram for the main species of fish larvae in the southern Gulf of Mexico (>90%) with environmental factors represented by vectors, Temp: temperature, Sal: salinity, EP: potential energy anomaly. A) May, B) August, C) November, D) February.

On the other hand, Pleuronectiformes larvae, including those of the Bothidae, Paralichthydae and Cynoglosidae, presented a wide distribution throughout the water column, with relatively high densities in the deep layers.

The deep levels (45-105 m) were characterized by the presence of fish larvae of oceanic dwellers, including *Bregmaceros atlanticus* and members of the families Myctophidae, Gonostomatidae and Phosichthyids (Flores-Coto & Ordoñez-López, 1991; Zavala-Garcia & Flores-Coto, 1994; Gôngora-Goçalo *et al.*, 2011).

The recorded distribution patterns reflect the behavior and preference of each species to maintain a certain position in the water column. According to Olla and Davis (1990), fish larvae possess behavior mechanisms that enable them to alter their position in the water column to deal with environmental gradients and select favorable ones. On the other hand, the preference of a certain depth stratum has been associated with biological and environmental stimuli that ensure the best larval survival (Boehlert & Mundy, 1988; Heath, 1992; Cha *et al.*, 1994; Olivar & Sabatés, 1997; Aceves-Medina *et al.*, 2008).

During spring, summer and autumn, the vertical distribution pattern of larvae on the outer shelf indicated the presence of two groups of species in the water column, a neritic group that mostly occupied the surface layer (0-18 m) and a mesopelagic group confined to the deeper layer (45-105 m). Apart from the larval habit to remain in a particular layer, distribution patterns may be related to the water column hydrodynamics. During the seasons of this study, the neritic organisms were generally confined to the mixing surface layer at ~30 m.

The CCA corroborated a direct relationship between the neritic species and high values of salinity and temperature, mainly in the upper layers, as has been reported by Tzeng and Wang (1993) and Miranda *et al.* (2006), while mesopelagic larvae presented a greater affinity with high values of stratification.

The presence of the same two groups of species was observed in winter as well. However, the vertical distribution of some mesopelagic species was not confined to the deep layer. Larvae of several species were distributed more widely in the water column. This may be related to the depth of the mixing layer which at this time of the year reached 70 m and favored the mixing of surface and deep species. This was confirmed by the CCA data for this season.

The distribution indicates a species-specific depth selection behavior dependent on a particular environmental condition of the water column.

Such changes in the distribution of species during mixing processes have been documented by various authors for other regions, and it has been concluded that vertical mixing may modify patterns of vertical distribution of planktonic organisms (Incze *et al.,* 1990; Haury *et al.,* 1990; Legadeuc *et al.,* 1997; Farstey *et al.,* 2002).

The results make it possible to observe a strong contrast between the high larval density at the surface, mainly of neritic species, and the low larval densities in the deep layer that correspond to the mesopelagic species for the four seasons. The greatest difference between the surface and the deep layers was observed in the spring and the smallest in the winter, probably because at that time a greater number of larvae of mesopelagic species ascended from deeper levels that were not sampled.

The greater concentration of larvae in the surface layer of the oceans, generally above 50 m, has been linked to food availability (Röpke, 1993; Conway *et al.*, 1997; Gray, 1998; Sabatés, 2004; Sánchez-Velasco *et al.,* 2009). Rodríguez *et al.* (2006) also mentioned that there is a trophic relationship between fish larvae and mesozooplankton, and consequently the distribution of prey may play an important role in the vertical distribution of larvae.

The study area that includes the first 105 m of the water column is characterized by the presence of two major layers, a surface layer (0 to 18 m) with a greater abundance of neritic species and a deeper layer (45 to 105 m) with more species that have an affinity for oceanic environments.

The mixing process in the water column was the most important physical factor to affect the vertical distribution of larvae, particularly in winter. However, regarding the habits of the larvae of each species, the preference to stay of a certain depth was the most important biological factor that determined their distribution in the water column.

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