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ARTICLE

Environmental factors affecting structure and spatial patterns of larval fish assemblages in the southern Gulf of Mexico

Factores ambientales que afectan la estructura y patrones espaciales de las asociaciones de larvas de peces en el sur del Golfo de México

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Resumen.- Se estudiaron los factores ambientales que afectan las asociaciones de larvas de peces en el sur del Golfo de México. Las muestras se obtuvieron con redes Bongo de superficie a 200 m, en 46 estaciones, en primavera 2006. A cada taxón de larvas se le asignó el hábitat de sus adultos. Las asociaciones de larvas se definieron por el índice de Bray-Curtis. Se registró un total de 182 taxones, la mayoría oceánicos, de plataforma media y arrecifales. Se definieron 3 comunidades, Yucatán (YA), Tabasco-Campeche (TCA) y Oceánica (OA). YA se ubicó sobre el Banco de Campeche, en la amplia plataforma de Yucatán, donde el proceso hidrodinámico más importante es una rama de la corriente de Yucatán. TCA ocupó la plataforma de Tabasco y suroeste de la plataforma de Campeche, caracterizada por la descarga de aguas continentales. OA ocupó el área oceánica de la Bahía de Campeche, donde el proceso hidrodinámico dominante es un giro ciclónico casi permanente. Como resultado de diferentes hechos hidrográficos, sean corrientes oceánicas, presencia de giros o descargas de aguas dulces, y la topografía; la plataforma de Tabasco, el Banco de Campeche (plataforma de Yucatán) y la Bahía de Campeche constituyen regiones con escenarios ambientales claramente contrastantes. La distribución geográfica de las 3 asociaciones de larvas se ajusta bien con estas 3 áreas de diferente hidrodinámica. La estructura y distribución espacial de las asociaciones de larvas está determinada en primer lugar por el hábitat y áreas de desove de sus adultos, siendo después modulada por las forzantes hidrográficas que caracterizan cada área.

Palabras clave: Asociaciones de larvas de peces, hidrodinámica, Golfo de México

Abstract.- The environmental factors that affect larval fish assemblages in the southern Gulf of Mexico were studied. Samples were collected with a Bongo net from the surface to a depth of 200 m, at 46 sampling stations, during spring 2006. The adult habitat was assigned to each larval fish taxon. Larval assemblages were defined by the Bray-Curtis index. A total of 182 taxa were found, of which most were oceanic, mid shelf and reef. Three assemblages were defined: Yucatan (YA), Tabasco-Campeche (TCA) and Oceanic (OA). The YA was located on the Campeche Bank, the wide Yucatan shelf where the most important hydrodynamic processes is a branch of Yucatan current. The TCA occupied the shelf of Tabasco and the southwestern shelf of Campeche, characterized by the continental freshwater discharge. The OA occupied the oceanic area of Campeche Bay, where the dominant hydrodynamic process is an almost permanent cyclonic gyre. As a result of the different hydrographic features, which are ocean currents, presence of gyres, freshwater discharge, and the topography; the Tabasco shelf, Campeche Bank (Yucatan shelf) and Campeche Bay constitute different regions. They are regions with clearly contrasting environmental scenarios. The geographic distribution of the 3 assemblages fitted well with these 3 hydrodynamically different areas. The structure and spatial distribution of the larval assemblages was determined first by the habitat of the adults and the spawning areas, and then being modulated by the hydrographic features that characterize each area.

Key words: Larval fish assemblages, hydrodynamics, Gulf of Mexico

INTRODUCTION

The composition, abundance and distribution of larval fish assemblages in any area depend first on biological factors such as the structure of adult fish communities, which in turn is conditioned by the characteristics of the habitat and especially on the species reproductive habits that are related to the location and time of spawning, resulting from an evolutionary process aiming at maximizing the survival of the offspring; and the hydrodynamics of the area that constitute a preponderant factor for the planktonic stages, eggs and larvae.

The southern Gulf of Mexico (Campeche Bank and Campeche Bay) presents a great variety of fish habitats that include open ocean areas, continental shelves that receive freshwater discharges, and estuaries and coastal lagoons that provide nursery areas for many fish species.

To this variety of habitats one must add that the hydrodynamics of the region are dominated by several hydrodynamic processes that generate different hydrographic scenarios. Several regions have been identified: Campeche Bank, Veracruz shelf, Tabasco and Campeche shelves and Campeche Bay.

Campeche Bank is a wide shelf north and northwest of the Yucatan peninsula, basically a calcareous area with its western boundary at the Campeche canyon; here the main predominant feature is a westward and southwestward circulation along the northern and western littorals of the peninsula, respectively, throughout the year as result of a branch of the Yucatan current that flows along the Campeche Bank carrying water from the upwelling off Cabo Catoche (Merino 1997, Portilla-Casillas *et al*. 2003, Zavala-Hidalgo *et al*. 2003). In the Campeche Bank there are series of small reefs, some of which have formed islands, and the coastal lagoons adjacent to this shelf have no freshwater discharges or any connection with rivers.

Other region is the Tabasco and Campeche shelf. The Veracruz shelf presents a seasonal circulation that moves southeast from September to March and northwest from May to August, consequently the circulation on the Tabasco and Campeche shelves is affected by the confluence of the northerly current coming from the Campeche Bank and the southerly current coming from the Veracruz shelf during Autumn-Winter (Zavala-Hidalgo *et al*. 2003). In the area the most important hydrodynamic process is the freshwater discharge from the main river-lagoon systems, among which the most important rivers are the Grijalva, Usumacinta, San Pedro y San Pablo and Coatzacoalcos along the Tabasco and southern Veracruz coasts.

A third region is Campeche Bay, which includes the region south of 22°N but excludes the continental shelves, the eastern boundary at the Campeche canyon, the region presents as the main hydrographic feature a semi-permanent cyclonic circulation that covers mainly the southwestern area and also the narrow Veracruz shelf and the most external part of the Campeche and Yucatan shelves (Padilla *et al.* 1990, Salas de León *et al.* 1992, Signoret *et al.* 2006), as well as a weak northward current in its western region, as well as some intermittent anticyclones (Pérez-Brunius *et al.* 2013).

These regions are defined by the forcing that affects them. The winds have a seasonal component in the western Gulf, mostly with northeasters in Autumn-Winter and southeasters in the late Spring and Summer. These winds are the main forcing of the Veracruz shelf currents. On the Campeche Bank, the winds are easterlies throughout the year and are the main cause of the circulation pattern. The cyclonic circulation in Campeche Bay has being attributed to wind stress curl, which is mainly positive in the area, but also to the northern Gulf of Mexico eddies when they interact with the continental slope and move southward (Sutyrin *et al*. 2003, Romanou *et al*. 2004, Vázquez de la Cerda *et al*. 2005).

These and other differences have led to a regionalization of the Gulf of Mexico that has considered a variety of criteria including the sedimentary geology (Araujo-Mendieta *et al*. 2003), irradiance (Callejas-Jiménez *et al*. 2012), chlorophyll concentration (Salmerón-García *et al*. 2011) and hydrological processes (Zavala-Hidalgo & Fernández-Eguiarte 2006).

To date, most studies on the ichthyoplankton in the southern Gulf of Mexico have focused on the region south of 21°N, with many studies restricted to the continental shelves of Tabasco and Campeche (Flores-Coto *et al*. 1988, 2009). Regarding the ichthyoplankton of the Yucatan shelf, there is scarce information (Sánchez-Velasco & Flores-Coto 1994, Falfán-Vázquez *et al*. 2008). The distribution of larvae in the studied area reflects the reproductive strategies of the adults (Flores-Coto *et al*. 1993, Sanvicente-Añorve *et al*. 1998). The part played by the main hydrological factors that affect this distribution, such as the freshwater discharges and the main circulation patterns, has also been analyzed (Sanvicente-Añorve *et al*. 1998, Salas de Leon *et al.* 1998). However, no previous study has included the whole southern Gulf of Mexico to obtain an integral vision of the dominant physical conditions and their effect on the formation of fish larvae communities in the area. Therefore, the goal of this study was to determine the biological and environmental factors that affect larval fish assemblages in the southern Gulf of Mexico.

MATERIALS AND METHODS

The study area lies in the southern Gulf of Mexico between 18º-23ºN and 87º-97ºW (Fig. 1). Biological and physical parameters were collected from May 19 to June 18 2006, aboard the research vessel 'Justo Sierra' of the UNAM from a network of 46 stations.

Temperature and salinity data were recorded with a calibrated CTD probe (III/Woce) and turbidity (Nephelometric Turbidity Units) with a Hach Model 0220 nephelometer (APHA 2005). Abiotic data included in the analyses were those recorded from the surface to 200 m depth, or less depending of the depth of station.

Zooplankton samples were collected with 60 cm mouth diameter and 505 and 333 mm mesh size Bongo nets. The hauls were oblique from the surface to a maximum depth of 200 m or where the depth permitted, each following a circular trajectory at a speed of 2-3 knots. The volume of water filtered was calculated with calibrated flowmeters (General Oceanic, model 2030R) placed at the mouth of each net. Samples were fixed with 4% formaldehyde, buffered with sodium borate. Fish larvae were removed from the 505 mm mesh samples and identified to the species level when possible (Richards 2006, Fahay 2007). Larval abundance was standardized as number of larvae per 100 m^3.

Bray-Curtis dissimilarity index was used to define species assemblages (Bray & Curtis 1957) using data transformed to ln(x+1). A cluster was built from the dissimilarity matrix using the ANACOM program (De la Cruz 1994).

The main species of each assemblage were considered to perform a Canonical Correspondence Analysis, in order to elucidate the possible relationship between species distribution and physical environmental variables. To define the most important species was used 3% of the Importance Value index (IVI) which considers the sum of the abundance and frequency percentage, the final will yield a maximal value of 200%.

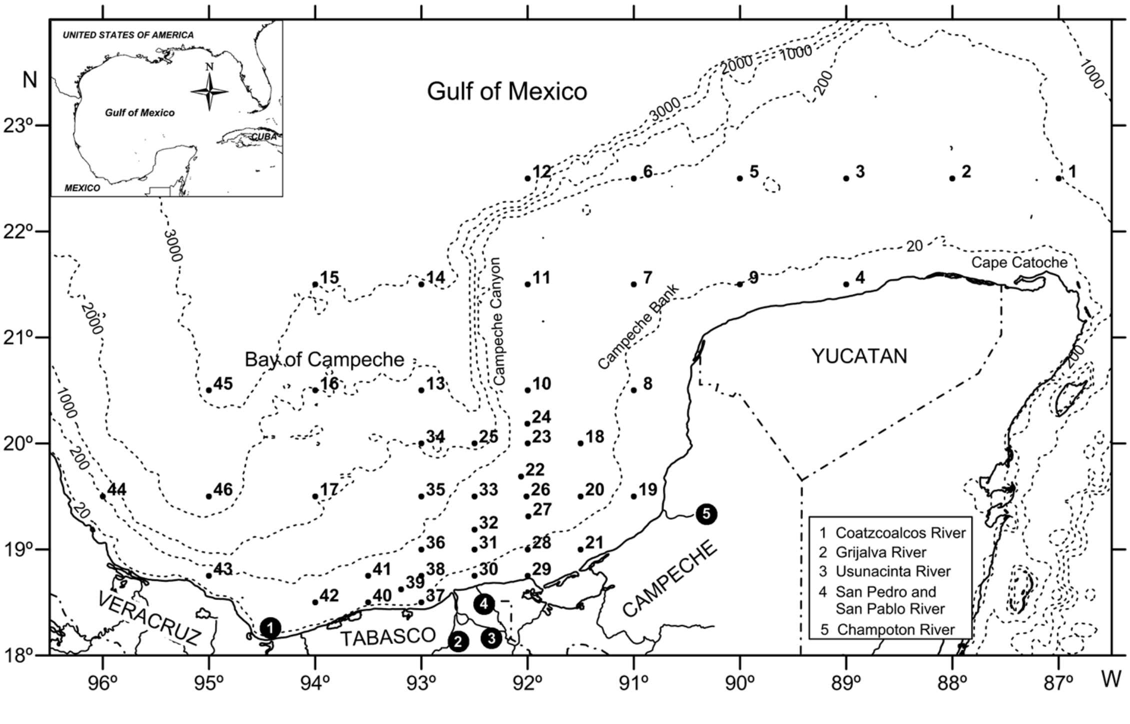

Figure 1. Study area and sampling stations / Área de estudio y estaciones de muestreo

The habitat of the corresponding adults was assigned to each taxon in order to analyze the frequency and abundance of each type in the different assemblages, assuming that there would be differences essentially due to the hydrodynamics of the areas occupied by each assemblage. The habitats considered were neritic, oceanic, outer shelf, reef, mid shelf and coastal. Families (not genera or species) with a very wide distribution were including in the neritic habitat.

Results

Hydrology and circulation

Salinity, temperature, and turbidity data as average of the 200 m surface layer or to the depth that the stations allowed it, were analyzed.

Salinity was very homogeneous throughout most the area, with values around 36.5 in the oceanic area, and 36.75 on the Campeche Bank. This homogeneousness is broken along the Tabasco and south of Veracruz coasts, off the main freshwater discharge systems were the lower salinities were recorded and small area with high values off the Champoton (Fig. 2A).

The lowers temperatures (~23ºC) were recorded on oceanic area of Campeche bay; in contrast, higher values (> 26ºC) occurred over the continental shelf from Veracruz to Campeche, particularly off the Términos Lagoon in a very wide area were the highest were recorded. On the Campeche Bank the temperature fluctuates between 24 and 26ºC, except on the most oriental portion (Fig. 2B).

Turbidity as well as the salinity was very homogeneous, with average values lower on the Yucatan shelf (0.30) and greater on the Campeche-Tabasco shelf (0.44) off the main systems of continental water discharges, and intermediate values in the oceanic area (0.35) (Fig. 2C).

During the sampling period the surface geostrophic currents, estimated from altimetry products generated in the web site of the Colorado Center for Astrodynamics Research[1], show that weak currents occurred, with a predominant minimum pattern in the Campeche Bay associated with a cyclonic circulation and a more intense cyclone (minimum) located in the southwestern region. North of the Bay of Campeche an anticyclone (hgh) is observed. The altimetry over the Campeche Bank is less reliable since is a shallow region and is expected to have a westward circulation as previous studies have reported (Zavala-Hidalgo *et al*. 2003, Enriquez *et al*. 2010) (Fig. 3).

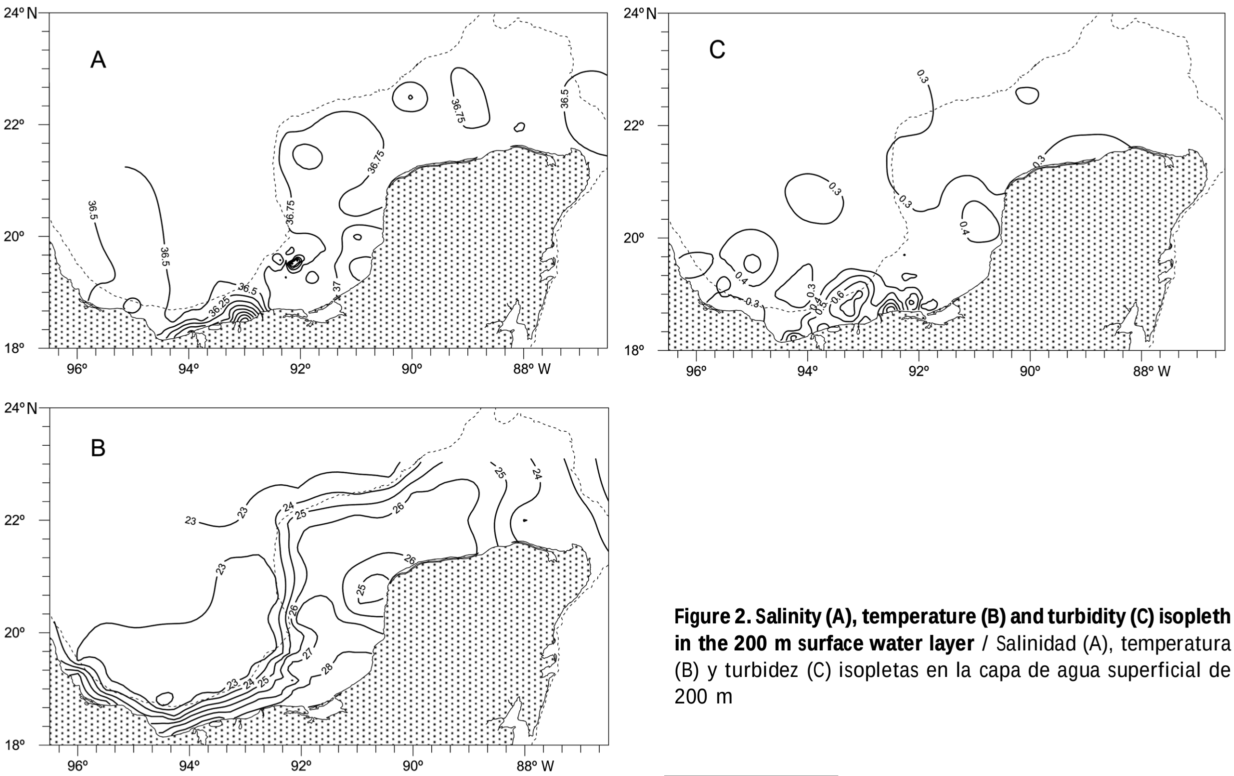

Figure 2. Salinity (A), temperature (B) and turbidity (C) isopleth in the 200 m surface water layer / Salinidad (A), temperatura (B) y turbidez (C) isopletas en la capa de agua superficial de 200 m

[1]<http://eddy.colorado.edu/ccar/ssh/nrt_gom_grid_viewer>

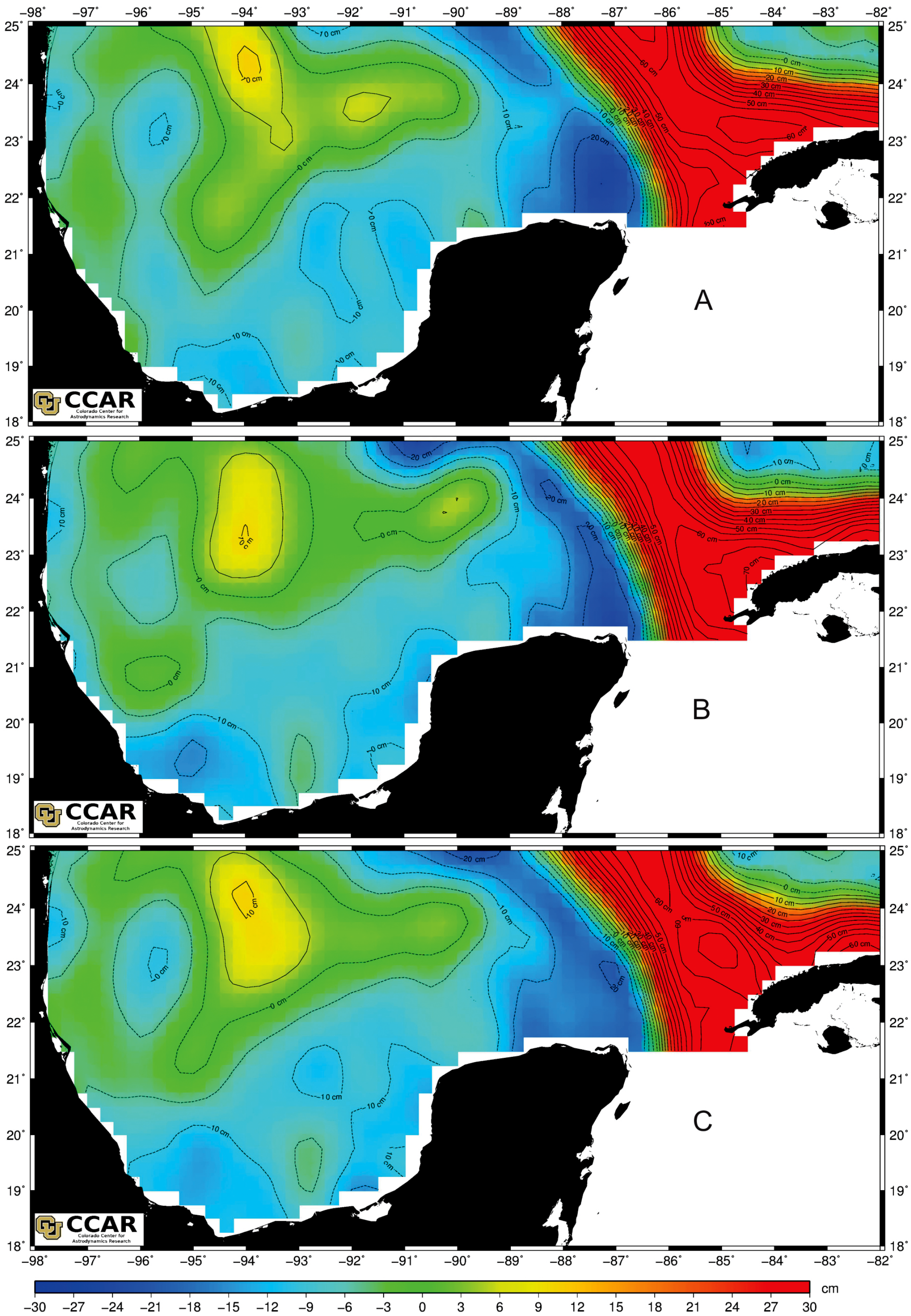

Figure 3. Mesoscale altimetry of the Gulf of Mexico. A) May 15, 2006, B) May 30, 2006, C) June 15, 2006 / Altimetría a mesoescala del Golfo de México. A) Mayo 15, 2006, B) Mayo 30, 2006, C) Junio 15, 2006

Larval composition

A total of 182 taxa were recorded (Table 1) of which, considering the habitat of their adults, most were oceanic (29.6%), mid shelf (26.3%) and reef (25.2%) species and the others were coastal (10.4%), neritic (4.4%) and outer shelf (3.3%) species.

The Bray-Curtis dissimilarity analysis defined 3 assemblages (Figs. 4 and 5): Yucatan assemblage (YA), Tabasco-Campeche assemblage (TCA) and Oceanic assemblage (OA), with geographic distributions that fitted well with 3 different hydrodynamic areas.

The Yucatan assemblage was located in the Campeche Bank, the wide Yucatan shelf with its western boundary at the Campeche canyon. The Tabasco-Campeche assemblage occupied the Tabasco and Campeche continental shelves. The Oceanic assemblage occupied the oceanic area of Campeche Bay with its southern boundary at the continental shelf and its eastern boundary at the Campeche canyon.

The greatest number of taxa was 113 for the TCA and the lowest was 75 for the YA, while 91 taxa were recorded for the OA. The average densities were 103.16, 26.76 and 8.15 ind. 100 m^{-3}, respectively (Fig. 5A).

The results indicate that the percentages for the oceanic, mid shelf and reef habitats for the identified fish larvae taxa were very similar, however, the percentages in the different assemblages varied in relation to the area that each occupied, indicating a predominance of one type of habitat for each (Fig. 6).

Of the 75 taxa recorded for the YA, most corresponded to organisms of reef (36.5%) and mid shelf (33.8%) habitats (Fig. 6A), with 19 exclusive taxa of which 37% were reef organisms (Fig. 6B).

Of the 91 taxa recorded for the OA, more than half (53%) were oceanic and 20% were mid shelf organisms (Fig. 6A), with 48 exclusive taxa of which 83.3% were oceanic organisms. This assemblage presented the lesser density of organisms (Fig. 6B).

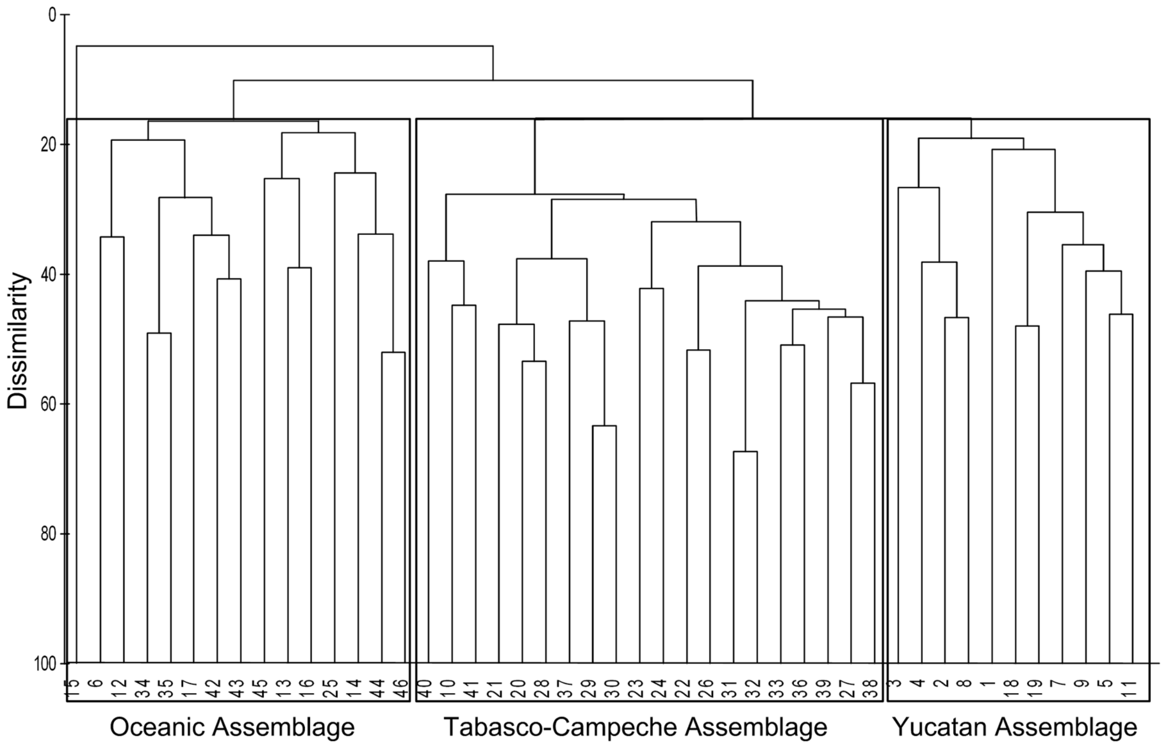

Figure 4. Dissimilarity dendrogram, defining 3 assemblages / Dendrograma de disimilitud, definiendo 3 asociaciones

Of the 113 taxa recorded for the TCA, most were mid shelf (36.6%) and reef (34.0%) organisms (Fig. 6A), with 45 exclusive taxa of which more than 82% were mid shelf, coastal and reef organisms (Fig. 6B).

The most abundant and exclusive species and genera of each assemblage agree the area in which they were found, thus, the most abundant species in the OA were *Notolichnus valdiviae* Brauer, 1904, *Benthosema suborbitale* Gilbert, 1913 and *Diaphus* spp. of the oceanic habitat, together with *Bregmaceros cantori*, Milliken & Houde, 1984 and the most abundant exclusive species, apart from the first two species stated above, were *Symbolophorus rufinus* Tåning, 1928, *Hygophum reinhartii* Lütken, 1892 and *Hygophum hygomii* Lütken, 1892 of the oceanic habitat.

The dominant organisms in the YA, located on the calcareous shelves of Yucatan and Campeche, included the reef species *Pseudogramma gregoryi* Breder, 1927 and *Prionotus* spp., the mid shelf species *Decapterus punctatus* Cuvier, 1829 and *Lutjanus campechanus* Poey, 1860 and the coastal species *Stephanolepis* spp. and *Chloroscombrus chrysurus* Linnaeus, 1766. Among the most abundant exclusive taxa, apart from *Stephanolepis* and *P. gregoryi* already mentioned, were the reef species *Diplogramus pauciradiatus* Gill, 1865 and the mid shelf species *Decapterus* spp.

The dominant organisms in the TCA were the mid shelf species *B. cantori*, *Symphurus plagiusa* Linnaeus, 1766 and *Syacium gunteri* Ginsburg, 1933 and the coastal species *C. chrysurus*, apart from *Anchoa* spp. that has a wide distribution. Among the abundant exclusive taxa, the dominant species were the mid shelf *Diplectrum* spp. and *Selene setapinnis* Mitchill, 1815, the coastal *Cynoscion arenarius* Ginsburg, 1930 and *Micropogonias* spp., and the reef-dwelling *Balistes capriscus* Gmelin, 1789.

Of the 182 taxa, only 25 were present in the 3 assemblages, which is less than 14%. Only 3 oceanic taxa were shared by the YA and the OA. The OA and the TCA shared 15 taxa, most of which were oceanic and mid shelf organisms. The greatest number of shared taxa (28) occurred in the YA and the TCA, most of which were reef, mid shelf and coastal organisms, and none oceanic as may be expected.

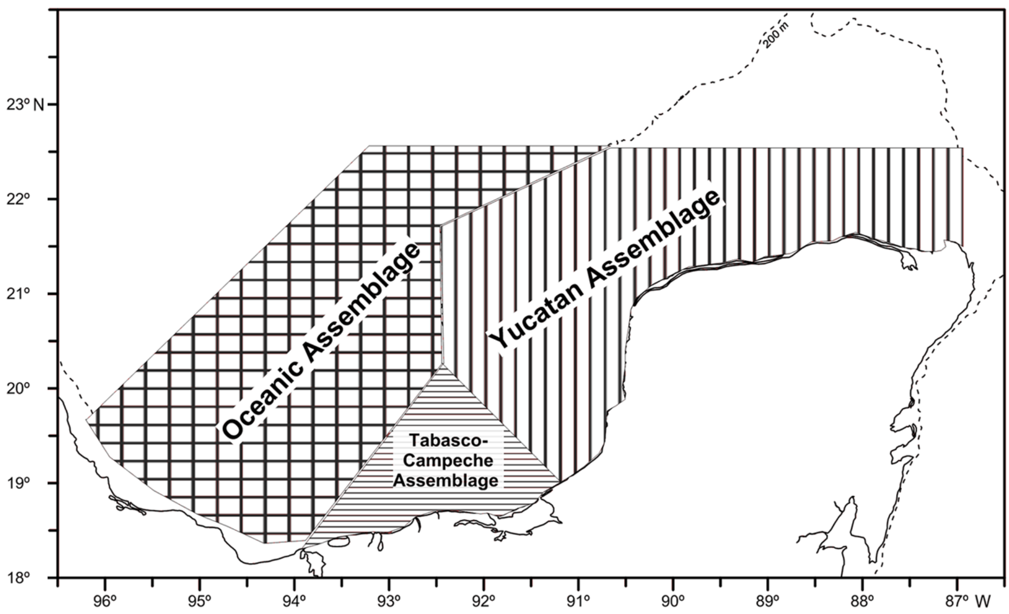

Figure 5. Geographical location of the areas occupied by the assemblages / Ubicación geográfica de las zonas ocupadas por las asociaciones

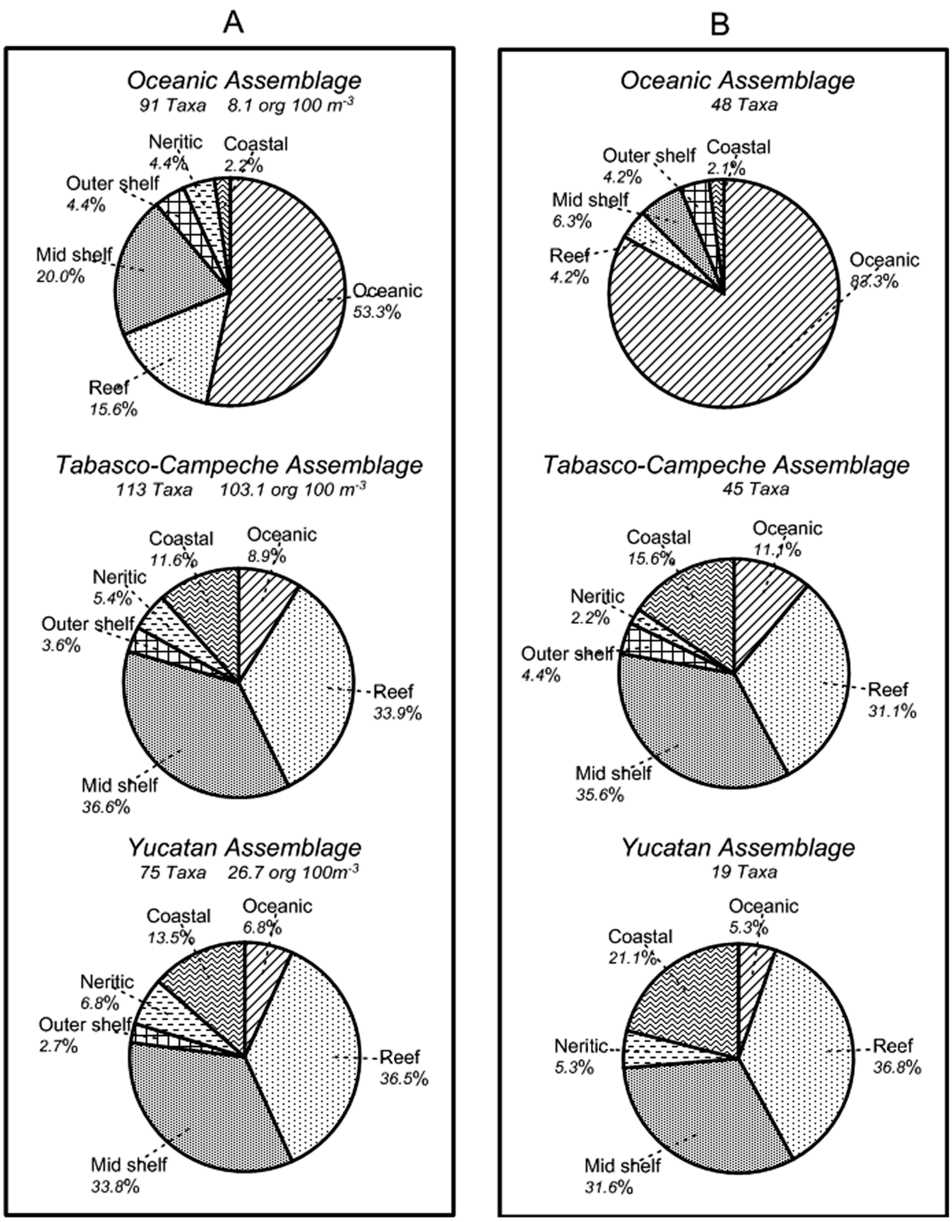

Figure 6. Proportion of habitats represented in each assemblage: A) all taxa, B) taxa exclusive of each assemblage / Proporción de hábitats representados en cada asociación: A) todos los taxones, B) taxones exclusivos de cada asociación

Table 1. Recorded larval fish taxa from the Southern Gulf of Mexico, May, 2006. Habitat (H), Total abundance (Ab), Percentage of total abundance (Ab%) and Frequency (F). Adult taxa habitat: Reef (R), Coastal (C), Neritic (N), Oceanic (O), Mid shelf (MS), Outer shelf (OS) and Undefined (X) / Taxones de larvas de peces registrados en el sur del Golfo de México, mayo de 2006. Hábitat (H), abundancia total (Ab), porcentaje de abundancia total (Ab%) y frecuencia (F). Hábitat de los taxones adultos: Arrecife (R), Costero (C), Nerítico (N), Oceánico (O), de plataforma media (MS), plataforma externa (OS) y no definido (X)

Taxa	H	Ab	Ab%	F
Gobiidae	X	4372.2	23.360	40
Anchoa spp.	N	2648.4	14.150	14
Chloroscombrus chrysurus	C	1455.9	7.779	15
Clupeidae	N	1112.4	5.944	21
Bregmaceros cantori	OS	874.3	4.671	22
Gerreidae	N	491.4	2.625	22
Symphurus plagiusa	OS	294.4	1.573	12
Syacium gunteri	OS	217.3	1.161	17
Stephanolepis spp.	C	188.3	1.006	1
Lutjanus campechanus	OS	174.8	0.934	17
Decapterus punctatus	OS	149.9	0.801	11
Cynoscion arenarius	C	137.4	0.734	7
Diplectrum spp.	OS	123.5	0.660	10
Selene setapinnis	OS	122.5	0.654	11
Serranidae	N	115.6	0.618	6
Trachurus lathami	OS	99.4	0.531	19
Balistes capriscus	C	92.1	0.492	16
Cyclopsetta fimbriata	OS	91.4	0.488	13
Selar crumenophthalmus	OS	91.1	0.487	19
Labridae	R	83.4	0.445	11
Diaphus spp,	MS	71.4	0.381	20
Syacium papillosum	OS	65.3	0.349	11
Prionotus spp.	R	59.0	0.315	8
Syacium spp.	OS	51.3	0.274	7
Diplectrum t - 1	OS	45.0	0.240	4
Callionymidae	R	39.2	0.210	11
Sphyraena guachancho	C	37.3	0.199	13
Anguilliformes	R	37.1	0.198	10
Lepophidium spp.	OS	35.4	0.189	10
Micropogonias spp.	C	32.3	0.173	3
Microdesmus longipinnis	OS	30.8	0.165	9
Mugilidae	OS	29.9	0.160	4
Aluterus spp.	R	29.6	0.158	10
Saurida brasiliensis	MS	28.8	0.154	3
Apogonidae	R	28.5	0.153	7
Synodus spp.	R	28.4	0.152	7
Bothus ocellatus	OS	26.3	0.140	15
Pseudogramma gregori	R	24.6	0.132	1
Citharichthys spp.	OS	23.8	0.127	3
Serranus spp.	OS	22.1	0.118	11
Microdesmus bahianus	OS	21.9	0.117	8

Taxa	H	Ab	Ab%	F
Auxis spp.	OS	20.2	0.108	7
Ophidion spp.	R	19.0	0.101	7
Prionotus evolans	R	18.1	0.096	5
Decapterus spp.	OS	17.3	0.093	1
Rhomboplites aurorubens	OS	17.2	0.092	5
Citharichthys spilopterus	OS	17.0	0.091	3
Lutjanus spp.	OS	16.5	0.088	3
Synodus foetens	R	16.4	0.088	5
Scarus spp.	R	15.6	0.083	4
Diodontidae	R	15.2	0.081	7
Notolychnus valdiviae	O	14.6	0.078	6
Mullidae	R	14.2	0.076	7
Lepophidium t -1	OS	13.6	0.073	3
Benthosema suborbitale	O	12.4	0.066	7
Chromis spp.	R	11.7	0.063	1
Selene spp.	OS	11.4	0.061	3
Auxis rochei	OS	10.7	0.057	3
Diplectrum t - 2	OS	10.6	0.057	4
Ceratoscopelus warmingii	O	10.3	0.055	5
Carangidae	N	10.2	0.054	3
Lampadena spp.	O	9.3	0.050	2
Bairdiella chrysoura	C	9.2	0.049	3
Scorpaenidae	R	9.0	0.048	7
Etropus crossotus	C	8.8	0.047	4
Synodus poeyi	R	8.6	0.046	2
Cyclothone spp.	O	8.4	0.045	5
Cyclothone braueri	O	7.9	0.042	6
Menticirrhus spp.	C	7.8	0.042	2
Ophidion nocomis	R	7.7	0.041	3
Pomacentridae	R	7.7	0.041	2
Ophichthus cruentifer	MS	7.6	0.041	6
Opistognathidae	R	7.5	0.040	3
Tetraodontidae	R	7.4	0.040	3
Stellifer lanceolatus	C	7.3	0.039	1
Citharichthys gymnorhinus	OS	7.3	0.039	3
Diogenichthys atlanticus	O	7.2	0.038	3
Aluterus scriptus	R	7.2	0.038	1
Symbolophorus rufinus	O	7.1	0.038	4
Euthynnus alletteratus	OS	7.0	0.037	5
Peprilus alepidotus	C	7.0	0.037	3
Balistidae	R	6.7	0.036	2

Taxa	H	Ab	Ab%	F
Diplogrammus pauciradiatus	R	6.2	0.033	1
Engyophrys senta	OS	6.0	0.032	4
Hygophum reinhardtii	O	5.6	0.030	5
Etropus spp.	C	5.6	0.030	1
Monacanthidae	R	5.5	0.029	2
Myctophum nitidulum	O	5.4	0.029	5
Micropogonias undulatus	C	5.2	0.028	1
Hygophum hygomii	O	5.1	0.027	2
Myrophis punctatus	O	4.9	0.026	2
Oligoplites saurus	C	4.7	0.025	3
Mugil spp.	OS	4.7	0.025	4
Scomberomorus cavalla	OS	4.6	0.025	5
Myctophum asperum	O	4.6	0.025	3
Gonostoma atlanticum	O	4.6	0.025	4
Decapterus macarellus	OS	4.6	0.024	2
Sternoptyx spp.	O	4.5	0.024	2
Gonostomatidae	O	4.4	0.023	3
Myctophidae	O	4.3	0.023	2
Caranx crysos	OS	4.1	0.022	3
Anguillidae	R	4.0	0.021	4
Apogon spp.	R	3.8	0.020	3
Parablennius marmoreus	R	3.7	0.020	1
Clepticus parri	R	3.6	0.019	1
Bregmaceros atlanticus	O	3.6	0.019	4
Hygophum macrochir	O	3.6	0.019	2
Microdesmus carri	OS	3.6	0.019	1
Lepidophanes guentheri	O	3.5	0.019	2
Percophidae	O	3.4	0.018	2
Ariommatidae	MS	3.4	0.018	1
Ophidion selenops	R	3.4	0.018	2
Belonidae	R	3.2	0.017	1
Sparisoma spp.	R	3.2	0.017	3
Notoscopelus spp.	O	3.0	0.016	2
Vinciguerria nimbaria	O	3.0	0.016	3
Trichiurus lepturus	OS	3.0	0.016	3
Sphaeroides spp.	R	2.9	0.016	3
Hygophum taaningi	O	2.8	0.015	2
Ophidiidae	R	2.8	0.015	3
Myctophum affine	O	2.8	0.015	3
Trichopsetta ventralis	OS	2.8	0.015	1
Katsuwonus pelamis	O	2.8	0.015	1

Table 1. Continued / Continuación

Taxa	H	Ab	Ab%	F
Vinciguerria poweriae	O	2.7	0.014	2
Heteropriacanthus cruentatus	R	2.5	0.014	1
Cynoscion nothus	C	2.4	0.013	2
Paralepididae	O	2.2	0.012	2
Auxis thazard	OS	2.1	0.011	1
Citharichthys arctifrons	OS	2.0	0.011	2
Epinephelus spp.	OS	1.9	0.010	2
Scombridae	N	1.9	0.010	2
Lestidiops affinis	O	1.9	0.010	2
Thunnus spp.	O	1.9	0.010	2
Myctophum selenops	O	1.8	0.009	2
Caranx spp.	OS	1.7	0.009	1
Sphyraena spp.	C	1.7	0.009	1
Fistularidae	N	1.7	0.009	2
Polynemidae	C	1.6	0.009	1
Symphurus spp.	OS	1.6	0.009	1
Vinciguerria attenuata	O	1.6	0.008	1
Chauliodus sloani	O	1.6	0.008	1
Aluterus schoepfii	R	1.5	0.008	1
Ostraciidae	R	1.5	0.008	1
Myctophum spp.	O	1.4	0.007	1
Cerdale floridana	R	1.2	0.007	1
Scombreromorus regalis	OS	1.2	0.007	1
Chasmodes spp.	C	1.2	0.006	1
Bythitidae	R	1.2	0.006	1
Valenciennellus tripunctulatus	O	1.2	0.006	1
Liopropoma spp.	OS	1.1	0.006	2
Caulophrynidae	O	1.1	0.006	1
Exocoetidae	N	1.1	0.006	1
Carapidae	OS	1.1	0.006	1

Taxa	H	Ab	Ab%	F
Ogcocephalidae	R	1.0	0.006	1
Rypticus spp.	R	1.0	0.006	1
Scomberomorus maculatus	OS	1.0	0.006	1
Maurolicus muelleri	O	1.0	0.005	1
Haemulidae	R	1.0	0.005	1
Melanostomiidae	O	1.0	0.005	1
Etropus microstomus	C	1.0	0.005	1
Pollichthys mauli	O	1.0	0.005	1
Leptostomias spp.	O	1.0	0.005	1
Coryphaena spp.	O	1.0	0.005	1
Albuliformes	R	1.0	0.005	1
Gonostoma elongatum	O	0.9	0.005	1
Vinciguerria spp.	O	0.9	0.005	1
Idiacanthus fasciola	O	0.9	0.005	1
Centrobranchus nigroocellatus	O	0.9	0.005	1
Acropomatidae	MS	0.9	0.005	1
Ophidion marginatum	R	0.9	0.005	1
Coryphaena equiselis	O	0.9	0.005	1
Pontinus spp.	R	0.9	0.005	1
Hygophum spp.	O	0.9	0.005	1
Canthigaster rostrata	R	0.8	0.005	1
Scopelarchus spp.	O	0.8	0.004	1
Lepidophanes spp.	O	0.8	0.004	1
Scopelarchus analis	O	0.8	0.004	1
Macroparalepis affinis	O	0.8	0.004	1
Macroparalepis brevis	O	0.8	0.004	1
Diaphus rafinesquii	MS	0.8	0.004	1
Argyropelecus spp.	O	0.8	0.004	1
Myctophum obtusirostre	O	0.8	0.004	1

With 37 taxa as resulting of 3% of IVI, a CCA was performed. The distribution of taxa in relation to the axes show 3 groups which nearly correspond to the 3 assemblages taxa, aside of those which share among them (Fig. 7). The CTA taxa were related with high temperature and turbidity, as *S. setapinis*, *B*, *crapisicus*, *S. guachancho*, *S. plagiusa*, *C. arenarius*, among others. In contrast, the OA taxa appear related to low temperature and turbidity as *B. atlanticus*, *M. asperum*, *H. reinhartii*, *B. suborbitale*, *G. atlanticum*, *S. rufinus*, among others. The YA taxa seem to be more related with low turbidity and high salinity, as *P. gregoryi*, *D. punctatus*, *Serranus* spp., and *L. campechanus* (Fig. 7).

Discussion

Assemblages and regionalization

The 3 fish larvae assemblages defined by the similarity analysis (YA, TCA and OA) showed a geographic distribution that fitted well with the 3 different areas resulting from hydrological processes (Zavala-Hidalgo & Fernández-Eguiarte 2006), which it could be mean that, together with the biological aspect that corresponds to the habitat of the adults and their reproductive habits, the assemblages were strongly affected by the dominant hydrodynamics in each area, as occur in other parts of the world (Alemany *et al*. 2006, Sabates *et al*. 2007).

The CCA helps to support this idea, since it allows to distinguish groups of taxa affected to a greater or lesser extent by some of the hydrographic parameters analyzed; therefore, OA taxa are related to low temperatures, which are commonly recorded in the oceanic area of the Campeche Bay and contrast with those of the adjacent continental shelf (Monreal-Gomez *et al*. 1992). On the other hand, the taxa of the TCA appear linked at high temperatures and especially to high turbidity which makes sense if we know that the location of this assemblage is exactly off the main download area of inland waters

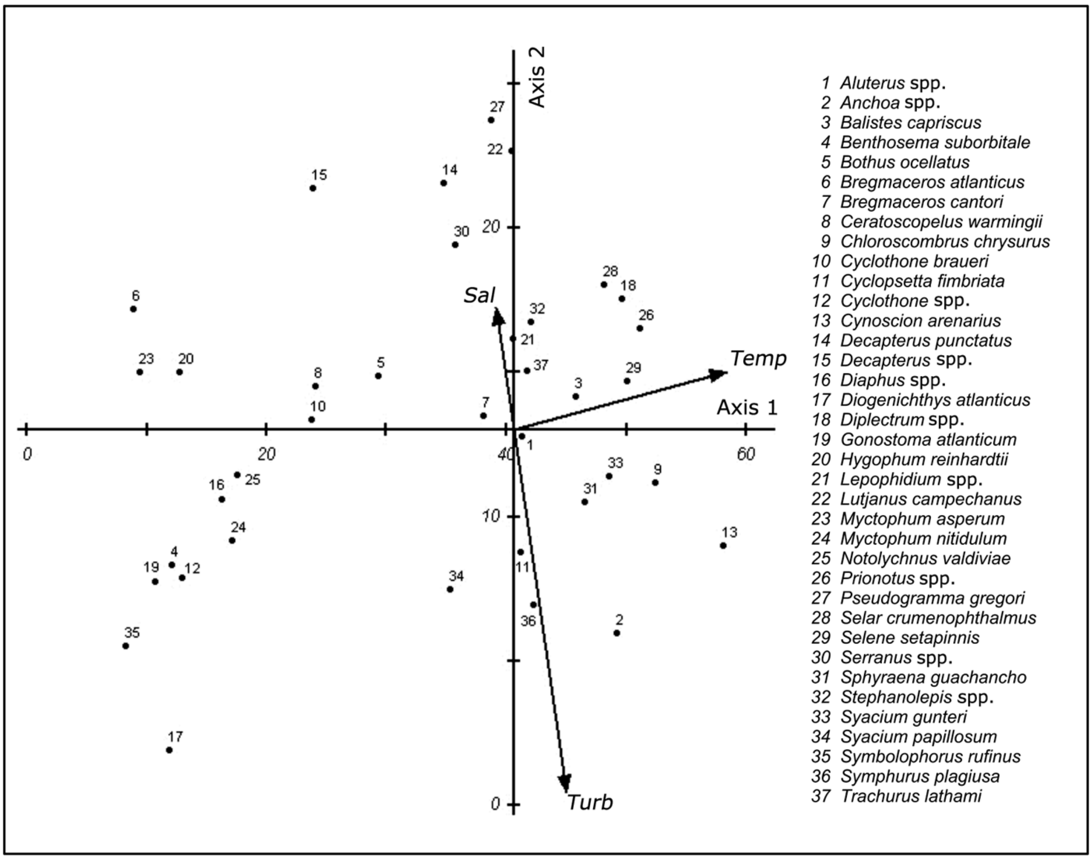

Figure 7. Canonical correspondence analysis biplot of the most abundant and frequent taxa (IVI >3%) from the Oceanic, Tabasco-Campeche and Yucatan assemblages, defined by dissimilarity analysis / Análisis Canónico de Correspondencia de los taxones más abundantes y frecuentes (IVI >3%) de las asociaciones Oceánica, Tabasco-Campeche y Yucatán,

carrying large amount of sediments and organic matter, which consequently creates areas of low concentration of oxygen, as showed by Padilla-Pilotze *et al.* (1990). Taxa of YA appear related to high salinity and low turbidity, which seems a logical condition if we know that the waters covering the Yucatan shelf are a branch of the Yucatan current with more oceanic that coastal character (Merino 1997, Mühling *et al.* 2013)

The composition and distribution of fish larvae species in Campeche Bank and Campeche Bay depend first on the habitat and the reproductive strategies of the adults, which include the spawning areas (Flores-Coto *et al.* 1988, 1993, Sanvicente-Añorve *et al.* 2000, Espinosa-Fuentes & Flores-Coto 2004). This is a general fact worldwide (Rakocinski *et al.* 1996, Sabatés & Olivar 1996, Miller 2002, Marancik *et al.* 2005, Sabatés *et al.* 2007), for which the complement establishing differences among the assemblages are the factors that determine the hydrodynamics of each region.

These and other differences have led to a regionalization of the Gulf of Mexico that has considered a variety of criteria including the sedimentary geology (Araujo-Mendieta *et al.* 2003), irradiance (Callejas-Jiménez *et al.* 2012), chlorophyll concentration (Salmerón-García *et al.* 2011) and hydrodynamical processes (Zavala-Hidalgo & Fernández-Eguiarte 2006).

However, the best fit for the 3 assemblages corresponded closely to areas 2, 3 and 6 of the regionalization proposed by Zavala-Hidalgo & Fernández-Eguiarte (2006) (Fig. 8), though there is also a close correspondence between the physiographic provinces (Araujo-Mendieta *et al*. 2003) formed over thousands of years and the assemblages recorded here. This must also mean that the hydrographic factors that determine the distribution patterns of fish larvae have prevailed over thousands of years.

Boundaries and interactions of the areas of the assemblages

The interaction that takes place among areas makes their geographic boundaries dynamic, as may be seen in the records of oceanic organisms on the Yucatan, Campeche and Tabasco shelves and of mid shelf organisms in the oceanic region. The common and shared taxa indicate that advection, diffusion and dispersion processes generated a greater interaction between the Yucatan assemblage and the Tabasco-Campeche assemblage, and a lesser interaction between these and the oceanic community. In particular, the boundary between the YA and OA, TCA coincides with the type of sediment on the shelves, as they are calcareous on the Campeche Bank and terrigenous off Tabasco (Ayala-Castañares & Gutiérrez-Estrada 1990).

Previous studies carried out in the region (Flores-Coto *et al*. 1988, 1993, 2009; Sanvicente-Añorve *et al*. 1998, Espinosa-Fuentes & Flores-Coto 2004) have shown that there is an area where the oceanic and neritic populations mix. This area is located along the continental slope, but may extend towards the mid shelf or the oceanic area.

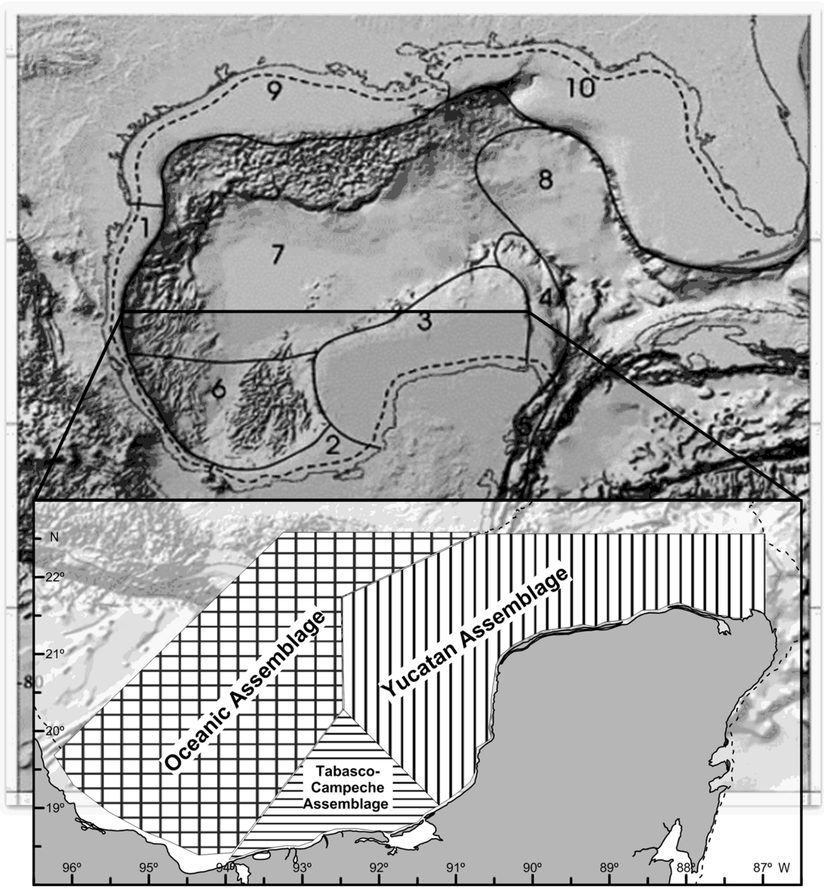

Figure 8. Comparative geographical areas in the hydrographical regionalization (Zavala-Hidalgo & Fernández-Eguiarte 2006) and the assemblages defined in this study / Áreas geográficas comparativas en la regionalización hidrográfica (Zavala-Hidalgo & Fernández-Eguiarte 2006) y las asociaciones definidas en el presente estudio

However, the low number of oceanic taxa in neritic assemblages indicates a low influence of the oceanic community on the neritic communities. In addition, the Campeche Bank current always follows westward direction and may reach the Tabasco shelf, thus, it must have a greater influence on the oceanic and Campeche-Tabasco communities than the other way round, which explains the relatively high number of reef taxa in these communities, considering that the reefs are found only on the Campeche Bank (Carricat-Ganivet & Horta-Puga 1993, Oliver *et al*. 2004). It may be that many larvae of reef dwelling parents use the westward currents to occupy the area of the Tabasco-Campeche communities as a nursery area and, as juveniles, return to the reefs on the Yucatan shelf and part of the Campeche shelf.

Important factors that generate boundaries between the assemblages are the gyres in Campeche Bay. The importance of the gyres regarding the distribution of planktonic organisms in the area may seem obvious, and has already been mentioned by Salas *et al*. (1998). However, the role that they play in Campeche Bay may be emphasized, as they limit the movement of coastal marine sediments towards the center of the Gulf bringing a recirculation within the bay (Gutiérrez-Estrada *et al*. 2003), and it may be assumed that this also happens with fish larvae and other planktonic organisms.

The gyre in Campeche Bay reaches the narrow shelves of Veracruz and western Tabasco, while it does not reach the inner Yucatan shelf or does so to a lesser degree, and it generates a boundary for the neritic waters at the continental slope off Tabasco and Campeche (Salas *et al*. 1992, 1998, Vidal-Lorandi *et al*. 2003, Signoret *et al*. 2006).

Boundaries are also generated by the freshwater discharges in the southern Gulf of Mexico. Several authors have recorded the presence of a front that may be detected in an almost permanent horizontal salinity gradient (Czitrom *et al*. 1986, Shirasago 1991, Monreal-Gómez *et al*. 1992).

The distribution of the salinity, temperature and turbidity values recorded in this study, though not establishing clear boundaries between the areas occupied by each assemblage, did present a close correspondence with them. In particular, the area with the lowest temperatures fitted well with the OA, and the area with the greatest turbidity, and to a lesser degree the lower salinity values, corresponded to the area occupied by the TCA. It is the combination of the circulation patterns, water properties and type of sediments which explains the region differences.

Persistence of the assemblages

The low number of shared taxa and the difference in the density of the more abundant taxa reflect the persistence of each assemblage in its respective area, where hydrodynamics play an important role, since the collision of currents and gyres generate hydrographic convergences, such as fronts, that act as barriers and restrict the movement of organisms from one area to another (Sabatés & Olivar 1996).

No one factor by itself can be considered as determinant of the formation, location and persistence of any assemblage, it must be the sum of the partiality of each factor. Obviously, seasonal changes of water masses, currents, vertical mixing intensity of processes will determine the final pattern of the distribution of the assemblages (Alemany *et al*. 2006, Sabates *et al*. 2007, Mühling *et al*. 2013).

Converging fronts overcome diffusive and advective flows (Miller 2002) and help maintain the assemblages within their areas. It must be understood that, notwithstanding that the larvae have a limited capacity to swim, they are not passive particles and thus 'ichthyoplanktonic assemblages may reflect larval behavioral responses to environmental signals' (Miller 2002).

It may be summarized that, apart from the different boundaries and interactions between the areas where the three assemblages were located, their formation was determined first by the habitat and spawning area of the adults, and next by the dominant physical factors that generate boundaries in each area and allow the formation of individual assemblages.

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