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Holoplanktonic polychaetes from the Gulf of Tehuantepec, Mexico

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Abstract: Composition, abundance, and main assemblages of holoplanktonic polychaetes were analysed in the Gulf of Tehuantepec. This Gulf, in Mexican waters of the eastern tropical Pacific, is a very productive system due to an upwelling during the winter. Zooplankton samples were taken over a station grid covering neritic and oceanic waters during March and November 1978. Most species showed their highest densities in the oceanic region. In the western Gulf, the area sampled in both seasons, mean polychaete abundance was higher in November (549.2 ind.1000 m^{-3}) than in March (143.8 ind.1000 m^{-3}). A regression tree analysis showed that pH and dissolved oxygen were the main factors affecting the total polychaete abundance over the study area during March. Identified families were: Lopadorhynchidae (88.8%), Alciopidae (6.6%), Iospilidae (2.8%), Tomopteridae (1.1%) and Typhloscolecidae (0.7%). The dominant species, *Pelagobia longicirrata,* accounted for 86.5% of the total polychaete abundance. A Bray-Curtis analysis identified two main polychaete assemblages during March: "oceanic" and "neritic". Species richness and mean polychaete abundance were higher in the "oceanic" assemblage, and *P. longicirrata*, *Plotohelmis capitata*, *Rhynchonerella gracilis* and *Lopadorhynchus henseni* were the most frequent and abundant species in this assemblage. In the "neritic" assemblage, the iospilids *Phalacrophorus uniformis* and *Iospilus phalacroides* registered the highest relative abundance. It is suggested that the structure of holoplanktonic polychaete assemblages could be determined by the feeding habits of the species and their tolerance to the variability in environmental conditions.

Résumé : La composition, l'abondance et les principaux assemblages de polychètes holoplanctoniques du Golfe de Tehuantepec sont analysés. Ce Golfe, situé dans les eaux mexicaines de l'est du Pacifique tropical, est un système très productif en raison d'un upwelling hivernal. Le zooplancton a été échantillonné sur un quadrillage couvrant les eaux néritiques et océaniques en mars et novembre 1978. Les plus fortes densités sont obtenues dans la région océanique pour la plupart des espèces. Dans la partie ouest du Golfe, région échantillonnée pendant les deux saisons, l'abondance moyenne des polychètes est plus élevée en novembre (549,2 ind.1000 m^{-3}) qu'en mars (143,8 ind.1000 m^{-3}). L'analyse par arbres de régression montre que le pH et l'oxygène dissous sont les principaux facteurs affectant l'abondance totale des Polychètes sur la zone d'étude en mars. Les familles identifiées sont: Lopadorhynchidae (88,8%), Alciopidae (6,6%), Iospilidae (2,8%), Tomopteridae (1,1%) et Typhloscolecidae (0,7%). L'espèce dominante, *Pelagobia longicirrata,* représente 86,5% de l'abondance totale. Une analyse de Bray-Curtis permet d'identifier deux principaux assemblages en mars: un assemblage "océanique" et un assemblage "néritique". La richesse spécifique et l'abondance moyenne des polychètes sont plus élevées dans l'assemblage "océanique", *P. longicirrata*, *Plotohelmis capitata*, *Rhynchonerella gracilis* et *Lopadorhynchus henseni* sont les espèces les plus fréquentes et les plus abondantes de cet assemblage. Les plus fortes abondances relatives des

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Iospilidae sont obtenues dans l'assemblage "néritique". La structure des assemblages de polychètes holoplanctoniques pourrait s'expliquer par le comportement alimentaire des espèces et leur tolérance vis à vis de la variabilité des conditions environnementales.

Keywords: Polychaeta, Holoplankton, Lopadorhynchidae, Oxygen minimum zone, Tropical Pacific Ocean

Introduction

Polychaete annelids are a large and diverse group. Most of the species inhabit the benthic environment, although several species have evolved to colonize the pelagic realm (Fernández-Álamo & Thuesen, 1999). Most of the benthic families have planktonic stages, such as sexually mature forms or larval stages (Day, 1967). According to Støp-Bowitz (1996), from the 85 Polychaeta families, only eight are exclusively holopelagic.

Holoplanktonic polychaetes are widely distributed in the oceans, mainly in the open sea. Most species are found in the 50 m thick surface layer, although several forms have bathypelagic habits (Støp-Bowitz, 1996). These animals have developed special characteristics to survive in the pelagic environment, such as flattened or gelatinous transparent bodies, long appendages, sperm storage in females, and complex muscled eyes to search for preys (Fernández-Álamo & Thuesen, 1999). In spite of their low abundance in the plankton, they play an important role in organic matter mineralization in the water column (Uttal & Buck, 1996) and in the plankton food web. Their trophic ecology is complex, with a wide range of feeding strategies. Most species are active predators and use their quick eversible proboscis to attack other zooplankters, such as fish larvae, siphonophores, chaetognaths and appendicularians (Rakusa-Suszczewski, 1968). Some species are filter-feeders or phytophagous (Day, 1967), others are ectoparasites (Øresland & Pleijel, 1991), and only few species are able to capture falling detritus in a mucous web, or to grasp detrital material with their ciliated tentacles (Uttal & Buck, 1996).

Most studies on holoplanktonic polychaetes have emphasized taxonomy, but ecological or evolutionary aspects are poorly known. In Mexican Pacific waters, few studies have analysed the distribution and abundance of holoplanktonic polychaetes around the Baja California Peninsula (Fernández-Álamo, 1992, 1996) and the latitudinal changes in their assemblage structure in the California Current System (Fernández-Álamo et al., 2003).

The Gulf of Tehuantepec, Mexico, on the fringe of the eastern tropical Pacific, is a very complex system due to a variable shelf width, to the influence of lagoonal waters, but mainly to a periodic aeolian upwelling that occurs from November to February (Gallegos-García & Barberán-Falcón, 1998). In consequence, this area is characterized by high primary and secondary production (Lara-Lara et al., 1998; Ayala-Duval et al., 1996) supporting important fisheries that represent a considerable economic resource for the coastal human population. In spite of the economic and ecological importance of this Gulf, the knowledge of the pelagic ecosystem is still limited (Färber-Lorda et al., 1994; Ayala-Duval et al., 1996; Fernández-Álamo et al., 2000) and there is a need to improve the understanding of the plankton system. In this study, we analyse the composition, abundance, and main holoplanktonic polychaete assemblages in the Gulf of Tehuantepec in relation to some hydrological characteristics.

Study area

The Gulf of Tehuantepec, Mexico, is located between 13°30'-16°30' N and 92°30'-96° W in the tropical fringe of the Eastern Pacific (Fig. 1). In this area, the continental shelf is about 25 km wide in the western part and 200 km in the eastern section. The central part of the Gulf is influenced by the discharge of important lagoonal systems. The Tehuantepec Isthmus, which separates the Gulf of Tehuantepec from the Gulf of Mexico, is only 40 km wide and 200 m high and, from November to February, the "tehuanos", strong winds (~8 $m.s^{-1}$) coming from the Gulf of Mexico, are funneled across the isthmus between two great mountain chains of 2000 m high (Stumpf & Legeckis, 1977; Gallegos-García & Barberán-Falcón, 1998). The "tehuanos" cause advection of large volumes of surface water offshore that are replaced by colder subsurface waters; hence, surface temperatures can drop by as much as 8 ºC in relation to the surrounding waters (Stumpf, 1975) and a large anticyclonic gyre develops and moves towards the west (Stumpf & Legeckis, 1977; Gallegos-García & Barberán-Falcón, 1998). When the "tehuanos" cease or become moderate, the normal east-west surface circulation is re-established and surface temperatures increase to 25-30º C (Gallegos-García & Barberán-Falcón, 1998). The pelagic environment in this region is characterized by the oxygen minimum zone (OMZ), a widespread feature in the eastern Pacific caused by a combination of high oxygen consumption by zooplankton and bacteria, degradation of

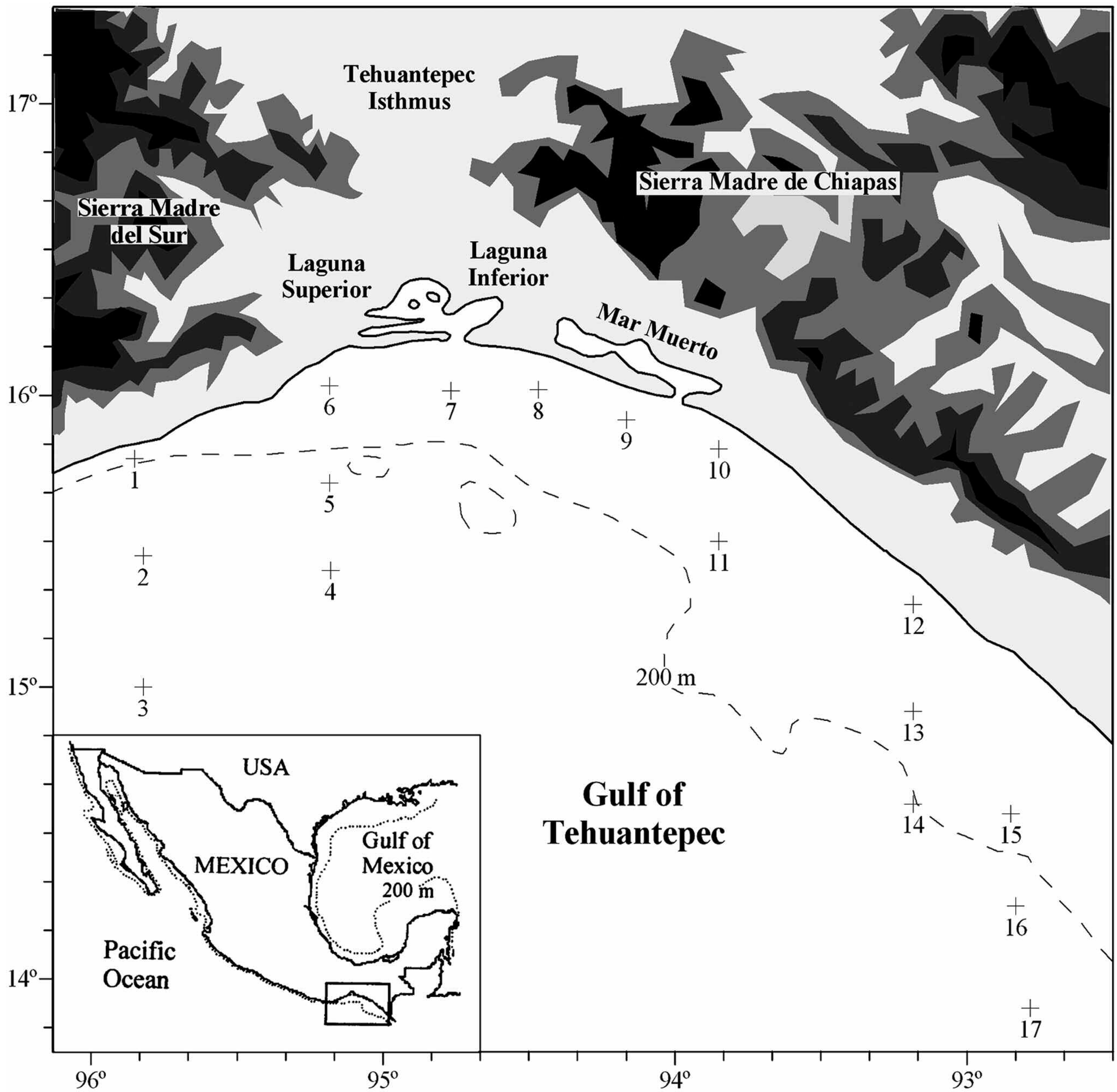

Figure 1. Study area and location of sampling stations.
Figure 1. Zone d'étude et localisation des stations de prélèvements.

primary producers, and a poor ventilation of intermediate waters due to a strong thermocline that prevents the exchange of oxygen-richer water from above (Wyrtki, 1962). Oxygen concentration is higher (4-5 ml L^{-1}) near the surface and decreases rapidly with depth, reaching concentrations of 0.5 ml L^{-1} or less at 75-100 m (Pérez-Cruz & Machain-Castillo, 1990).

Material and methods

Sampling was carried out during March and November 1978 in the Gulf of Tehuantepec. Station grid covered neritic and oceanic waters during March (Fig. 1); however, during November, due to the strong "tehuanos" winds, only five/six oceanographic stations of the western part were

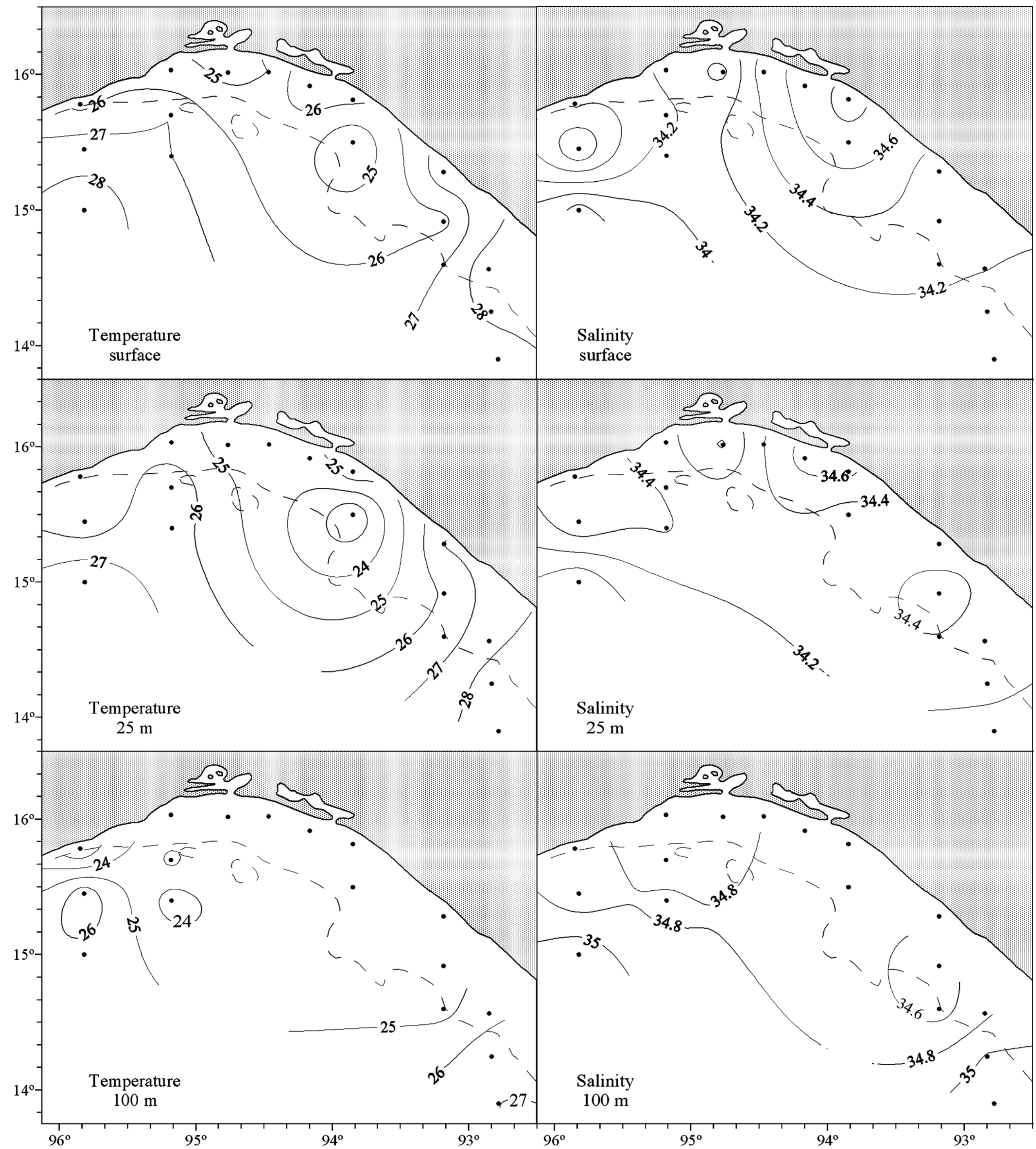

Figure 2. Horizontal planes of temperature and salinity in the Gulf of Tehuantepec during March 1978.
Figure 2. Plans horizontaux de température et salinité dans le Golfe de Tehuantepec en mars 1978.

sampled for biological/hydrological purposes. Hydrographic observations were made at several discrete depths (0, 25, 50, 100, 150, 200, 250, and 300 m) at each sampling station. Temperature was measured with reversing thermometers attached to Nansen water bottles, from which salinity, pH, and dissolved oxygen were measured. Zooplankton samples were taken in oblique tows using a conical 1-m diameter, 3-m long, and 500-µm mesh net in the upper 200 m, according to the bathymetry. A flowmeter was placed in the net to measure the volume of the sampled water, which varied between 15 and 552 m^3 (mean = 155 m^3). Samples were fixed in 10% formalin neutralized with sodium borate. All polychaetes were separated from samples, and abundance data were standardized to number of individuals in 1000 m^3 (ind.1000 m^{-3}). To define the main environmental factors affecting changes in abundance of polychaetes, a Regression Tree (RT) analysis was developed with log-transformed polychaete abundance as response variable, and temperature, salinity, dissolved oxygen, and pH as predictor variables. These abiotic parameters represented the mean integrated values in the upper 200m, where the biological sampling was done. In order to identify main polychaete assemblages, a Bray-Curtis Dissimilarity Index was applied to two log-transformed data matrices (March and March/November) of species composition, and the average linkage group method was employed as clustering algorithm.

Results

Hydrology

During March, mean integrated values showed lower salinity records in neritic waters (< 36.6), where higher temperatures (24 to 26ºC) were also registered. Regarding horizontal planes, surface temperatures in the Gulf of Tehuantepec fluctuated between 25 and 28ºC, with the lowest temperatures (~25ºC) registered in neritic waters, to the south-east of Mar Muerto Lagoon (Fig. 2). Temperatures at 25 m depth (23 to 28ºC) were slightly lower than at the surface, but distribution was very similar. At 100 m depth, temperatures fluctuated between 22 and 26.7ºC in the western oceanic region, and between 24.7 and 27ºC in the eastern part, indicating a slight stratification in the former region. Vertical temperature profiles indicated that the thermocline roughly corresponded to the 50 m depth. Salinity fluctuated between 33.8 and 34.6 at the surface and between 34 and 34.8 at 25 m depth. At 100 m depth, salinity values were very homogeneous and varied between 34.7 and 35.1 (Fig. 2).

Mean integrated values of pH and dissolved oxygen (ml L^{-1}) showed their highest records (> 7.6 for pH, and > 2 ml L^{-1} for dissolved oxygen) in neritic waters. The highest mean pH values (7.8 to 8) were registered in front of the lagoons and the lowest (7.2 to 7.4) in the western oceanic region. Also, the lowest dissolved oxygen values (0.54 to 1.15 ml L^{-1}) were registered in the western oceanic area, whereas the highest values (2.7 to 3.57 ml L^{-1}) were observed over the coastal stations. Vertical oxygen profiles in the oceanic area indicated that the “oxycline” corresponded with the 50-75 m layer. Dissolved oxygen values fluctuated between 2.3 and 3.4 ml L^{-1} above this layer, and between 0.1 and 1 ml L^{-1} below it.

During November, beginning of the upwelling period, these parameters were measured only in the western region of the study area. Mean water column temperatures reached their lowest values at stations 4 and 5 (21 to 23ºC), and the highest (~ 27ºC) at coastal stations 1 and 6. Mean salinity values (~ 34.7) were very homogeneous over the oceanic area, and the lowest values (32.7) were registered at coastal station 6. Mean pH values fluctuated between 6.56 and 7.35 over the sampled area. The lowest mean oxygen values (< 1.0 ml L^{-1}) were registered at oceanic stations, and vertical profiles indicated that the “oxycline” corresponded with the 25-75 m layer.

Abundance and composition

During March, polychaetes were widely distributed in both neritic and oceanic regions, although the highest densities were registered in the oceanic region (Fig. 3). In the western Gulf, the area sampled in both seasons, mean polychaete abundance was at least three times larger in November (549.2 ind.1000 m^{-3}) than in March (143.8 ind.1000 m^{-3}). RT analysis applied to data from March revealed that the pH was the main factor separating high and low polychaete abundance in the study area. The highest pH values (> 7.87) registered in the coastal stations (6, 8, 10, 12) were associated with the lowest polychaete abundance values (Fig. 4). Dissolved oxygen and salinity appeared to be also important at the lowest levels of the RT hierarchical structure. Thus, the area with the highest mean polychaete abundance (623.8 ind.1000 m^{-3}; stations 3, 4, 16 and 17) was associated with values of salinity and dissolved oxygen above 34.65 and 1.09 ml L^{-1} respectively (Fig. 4).

Regarding composition, 24 holoplanktonic polychaete species belonging to five families were identified (Table 1). The most abundant family was Lopadorhynchidae (88.8%), followed by Alciopidae (6.6%), Iospilidae (2.8%), Tomopteridae (1.1%) and Typhloscolecidae (0.7%). The dominant species was *Pelagobia longicirrata* Greeff, 1879, accounting for 86.5% of the total abundance and collected in all sampling stations during both seasons. Other less important species were *Phalacrophorus uniformis* Reibisch, 1895 (2.6%), *Rhynchonerella gracilis* Costa, 1862 (2.3%), *Plotohelmis capitata* (Greeff, 1876) (2.2%) and *Rhynchonerella moebii* (Apstein, 1893) (1.3%). The remaining 17 species represented 5.1% of the total abundance. Most species were present at higher densities in the oceanic than in the neritic region.

Holoplanktonic polychaete assemblages

A Bray-Curtis Dissimilarity Index applied to the data matrix from March revealed the presence of two main holo-

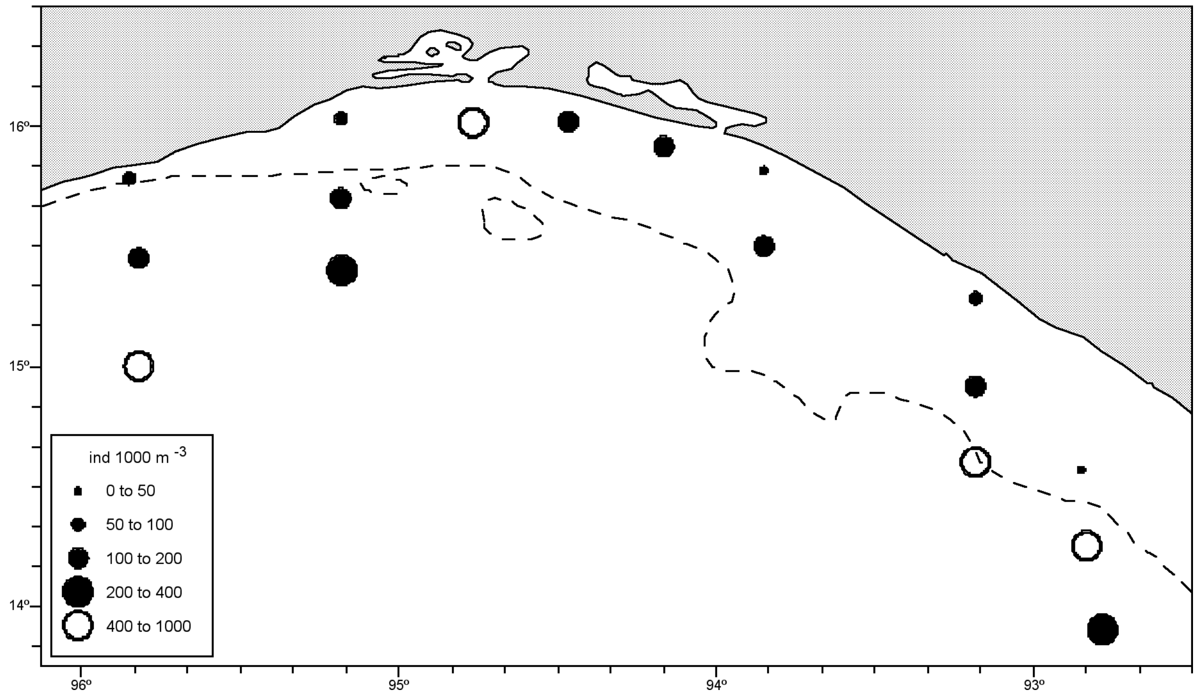

Figure 3. Total holoplanktonic polychaete abundance in the Gulf of Tehuantepec during March 1978.
Figure 3. Abondance totale des polychètes holoplanctoniques du Golfe de Tehuantepec en mars 1978.

planktonic polychaete assemblages in the Gulf of Tehuantepec: the "neritic" and the "oceanic" assemblages, located respectively over and beyond the continental shelf (Fig. 5). The same analysis applied to the data matrix from March/November practically defined the same assemblages. The main difference was that stations 1 and 5 from March were attached to the "neritic" group, whereas those from November were attached to the "oceanic" one (Fig. 6), indicating that these stations corresponded to a transitional zone between assemblages.

During March, mean polychaete abundance and species richness (21) was higher in the "oceanic" assemblage; *Pelagobia longicirrata*, *Plotohelmis capitata*, *Rhynchonerella gracilis,* and *Lopadorhynchus henseni* Reibisch, 1893, registered their highest frequency and abundance values in this assemblage. The first two species were three times more abundant in the "oceanic" than in the "neritic" assemblage (Table 2), and *R. gracilis* and *L. henseni* occurred only in the "oceanic" assemblage. Other uncommon species, such as *Krohnia lepidota* (Krohn, 1845)*, Plotohelmis tenuis* (Apstein, 1900)*, Vanadis minuta* Treadwell, 1906*, Lopadorhynchus kronii* Claparède, 1880, and *Sagitella kowalewski* Wagner, 1872*,* were recorded only in this group. A small number of species registered their highest density and frequency of occurrence in the "neritic" assemblage, such as the iospilids *Phalacrophorus uniformis* and *Iospilus phalacroides* Viguier, 1886 (Table 2).

Discussion

Abundance and composition

In the Gulf of Tehuantepec, holoplanktonic polychaetes were widely distributed in both neritic and oceanic waters during March, although total polychaete abundance was highest in areas beyond the shelf (Fig. 3). These results agree with previous observations, since many authors have indicated that these animals inhabit mainly the open sea (Day, 1967; Støp-Bowitz, 1996). At least for the western region, polychaete density was higher during November as it has been also found for copepods (Fernández-Álamo et al., 2000). These high values could be due to the upwelling process that takes place from November to February and causes an increase in primary and secondary productivity (Ayala-Duval et al., 1996; Lara-Lara et al., 1998).

RT analysis showed that pH and dissolved oxygen were the main factors influencing geographical variability in polychaete abundance in the Gulf of Tehuantepec during March. Many chemical and biological processes in aquatic

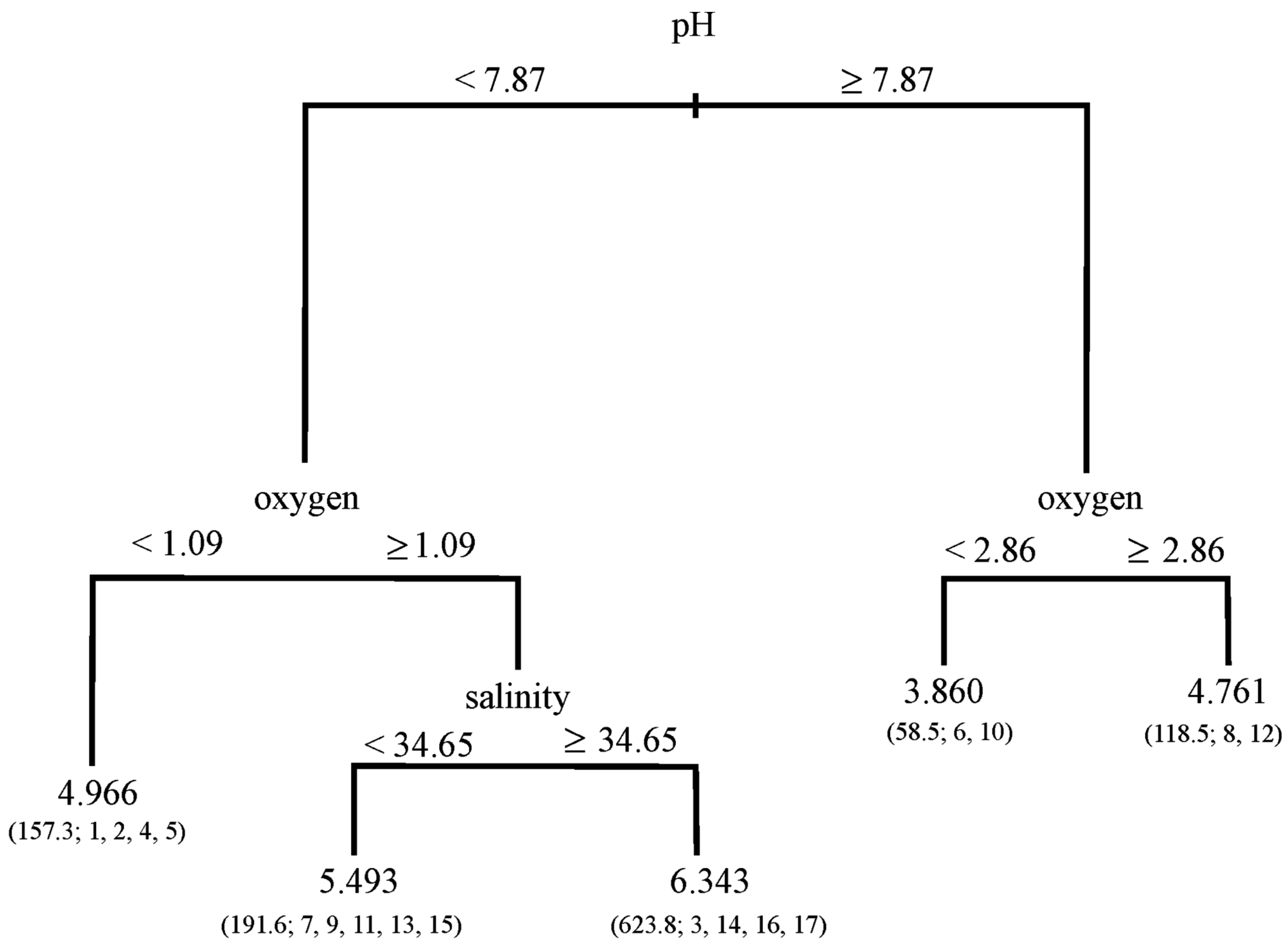

Figure 4. Regression tree analysis applied to log-transformed polychaete abundance as response variable, and temperature, salinity, dissolved oxygen and pH as predictor variables. Gulf of Tehuantepec, March 1978 (mean polychaete abundance; stations).

Figure 4. Résultats de l'analyse par arbres de régression avec les abondances de polychètes (transformées en log) comme réponse et les paramètres température, salinité, oxygène dissous et pH comme prédicteurs. Golfe de Tehuantepec, mars 1978 (abondance moyenne des polychètes; stations).

systems are affected by the pH and, outside its seawater range (7.5 to 8.5), it alters the physiological activities of most organisms. In spite that the pH values registered in this study were within the normal range for seawater, we observed an inverse relationship between mean pH values and total polychaete abundance (Fig. 4). The pH values here registered are consistent with pH values of other upwelling areas (Simpson & Zirino, 1980). These authors indicated that in the Peruvian upwelling region, cold, nutrient-rich waters are characterized by low pH (7.7 to 7.8). To our knowledge, no relationship has been found between total abundance of zooplankters and pH values within their normal seawater range. In karstic systems, Cervantes-Martínez et al. (2002) found an inverse relationship between zooplankton biomass and pH values. Undoubtedly, the most important gas in water is oxygen, as its role in metabolic processes is essential to all forms of life and it affects the distribution of pelagic organisms at several spatial scales. In the east coast of the Pacific Ocean, the widespread OMZ exerts a severe impact on the distribution of zooplankton (Judkins, 1980; Saltzman & Wishner, 1997). Above a Pacific seamount, Saltzman & Wishner (1997) found that pelagic polychaetes distributed mostly at the thermocline (30-100 m; 36.2%), and at the upper (100-300 m; 28.9%) and lower OMZ (1000-1300 m; 30%) interfaces. They hypothesized that the upper OMZ zooplankton community was associated with detrital material accumulating below the thermocline. In the Peruvian upwelling region, Judkins (1980) found that polychaetes (mainly the genus *Tompteris* Eschscholtz, 1825), as well as most zooplankton taxa, aggregated a few meters above the 0.1 ml L^{-1} isopleth. In this work, it was not our objective to analyse

Table 1. Holoplanktonic polychaete species collected in the Gulf of Tehuantepec during March and November 1978. Taxonomic classification after Rouse & Pleijel (2001).

Tableau 1. Liste des espèces de polychètes holoplanctoniques récoltées dans le Golfe de Tehuantepec en mars et novembre 1978. Classification taxonomique de Rouse & Pleijel (2001).

	Mean abundance (ind 1000 m^{-3})		% of the total abundance
	March (n = 17)	November (n = 5)	
Alciopidae			
Alciopina parasitica Claparède & Panceri, 1867	1.3	3.0	0.52
Krohnia lepidota (Krohn, 1845)	0.3	_	0.07
Plotohelmis capitata (Greeff, 1876)	7.2	6.6	2.18
Plotohelmis tenuis (Apstein, 1900)	0.7	0.4	0.20
Rhynchonerella gracilis Costa, 1862	7.8	5.8	2.28
Rhynchonerella moebii (Apstein, 1893)	4.1	4.8	1.31
Vanadis longissima (Levinsen, 1885)	_	0.4	0.03
Vanadis minuta Treadwell, 1906	0.1	_	0.03
Vanadis tagensis Dales, 1955	_	0.4	0.03
Lopadorhynchidae			
Lopadorhynchus nationalis Reibisch, 1895	3.1	0.8	0.76
Lopadorhynchus brevis Grube, 1855	2.6	0.4	0.62
Lopadorhynchus henseni Reibisch, 1893	3.5	_	0.85
Lopadorhynchus krohnii Claparède, 1880	0.2	_	0.04
Pelagobia longicirrata Greeff, 1879	213.5	516.6	86.52
Iospilidae			
Iospilus phalacroides Viguier, 1886	0.6	_	0.14
Phalacrophorus pictus Greeff, 1879	0.4	_	0.06
Phalacrophorus uniformis Reibisch, 1895	9.0	6.2	2.59
Tompteridae			
Tomopteris elegans Chun, 1888	0.6	_	0.11
Tomopteris euchaeta Chun, 1888	0.7	_	0.17
Tomopteris nationalis Apstein, 1900	2.3	_	0.52
Tomopteris planktonis Apstein, 1900	1.2	0.4	0.30
Typhloscolecidae			
Sagitella kowalewski Wagner, 1872	0.1	0.4	0.06
Travisiopsis dubia Støp-Bowitz, 1948	0.7	3.0	0.38
Typhloscolex mulleri Busch, 1851	1.0	_	0.24

the vertical distribution of polychaete abundance; however, we think that the encroachment of the OMZ concentrates zooplankton into the surface layer, as Judkins (1980) also suggested.

In this study, Lopadorhynchidae (88.8%) was the most abundant family, especially due to the presence of *Pelagobia longicirrata*. Rouse & Pleijel (2001) indicated this family to be cosmopolitan although more common in warm and tropical waters. The dominant species in this study, *P. longicirrata* (86.5%), is widely distributed in the Atlantic, Mediterranean and Indian Oceans (Berkeley & Berkeley, 1960). This species is among the most abundant and frequent species of the holoplanktonic polychaetes in the Antarctic Sea, southeastern Pacific and Gulf of California (Sicinski, 1988; Fernández-Álamo, 1983, 1992; Dinofrio, 1997).

The alciopids represented 6.5% of the total abundance, with *Rhynchonerella gracilis, Plotohelmis capitata* and *R. moebii* being the most common species (Table 1). The characteristics that may explain the relatively high abundance of alciopids in the pelagic system are a strong proboscis and the complex, large, telescopic eyes controlled by muscles that allow the eyes to change direction and enable individuals to recognize the size and shape of the prey items (Fernández-Álamo & Thuesen, 1999). Among the alciopid species here recorded, *P. capitata* is the most abundant species in waters of the outer shelf around Madagascar during April and May (Day, 1975), but it is uncommon in Peruvian waters (Berkeley & Berkeley, 1961). *Rhynchonerella moebii* has also been reported in the Mediterranean (Apstein, 1900, in Berkeley & Berkeley, 1961), the North Atlantic (Wesenberg-Lund, 1939, in

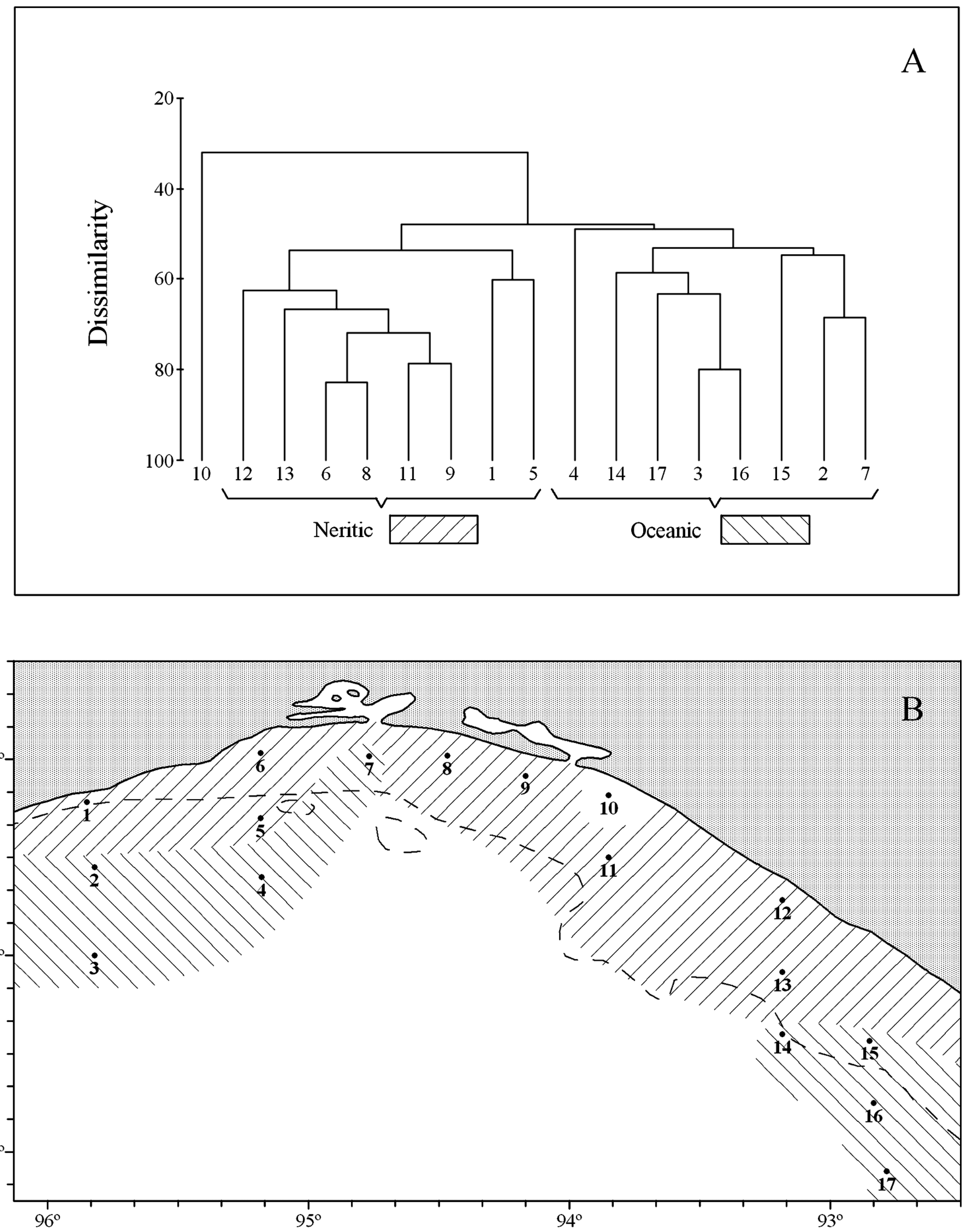

Figure 5. A. Identification of main holoplanktonic polychaete assemblages based on a Bray-Curtis cluster analysis. **B.** Geographical location of the assemblages. Gulf of Tehuantepec, March 1978.

Figure 5. A. Identification des principaux assemblages de polychètes holoplanctoniques par la méthode de groupement de Bray-Curtis. **B.** Localisation géographique de ces assemblages. Golfe de Tehuantepec, mars 1978.

Table 2. Relative abundance of holoplanktonic polychaete species in the assemblages identified in the Gulf of Tehuantepec during March 1978. *X* = mean abundance (ind 1000 m^{-3}), *F* = percentage of occurrence, *n* = number of stations.

Tableau 2. Abondance relative des espèces de polychètes holoplanctoniques dans les différents assemblages identifiés dans le Golfe de Tehuantepec en mars 1978. *X* = abondance moyenne (ind 1000 m^{-3}), *F* = pourcentage d'occurrence, *n* = nombre de stations.

	NERITIC (*n* = 8)		OCEANIC (*n* = 8)	
	X	*F*	*X*	*F*
Alciopina parasitica	0.3	12.5	2.5	62.5
Krohnia lepidota	_	_	0.6	12.5
Plotohelmis capitata	3.8	87.5	11.5	75.0
Plotohelmis tenuis	_	_	1.5	25.0
Rhynchonerella gracilis	_	_	16.6	100.0
Rhynchonerella moebii	2.5	37.5	6.1	75.0
Vanadis minuta	_	_	0.3	12.5
Lopadorhynchus nationalis	2.0	75.0	4.6	87.5
Lopadorhynchus brevis	1.9	25.0	3.6	50.0
Lopadorhynchus henseni	_	_	7.5	62.5
Lopadorhynchus krohnii	_	_	0.4	12.5
Pelagobia longicirrata	102.0	100.0	349.0	100.0
Iospilus phalacroides	1.3	25.0	_	_
Phalacrophorus pictus	0.3	12.5	0.5	25.0
Phalacrophorus uniformis	10.3	75.0	8.9	62.5
Tomopteris elegans	0.3	12.5	0.6	25.0
Tomopteris euchaeta	0.3	12.5	1.3	25.0
Tomopteris nationalis	0.9	37.5	4.0	50.0
Tomopteris planktonis	1.1	50.0	1.5	37.5
Sagitella kowalewski	_	_	0.3	12.5
Travisiopsis dubia	0.3	12.5	0.9	37.5
Typhloscolex mulleri	0.5	25.0	1.6	37.5

Berkeley & Berkeley, 1961), the North Pacific (Dales, 1957), Peruvian waters (Berkeley & Berkeley, 1961), and eastern tropical Pacific (Fernández-Álamo, 1983). According to Dales (1957), *R. gracilis* is a rare species, however Fernández-Álamo (1983) found this species widely distributed in the eastern tropical Pacific. *Alciopina parasitica* Claparède & Panceri, 1867, was rare in our survey region and occurred mainly in the oceanic area, in agreement with Dales' (1957) results.

Iospilids were the third most abundant family (2.8%) in this study and *Phalacrophorus uniformis* was its best represented species (2.6%). These holoplanktonic polychaetes appear to be cosmopolitan (Rouse & Pleijel, 2001). The records of *P. uniformis* include the northwest Australian Sea (Peter, 1974), the Atlantic (Day, 1967), the eastern tropical Pacific (Fernández-Álamo, 1983) and the California Current System (Fernández-Álamo et al., 2003).

Tomopterids accounted for 1.1% of the total abundance. However, in the California Current System, this family accounted for 87.3% of the holoplanktonic polychaetes (Fernández-Álamo et al., 2003). Distribution of tomopterids is worldwide, including oceanic and near-shore waters, from the surface to a few hundred meters depth (Rouse & Pleijel, 2001). Feeding habits of these animals are variable. Some have a short pharynx and ingest the whole prey, or suck out the body fluids; other tomopterid forms lack prey-catching organs and eat microscopic preys (Day, 1967; Fernández-Álamo & Thuesen, 1999). All the species in this study have also been found in the California Current System and in the southeastern Pacific (Fernández-Álamo, 1983; Fernández-Álamo et al., 2003).

Typhloscolecidae was the least abundant family (0.7%) in this study. They have a cosmopolitan distribution, from shallow waters down to abyssal depths (Uschakov, 1972). It has been suggested that they are ectoparasites of soft-bodied or gelatinous animals, such as chaetognaths (Øresland & Pleijel, 1991). As in the Tehuantepec Gulf, species of this family also depict low abundances in the California Current System (Fernández-Álamo et al., 2003). In the Indian Ocean and eastern tropical Pacific, Peter (1975) and Fernández-Álamo (1983) found *Typhloscolex mulleri* Busch, 1851 and *Sagitella kowalewski* as the most abundant species of the family; in our study area, *Travisiopsis dubia* Støp-Bowitz, 1948, recorded the highest abundance.

Holoplanktonic polychaete assemblages

Results of the present study indicate the presence of "neritic" and "oceanic" holoplanktonic polychaete assemblages during March, with a higher abundance of most species in the "oceanic" assemblage (Fig. 5; Table 2). Some of the most abundant species in this assemblage (*Pelagobia longicirrata* and *Plotohelmis capitata*) were also found in the "neritic" one, indicating a wide tolerance to environmental conditions (Berkeley & Berkeley, 1960; Day, 1975; Dinofrio, 1997; Fernández-Álamo, 1983). Some species that restricted their distribution to the "oceanic" assemblage, such as *Rhynchonerella gracilis* and *Lopadorhynchus henseni*, may have a low tolerance to variations in physical features.

Multivariate analysis applied to the data matrices from November (beginning of the upwelling period) and March indicated that geographical changes in the assemblages are more important than the composition itself, at least for the two sampled periods. However, we hypothesize that temporal succession phases in the occurrence of holoplanktonic polychaetes might also occur associated with particular

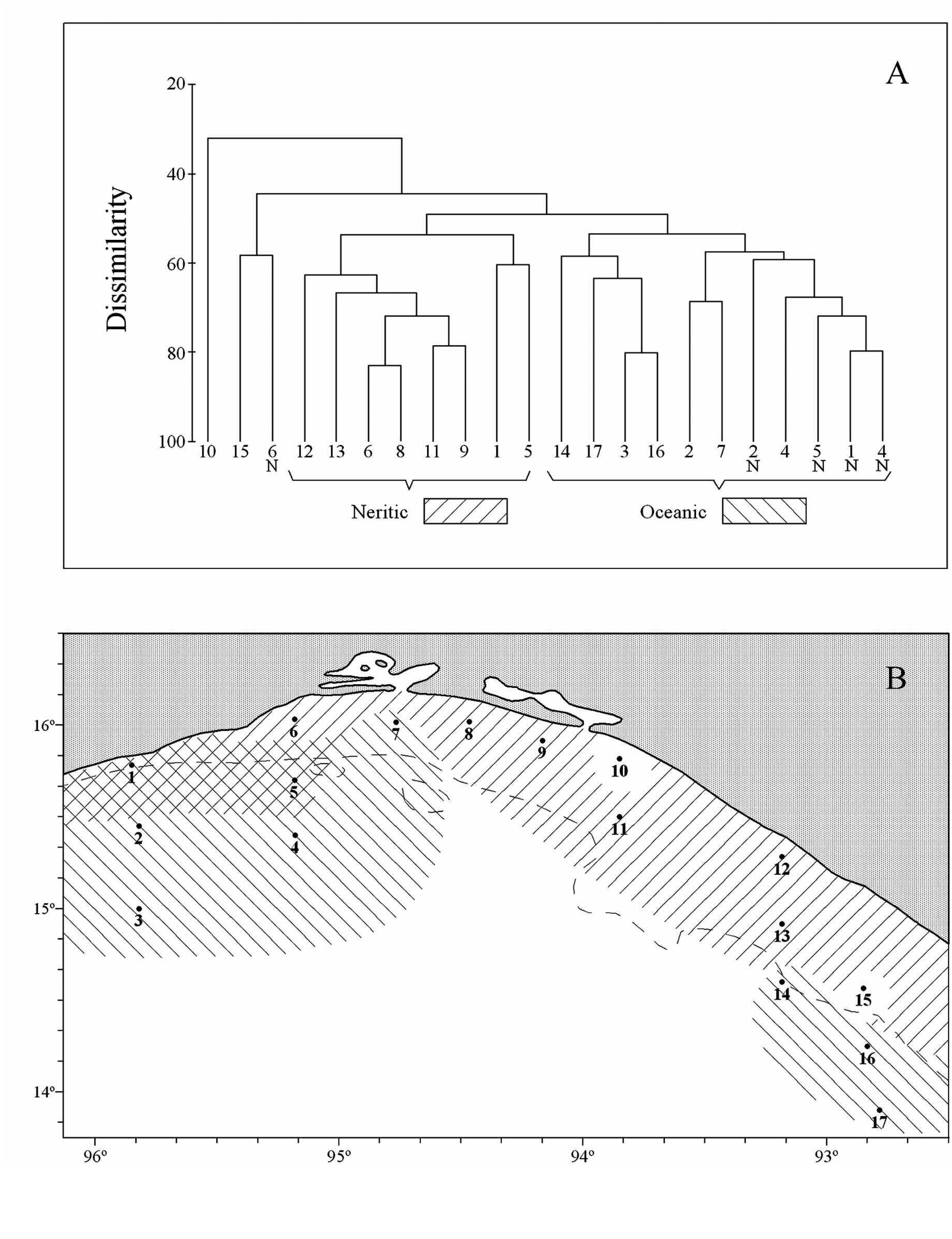

Figure 6. A. Identification of main holoplanktonic polychaete assemblages based on a Bray-Curtis cluster analysis. **B.** Geographical location of the assemblages. Gulf of Tehuantepec, March/November 1978. N = November.

Figure 6. A. Identification des principaux assemblages de polychètes holoplanctoniques par la méthode de groupement de Bray-Curtis. **B.** Localisation géographique de ces assemblages. Golfe de Tehuantepec, mars/novembre 1978. N = novembre.

upwelling periods, as it has been observed for other zooplankters in other upwelling areas (Timonin, 1993). The main changes might be associated with the relative dominance of phytophagous, carnivores, and detritivores at different levels of the water column, since, as several authors suggest (Judkins, 1980; Saltzman & Wishner, 1997), the OMZ has a deep impact on the vertical distribution of pelagic organisms.

Literature concerning polychaete assemblages is scarce, even for the benthic environment. Few studies have analysed planktonic polychaete assemblages (Day, 1975; Murina, 1997), but hardly any has focused specifically on holoplanktonic polychaete assemblages (Fernández-Álamo et al., 2003). Thus, few comparable studies to the present one exist. Around Madagascar, Day (1975) distinguished three environmental areas, named "inner neritic", "outer neritic", and "oceanic", and observed that the distribution of holoplanktonic and meroplanktonic polychaetes was related to these features. He found that *Iospilus phalacroides* and *Phalacrophorus pictus* Greeff, 1879, reached their maximum abundance in the "inner neritic" area during the summer. In the present study, *I. phalacroides* and *Phalacrophorus uniformis* were more abundant in the "neritic" assemblage. Day (1975) suggested that food supplies derived from the mangrove swamps influence distribution of these species. Our results support the suggestion (Day, 1967) that some iospilids, such as the genus *Iospilus* Viguier, 1886, are phytophagous or are filter-feeders, which might explain their abundance in the neritic region, where the phytoplankton concentration is higher (Lara-Lara et al., 1998). However, it has been observed that *Phalacrophorus* Greeff, 1879, has enormous jaws and is carnivorous (Day, 1967).

In a ~2,500 km transect along the California Current System, Fernández-Álamo et al. (2003) identified three distinctive holoplanktonic polychaete assemblages, whose geographical location was correlated to productivity and main water masses. Their results showed a "north group" associated with areas of high primary and secondary production and with the California Current and Subtropical Central water masses, a "south group" related to the Surface Equatorial Water, and a "transition group" between them. They reported the presence of *P. pictus* in the high production group, in agreement with Day's (1975) results.

In the Black Sea, Murina (1997) found that larvae of 22 meroplanktonic polychaete species could be grouped into five ecological groups according to some environmental features, such as temperature, salinity, depth, and distance to the coast.

In spite of the lack of information on pelagic polychaete distribution and trophic habits, all these findings suggest that the structure of holoplanktonic polychaete assemblages could be determined by the feeding habits of the species and to their tolerance to the variability in environmental conditions.

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