

A suggested local regions in the Southern Gulf of Mexico using a diatom database (1979-2002) and oceanic hidrographic features

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Abstract

A diatom data-base of 255 species obtained from 14 oceanographic cruises (14801 entries of 647 sampling sites) together with the analysis of oceanic features were used to establish four local regions in the southern Gulf of Mexico. In addition, common species for each region were designated. This study is based on the application of cluster analysis and the species frequency data. Material for this undertaking consisted of water and net samples obtained between June 1979 and December 2002. Results show that the most frequent species (> 40%) were: *Asterionellopsis glacialis*, *Bacteriastrum delicatulum*, *B. hyalinum*, *Chaetoceros affinis*, *C. coarctatus*, *C. compressus*, *C. curvisetus*, *C. danicus*, *C. decipiens*, *C. diversus*, *C. lorenzianus*, *C. pelagicus*, *C. peruvianus*, *Coscinodiscus radiatus*, *Cylindrotheca closterium*, *Guinardia flaccida*, *Hemiaulus hauckii*, *H. membranaceus*, *H. sinensis*, *Leptocylindrus danicus*, *Neocalyptrella robusta*, *Nitzschia bicapitata*, *Pleurosigma diverse-striatum*, *Proboscia alata*, *Pseudo-nitzschia pungens*, *Pseudosolenia calcar-avis*, *Rhizosolenia imbricata*, *R. setigera*, *Skeletonema costatum*, *Thalassionema bacillare*, *T. frauenfeldii*, *T. nitzschoides* and *Thalassiosira eccentrica*. The species composition for each region and season are discussed. It is concluded that sampling site assemblages are related to oceanographic conditions. A total list of species composition is given, forty-seven species taxa being new records for this area.

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Introduction

It is well known that diatoms are the dominant world-wide group; however, there are few records on the systematic and distribution in the southern Gulf of Mexico and contiguous waters. Although diatoms are powerful indicators of environmental conditions, there is still a need to fill with respect to the global knowledge in this region since they have provided valuable information for many years to determine climate variation and water quality (Rabalais *et al.*, 2001). This is important to consider since the southern Gulf of Mexico is highly productive and the oil industry makes this region economically critical because of the constant effluents of

untreated water into this region, the continuous oil spills and the presence of toxic substances (Ponce-Vélez and Botello, 2005).

Early diatom investigations in the southern gulf were undertaken for the first time by Adolf Schmidt, who in his *Atlas der Diatomacenkunde* (1874-1959) listed 319 taxa for this region. Later on, during the Soviet and Soviet-Cuban expeditions in the period of 1960-1980s there were several contributions summarized by Okolodkov (2003). However, in most of these studies, diatoms are mentioned only as a check list with no details. Recently Moreno-Ruiz *et al.* (1993); Moreno and Licea (1994); Licea (1994); Hernández-Becerril (1998), Hernández-Becerril and Flores (1998) and

Hernández-Becerril *et al.* (2008) have made concentrated efforts to describe on diatoms. Kravesky *et al.* (2009) have compiled a diatom list of 1000 species for the whole of the Gulf of Mexico; however, as they themselves have pointed out, many of these taxa need revision.

This study attempts to make a regionalization of the southern gulf by setting spatial bounds using diatom species. A first approach is to explore the use of cluster analysis in the field of species composition in order to understand the complexity of ecosystems in the study area. Our aim is to characterize the regions, as well as, their relationship with the oceanographic conditions referred to in the literature.

Materials and Methods

Study area: It is located in the southern Gulf of Mexico, between 18°15' and 24°05' N, and 86°12' and 97°38'. According to García (1973), the climate is warm sub-humid with rainy summers. Hydrographic conditions in the Southern Gulf of Mexico are highly influenced by the Loop Current (LC) and the Loop Current Rings (LCR) as well as by the occurrence of winter storms between October and April whose winds contribute to the cooling and mixing of the surface water column in this region. The presence of cold winds known locally as "Nortes" (Northwinds) cause the formation of cold

fronts that generate intense winds between October and April (Tapánes and González-Coya, 1980; Alatorre *et al.*, 1987).

A great number of water masses occur in the Gulf of Mexico; however, for the purpose of this study only the ones that affect the shelf of the southern region will be considered: The Caribbean Subtropical Subsurface Water (CSSW) is warm and salty (22.5°C and 36.6 psu, respectively); on its arrival at the Gulf of Mexico (GM) through the Yucatan Canal it forms the Loop Current that frequently encloses an anticyclonic gyre that flows clockwise; The Gulf of Mexico Subtropical Surface Water (GMSSW) is formed inside the gulf during winter when the cold atmospheric fronts cause the lowering of temperature and salinity. The Common Gulf Water (CGMW) is formed inside the gulf through two mechanisms: by convective mixing and the collision of the anticyclonic gyre with the continental shelf of Tamaulipas near the Mexican border creating a zone of horizontal divergence and convergence (Monreal-Gómez *et al.*, 2004).

This region has a predominantly cyclonic circulation mainly associated with the Yucatan Canal waters (Merrel and Morrison, 1981). Monreal-Gómez and Salas de León (1990) confirmed the presence of cyclonic gyres in a westerly direction that persist in the whole region from February until March and tend to vanish in April.

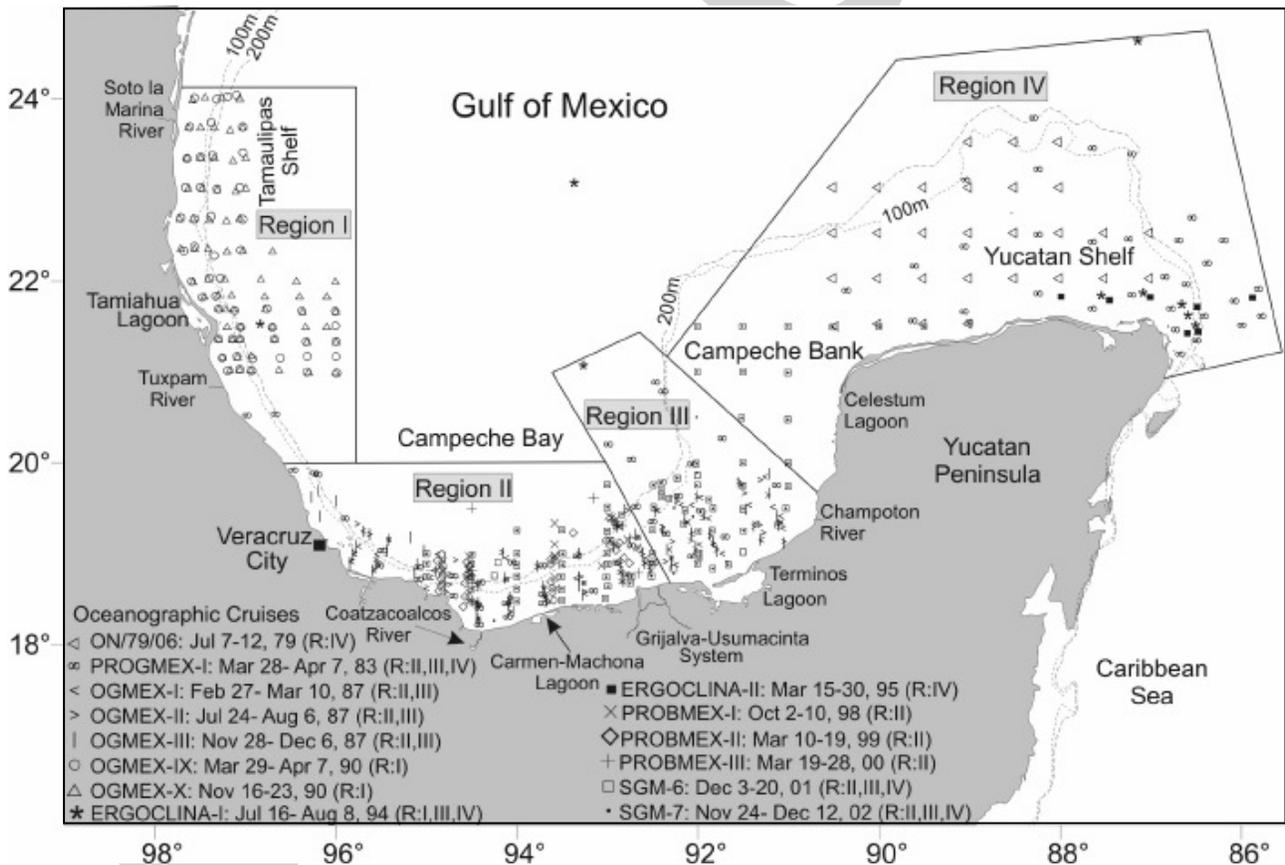


Fig. 1: Site locations of 14 oceanographic cruises in the southern Gulf of Mexico (647 sampling sites). The geographic regions were established on the base of cluster analyses of the diatom species composition and frequency. Parentheses indicate sampling of covered regions

In May the gyre disappears, and the circulation changes from east to west. The cyclonic gyre sets in in August and September throughout the whole region and lasts until December. In addition, the dominant cyclonic circulation and river-fronts create a dynamic system which gives this region a unique ecological condition. Besides, the rivers Coatzacoalcos and the Grijalva-Usumacinta (GU) represent approximately one-third of all fluvial discharges onto the Mexican coast in the southern Gulf (Tamayo 1990). There are several coastal lagoons that stand out for their estuarine outwelling to the coast. Additional information is found in López-Veneroni and González Lozano (2009) and Salas de León *et al* (2009).

The Yucatan Shelf is highly influenced by the upwelling that is north of Cape Catoche (Cochrane, 1969; Merino, 1997). Another significant feature is the shelf width around the peninsula which extends seaward for over 260 km, thus making it the widest continental shelf in the Caribbean region. In contrast, in the Caribbean margin, the shelf is very narrow (3 km wide), which causes water to upwell onto this shelf, where the water remains trapped within its euphotic zone for long periods; this might very well increase the fertilizing potential in this area (Furnas and Smayda, 1987; Pérez *et al.*, 1999). One part of the upwelled waters flows toward the west, leaving the shelf near the Alacranes Reef while the other part moves toward the coast, forming a cyclonic circulation to the north of Cape Catoche.

Sampling analyses: This study is based on a relational data-base obtained by the authors who studied the 255 species of diatoms with 14801 entries obtained during long-term oceanographic surveys in the Southern Gulf of Mexico (projects: PROGMEX, OGMEX and SGM). For this investigation, 14 oceanographic cruises were selected. Surveys were carried out on board the R/V *JUSTO SIERRA* between March 1983 and November 2002, with the exception of the cruise ON/79/06 in July 1979. The stations occupied during these cruises are shown in Figure 1 (647 sites were sampled). Vertical net tows were made at each station with a 30 and 45 μm mesh net and were preserved with 2% buffered formalin. Water samples were occasionally taken and fixed in Lugol's solution for the analysis on an inverted microscope. The sampling collection used for qualitative analyses is housed at the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (Collection: MEXU-UNAM). The species list with nomenclatural authorities was arranged alphabetically (Table 1)

Based on the presence/absence of the diatoms species of each cruise, several Cluster Analyses (CA) were carried out following Ward's method and Euclidean Distances (Everitt, 1993). Previously, the information of the species composition and the sampling collection dates was arranged according to the climatic characteristics in the study area by applying the criterion of Manzano-Sarabia and Salinas-Zavala (2008) and Yañez-Arancibia and Day (1982), who consider the dry season from November to April, the rainy season from May to September and the northwind season from October to March. The material used for each season of the year was: dry season (six cruises); rainy season (three cruises, there were only one sample

for Region I) and northwind season (five cruises). Unfortunately, none of the cruises was surveyed simultaneously covering the whole area; in the best case, three regions were covered in four cruises; on the other hand, some sampling sites changed in different cruises. The cluster analyses of figures 2-4 were the basis for establishing the regions indicated in figure 1. In addition, the criteria of Levin *et al.* (2001) and Longhurst (2007) were taken into account. The use of frequency was used as a complementary tool.

Results and Discussion

Diatom species composition: Table 1 shows the species used for this investigation, of which the most common genera were *Chaetoceros* (36 spp), *Thalassiosira* (20 spp), *Nitzschia* (18 spp) and *Rhizosolenia* (14 spp). Frequency data show that they were found widely distributed in the area. As can be seen, 204 species were found during the northwind season; 96 species were seen during the rainy season and 78 species were found throughout the year. A general view of the community revealed that the most frequent species (> than 40 % of relative frequency) were: *Asterionellopsis glacialis*, *Bacteriastrium delicatulum*, *B. hyalinum*, *Chaetoceros affinis*, *C. coarctatus*, *C. compressus*, *C. curvisetus*, *C. danicus*, *C. decipiens*, *C. diversus*, *C. lorenzianus*, *C. pelagicus*, *C. peruvianus*, *Coscinodiscus radiatus*, *Cylindrotheca closterium*, *Guinardia flaccida*, *Hemiaulus hauckii*, *H. membranaceus*, *H. sinensis*, *Leptocylindrus danicus*, *Neocalyptrella robusta*, *Nitzschia bicapitata*, *Pleurosigma diverse-striatum*, *Proboscia alata*, *Pseudo-nitzschia pungens*, *Pseudosolenia calcar-avis*, *Rhizosolenia imbricata*, *R. setigera*, *Skeletonema costatum*, *Thalassionema bacillare*, *T. frauenfeldii*, *T. nitzschoides* and *Thalassiosira eccentrica*.

Our results related to the species composition of the southern gulf agree well with the species reported by other authors in this study area (Khromov, 1969; Conger *et al.*, 1972; Krylov, 1974; Licea 1977, 1994; Hernández-Becerril *et al.*, 2008; Krayesky *et al.*, 2009). Most of the identified species correspond to neritic species, temperate and subtropical of cosmopolitan distribution according to Polat *et al* (2000).

Regions and site associations: To attempt to establish ecological regions at the sea is a difficult task since there are many factors involved besides the controversies pointed out by Longhurst (2007). Although the data have some limitations, we believe it is important to explore and discuss them with the available information as a first approach towards the understanding of the complexity of the ecosystems in the southern Gulf of Mexico.

Based on the analyses of 17 CA, four local regions were established in the southern gulf as follows: Region-I (R-I) includes the area between the rivers Soto Marina and Tuxpan; Region-II (R-II) encompasses the surrounding area of Veracruz harbor to the Carmen-Machona lagoons; Region-III (R-III) is limited from the outlet of GU river system to Champoton River, and Region-IV (R-IV) is located at the Yucatan shelf; in between, transition zones were found for all regions (Fig. 1). Licea *et al.* (2004) found similar regions

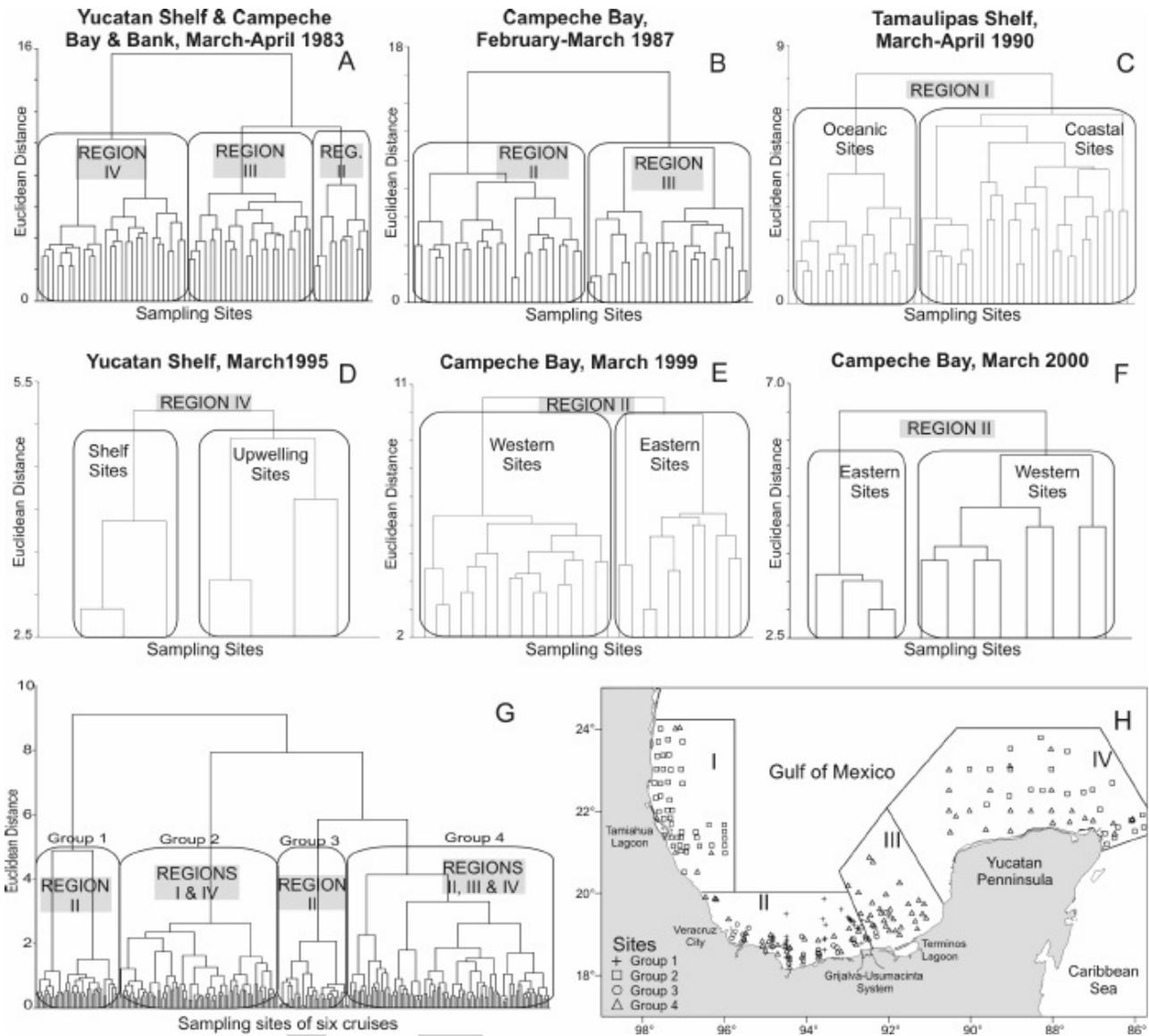


Fig. 2A-F: show the similarity among sampling sites (Presence/absence) of six cruises surveyed during the dry season. Sampling date and places are indicated in bold letters. Fig. G, represents a cluster including the total sampling sites of the above clusters (material used: 227 sites and 174 species). Fig. H, shows the location sites of the formed groups on the established regions, both obtained from Fig. G

based on the study of a data-base of dinoflagellates in the same area; however, they did not differentiate R-II and R-III of this study, which are the most conspicuous ecological regions due to species requirements and the regional hydrographic conditions that occur particularly in this area.

R-I differs greatly from R-II and R-III since this area is characterized as a mesotrophic ambient (Manzano-Sarabia and Salinas-Zavala, 2008), besides the collision of the anticyclonic gyres from the LC and their impact on the coastal area; in addition, their platform is very narrow and the influence of rivers is scarce (Vidal et al., 1992), The associated sites in this region are related only to some sites of the Yucatan shelf.

R-II and R-III are strongly related not only because of their diatom species composition, but also because the benthic communities (Hernández-Arana et al., 2003) and dwelling species of these regions are brackish, euryhalines and with the capacity of responding quickly to the turbulent conditions of river discharges and the stratification that show up in this area (Flöder and Burns, 2004; Matondkar et al., 2007). In these regions the species composition show greater heterogeneity, as much in space as in time, mainly toward the east in front of the Terminos Lagoon. On the other hand, several rivers discharge, and consequently a high level of nutrients is expected, as compared with the adjacent regions. These facts, combined with littoral circulation associated with cyclonic gyres drifting from a branch of the Loop Current (Monreal and Salas de León 1990) create

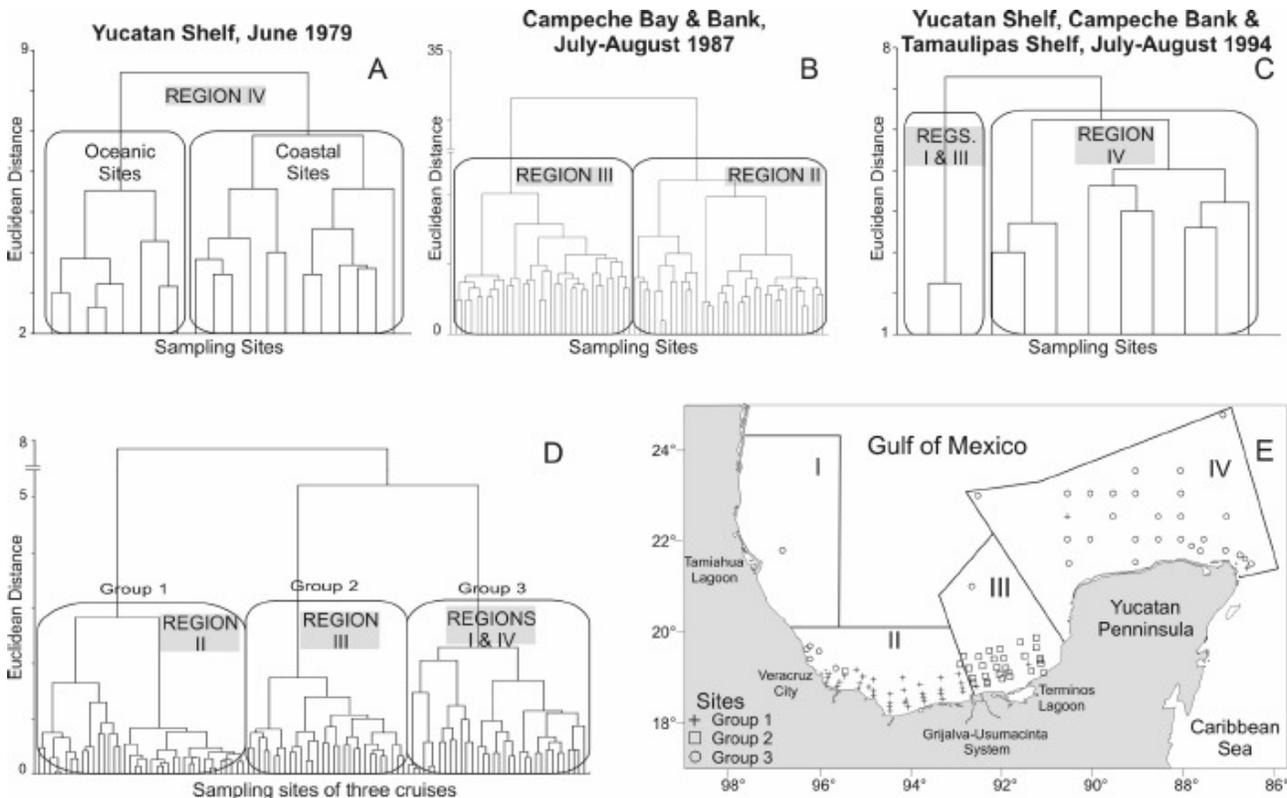


Fig. 3A-C: shows the similarity among sampling sites (Presence/absence) of three cruises surveyed during the rainy season; only one sample was obtained for Region I. Sampling date and places are indicated in bold letters. Fig. D, represents a cluster including the total sampling sites (material used: 104 sites and 96 species). Fig. E, shows the location sites of the formed groups on the established regions, both obtained from Fig. D

contrasting hydrographical conditions that may or may not support the survival of species, thus affecting their distribution. Another possible explanation is the intrusion of different water masses (CSSW; GMSSW; CGMW).

R-IV is well represented by big species, several of them of the family Rhizosoleniaceae, it being an area of little depth, high evaporation and no rivers; however, it is strongly influenced by the upwelling of the Yucatan shelf (Merino, 1997; Portilla-Casillas *et al.*, 2003). It was observed that this region shares species associations of the genera *Dactylosolen*, *Guinardia*, *Proboscia* and *Rhizosolenia*, with the Region I, whose species are typical of tropical and stable environments (Halegraeff and Jeffrey, 1984). On the other hand, it is important to consider that eddies can be expelled from the Loop Current towards the coast of Region I transporting species not only from the Caribbean Sea but also from the Yucatan shelf.

Dry season: During this season, it is noticed that there is a direct relationship among the oceanographic conditions of the area, such as, upwelling of the Yucatan shelf, the stratification of water masses, the collision of the gyre at the west coast of Tamaulipas shelf, as well as the difference of the fresh contribution of the rivers Coatzacoalcos and GU. These effects are evident in the clusters of figs. 2A-G. Figs. 2A-C show a clear delimitation of four groups distributed in four

regions; it is evident that each formed group corresponds to one region; something similar occurs in Figs. 2D-F. Fig. 2G shows a cluster including all the sampling sites where the formation of four groups distributed in four Regions is evident. Figs. 2E and F show the separation of the western and eastern sites, due to the difference in discharge of the rivers. Licea and Luna (1999) previously registered these differences in the productivity of this region; more recently Salas de León *et al.* (2008) have confirmed that this region has eddies that explain the species mixture in this region. Likewise, the coastal sites of R-IV are similar to those of R-III and some of R-II. This is explained by the LC detached rings that occasionally shift on the Yucatan shelf toward the Bank of Campeche (Furnas & Smayda 1987). In addition, waters from the Yucatan upwelling flow along the north coast of Yucatan toward Campeche Bank (Portilla-Casillas *et al.* 2003). R-II is the most heterogeneous; it has sites of three groups: 1, 3 and 4 (Fig. 2G). Group 1 (cross symbol of Fig. 2H) corresponds to sites of the east portion of the study area; group two was found in R-I and R-IV (square symbols); while group three corresponds to sites located toward the west coast; the group 4 is distributed at Regions II, III and IV. As can be seen in figures 2G-H, the oceanic sites of R-IV are similar to the sites of R-I; this could be explained by the origin of the same water mass that comes from the ring's detachment of the LC, as Vidal *et al.* (1994) state in their studies of the water mass distribution in the western Gulf of Mexico.

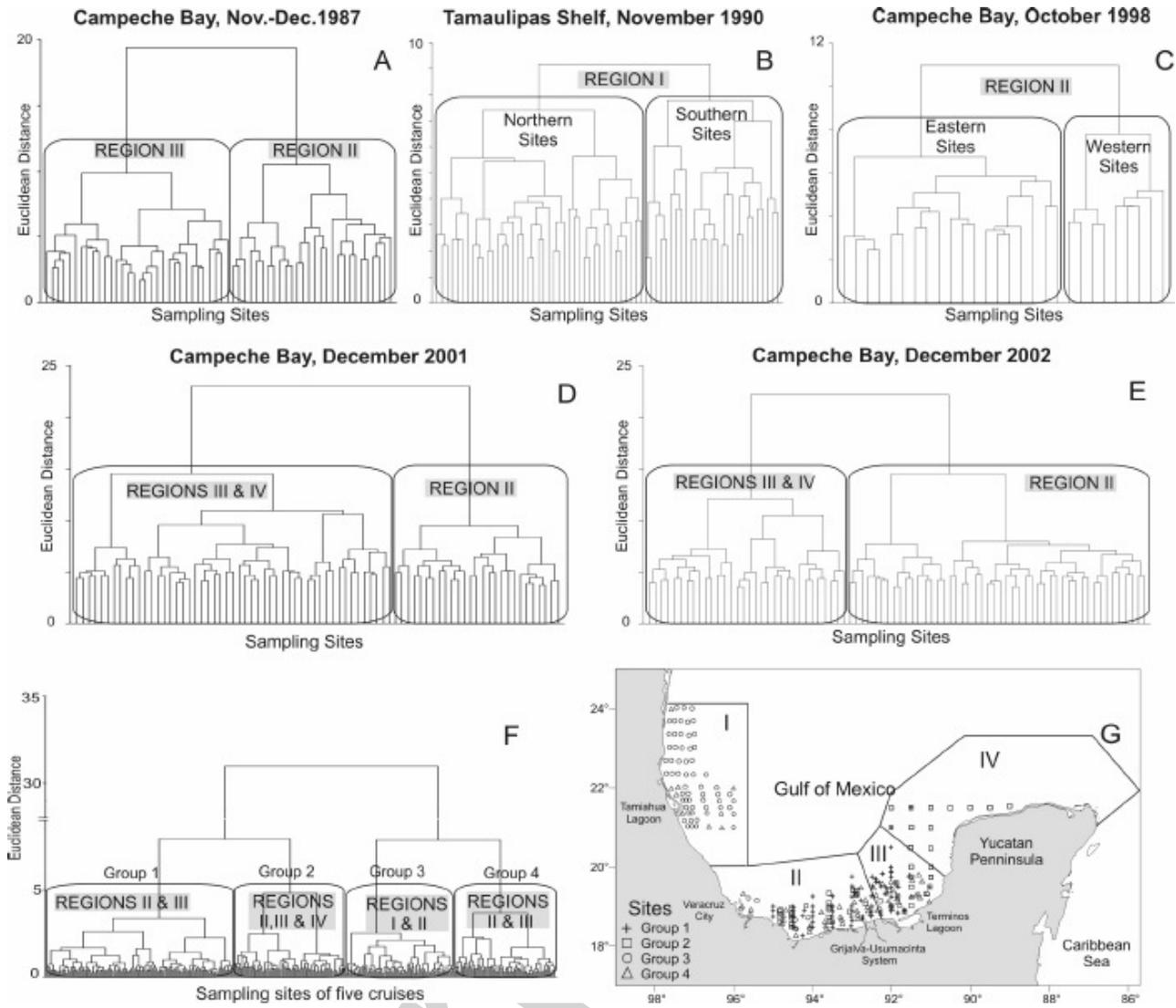


Fig. 4A-E: shows the similarity among sampling sites (Presence/absence) of five cruises surveyed during the northwind season; few samples were obtained for Region I. Sampling date and places are indicated in bold letters. **Fig. F,** represents a cluster including the total sampling sites (material used: 316 sites and 204 species). **Fig. G,** shows the location sites of the formed groups on the established regions, both obtained from Fig. F.

Rainy season: Fig. 3A-E show the similarities among sites of three cruises grouped for this season; only one sample was obtained for R-I. Fig. 3A shows the formation of two groups located on R-IV, separating the oceanic sites from the coastal ones; the influence of the upwelling of Cape Catoche was not perceived. Fig 3B shows a clear separation of two groups that are coincident with R-II and R-III and are related to the highest river discharge, particularly R-II. Fig. 3C shows the formation of two groups; the first one with few sites located in R-I and R-III; the second located in R-IV. Fig. 3D combines all sampling sites of the rainy season, showing the formation of groups 1 and 2 coincident with R-II and R-III (cross and square symbols of Fig. 3E); the third group was formed with sites located in R-I and R-IV (empty circles in Fig. 3E). A similar situation occurred during the dry season (see Fig. 2H, square symbols) having the same explanation of Vidal *et al.* (1994).

It must be taken into account that the anticyclonic gyres from the LC have no constant periodicity (intervals ranging from 3 to 25 months) as Monreal-Gómez *et al.* (2004) have pointed out for this zone; thus, both effects could be related to this physical process. Additionally the constant presence of hurricanes, typical of this time of the year undoubtedly could have an effect on the coasts of this region.

Northwind season: Figures 4A-G, show the similarities between sites of five cruises for this season; few samples were obtained for R-IV. Fig. 4F shows the formation of four groups distributed in four regions: Group 1 is located in R-II and R-III; group two, in R-II, R-III and R-IV; group three, in R-I and R-II and group four, in R-II and R-III. It is interesting to note that group one and four are located in R-II and R-III (Campeche Bay).

Table - 1: List of species from the southern Gulf of Mexico. FR=Frequency; (+) = Dry season; (=) = Rainy season; (%) = Northwind season. Species in bold letters are new records for the Southern Gulf of Mexico (NR)

TAXA	FR
Actinocyclus circellus Watkins NR +	0.2
A. curvatulus Jan. NR +	0.3
<i>A. octonarius</i> Ehr. + ■	7.3
A. octonarius var. crassus (W. Sm.) Hendey NR + ■	0.3
A. octonarius var. ralfsii (W. Sm.) Hendey NR +	0.2
A. octonarius var. sparsus (Greg.) Hendey NR +	0.3
<i>A. octonarius</i> var. <i>tenellus</i> (Bréb.) ex Villareal et Fryxell +	2.9
A. subtilis (Greg.) Ralfs NR + ■	1.7
<i>Actinoptychus senarius</i> Ehr. + ▲ ■	9.9
<i>Alveus marinus</i> (Grun.) Kaczmarek et Fryxell + ■	2.6
<i>Amphora bigibba</i> Grun. ▲	0.2
<i>A. contracta</i> Grun. ■	0.2
A. costata var. inflata (Grun.) H. Perag. et Perag. NR ▲	0.2
<i>A. decussata</i> Grun. ▲	0.2
<i>A. exigua</i> Greg. ▲	0.2
<i>A. ovalis</i> (Kütz.) Kütz. + ■	1.5
<i>A. proteus</i> Greg. ■	0.2
A. reichardiana Grun. NR ■	0.2
<i>Asterionellopsis glacialis</i> (Castr.) Round + ▲ ■	18.5
<i>Asterolampra marylandica</i> Ehr. + ■	0.2
Asteromphalus arachne (Bréb.) Ralfs NR + ■	0.6
A. cleveanus Grun. NR +	3.2
<i>A. flabellatus</i> (Bréb.) Grev. + ■	1.7
<i>A. heptactis</i> (Bréb.) Ralfs + ■	7.6
<i>A. robustus</i> Castr. + ■	2.3
<i>A. sarcophagus</i> Wall. +	0.2
<i>A. shadbolianus</i> (Grev.) Ralfs in Pritch. ■	0.2
A. stellatus (Grev.) Ralfs in Pritch. NR ■	0.2
<i>Aulacoseira granulata</i> (Ehr.) Simonsen + ■	2.3
<i>Azpeitia neocrenulata</i> (Van Landingham) Fryxell et Watkins + ■	1.2
<i>A. nodulifera</i> Fryxell et Sims. + ▲ ■	19.2
<i>Bacillaria paxillifer</i> (Müller) Hendey + ■	7.7
<i>Bacteriastrium delicatulum</i> Cl. + ▲ ■	38.6
<i>B. elongatum</i> Cl. + ▲ ■	14.5
<i>B. furcatum</i> Shadb. + ■	13.4
<i>B. hyalinum</i> Laud. + ▲ ■	31.4
Bellerochea horologicalis Von Stosch NR ■	0.3
<i>B. malleus</i> (Brightw.) Van Heurck ■	0.8
<i>Biddulphia alternans</i> (J. W. Bailey) Van Heurck ■	0.3
<i>B. biddulphiana</i> (Smith) Boyer ■	3.2
<i>B. tridens</i> (Ehr.) Ehr. ■	0.8
<i>Bleakeleya notata</i> (Grun.) Round + ▲ ■	2.6
<i>Caloneis liber</i> (W. Sm.) P. T. Cl. ■	0.2
Campylodiscus braziliensis Deby NR +	0.2
C. clypeus Ehr. NR ■	0.5
C. decorus Bréb. NR +	0.2
<i>C. samoensis</i> Grun. ■	0.5
<i>Campylosira cymbelliformis</i> (Schm.) Grun. ex Van Heurck +	0.2
<i>Ceratalina pelagica</i> (Cl.) Hendey + ▲ ■	17.2
<i>Cerataulus smithii</i> Ralfs in Pritch. +	0.2
Cerataulus turgidus (Ehr.) Ehr. NR +	0.3
<i>Chaetoceros affinis</i> Laud. + ▲ ■	28.1
C. affinis var. willei (Gran) Hust. NR + ■	1.2
<i>C. anastomosans</i> Grun. + ▲ ■	1.1
<i>C. atlanticus</i> Cl. + ▲ ■	5.1
C. atlanticus var. neapolitana (Schröd.) Hust. NR +	0.8
<i>C. borealis</i> Bailey ■	1.7
<i>C. brevis</i> Schütt + ▲ ■	6.6
<i>C. coarctatus</i> Laud. + ▲ ■	43.1
C. compressus Laud. NR + ▲ ■	32.0
<i>C. concavicornis</i> Mangin + ■	1.2
<i>C. constrictus</i> Gran + ▲ ■	9.0
<i>C. curvisetus</i> Cl. + ▲ ■	39.9
<i>C. dadayi</i> Pav. ■	2.5
<i>C. danicus</i> Cl. + ▲ ■	26.0
<i>C. debilis</i> Cl. + ■	0.6
<i>C. decipiens</i> Cl. + ▲ ■	47.6
<i>C. dichæta</i> Ehr. +	0.5
<i>C. didymus</i> Ehr. + ■	15.6
<i>C. diversus</i> Cl. + ▲ ■	47.9
<i>C. eibenii</i> Grun. ■	2.6
<i>C. lacinosus</i> Schütt + ▲ ■	13.8
C. lorenzianus f. singularis Takano NR ■	1.5
<i>C. lorenzianus</i> Grun. + ▲ ■	58.6
<i>C. messanensis</i> Castr. + ▲ ■	8.7
<i>C. pelagicus</i> Cl. + ▲ ■	36.0
C. perpusillus Cl. NR ■	1.2
<i>C. peruvianus</i> Brightw. + ▲ ■	47.3
<i>C. pseudocurvisetus</i> Mangin + ▲ ■	4.5
<i>C. radicans</i> Schütt + ■	2.3
<i>C. rostratus</i> Laud. ■	0.8
<i>C. socialis</i> Laud. ■	0.2
<i>C. subtilis</i> Cl. ■	1.4
<i>C. subtilis</i> var. <i>abnormis</i> (Prosh.-Lav.) Prosh.-Lav. ■	0.2
<i>C. tetrastichon</i> Cl. ■	4.0
<i>C. tortissimus</i> Gran ■	7.1
<i>C. wighami</i> Brightw. ■	0.6
<i>Climacodium frauenfeldianum</i> Grun. + ■	8.3
Cocconeis britannica Nägeli in Kütz. NR +	0.2
<i>C. pseudomarginata</i> W. Greg. ■	0.2
<i>C. scutellum</i> Ehr. ■	0.2
<i>Corethron hystrix</i> Hensen + ▲ ■	14.7
<i>Coscinodiscus asteromphalus</i> Ehr. + ■	10.7
<i>C. centralis</i> Ehr. + ■	1.4
<i>C. concinnus</i> W. Sm. + ■	0.3
<i>C. gigas</i> Ehr. ■	5.6
<i>C. granii</i> Gough + ▲ ■	18.4
<i>C. jonesianus</i> (Grev.) Ostenf. + ■	0.8
<i>C. radiatus</i> Ehr. + ▲ ■	31.2
<i>C. rothii</i> (Ehr.) Grun. +	0.2
<i>C. wailesii</i> (Gran) Angst + ■	1.4
Cyclotella litoralis Lange et Syvertsen NR + ■	3.6
<i>C. maneghiniana</i> Kütz. + ■	0.8
<i>C. striata</i> (Kütz.) Grun. + ■	4.3
<i>C. stylorum</i> Brightw. +	2.9
<i>Cylindrotheca closterium</i> (Ehr.) Reimman et Lewin + ▲ ■	29.7
Cymatowitzschia marina (Lewis) Simonsen NR +	0.2
<i>Cymatopsis lorenziana</i> Grun. + ▲ ■	9.3
Cymbella mexicana (Ehr.) Cl. NR +	0.3
<i>Dactyliosolen fragillissimus</i> (Berg.) Hasle + ▲ ■	15.9
<i>D. phuketensis</i> (Sundström) Hasle ■	11.1
<i>Delphineis surirella</i> (Ehr.) Andrews + ▲ ■	15.5
D. minutissima (Hust.) Simonsen NR + ▲ ■	0.6
<i>Detonula pumila</i> (Castr.) Gran + ▲ ■	19.6
<i>Dimeregramma marinum</i> (Greg.) Ralfs in Pritch. +	0.2

<i>Diploneis bombus</i> (Ehr.) Cl. + ▲ ■	10.0	<i>N. pacifica</i> Cupp + ▲ ■	4.9
<i>D. crabro</i> Ehr. ■	2.5	<i>N. sicula</i> (Castr.) Hust. + ▲ ■	18.1
<i>D. decipiens</i> var. <i>paralella</i> A. Cl.-Euler NR +	0.3	<i>N. sigma</i> (Kütz.) W. Sm. + ▲ ■	13.0
<i>D. lineata</i> (Donk.) Cl. NR ■	0.2	<i>N. socialis</i> Greg. + ▲ ■	7.0
<i>D. sejuncta</i> f. <i>constricta</i> Hust. NR +	0.2	<i>N. vidovichi</i> Grun. NR ■	0.2
<i>D. splendida</i> var. <i>puella</i> (Schtdt) P. T. Cl. NR ■	0.2	<i>Odontella aurita</i> (Lyngbye) Agardh + ▲ ■	9.3
<i>D. subadvena</i> Hust. NR ■	0.2	<i>O. longicuris</i> (Grev.) Hoban ■	0.2
<i>D. vacillans</i> var. <i>renitens</i> (Schm.) P. T. Cl. NR ■	0.2	<i>O. mobiliensis</i> (Bailey) Grun. + ■	6.2
<i>D. weissflogii</i> (Schm.) P. T. Cl. + ■	2.2	<i>O. sinensis</i> (Grev.) Grun. + ▲ ■	11.4
<i>Ditylum brightwellii</i> (West) Grun. + ■	5.9	<i>Palmeria hardmanniana</i> Grev. ■	12.1
<i>Donkinia recta</i> (Donk.) Carruthers ■	0.3	<i>Paralia sulcata</i> (Ehr.) Cl. + ▲ ■	17.9
<i>Entomoneis alata</i> (Ehr.) Ehr. NR + ■	2.3	<i>Planktoniella sol</i> (Wall.) Schütt F. + ■	3.2
<i>E. pulchra</i> (J. W. Bailey) Reimer NR ■	0.3	<i>Pleurosigma angulatum</i> (Quekett) W. Sm. + ■	4.6
<i>Epithemia zebra</i> (Ehr.) Kütz. +	0.2	<i>P. diverse-striatum</i> Meister NR + ▲ ■	36.3
<i>Eucampia cornuta</i> (Cl.) Grun. ■	9.1	<i>P. normanii</i> Ralfs in Pritch. ■	7.3
<i>E. zodiacus</i> Ehr. + ▲ ■	9.3	<i>Podocystis adriatica</i> (Kütz.) Ralfs ■	0.2
<i>Eupodiscus radiatus</i> J. W. Bailey ■	1.1	<i>Podosira stelliger</i> (Bailey) A. Mann +	0.2
<i>Gossleriella tropica</i> Schütt + ■	1.4	<i>Proboscia alata</i> (Brightw.) Sundström + ■	24.4
<i>Guinardia cylindrus</i> (Cl.) Hasle ■	1.4	<i>P. alata</i> f. <i>gracillima</i> (Cl.) Lincea et Moreno NR + ■	16.7
<i>G. delicatula</i> (Cl.) Hasle + ■	4.9	<i>P. alata</i> f. <i>indica</i> (H. Perag.) Lincea et Moreno NR + ■	16.2
<i>G. fiaccida</i> (Castr.) Perag. + ▲ ■	49.9	<i>Psammodiscus nitidus</i> (W. Greg) Round et D. G. Mann +	0.2
<i>G. striata</i> (Stolt.) Hasle + ■	21.2	<i>Psammodictyon constrictum</i> (Greg.) D. G. Mann + ■	1.5
<i>Haslea wawrikan</i> (Hust.) Simonsen + ▲ ■	25.7	<i>P. panduriforme</i> (Greg.) D.G. Mann + ▲ ■	2.2
<i>Helicotheca tamesis</i> (Shrubs.) Richard ■	9.6	<i>Pseudo-nitzschia multiseries</i> (Hasle) Hasle ▲ ■	0.9
<i>Hemiaulus hauckii</i> Grun. in Van Heurck + ▲ ■	53.3	<i>P. pseudodelicatissima</i> (Hasle) Hasle + ▲ ■	22.4
<i>H. membranaceus</i> Cl. + ▲ ■	57.3	<i>P. pungens</i> (Grun. ex Cl.) Hasle + ▲ ■	38.2
<i>H. sinensis</i> Grev. + ▲ ■	42.8	<i>P. seriata</i> (Cl.) H. Perag. + ▲	0.8
<i>Hemidiscus cuneiformis</i> var. <i>ventricosa</i> (Castr.) Hust. +	0.2	<i>P. subfraudulenta</i> (Hasle) Hasle + ▲ ■	6.6
<i>H. cuneiformis</i> var. <i>orbicularis</i> (Castr.) F. Hust. ■	0.2	<i>P. subpacific</i> (Hasle) Hasle +	1.1
<i>Lauderia annulata</i> Cl. + ▲ ■	10.8	<i>Pseudosolenia calcar-avis</i> (Schultze) Sundstöm + ▲ ■	51.8
<i>Leptocylindrus danicus</i> Cl. + ▲ ■	42.0	<i>Rhizosolenia acuminata</i> (H. Perag.) H. Perag. ■	11.4
<i>L. mediterraneus</i> (H. Perag.) Hasle + ■	3.6	<i>R. bergonii</i> H. Perag. + ■	15.1
<i>L. minimus</i> Gran + ■	1.5	<i>R. castracanei</i> H. Perag. + ■	9.4
<i>Lioloma elongatum</i> (Grun.) Hasle NR + ■	10.4	<i>R. clevei</i> Ostenf. ■	10.0
<i>L. pacificum</i> (Cupp) Hasle ■	14.2	<i>R. clevei</i> var. <i>comun</i> Sundström NR + ■	3.7
<i>Lithodesmium undulatum</i> Ehr. + ■	14.5	<i>R. crassa</i> Schimper in Karsten ■	8.7
<i>Lyrella clavata</i> (Greg.) D. G. Mann ■	0.2	<i>R. hebetata</i> f. <i>semispina</i> (Hensen) Gran NR +	1.1
<i>L. hennedyi</i> (W. Sm.) A. J. Stickle et D. G. Mann ■	0.3	<i>R. hebetata</i> Bailey ■	0.3
<i>L. lyra</i> (Ehr.) Karayeva ■	0.5	<i>R. hyalina</i> Ostenf. in Ostenf. et Schm. ■	0.2
<i>L. lyra</i> var. <i>recta</i> (Greville) Moreno ■	0.2	<i>R. imbricata</i> Brightw. + ▲ ■	28.1
<i>Mastogloia binotata</i> (Grun.) Cl. ■	0.2	<i>R. pungens</i> Cl.-Euler + ■	14.5
<i>M. rostrata</i> (Wall.) Hust. ▲ ■	13.8	<i>R. setigera</i> Brightw. + ▲ ■	29.5
<i>Meuniera membranacea</i> (Cl.) P. C. Silva ■	14.8	<i>R. styliformis</i> Brightw. + ■	14.4
<i>Minidiscus trioculatus</i> (Taylor) Hasle ■	1.1	<i>R. temperei</i> H. Perag. NR ■	5.3
<i>Neoclyptrella robusta</i> Hemández-Becerril et Meave del Castillo + ■	25.0	<i>Roperia tesellata</i> (Roper) Grun. ex Pelletan NR + ■	2.2
<i>Neodelphineis indica</i> (Taylor) Hasle +	0.2	<i>Skeletonema</i> spp. + ▲ ■	34.2
<i>N. pelagica</i> Takano + ▲ ■	9.6	<i>Stephanophyxis palmeriana</i> (Grev.) Grun. ■	6.2
<i>Nitzschia angularis</i> var. <i>affinis</i> (Grun.) Van Heurck ▲	0.2	<i>S. turris</i> (Grev.) Ralfs in Pritch. ■	0.2
<i>N. bicapitata</i> Cl. + ▲ ■	45.6	<i>Thalassionema bacillare</i> (Heiden) Kolbe + ▲ ■	39.7
<i>N. bifurcata</i> Kaczmarek et Lincea + ▲	1.4	<i>T. frauenfeldii</i> (Grun.) Temp. et Perag. + ▲ ■	34.9
<i>N. braarudii</i> Hasle +	1.9	<i>T. nitzschiioides</i> (Grun.) Mereschkowsky + ▲ ■	58.6
<i>N. capuluspalae</i> Simonsen NR ▲ ■	0.5	<i>T. nitzschiioides</i> var. <i>capitulata</i> (Castr.) Moreno +	0.2
<i>N. dietrichii</i> Simonsen + ▲ ■	8.5	<i>Thalassiosira allenii</i> Takano NR + ■	0.9
<i>N. dissipata</i> (Kütz.) Grun. + ▲ ■	4.0	<i>T. binata</i> Fryxell +	0.3
<i>N. frustulum</i> (Kütz.) Grun. in Cl. et Grun. + ▲ ■	0.3	<i>T. decipiens</i> (Grun.) Jörg. NR + ▲ ■	9.7
<i>N. gandersheimiensis</i> Krasske + ▲ ■	4.0	<i>T. delicatula</i> Ostenf. + ▲	0.2
<i>N. interruptestriata</i> (Heiden) Simonsen NR + ▲ ■	5.1	<i>T. diporocyclus</i> Hasle +	0.2
<i>N. longissima</i> (Bréb.) Ralfs in Pritch. + ▲ ■	9.9	<i>T. eccentrica</i> (Ehr.) Cl. + ▲ ■	41.9
<i>N. ossiformis</i> (Taylor) Simonsen + ▲	0.5	<i>T. elsayedii</i> Fryxell ■	0.8
<i>N. ovalis</i> Amott in Cl. et Grun. + ▲ ■	13.1	<i>T. lineata</i> Jousé + ▲ ■	1.5

<i>T. lineoides</i> Hersig et Fryxell + ▲	0.5
<i>T. mala</i> Takano + ▲ ■	5.3
<i>T. minima</i> Gaarder +	0.5
<i>T. nanolineata</i> (Mann) Hasle et Fryxell +	0.2
<i>T. oceanica</i> Hasle +	0.3
<i>T. oestrupii</i> Proschkina-Lavrenko + ▲ ■	13.1
<i>T. oestrupii</i> var. <i>venrikae</i> Fryxell et Hasle + ▲	4.5
<i>T. partheneia</i> Schrader + ▲ ■	3.6
<i>T. punctifera</i> (Gruow) Fryxell Simonsen et Hasle + ▲	0.6
<i>T. sacketti</i> Fryxell + ▲	0.3
<i>T. subtilis</i> (Ostenf.) Gran + ▲ ■	15.6
<i>T. tubifera</i> Fryxell ▲ ■	2.8
<i>Thalassiothrix longissima</i> P. T. Cl. et Grun. NR + ■	17.3
<i>Triceratium favus</i> Ehr. ■	3.2
<i>Triceratium favus</i> var. <i>quadrata</i> Grun. NR ■	3.2
<i>Triceratium pentacrinus</i> Wall. ■	0.5
<i>Trachyneis aspera</i> (Ehr.) P. T. Cl. ■	0.2
<i>Tryblionella apiculata</i> Greg. NR +	0.3
<i>Tryblionella hungarica</i> (Grun.) D. G. Mann +	0.2
<i>Tryblionella marginulata</i> (Grun.) D. G. Mann + ▲ ■	2.3

Comparing the cruises surveyed in the Bay of Campeche, it is observed that the clusters of R-II and R-III of the years 1987, 1998 have differences toward the east or west of the bay; while clusters of the years 2001 and 2002 are very similar (Figs. 3A, C, D and E). As for the R-I, two groups are observed; one in the sites located in the north coast of Tamiahua Lagoon and the other toward the southern sites (Fig. 3B). During this season of the year several critical transition zones are formed between the four regions, probably for the effect of the great instability that is observed during this time due to the influence of the winds from the north and the energy that they introduce to the ecosystem, which can be different every year. This could explain the heterogeneity of the formed groups, particularly in R-II and R-III. During this season the two groups of R-I (Fig. 3B), can be explained by the divergence effect generated in this area by the collision of the cyclonic and the anticyclonic gyres associated with this gyre, as well as a result of the detachment rings of the LC, as Vázquez de la Cerda *et al.* (2005) stated.

Species frequency: An additional approach to characterise the regions and sampling times was the selection of the species frequency > than 40%, that was also present alone in regions or seasons of the year, as well as other species with an exclusive presence, in one region although with low frequency.

Region I which is characterised by the highest frequency of *Bacteriastrium hyalinum*, (89.7%), additionally shares most of the species that have frequency > than 40% of the remaining regions. R-II is characterised by *Chaetoceros affinis*, *C. compressus*, *Cylindrotheca closterium*, *Rhizosolenia setigera* and *Skeletonema costatum*, which are also species that have a preference for brackish water. In addition, the presence of 33 species that was observed only in this region, belonging to the genus *Amphora*, *Asteromphalus*, *Cerataulus*, *Coscinodiscus*, *Diploneis*, *Nitzschia*, *Biddulphia*, *Caloneis*, *Cyclotella* and *Cymbella*. R-III, was characterised by *Chaetoceros danicus*, *Neocalyptrella robusta*, *Proboscia alata* and

Rhizosolenia imbricata, species of warm waters that adapt themselves to live well in a warmer area as it is this region. R-IV is characterized to by a very variable community represented by *Pseudosolenia calcar-avis*; as well as 16 species that, although they have very low frequency, have been observed only in this region and belong to the genus: *Amphora*, *Campylodiscus*, *Cocconeis*, *Diplones*, *Lyrella* and *Nitzschia* that are benthic and picoplanktic species (Table 1).

The dry season is characterized by the high frequency of *Chaetoceros decipiens*, *C. peruvianus* and *Pleurosigma diversestriatum*. The rainy season is represented by the highest frequency of picoplanktic species with brackish preference (*Asterionellopsis glaciales*, *Cylindrotheca closterium*, *Bacteriastrium hyalinum*, *Chaetoceros coarctatus*, *C. compressus*, *Rhizosolenia setigera*, and *Skeletonema costatum*) that are species with a high response capacity to estuarine outwelling coastal lagoons and rivers. During the northwind season, the species with high frequency were: *Chaetoceros brevis*, *C. constrictus*, *C. danicus*, *C. dictyota*, *Coscinodiscus radiatus*, *Neocalyptrella robusta*, *Proboscia alata* y *Rhizosolenia imbricata*; species that adapt themselves to the typical turbulence of this time.

Transition zones: Transition regions (the boundary between regions) certainly occurs at each region, as can be seen in figs. 2A, 2B; 3B, 3D, and 4A, 4D and 4E, where there are noticed changes in similarity between sites and consequently in species composition and even in seasonal or yearly variations. In fact, sharp boundaries were not observed and most probably they do not exist in the strict sense. The transition area between R-I and R-II spreads out between the coasts of Veracruz and the Tamiahua lagoon. The transition between R-II and R-III is given between the GU rivers and the Terminos lagoon. The transition between R-III and R-IV was observed between the Champoton river and the Celestum Lagoon.

Critical transition zones: Critical transition zones (CTZs) in the sense of Levin *et al.* (2001), who state that they are hybrid ecosystems that are strongly influenced by the ecosystems that they link, even though they may also contain different species. This situation occurred in all regions in our study area, even on sampling sites and climatic seasons. On the other hand, fronts are zones of greatest ecological discontinuity. In some cases, they can represent more than a leaky boundary between different regions; a good example are R-II and R-III, which are strongly influenced by river fronts of G-OR.

The transition zones between two ecological communities are, by definition, linear and less extensive than the communities they separate, they are associated with a gradient either in the physical environment or in an external stress. For this reason, the oceanographic historical information from the southern gulf has been an important tool to explain which factors are involved in a regionalization setting, since the regional oceanographic processes are important factors.

Longhurst (2007), in his book *Ecological Geography of the Sea* emphasizes the importance of the fronts, shelf-edges, upwelling,

river plumes, pycnoclines, eddies, as well as the scales of longer term responses. These are important factors for the establishment of regions in the ocean. He states that ecological boundaries will be least ambiguous where discontinuities in the physical environment are strongest. We observed this situation at the boundaries between all established regions.

In fact, boundaries in the established regions are related to the location fronts and greatest ecological discontinuities, since they can represent a boundary between different climatic regimes. This is associated with the physical dynamics of different fronts (rivers eddies, vortex, littoral transport; coastal processes; LC associated with ring detachments; estuarine influence on the continental shelf, drifting eddies, tropical storms and hurricanes, as well as the general circulation and water-mass exchange within the gulf), as was emphasized above. The constant generation of cyclones and hurricanes, especially during summer months certainly should affect the coastal areas. These frontogenesis phenomena clearly explain that R-II during the dry season separates into two groups. Moreover the boundary with R-III moves either toward the east or to the west, depending on the river's outflow and littoral circulation.

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