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ORIGINAL ARTICLE

Distribution of polychaete feeding guilds in sedimentary environments of the Campeche Bank, Southern Gulf of Mexico

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Abstract The aim of this study was to analyze the trophic structure of the polychaete assemblages found in the Campeche Bank, southern Gulf of Mexico and to examine the effect of the sediment composition on the spatial distribution of the feeding guilds. In all, 2,662 organisms belonging to 160 species and 16 feeding guilds were identified. Filter-feeders (*Fabricinuda trilobata* and *Bispira melanostigma*) dominated. Five groups of stations were defined based on feeding guilds: one, in the southwest, characterized by motile jawed burrowers (17.14% contribution); the second, from the southeast to the northwest, characterized by seven guilds (45.25%), mainly filter-feeders and surface deposit-feeders; the third, in the southwest, characterized by three guilds (42.13%), mainly discretely motile tentaculate filter-feeders and motile unarmed burrowers; group four, in the east, was characterized by sessile tentaculate filter-feeders (63.68%); and group five, in the center and to the north, was characterized by four guilds (53.69%), mainly discretely motile tentaculate filter-feeders. The variety of feeding guilds was higher in the northwest with seven guilds, and the lowest variety was found in the east and south with only one or two guilds. Contrary to the starting hypothesis, the sediment composition was not the main factor that determined the distribution of the polychaete feeding guilds. Instead, salinity and depth were more important for the spatial arrangement of the trophic groups. The feeding guilds of polychaetes proved to be more sensitive to environmental changes than density or diversity.

Keywords Polychaetes · Feeding guilds · Trophic structure · Benthic communities

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Introduction

The study of feeding guilds is important to understand spatial and temporal changes in benthic communities (Heip 1992; Wieking and Kröncke 2003) and parts of them such as polychaete assemblages (Paiva 1993; Muniz and Pires 1999). Polychaete feeding guilds are based on the relationships between food particle sizes, feeding habits and the motility patterns associated with feeding (Fauchald and Jumars 1979; Pagliosa 2005). A common assumption is that deposit-feeders are abundant in muddy habitats while suspension feeders dominate in sandy habitats (Gray 1981). Nevertheless, besides the frequent co-occurrence of the two groups, some species can modify their trophic habits in response to food availability, and also their ability to colonize bottoms with high sediment mobility, as exemplified by some spionids (Maurer and Leathem 1981). In addition, many species are not invariably associated with a single sediment type, but their trophic organization relates to factors such as organic content and granulometric characteristics of sediments (Snelgrove and Butman 1994). Pagliosa (2005) used feeding guilds to develop an ecological and environmental impact assessment in which feeding guilds were related to environmental parameters, disturbance, availability of resources or interspecific competition. Therefore, the pattern is not universal but might be highly dependent on habitat conditions (Pinedo et al. 1997). A fundamental question to analyze the feeding structure is how to separate species into feeding guilds. Fauchald and Jumars (1979) proposed a conceptual pattern to classify polychaete species according to their feeding features. A strong increase in studies on the diets and the biology of polychaetes in the last years has given rise to a major interest in the use of feeding guilds in studies on polychaete communities (Pagliosa 2005). However, the original feeding scheme by Fauchald and Jumars (1979) has remained basically the same and few studies have analyzed the significance of the complete pattern in the study of polychaetes assemblages (Maurer and Leathem 1981; Maurer et al. 1981; Dauer 1984; Gambi and Giangrande 1985; Gaston 1987; Muniz and Pires 1999; Pagliosa 2005). Despite some early criticism of the original feeding classification (Dauer et al. 1981; Dauer 1984), it seems necessary to revive the use of this important tool for the analysis of communities and to emphasize its importance for ecological and environmental benthic studies.

In the Gulf of Mexico, polychaetes represent a key group in terms of abundance and diversity on the continental shelf (Fauchald et al. 2009). In the Campeche Bank, distribution and diversity of polychaetes have been shown to be mainly influenced by the sediment composition, with diversity increasing with sand content (Hernández Arana et al. 2003; Domínguez Castanedo et al. 2007), but studies on their trophic structure are virtually absent. Thus, the aim of this study was to analyze the changes in the species composition and feeding guilds of the polychaete assemblages in the Campeche Bank, with the hypothesis that most of the variation of the spatial distribution of the polychaete feeding guilds would be associated to the changes in sediment composition present in the Campeche Bank. That is, the feeding guilds were expected to respond to the environmental sediment gradient by the increase of the filter-feeders to the east and northeast where sediments show an increasing percentage of sand, while burrowers and surface deposit-feeders were expected to increase toward the west and south with a decreasing percentage of sand. This kind of study is relevant in a region such as the Campeche Bank where natural and anthropogenic impacts are important (Granados Barba 2001; Hernández Arana et al. 2003; Hernández Arana et al. 2005) and the information obtained could provide a useful tool in environmental monitoring of the area.

Methods

Study area

The Campeche Bank (18°49′–21°35′N and 91°00′–92°10′W) is located in the southern Gulf of Mexico. During the winter, it is influenced by strong winds from the north, known as “nortes”, while in the summer, tropical storms or hurricanes from the southeast and abundant rains are common, together with the resultant river discharges. These phenomena cause seasonal changes in the physico-chemical characteristics of both the water and the sediments (Hernández Arana et al. 2005; Granados Barba et al. 2009). There is a gradual shift from terrigenous (west) to carbonate (east) sediments due to the absence of rivers in the east. A transitional zone with seasonally varying limits is characterized by a mixture of sediments (Yáñez Arancibia and Sánchez Gil 1983; Granados Barba 2001; Domínguez Castanedo et al. 2007). The Campeche Bank shows a large shelf (150 km wide) unaffected by rivers and with carbonate sediments (Fig. 1). The establishment and distribution of the local macrobenthic fauna is influenced by all these factors (Hernández Arana et al. 2003). The diversity of polychaetes is low in the transitional zone, influenced by the Grijalva–Usumacinta river discharge, and it is high in the east of the Campeche Bank. There are also species replacements from the terrigenous to the carbonate sediments, from lumbrinerid species in the terrigenous sediments to spionids in the transitional zone and to sabellids in the carbonate sediments (Domínguez Castanedo et al. 2007).

Sampling and data analysis

The biological material was collected during the “nortes” season (December 2001) on board the R/V “Justo Sierra” in 21 stations distributed in a grid in the inner continental shelf

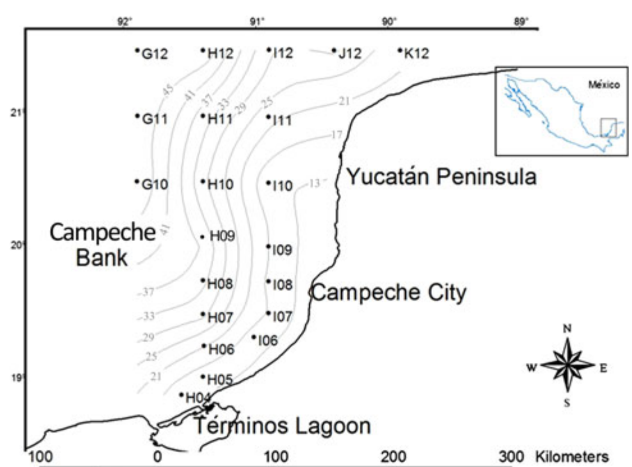

Fig. 1 Study area. Campeche Bank with the sampling stations (isobaths in meters)

(15–49 m) of the study area (Fig. 1). A Reineck box corer (2.5 m^2) was used to sample a uniform area of 0.08 m^2 per sample (with no replicates).The sediment was then sieved through a 0.5-mm mesh. The organisms were fixed with 4% formaldehyde and preserved in 70% ethanol. The polychaetes were identified to species level and transferred to the National Polychaete Collection in the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (CPICML-UNAM, DFE.IN.061.0598) (Table 1).

In this study, we followed the classification by Fauchald and Jumars (1979) which is based on a set of relationships between food particle size and composition, the mechanisms involved in food ingestion, and motility patterns associated with the feeding processes. Accordingly, polychaetes can be divided in five or six trophic categories: carnivores (C); surface deposit-feeders (S); burrowers (B); filter-feeders (F); herbivores (H); and omnivores (O). These categories combined with the three types of feeding motility [motile (M); discretely motile (D); and sessile (S)], and the three types of buccal structures used in food encounter and ingestion [jawed (J); tentaculate (T); and "other structures", usually sac-like pharynxes (X)], produce 22 feeding guilds that are biologically acceptable (Fauchald and Jumars 1979).

The density (ind./0.08 m^2) of the polychaetes of each feeding guild was analyzed by multivariate statistical methods of ordination. The differences in density values between stations and feeding guilds were evaluated by a *t*-test of dependent samples. After the fourth root transformation of the data, a similarity matrix was constructed with the 21 stations and also with the 16 feeding guilds using the Bray-Curtis index. An NMDS ordination was used to analyze the relationships among the feeding guilds. The SIMPER analysis was used to determine the species contribution to the groups with the PRIMER v.5 software (Field et al. 1982; Clarke and Gorley 2001). The distribution of the groups of the feeding guilds from the NMDS is shown on a map with the ArcView Gis 3.2 software.

A canonical correspondence analysis (CCA) using the CANOCO program (ter Braak 1988) was also carried out in order to show in a single diagram the direct interpretation of the relationships between species, stations and environmental factors. The relationship between feeding guilds and environmental variables was tested by the Monte-Carlo permutation test (Manly 1990).

Results

Community structure

In all, 2,662 polychaetes (160 species belonging to 44 families) were collected and classified into 16 feeding guilds (Table 1).

According to spatial variations in density and species composition, the more abundant fauna was found in shallow sandy sediments near the coast (in front of the city of Campeche): stations I09 (209.8 ind./0.08 m^2; mean 1.31 ind./spp. * 0.08 m^2), I08 (98.6 ind/0.08 m^2; mean 0.616 ind./spp. * 0.08 m^2), and I07 (31.4 ind/0.08 m^2; mean 0.196 ind./spp.*0.08 m^2) (Fig. 2). However, the *t*-test showed that only in station I07, the higher values observed were significantly different from other stations (t value = 1.9849, $P = 0.0489$), since in station I09 the higher density was mainly due to the sabellids *Fabricinuda trilobata* (90.2 ind./0.08 m^2) and *Bispira melanostigma* (85.6 ind./0.08 m^2), and in station I08 the density values were associated only with *B. melanostigma* (88 ind./0.08 m^2). On the other hand, the densities were significantly lower in shallow transitional (mixed terrigenous and carbonate) sediments from the southernmost stations: H04 (4.75 ind./0.08 m^2; t value = 2.71, $P = 0.007$) and H05 (1.6 ind./0.08 m^2; t value = 2.02, $P = 0.0451$).

Ordination analysis

The NMDS analysis based on feeding guilds (Fig. 3), showed five main groups of stations. The first (H07 and H08 stations) was represented by the BMJ feeding guild species (17.1% average similarity) and was located to the west, in front of the Términos lagoon and subjected to the influence of the Grijalva–Usumacinta river discharges (Fig. 4). This group included the fauna with the lowest densities and number of species, occurring at depths of 30–34 m with a sand content of 1.4–6.2%.

The second group (stations G10, G11, G12, H09, H10, H11, I06, I07, and I10) was characterized by HMJ, FDT, BMX, FST, SDT, SMT, and HDJ guilds (45.3% average similarity), thus displaying the highest variety of feeding guilds, and was located from the southeast toward the north (Fig. 4) in depths of 15–49 m, with an average of 58.5% in sand content.

The third group (H04, H05, I12, and K12) was characterized by FDT, BMX, and SDT guilds (42.1% average similarity); this group was split: one part in the southwest and the other in the northeast (Fig. 4), in shallow depths (15 m) near the coastline with 6.3–97.1% of sand.

The fourth group (I08 and I09) was characterized by the FST guild (63.7% average similarity) and was located to the east of the study area (Fig. 4), in front of the city of Campeche, in shallow sandy bottoms (16.5 m; 95% sand). The fifth group (H06, H12, I12, and J12) was characterized by FDT, CMJ, BMX, and HMJ guilds (53.7% average similarity). This group corresponded to the stations found toward north (Fig. 4), in depths of 21–48.7 m and 26.4–98.9% of sand.

Table 1 Species registered in the inner shelf of Campeche Bank with their relative densities and their feeding guilds

	Species	Density (%)	Trophic group	Feeding guilds	
1	*Aglaophamus verrilli*	0.43	Carnivore	CMJ	
2	Ampharetidae Genus A	0.04	Surface deposit feeder	SST	
3	*Amphicteis gunneri*	0.04	Surface deposit feeder	SST	
4	*Ancistrosyllis* sp. A	0.04	Carnivore	CMJ	
5	*Aphelochaeta* sp. 1	0.12	Surface deposit feeder	SMT	SDT
6	*Aphelochaeta* sp. 2	0.28	Surface deposit feeder	SMT	SDT
7	*Aphelochaeta* sp. 3	0.18	Surface deposit feeder	SMT	SDT
8	*Aphelochaeta* sp. 4	0.04	Surface deposit feeder	SMT	SDT
9	*Aricidea (Acmira) finitima*	0.16	Herbivore	HMX	SMX
10	*Aricidea (Acmira) philbinae*	0.17	Herbivore	HMX	SMX
11	*Aricidea (Acmira)* sp. 1	0.06	Herbivore	HMX	SMX
12	*Aricidea (Acmira)* sp. 2	0.96	Herbivore	HMX	SMX
13	*Aricidea (Acmira)* sp. 3	0.13	Herbivore	HMX	SMX
14	*Aricidea (Acmira) taylori*	0.32	Herbivore	HMX	SMX
15	*Aricidea (Allia) bryani*	0.04	Herbivore	HMX	SMX
16	*Aricidea (Allia)* sp. 1	0.02	Herbivore	HMX	SMX
17	*Armandia maculata*	3.28	Subsurface deposit feeder	BMX	
18	*Axiothella* sp. A	0.04	Subsurface deposit feeder	BSX	
19	*Axiothella* sp. 1	0.04	Subsurface deposit feeder	BSX	
20	*Bispira melanostigma*	33.25	Filter feeder	FST	
21	*Capitella* sp.	0.20	Subsurface deposit feeder	BMX	SMX
22	Capitellidae Genus 1	0.04	Subsurface deposit feeder	BMX	SMX
23	Capitellidae Genus 2	0.53	Subsurface deposit feeder	BMX	SMX
24	*Caulleriella* cf. *zetlandica*	0.08	Surface deposit feeder	SMT	SDT
25	*Caulleriella* sp. 1	0.37	Surface deposit feeder	SMT	SDT
26	*Ceratocephale oculata*	0.19	Omnivore	HMJ	CMJ, CDJ, SDJ
27	*Ceratonereis irritabilis*	0.05	Omnivore	HMJ	CMJ, CDJ, SDJ
28	*Ceratonereis versipedata*	0.11	Omnivore	HMJ	CMJ, CDJ, SDJ
29	*Chaetopterus variopedatus*	0.04	Filter feeder	FSP	
30	*Chaetozone* sp. 1	0.03	Surface deposit feeder	SMT	SDT
31	*Chaetozone* sp. 2	0.03	Surface deposit feeder	SMT	SDT
32	*Chone americana*	0.05	Filter feeder	FST	
33	*Chone duneri*	0.27	Filter feeder	FST	
34	*Cirrophorus lyra*	0.28	Herbivore	HMX	SMX
35	*Clymenella* sp.	0.09	Subsurface deposit feeder	BSX	
36	*Cossura delta*	1.40	Subsurface deposit feeder	BMX	
37	*Dasybranchus lumbricoides*	0.12	Subsurface deposit feeder	BMX	SMX
38	*Dasybranchus lunulatus*	0.34	Subsurface deposit feeder	BMX	SMX
39	*Demonax microphthalmus*	0.05	Filter feeder	FST	
40	*Diopatra* cf. *papillata*	0.04	Omnivore	HDJ	CMJ, CDJ, SDJ
41	*Diopatra cuprea*	0.12	Omnivore	HDJ	CMJ, CDJ, SDJ
42	*Diopatra neotridens*	0.07	Omnivore	HDJ	CMJ, CDJ, SDJ
43	*Diopatra tridentata*	0.02	Omnivore	HDJ	CMJ, CDJ, SDJ
44	*Syllis ferrugina*	0.30	Carnivore	CMJ	
45	*Eupolymnia nebulosa*	0.05	Surface deposit feeder	SST	
46	*Eurythoe complanata*	0.04	Carnivore	CMX	
47	*Exogone dispar*	0.09	Herbivore	HMJ	CMJ
48	*Exogone lourei*	0.20	Herbivore	HMJ	CMJ

Table 1 continued

	Species	Density (%)	Trophic group	Feeding guilds	
49	*Paraexogone atlantica*	0.30	Herbivore	HMJ	CMJ
50	*Paraexogone caribensis*	0.43	Herbivore	HMJ	CMJ
51	*Exogone* cf. *breviantennata*	0.08	Herbivore	HMJ	CMJ
52	*Fabricinuda trilobata*	23.23	Filter feeder	FST	SDT
53	*Glycera americana*	0.07	Carnivore	CDJ	BMJ
54	*Glycera brevicirris*	0.11	Carnivore	CDJ	BMJ
55	*Glycera papillosa*	0.53	Carnivore	CDJ	BMJ
56	*Grubeulepis mexicana*	0.21	Carnivore	CMJ	
57	*Hesionura coineaui*	0.04	Carnivore	CMS	
58	*Kinbergonuphis* cf. *cedroensis*	0.42	Omnivore	HDJ	CMJ, CDJ, SDJ
59	*Kinbergonuphis orenzansi*	0.03	Omnivore	HDJ	CMJ, CDJ, SDJ
60	*Kinbergonuphis pulchra*	0.45	Omnivore	HDJ	CMJ, CDJ, SDJ
61	*Kinbergonuphis simoni*	0.37	Omnivore	HDJ	CMJ, CDJ, SDJ
62	*Kinbergonuphis* sp. 1	0.04	Omnivore	HDJ	CMJ, CDJ, SDJ
63	*Kinbergonuphis* sp. 2	0.14	Omnivore	HDJ	CMJ, CDJ, SDJ
64	*Laonice cirrata*	0.30	Filter feeder	FDT	SDT
65	*Leiocapitella* sp. B	0.05	Subsurface deposit feeder	BMX	SMX
66	*Leiocapitella* sp. 1	0.08	Subsurface deposit feeder	BMX	SMX
67	*Leiocapitella* sp. 2	0.04	Subsurface deposit feeder	BMX	SMX
68	*Leiocapitella* sp. A	0.25	Subsurface deposit feeder	BMX	SMX
69	*Leiochrides* sp. 1	0.04	Subsurface deposit feeder	BMX	SMX
70	*Lepidasthenia varius*	0.04	Carnivore	CMJ	CDJ
71	*Levinsenia gracilis*	0.66	Herbivore	HMX	SMX
72	*Litocorsa antennata*	0.15	Carnivore	CMJ	
73	*Lumbrinerides aberrans*	0.04	Omnivore	HMJ	CMJ, CDJ, BMJ
74	*Lumbrinerides* sp. 1	0.03	Omnivore	HMJ	CMJ, CDJ, BMJ
75	*Lumbrineris cingulata*	0.04	Omnivore	HMJ	CMJ, CDJ, BMJ
76	*Lumbrineris latrelli*	0.17	Omnivore	HMJ	CMJ, CDJ, BMJ
77	*Lumbrineris* sp. 1	0.04	Omnivore	HMJ	CMJ, CDJ, BMJ
78	*Lumbrineris* sp. 2	0.11	Omnivore	HMJ	CMJ, CDJ, BMJ
79	*Lumbrineris* sp. 3	0.03	Omnivore	HMJ	CMJ, CDJ, BMJ
80	*Lysilla* sp. A	0.30	Surface deposit feeder	SDT	
81	*Magelona pettiboneae*	0.96	Surface deposit feeder	SDT	
82	*Magelona phyllisae*	0.09	Surface deposit feeder	SDT	
83	*Magelona polydentata*	0.61	Surface deposit feeder	SDT	
84	*Magelona* sp. B	0.10	Surface deposit feeder	SDT	
85	*Magelona* sp. G	0.78	Surface deposit feeder	SDT	
86	*Magelona* sp. L	0.04	Surface deposit feeder	SDT	
87	*Malacoceros indicus*	0.26	Filter feeder	FDT	SDT
88	*Malacoceros* sp. 1	0.04	Filter feeder	FDT	SDT
89	*Malmgreniella* sp.	0.04	Carnivore	CMJ	CDJ
90	*Mediomastus californiensis*	1.05	Subsurface deposit feeder	BMX	SMX
91	*Megalomma bioculatum*	0.32	Filter feeder	FST	
92	*Microspio pigmentata*	0.08	Filter feeder	FDT	SDT
93	*Monticellina baptisteae*	0.30	Surface deposit feeder	SMT	SDT
94	*Monticellina dorsobranchialis*	0.24	Surface deposit feeder	SMT	SDT
95	*Monticellina* sp. 1	0.04	Surface deposit feeder	SMT	SDT
96	*Mooreonuphis* sp. 1	0.08	Omnivore	HDJ	CMJ, CDJ, SDJ

Table 1 continued

	Species	Density (%)	Trophic group	Feeding guilds	
97	*Mooreonuphis* cf. *nebulosa*	0.04	Omnivore	HDJ	CMJ, CDJ, SDJ
98	*Neanthes micromma*	0.55	Omnivore	HMJ	CMJ, CDJ, SDJ
99	*Nematonereis hebes*	0.05	Omnivore	HMJ	CMJ, CDJ
100	*Nephtys incisa*	0.49	Subsurface deposit feeder	BMJ	
101	*Nephtys squamosa*	0.25	Subsurface deposit feeder	BMJ	
102	*Ninoë brasilensis*	0.04	Omnivore	HMJ	CMJ, CDJ, BMJ
103	*Ninoë leptognatha*	0.07	Omnivore	HMJ	CMJ, CDJ, BMJ
104	*Notomastus americanus*	0.07	Subsurface deposit feeder	BMX	SMX
105	*Notomastus daueri*	0.04	Subsurface deposit feeder	BMX	SMX
106	*Notomastus hemipodus*	0.09	Subsurface deposit feeder	BMX	SMX
107	*Notomastus lineatus*	0.05	Subsurface deposit feeder	BMX	SMX
108	*Notomastus lobatus*	0.09	Subsurface deposit feeder	BMX	SMX
109	*Notomastus tenuis*	0.13	Subsurface deposit feeder	BMX	SMX
110	*Odontosyllis enopla*	0.04	Carnivore	CMJ	
111	*Ophiogoniada lyra*	0.04	Carnivore	CDJ	
112	*Orbinia* sp. 1	1.86	Subsurface deposit feeder	BMX	
113	*Owenia* sp. A	0.34	Filter feeder	FDT	SDT
114	*Paramphinome jeffreysi*	0.11	Carnivore	CMX	
115	*Paramphinome* sp. B	0.09	Carnivore	CMX	
116	*Parapionosyllis uebelakerae*	0.15	Herbivore	HMJ	CMJ
117	*Paraprionospio yokoyamai*	5.48	Filter feeder	FDT	SDT
118	*Pectinaria gouldii*	0.05	Subsurface deposit feeder	BMX	
119	*Phyllodoce (Phyllodoce) arenae*	0.02	Carnivore	CMS	
120	*Phylo* sp. 1	0.03	Subsurface deposit feeder	BMX	
121	*Pionosyllis* sp. A	0.30	Carnivore	CMJ	
122	*Piromis roberti*	0.04	Surface deposit feeder	SDT	SMT
123	*Pisione wolfi*	0.04	Subsurface deposit feeder	BMX	
124	*Poecilochaetus johnsoni*	0.20	Surface deposit feeder	SDT	
125	*Prinospio (Prionospio) dubia*	0.72	Filter feeder	FDT	SDT
126	*Prionospio (Apoprionospio) dayi*	0.32	Filter feeder	FDT	SDT
127	*Prionospio (Minuspio) delta*	0.63	Filter feeder	FDT	SDT
128	*Prionospio (Minuspio) multibranchiata*	0.11	Filter feeder	FDT	SDT
129	*Prionospio (Minuspio) perkinsi*	0.08	Filter feeder	FDT	SDT
130	*Prionospio (Minuspio)* sp. 1	0.34	Filter feeder	FDT	SDT
131	*Prionospio (Minuspio)* sp. 2	0.50	Filter feeder	FDT	SDT
132	*Prionospio (Minuspio)* sp. 3	0.24	Filter feeder	FDT	SDT
133	*Prionospio (Minuspio) cirrifera*	0.13	Filter feeder	FDT	SDT
134	*Prionospio (Prionospio)* sp. 1	0.13	Filter feeder	FDT	SDT
135	*Prionospio (Prionospio) cristata*	1.75	Filter feeder	FDT	SDT
136	*Protodorvillea kefersteini*	0.14	Omnivore	HMJ	CMJ, SMJ
137	*Pseudopolydora* sp. 1	0.04	Filter feeder	FDT	SDT
138	*Rhynothelepus* sp.	0.15	Surface deposit feeder	SST	
139	*Rullierinereis mexicana*	0.04	Omnivore	HMJ	CMJ, CDJ, SDJ
140	*Scolelepis (Parascolelepis) texana*	0.17	Filter feeder	FDT	SDT
141	*Scolelepis squamata*	0.04	Filter feeder	FDT	SDT
142	*Scoletoma* cf. *ernesti*	0.06	Omnivore	HMJ	CMJ, CDJ, BMJ
143	*Scoletoma* sp. 1	0.11	Omnivore	HMJ	CMJ, CDJ, BMJ
144	*Scoletoma* sp. 2	0.71	Omnivore	HMJ	CMJ, CDJ, BMJ

Table 1 continued

	Species	Density (%)	Trophic group	Feeding guilds	
145	*Scoletoma* sp. 3	0.12	Omnivore	HMJ	CMJ, CDJ, BMJ
146	*Scoletoma* sp. 4	0.11	Omnivore	HMJ	CMJ, CDJ, BMJ
147	*Scoletoma verrilli*	2.06	Omnivore	HMJ	CMJ, CDJ, BMJ
148	*Scoloplos (Leodamas) rubra*	0.58	Subsurface deposit feeder	BMX	
149	*Scoloplos (Scoloplos) acmeceps*	0.04	Subsurface deposit feeder	BMX	
150	*Scoloplos (Scoloplos) texana*	0.04	Subsurface deposit feeder	BMX	
151	*Sigambra elongata*	0.26	Carnivore	CMJ	
152	*Sphaerodoropsis vittori*	0.04	Subsurface deposit feeder	BMX	
153	*Sphaerosyllis* sp.	0.04	Herbivore	HMJ	CMJ
154	*Spio pettiboneae*	0.08	Filter feeder	FDT	SDT
155	*Spiophanes bombyx*	0.11	Filter feeder	FDT	SDT
156	*Sternaspis scutata*	0.04	Subsurface deposit feeder	BMX	
157	*Sthenelanella* sp.	0.30	Carnivore	CMJ	
158	*Syllis ortizi*	0.04	Carnivore	CMJ	
159	*Terebellides carmenensis*	0.23	Surface deposit feeder	SST	
160	*Terebellides parvus*	0.13	Surface deposit feeder	SST	

The species named A, B, etc. were identified with the Taxonomic Guide to the polychaetes of the Northern Gulf of Mexico (Uebelacker and Johnson 1984) and they have not been formally named yet, so we kept them as in the guide. The species named 1, 2, etc. are considered potentially new to science and need further revision

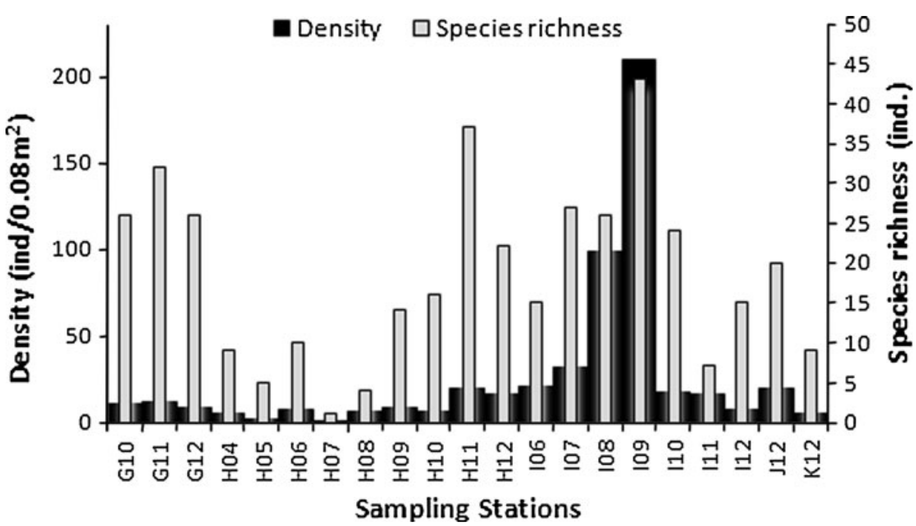

Fig. 2 Polychaete densities and species richness in the Campeche Bank

The arrangement of the stations in the NMDS analysis in the study area, showed that no clear distribution pattern emerges that can be attributed to the feeding guilds (Fig. 4). The dominating guild, constituted by the filter-feeders, was the only guild to show a trend. The FST guild (301.7 ind/0.08 m^2) was more abundant in group 4, located to the east of the study area; its density decreased to the west as shown in Fig. 3. The FDT guild (62.6 ind/0.08 m^2, present in 85.7% of the stations) was more abundant in group 5, located to the north, and its density decreased to the east and south of the Bank. So, the sessile and discretely motile filter-feeders decreased toward west and south of the Campeche Bank. In the remaining guilds, lower density values were observed and their distribution was heterogeneous across the Campeche Bank.

The correlation of feeding guilds to environmental data, according to the canonical analysis, was 0.82 for the first axis and 0.74 for the second axis. The Monte-Carlo test was significant ($P = 0.04$) and only the first two axes were analyzed, explaining 78.8% of the variation of the feeding guilds by the effect of the environmental variables. The spatial variations in the distribution of the feeding guilds were not significantly associated with the sediment composition. A significant correlation was found, however, with

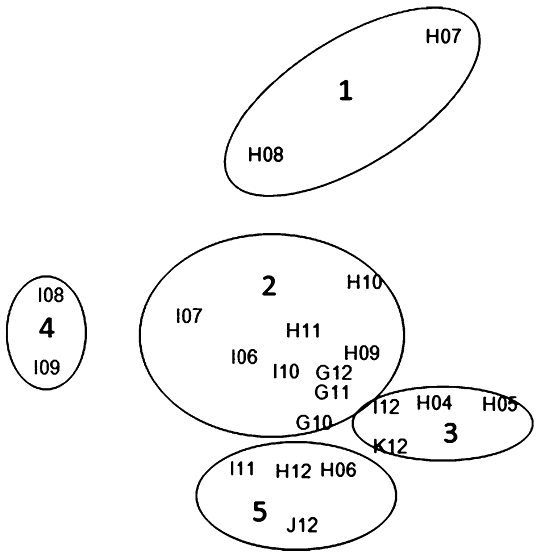

Fig. 3 NMDS analysis of the sampling stations based on the densities of the polychaete feeding guilds (groups numbered 1–5)

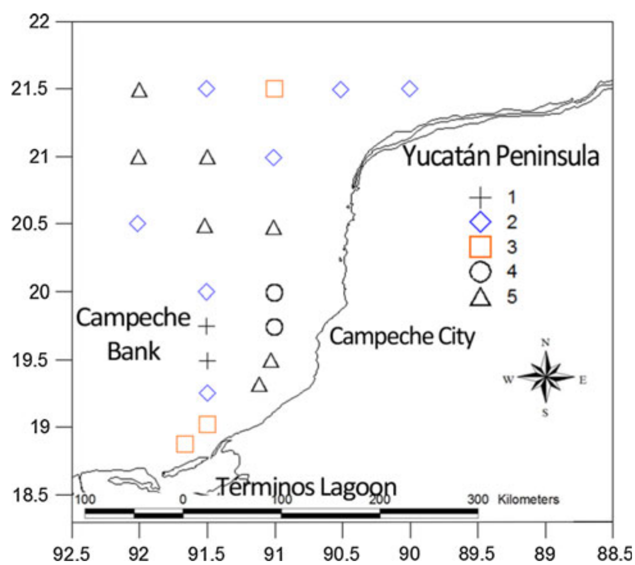

Fig. 4 Distribution of the groups obtained in the NMDS analysis according to their feeding guilds. Group I: BMJ guild; Group 2: HMJ, FDT, BMX, FST, SDT, SMT, and HDJ; Group 3: FDT, BMX, and SDT; Group 4: FST and Group 5: FDT, CMJ, BMX, and HMJ

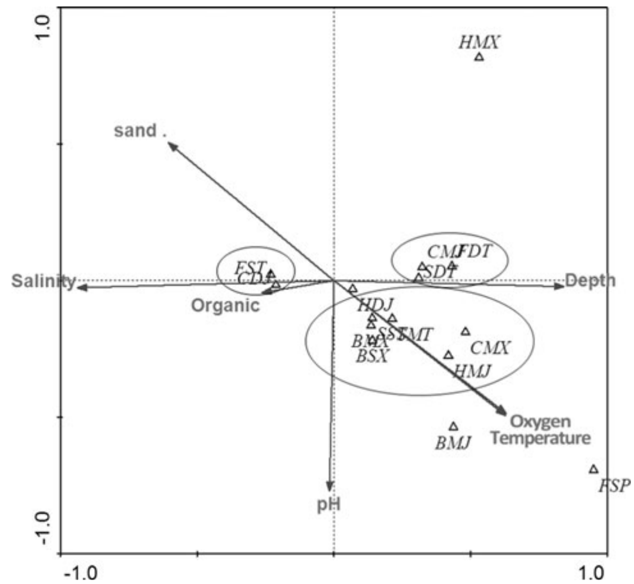

Fig. 5 Canonical correspondence analysis (CCA) ordination diagram showing the feeding guilds and environmental variables relative to axes I and II

salinity (0.77) and depth (0.69) in the first axis of the CCA, while pH (0.57) and sand percentage (0.38) were significant in the second axis. Salinity (−0.92), temperature (0.73), and oxygen (0.73) variations were clearly correlated to depth.

Most of the feeding guilds (CMX, HMJ, HDJ, BMX, BSX, SST, SMT) were distributed in deeper environments with medium values of salinity and sand in the northwest of the study area (Fig. 5). On the other hand, the FST and CDJ guilds were found in shallow stations with high salinity, organic carbon content, and sand content from the northwest to the east, while the CMJ, FDT, and SDT guilds were located in deeper stations with medium values of salinity and sand from the center to the northwest. The FSP and BMJ guilds were found in deep stations with low salinities, high pH, and muddy bottoms in the west of the Bank. The HMX guild dominated in the deep stations with low salinity and muddy sediments, but contrary to FSP and BMJ, it was distributed in zones with the lowest levels of pH, mainly in the center and north. Then, the filter-feeders showed an ability to tolerate a wider range of changes in environmental conditions, while both the sessile and discretely motile were present only in habitats with at least 7% sand and clearly dominated in sediments with greater than or equal to 50% of sand, to the northwest and east of the Bank. The sessile pumping filter-feeders were present only in deep, muddy sediments with high pH values (station H09). The carnivores also tolerated a wide range of environmental conditions and were located in several regions of the Campeche Bank. The motile jawed carnivores preferred average depths (25 m), while the motile unarmed preferred deeper stations, both in low salinities and average to low sand content of the sediments. The discretely motile jawed carnivores, on the contrary, preferred the shallow stations with high salinity values. The motile and discretely motile jawed herbivores tolerated average depths, low salinities, low pH values and low sand percentage. The unarmed motile herbivores tolerated high depths and sand content. On the other hand, the subsurface deposit-feeders do not seem to tolerate significant changes in environmental conditions, and the same probably applies to the burrowers, which occurred only at average depths with low salinities and low sand content in the sediments.

Discussion

According to Snelgrove et al. (1997), polychaetes in any benthic community display a wide range of feeding types, although in most soft-bottom communities, suspension (filter-feeders) and deposit-feeders (surface deposit-feeders and burrowers) dominate. In this study the filter-feeders, sessile and discretely motile, tentaculate organisms (FST, FDT) were the most abundant and frequent, although there was also a remarkable contribution of the motile jawed burrowers (BMX) guild. In the Campeche Bank, the highest variety of feeding guilds was found to the north-west where high diversities of polychaetes had already been reported. In contrast, the lowest variety of feeding guilds was found in the southwest of the Campeche Bank where polychaete species diversity is low (Domínguez Castanedo et al. 2007).

Contrary to our expectations, the sediment type was not the main factor influencing the distribution of the feeding guilds in the Campeche Bank. Basically, it was depth that determined the distribution of the feeding guilds even though the range analyzed was only 15–49 m. The variables correlated with depth, mainly salinity and secondarily temperature and oxygen, were also important for the changes in trophic structure. The highest variety of feeding guilds at the deepest stations can be linked to the relative stability of the water–sediment interface found at greater depths (Paiva 1993). As also stated by Fauchald and Jumars (1979), Maurer and Leathem (1981) found that sessile organisms were generally associated with less dynamic and more stable sediments encountered in the deepest environments. Actually, this pattern was also observed in the Campeche Bank, where the FSP and FDT guilds (sabellids and spionids) were very abundant at the deepest stations, located in the middle and outer shelf, which are relatively far from the Grijalva–Usumacinta river discharges. According to Muniz and Pires (1999), the river discharges with their input of terrigenous sediments and suspended particulates obstruct the feeding structures of filter-feeders. Besides, the considerable extension of the continental shelf allows the seasonal upwelling water to remain in the shelf along the euphotic zone for a longer time (Merino 1997), supporting the settling of the filtering species.

High densities of burrowers and surface deposit-feeders were expected to occur close to the Grijalva–Usumacinta discharges in the muddy sediments, but subsurface deposit-feeders as well as tentaculate, motile, discrete motile, and motile unarmed burrowers were also very abundant at sandy stations in the center and to the east of the Campeche Bank. In these zones, high values of organic carbon content were registered, although the sediment was coarse, because of the high quantity of organic matter discharged by the Grijalva–Usumacinta river, which is the second major river in the Gulf of Mexico (after the Mississippi river) with a discharge of 4,402 $m^3 s^{-1}$ (Yáñez Arancibia and Day 2004). This organic matter is transported to the east of the Bank by the main current present during the “nortes” season. The local circulation pattern is from east to west along the coastline and due to the shallow and extended nature of the continental shelf low hydrodynamics prevail in the Campeche Bank (Salas de León et al. 1992) which favor the deposition of the organic carbon in shallower stations in the east. This pattern creates an environment suitable for surface deposit-feeders and burrowers in the eastern sandy stations as also mentioned in other studies (Gambi and Giangrande 1985; Muniz and Pires 1999).

The polychaete feeding guilds represent a fine tool that is more sensitive to detect environmental changes than are density and diversity values, particularly when the guilds are influenced by environmental factors other than sediment type.

The original scheme proposed by Fauchald and Jumars (1979) has remained so far almost unchanged, but adding the omnivore guild to the feeding modes, as suggested by Cheung et al. (2008), may improve the analysis of trophic patterns in the benthic environments. There are some species that can change their feeding mode depending on the availability of resources (Lindsay and Woodin 1995; Hentschel and Larson 2005). In the Campeche Bank, for example, *Scoletoma verrilli*, one of the most abundant species of the region, has the capacity to exploit different food resources as herbivore, carnivore or motile jawed burrower.

Although the use of polychaete feeding guilds in the analysis of community structures has encountered some objections, we agree with the conclusions of Pagliosa (2005), considering the use of these guilds a suitable tool to analyze polychaete assemblage patterns. Just as the community structure of polychaetes can reflect the condition of the environment, the same applies to feeding guilds, because they are dependent on the environmental variables (Pagliosa 2005) and not only or mainly on sediment type.

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