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Macrofaunal density and biomass in the Campeche Canyon, Southwestern Gulf of Mexico

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ABSTRACT

The composition, density and community structure of the benthic macrofauna were investigated in sediments of the Campeche Canyon in the SW Gulf of Mexico. Total macrofaunal density ranged from 9466 ± 2736 ind m^{-2} at the continental shelf station to 1550 ± 195 ind m^{-2} in the canyon. Density values significantly diminished with distance from the coast and depth; only a few stations in the center of the canyon displayed larger density values (E-37 with 4666 ± 1530 ind m^{-2}, E-36 with 5791 ± 642 ind m^{-2} and E-26 with 6925 ± 2258 ind m^{-2}). Densities were positively correlated to organic nitrogen in the sediment ($r = 0.82$) and coarse silt ($r = 0.43$), and negatively with depth ($r = -0.74$) and distance from the coast ($r = -0.68$). At all stations, the polychaete worms contributed most to the multi-species community structure. The nematodes and Foraminifera displayed their highest densities in the center of the canyon. The biomass values declined significantly with depth. We conclude that the macrofauna density and biomass changed in response to organic matter contents in the sediment, both with distance from the coast and with depth.

1. Introduction

Studies focusing on benthic macrofaunal communities in canyons have been conducted mostly in temperate and subtropical zones. The resulting information is diverse and has created controversy among scientists who attribute the variability to canyon types (Jorissen et al., 1994), diversity and dominance of sources of organic matter chemoautotrophic seepage (McHugh et al., 1992; Dron et al., 1987), photoautotrophic export to the seafloor (Sorbe, 1999; Laborde et al., 1999; Heussner et al., 1999), lateral transport (Cremer et al., 1999; Klaucke et al., 2000; Puig et al., 2000, 2003), hydrodynamics (Shepard et al., 1974; Gardner, 1989; Durrieu de Madron, 1994), seasonality (Pfannkuche and Soltwedel, 1998; Sorbe, 1999; Schmiedl et al., 2000), food availability (Stefanescu et al., 1994; Cartes, 1998; Gili et al., 2000) or different sediment factors (de Bovée et al., 1990; Vetter, 1995; Thistle et al., 1999).

The transport of sediment by turbidity currents originating from the discharge of rivers, marine currents, or unpredictable coastal storms that favor erosion of soft sediments by resuspension of material, are at the origin of canyons (Segall et al., 1989). This process results in a dense mixture of water and sediment that moves along the seabed transporting plant debris and the smallest faunal components (Keen, 1968). Sediment instability is an important ecosystem disturbance factor in canyon environments; the occurrence of small-scale mass wasting and bottom scour by currents influences the composition, abundance, and occurrence of benthic fauna in the canyon (Emery and Uchupi, 1984). The input of organic matter results in aggregations of large densities of organisms (Duineveld et al., 2001; Vetter, 1995) that are larger than at similar depths outside the canyons (Vetter and Dayton, 1999; Houston and Haedrich, 1984). Benthic macrofaunal species richness and density decrease with depth (Flach et al., 1998) and distance from the coast along continental slopes (Thistle et al., 1999) and have an effect on the size structure of the fauna (Cosson et al., 1997). In the tropics, canyons are biodiversity hotspots (i.e. Cañón de La Aguja, SW Caribbean) with large numbers of endemic species (Ardila et al., 2005).

The objectives of this paper are to (1) describe the taxonomic composition and richness, density, and biomass of the benthic macrofauna along a distance-from-land gradient in the Campeche Canyon in the southwestern Gulf of Mexico and (2) relate the taxonomic composition and abundance to some environmental factors in the sediment controlling the variability of the community in the canyon.

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2. Materials and methods

2.1. Study area

The Campeche Canyon is located in the SW sector of the Gulf of Mexico (Fig. 1). The boundary to the east is the Campeche Escarpment, to the west the Campeche shelf, and the Campeche knolls subprovince to the north (Bryant et al., 1991). The canyon is the boundary between the carbonate and the terrigenous sediment provinces in the SW Gulf of Mexico; its origin is related to the tectonic history of the zone and the opening of the Gulf during the Jurassic (Weaver, 1950). The major axis of the canyon runs 125 km from 20°00′ latitude N and 92°22′ longitude W to 21°00′ latitude N and 92°42′ longitude W and has a maximum width of 30 km (Creager, 1958), starting at a depth of 160 m on the outer continental shelf and extending to a maximum depth of 2800 m in the offshore waters of the Campeche Bay (Salas et al., 2004).

The canyon is an active area for the export of biogenic carbon. The suspended particles reach concentrations of 2.8–33.1 mg L^{-1}; the maximum chlorophyll concentrations vary between 0.15 and 0.29 mg Chl-*a* m^{-3} at depths of 78 and 89 m in the water column. The transport of nutrients from deeper water masses to the euphotic zone promotes high primary productivity in localized areas with well-oxygenated waters all the way to the bottom. An oxygen minimum zone occurs seasonally within the 500-m depth layer as a result of water upwelling and the intense flux of organic particles exported to the abyss (Morey et al., 2005). The main water masses that characterize the canyon seafloor are the Antarctic Intermediate Water (AAIW) and the North Atlantic Deep Water (NADW) below 1000 m (Nowlin and McLellan, 1967; Nowlin et al., 1969).

2.2. Collection and treatment of samples

2.2.1. Field work

Samples were collected onboard the R/V *Justo Sierra* during the PROMEBIO I (*Procesos Oceánicos y Mecanismos de Producción Biológica en el sur del Golfo de México*) cruise at eight georeferenced stations along the main axis of the Campeche Canyon (Table 1). Sediment samples were collected with replication, by sending a US-NEL boxcorer with an area of 0.16 m^2 to the bottom three times at each station, from which macrofauna samples were obtained, sieved through 250 μm mesh onboard and kept separate for the analyses after they were fixed with ethanol and stained with Rose Bengal. Each replicate was stored in a separate jar and labeled for later sorting in the laboratory. In addition, subsamples were collected to determine the organic carbon (C_{org}) and nitrogen (N_{org}) contents, the grain size, and the amount of chlorophyll *a* (Chl-*a*) present in the superficial sediment. The samples for grain size analysis were stored at room temperature. The samples collected for elemental carbon, nitrogen, and pigments analysis were stored in centrifuge tubes and frozen at −20 °C. At each site, temperature and salinity were determined from both the continuous CTD records and bottom water samples collected with Niskin bottles on a rosette.

2.2.2. Laboratory methods

The sediment samples collected for macrofauna were sorted and specimens identified to major taxa (genera, families, orders). Abundance and biomass were determined, the latter using a Sartorius analytical balance. The information was recorded on worksheets, density (ind m^{-2}) determined, and biomass recorded as fixed wet mass (mg fwm) was transformed into biomass and expressed as mg C m^{-2} using the constants described by Rowe (1983).

Grain size was analyzed using the Particle Sizer Analysette 20 Sedimentograph by photo-extinction measuring the degree of attenuation of light created by the suspended particles in the settling column. The samples collected for elemental organic carbon and nitrogen analysis were acidified with a 0.1 N HCl solution and analyzed in an EA FISONS model EA1108 elemental analyzer following the protocol described in Pella (1990). The results were expressed in percentages of the amount available per element in 1 mg of sediment. The C/N ratios were calculated to determine the input of organic materials to the seafloor. The pigment analysis determined Chl-*a* concentrations with a Turner Designs bench fluorometer model 10-AU at a wavelength of 680 nm (Arar and Collins, 1997).

2.3. Data analyses

A correlation analysis that included both the environmental variables and synthetic community structure variables was conducted to describe the relationship between the habitat environmental factors and the biotic data. The diversity index H' was computed based on natural logarithms; the evenness of species distributions in the samples was also computed. Chi-squared tests were used to measure patchiness in the macrofaunal community at each site using the three replicate box-core data in order to describe the randomly, aggregated, or uniformly distributed nature of the densities across the samples (Lambshead and Hodda, 1994; Rice and Lambshead, 1994).

Significance of the differences found in the density and biomass values among samples and depth zones was tested using a one-way analysis of variance (ANOVA). The relationships between taxonomic composition and environmental factors were studied by canonical redundancy analysis (RDA). Canonical redundancy analysis (RDA) is an appropriate method to explain beta diversity, which is the variation in taxonomic composition among sites, by environmental variables (Legendre et al., 2005). The taxonomic composition table was Hellinger-transformed prior to the analysis, following Legendre and Gallagher (2001): the data are first transformed into relative abundances per site; then the relative abundances are subjected to a square-root transformation to reduce the influence of the most abundant taxa. The taxa–environment relationship was tested using a permutation test involving 999 random permutations. Significance of individual canonical eigenvalues was tested to establish the major factors and components that structure the community in the canyon. Continental shelf station E-42, which differed markedly in taxonomic composition, was not included in this analysis.

3. Results

3.1. Description of the habitat

3.1.1. Bottom temperature and salinity

All canyon stations had temperatures of 4.31 or 4.32 °C. The salinity values ranged from 36.10 on the shelf to 34.76 in the canyon (Table 2). Based on the T-S series, only two water masses were identified as being associated to the seafloor habitats: the Caribbean sub-superficial subtropical water mass on the shelf and the North-Atlantic deep water mass in the canyon.

3.1.2. Organic carbon and nitrogen content in sediment

The average C_{org} values ranged from 1.50% on the continental shelf (E-42) to 0.58% in the canyon. The average N_{org} values ranged

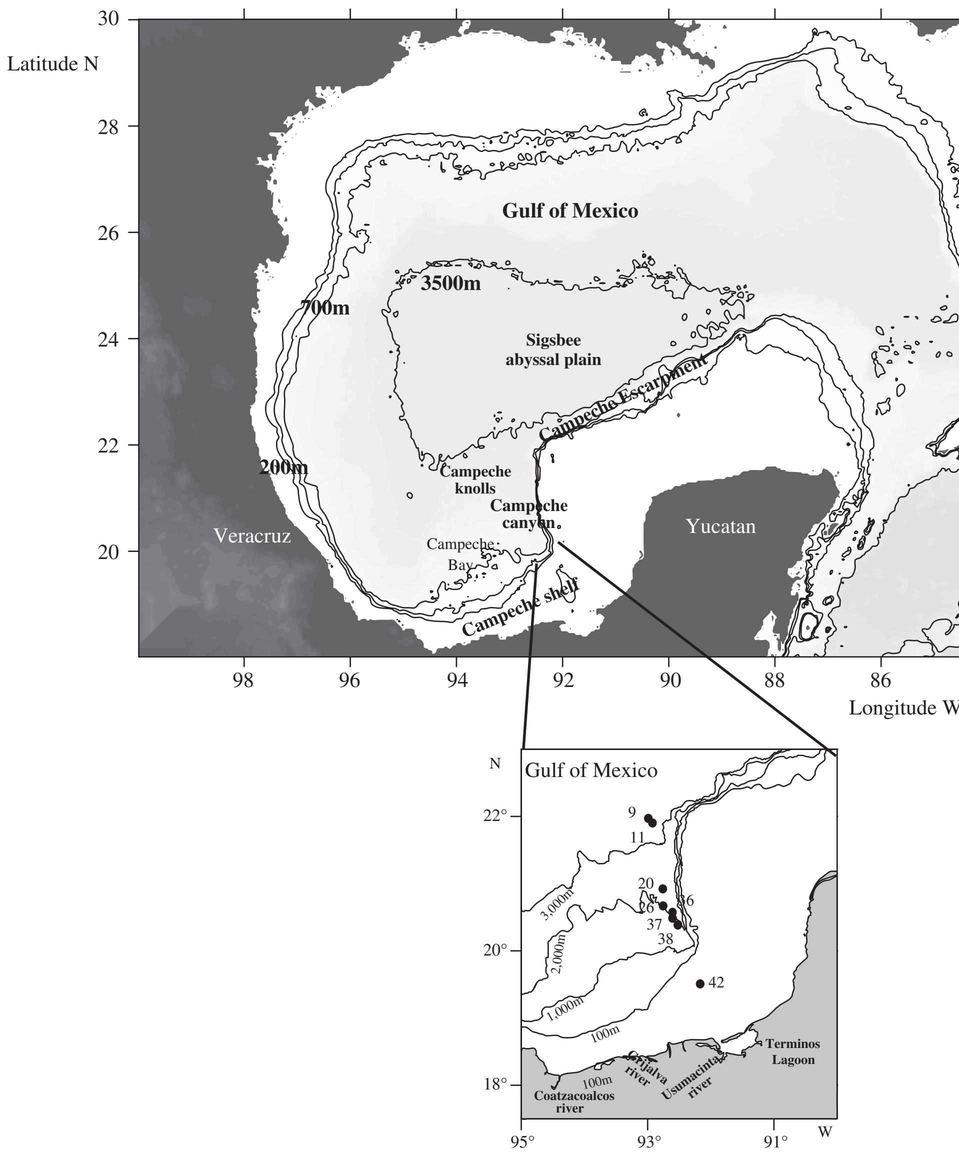


Fig. 1. Locations of the stations sampled in the Campeche Canyon in the SW Gulf of Mexico. Numbers in the small map show the station IDs.

Table 1
Geographic information on the locations where macrofauna samples were collected in the Campeche Canyon during the PROMEBIO.I cruise

Station	Depth (m)	Latitude N	Longitude W	Distance from the coast (km)
42	54	19°30′04.2″	92°10′06.0″	63.02
38	2320	20°23′00.0″	92°31′30.0″	81.77
37	2420	20°29′13.2″	92°36′34.2″	123.29
36	2460	20°34′36.0″	92°36′35.4″	129.48
26	2560	20°40′12.6″	92°45′25.8″	147.78
20	2750	20°55′33.0″	92°45′27.0″	167.78
11	2840	21°05′03.0″	92°55′33.0″	186.41
9	2900	23°58′34.8″	92°59′35.4″	222.86

from 0.16% to 0.08% (Table 2). Both C_{org} and N_{org} values decreased with depth and distance from the coast; the largest values were recorded in the central area of the canyon ($C_{org} = 1.14\%$, $N_{org} = 0.15\%$), where the values were almost twice as large as those recorded at nearby stations ($C_{org} = 0.58\%$, 0.76%; $N_{org} = 0.08\%$, 0.10%). The C_{org} and N_{org} percentages were positively correlated ($r = 0.94$). The average values of the C/N ratio ranged from 9.10 on the shelf to 7.12 in the canyon. The C/N ratio in the canyon increased with depth (7.28–7.98), with the exception of Station E-20 in the central portion of the canyon which displayed the smallest values (7.12).

3.1.3. Pigments in sediment

The pigment values in the sediment ranged from 159.25 μg Chl-*a* cm^{-2} on the shelf to 0.18 μg Chl-*a* cm^{-2} in the canyon. The stations located in the center of the canyon (E-37 and E-26) displayed notably larger (22.0 and 6.49 μg Chl-*a* cm^{-2}) average values than those found in peripheral areas of the canyon (around 0.2 μg Chl-*a* cm^{-2}). Pigment values showed a diminishing trend with increasing depth and were related [ln(Chl-*a*)] to the organic carbon ($r = 0.87$, Fig. 2) and (Chl-*a*) to the nitrogen contents in the sediment ($r = 0.57$).

3.1.4. Grain size

The superficial sediment was composed mainly of clay and coarse silt, which contributed together up to 96% of the sediment composition (Table 2).

Table 2
Environmental factors at the locations sampled in the Campeche Canyon: mean values of sediment organic carbon and nitrogen, C/N ratio, pigments in the sediment and percentage contribution of the grain size characteristics

Location	Temperature (°C)	Salinity	% C	% N	C/N	μg Chl-*a* cm^{-2}	% Clay	% Coarse silt	% Very fine sand	% Fine sand
E-42	22.46	36.10	1.49±0.01	0.16±0.001	9.10±0.01	159.25±0.55	61.1	30.5	8.2	0
E-38	4.32	34.78	0.90±0.00	0.12±0.001	7.28±0.04	0.25±0.03	96.0	3.6	0.2	0
E-37	4.32	34.78	0.90±0.00	0.12±0.000	7.55±0.03	20.98±0.69	64.3	21.5	14	0
E-36	4.31	34.78	0.76±0.01	0.10±0.000	7.32±0.08	0.22±0.01	73.4	19.7	6.8	0
E-26	4.31	34.77	1.14±0.01	0.15±0.001	7.81±0.01	6.39±0.59	47.4	21.8	17.6	13.8
E-20	4.31	34.77	0.58±0.00	0.08±0.000	7.12±0.01	0.20±0.01	39.1	24.4	24.8	11.5
E-11	4.31	34.76	0.69±0.01	0.09±0.001	8.11±0.05	0.19±0.01	60.6	11.6	25.6	0.9
E-9	4.31	34.76	0.73±0.01	0.09±0.001	7.98±0.03	0.18±0.01	43.5	23.3	18.4	14.7

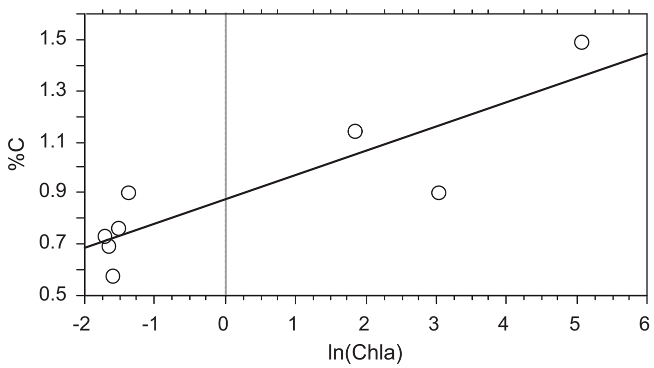


Fig. 2. Relationship between chlorophyll *a* (Chl-*a*) and % organic carbon (%C) at eight stations in the Campeche Canyon in the SW Gulf of Mexico.

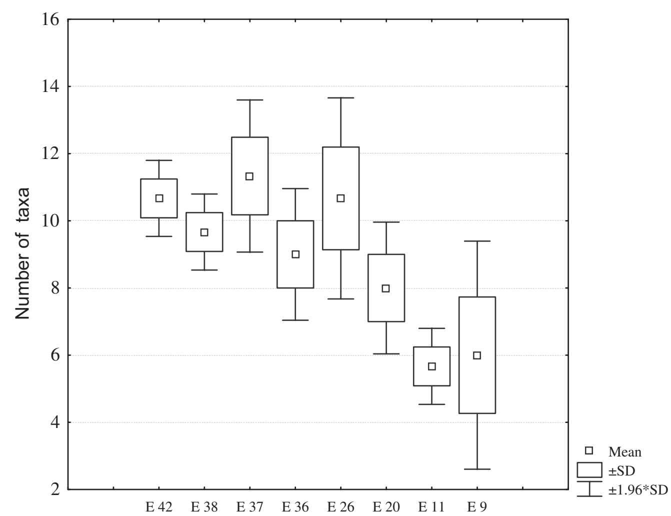


Fig. 3. Taxonomic richness of the macrofaunal benthic community at eight sampling stations in the Campeche Canyon, SW Gulf of Mexico, ordered by depth and distance from the coast along the abscissa. The graph shows the mean, standard deviation and standard error of the mean. E: the station ID number.

3.2. *The macrobenthic community structure*

3.2.1. *Taxonomic composition*

A total of 4367 specimens were sorted from the sediment. The 20 identified taxa were grouped into 12 classes, one subclass, two superorders, and six orders. Crustaceans were the most diversified taxon, represented by five classes. The largest taxonomic richness occurred near the canyon's head with 11.33±1.15 taxa. The number of taxa diminished with increasing depth and distance from the coast (Fig. 3) with 5.67±0.58 taxa near the canyon's mouth. The taxonomic richness was related to the organic nitrogen contents of the sediment ($r = 0.72$), distance to the coast ($r = -0.72$), and depth ($r = -0.46$). The change in taxonomic richness (s) was positively correlated ($r = 0.79$) to the total abundance of macrofauna.

The relationship between the taxonomic richness, the diversity index H' and the evenness index showed differences between the samples from the shelf ($\mathrm{Ln_{taxa}}<3$, $H<1$, $\mathrm{Ln}\,E/\mathrm{Ln_{taxa}}<-0.55$) and the canyon ($\mathrm{Ln_{taxa}}>3$, $H>1$, $\mathrm{Ln}\,E/\mathrm{Ln_{taxa}}>-0.55$). Chi-squared tests used here to measure patchiness in the whole macrofaunal community showed a significantly aggregated dispersion in both the total or by taxa and by station (97045.38, df 160, $p = 0.00$) and pooled or by station (35047.45, df 7, $p = 0.00$) values.

3.2.2. *Density*

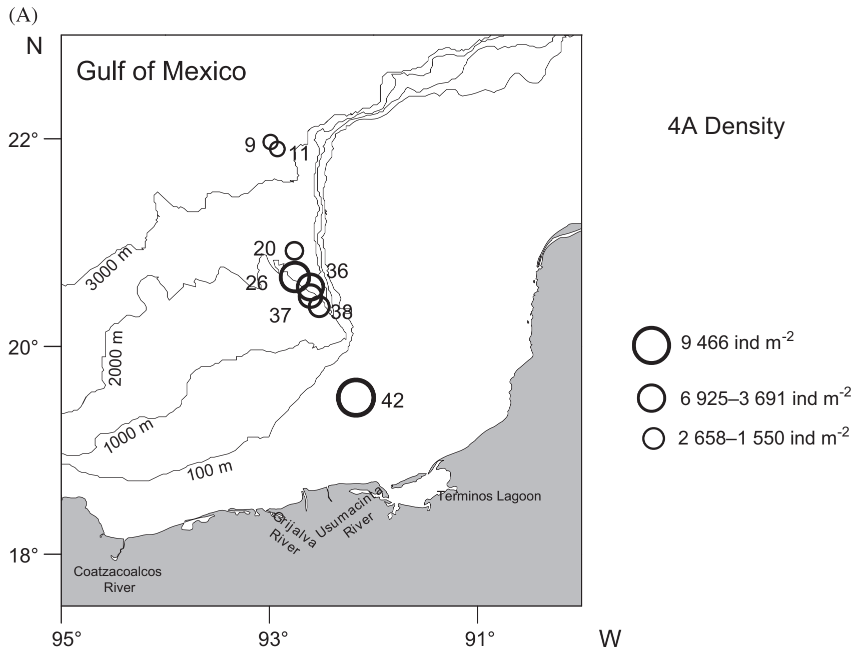
The mean animal density values ranged from 9466±2736 ind m^{-2} at the continental shelf station to 1550±195 ind m^{-2} in the canyon. Density values diminished with distance from the coast and with depth (Fig. 4A); only a few stations in the center of the canyon displayed larger values (E-37 with 4666±1530 ind m^{-2}, E-36 with 5791±642 ind m^{-2} and E-26 with 6925±2258 ind m^{-2}; Fig. 4A). The polychaete worms had the largest percentage density (43.67%); they were followed by the nematodes (24.48%), the foraminifera (16.10%) and the harpacticoid copepods (5.29%). These relative contributions to density changed with depth and taxon. The nematodes and foraminifera displayed a parabolic pattern, with the largest density recorded at stations located in the center of the canyon. Mean density values were significantly different among stations (ANOVA $F_{(7,\ 16)} = 10.86$, $p<0.0000$). Density values were positively correlated to percentages of organic nitrogen in the sediment ($r = 0.82$) and the occurrence of coarse silt ($r = 0.43$), and negatively to depth ($r = -0.74$) and distance from the coast ($r = -0.68$).

3.2.3. *Biomass*

The largest biomass values were recorded in the canyon's head: 27.44±1.17 mg C m^{-2} at station E-38 (2320 m) and 3.64±0.04 mg C m^{-2} at station E-37 (2420 m). The smallest mean value was recorded in the canyon's mouth or fan: 0.03±0.01 mg C m^{-2} at station E-9 (2900 m depth; Fig. 4B). Hydroids and agglutinating foraminifera contributed 96.64% of the total biomass, followed by bivalves (1.33%), polychaete worms (0.52%), and foraminifera (0.42%). The other taxa only contributed 1.09% of the total biomass. The biomass values displayed significant differences with depth (ANOVA $F_{(7,\ 16)} = 823.20$, $p<0.00000$).

3.2.4. *Canonical redundancy analysis (RDA)*

The selected explanatory variables (depth, distance from the coast, % N) explained $R^2 = 0.497$ ($R^2_{\mathrm{adjusted}} = 0.329$) of the variance



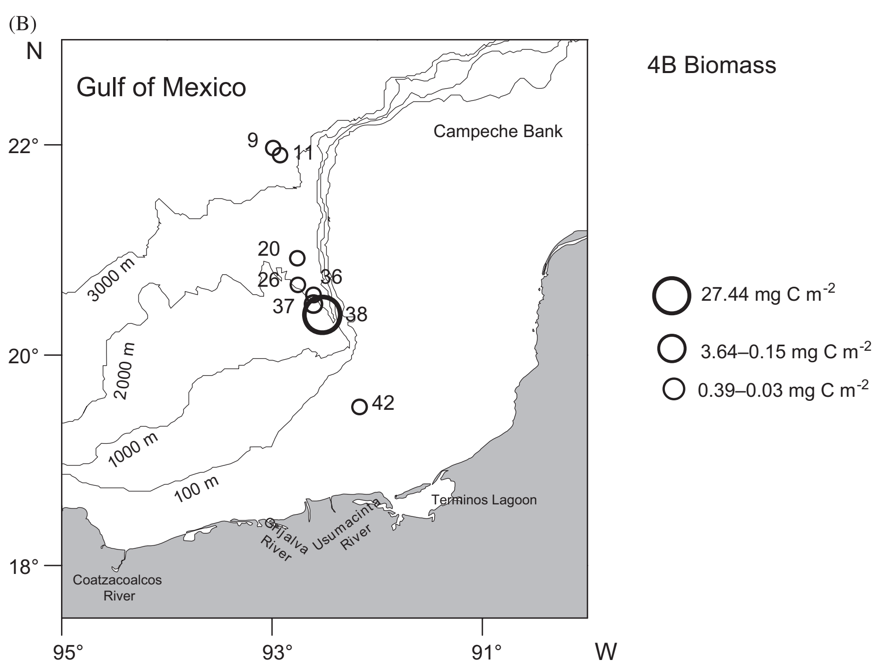


Fig. 4. (A) Geographic variability of the macrofaunal mean density values (ind m^{-2}) in the Campeche Canyon in the SW Gulf of Mexico. (B) Geographic variability of the macrofaunal mean biomass values (mg C m^{-2}) in the Campeche Canyon in the SW Gulf of Mexico. The numbers are the station identifiers. Circle size varies in relation to biomass, following the scale shown by the graph.

of the Hellinger-transformed taxonomic data (20 taxa) from the seven canyon stations. The model was highly significant ($p = 0.001$ after 999 random permutations). Two canonical axes were significant (Table 3). The first ordination axis (23% of the species variance, $p = 0.001$) represents an inshore–offshore gradient following the axis of the canyon; most of the taxa vary in response to the environmental factors (Fig. 5). Crustaceans (harpacticoid copepods and cumacea), hydroids, and foraminifera, characterize the head of the canyon with largest biomass values and high taxonomic richness. The central portion of the canyon had lower richness values; ostracods and echinoderms were the dominant faunal components. The stations at the mouth of the

Table 3
Canonical redundancy analysis (RDA) of the Campeche Canyon macrofaunal abundance data by the chemical and geographic explanatory variables: proportion of the beta variability explained by the first 4 canonical axes and tests of significance of the axes

	1	2	3	4
Eigenvalues	0.233	0.125	0.068	0.051
Taxa-environmental factors correlations	0.917	0.819	0.828	0.820
Cumul. % variance of taxonomic data	23.3	35.8	42.6	47.8
Probabilities (after 999 permutations)	0.001*	0.021*	0.208	0.338

* $p \leqslant 0.05$.

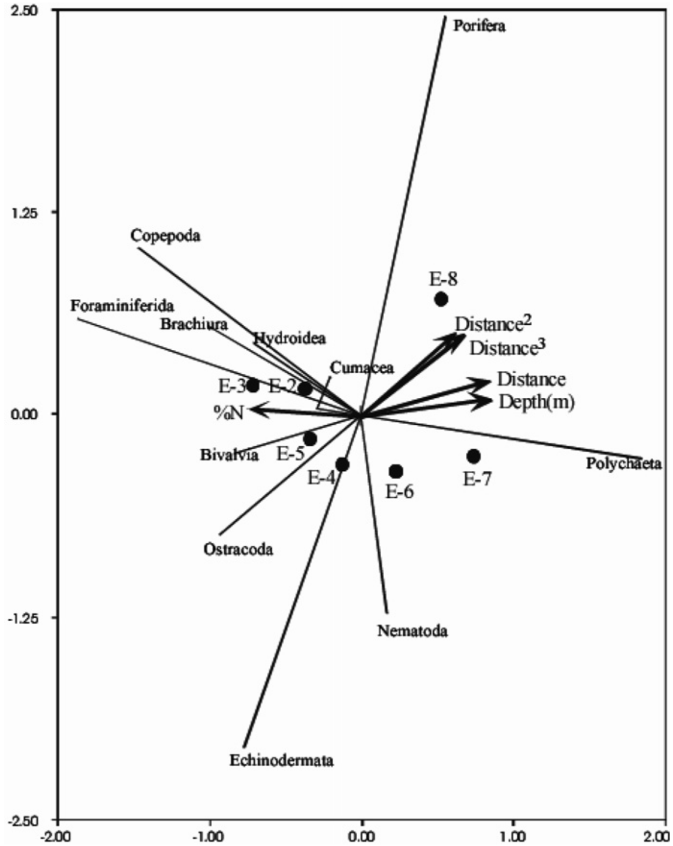


Fig. 5. Canonical redundancy analysis (RDA) triplot for seven stations in the Campeche Canyon, SW Gulf of Mexico, showing the stations, macrofaunal taxa, and the five selected environmental variables. Black dots represent the sampling stations, arrows the environmental variables, and lines the taxa.

canyon were characterized by the dominance of nematodes and polychaete worms.

4. Discussion

4.1. Taxonomic richness

Although measures of biodiversity along environmental gradients are the focus of marine ecological research, a general lack of comparability between studies has been attributed to the lack of similar levels for the identification of taxa in the most difficult groups. The majority of biodiversity assessments use species as the base unit. Recent studies have suggested the use of taxonomic surrogacy, replacing species with higher-ranked taxa (genera, families, etc.), recognizing that the use of higher ranks may not produce comparable results (Bertrand et al., 2006). Others suggest that higher-taxon surrogacy (family or even order level) is useful and may prove an efficient method at larger spatial scales (Davidson, 2005) in deep-sea studies where many species and genera are new to science (Doerries and Van Dover, 2003). Polychaete and bivalves are commonly found in canyons. The general pattern of decreasing number of taxa with depth recorded in the Campeche Canyon is consistent with other canyons (Flach and Thomsen, 1998); it differs with those recorded by Vetter and Dayton (1998) and Houston and Haedrich (1984). The organic enrichment promoted by hydrodynamics, as recorded in the Atlantic canyons that have influence over taxonomic richness and abundance (Cosson et al., 1997), was found in the Campeche Canyon. The presence of polychaetes as dominant components within the canyon can be attributed to the organic enrichment transported by currents down the slope (Vetter and Dayton, 1998). The activity/inactivity of canyons affects species richness and complexity of benthic communities (Maurer et al., 1994).

4.2. Density

The general trend of density change was inversely and exponentially related to distance from the coast and depth (Rowe, 1983). Differences between canyons are attributed to geographical differences in food supply (Cosson et al., 1997), hydrodynamics (Vetter and Dayton, 1999; Koppelmann and Weikert, 2000) and oxygen concentration (Fenchel and Finlay, 1995). Density is usually higher in canyons than on the continental shelf and slope (Vetter, 1995) and attributed to a reduced transport of sediment and organics to the deeper seabed stations (Duineveld et al., 2001). This contrasts with the results observed in the Campeche Canyon, where a larger load of sediment and accumulation of organics was found at mid-depth. The benthic community in Campeche Canyon responds to the input of exported material generated at the surface, associated with mesoscale features, and herein recognized as a cyclonic ring of 10^4 km in diameter in the area (Salas et al., 2004). The presence of pigments in superficial sediment and higher % C_{org} and N correlated with the high densities of polychaetes. The C/N ratio (>7) suggests that POC is exported to the seafloor (Meyer, 1994). Larger export of labile material of photoautotrophic origin reaches benthic communities (Cosson et al., 1997) by pelagic–benthic coupling or transport by turbidity currents (Vetter and Dayton, 1998). In some canyons, organic particles are consumed mostly in the water column (Houston and Haedrich, 1984).

4.3. Biomass

Macrofaunal biomass patterns among canyons can decrease with distance from the coast and depth (Duineveld et al., 2001), remain homogeneous throughout the canyon (Houston and Haedrich, 1984), or exhibit other distribution patterns (Vetter and Dayton, 1998). Macrofaunal biomass in the central area of the Campeche Canyon is characterized by a large aggregation of small filter feeders that respond to upwelling and export of POC (Salas et al., 2004).

This study concludes that the continental shelf station greatly differed from the stations in the Campeche Canyon. It recognizes that the macrofauna changed with distance from the coast and depth in response to the organic matter and pigments in the sediment. A parabolic pattern was recorded with higher values at 2320 m depth in the central portion of the canyon.

Acknowledgments

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