



Trophic categories of soft-bottoms epibenthic deep-sea polychaetes from the southeastern Gulf of California (Mexico) in relation with environmental variables

NURIA MÉNDEZ

Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán. P.O. Box 811, Mazatlán 82000, Sinaloa, México. Corresponding author: nuri@ola.icmyl.unam.mx

Abstract. Deep-sea epibenthic polychaetes from the southeastern Gulf of California were collected with a benthic sledge between 360 and 2309 m depth. The material collected during four oceanographic cruises (2000 and 2001) included 52 epibenthic polychaete taxa representing 21 families. Thirty-five species and five genera were identified. Although no significant Spearman correlation was observed between the environmental variables with density and with trophic categories, some trends were observed according to feeding strategies in different environmental conditions: sediment grain size and organic matter had a stronger influence than depth, temperature and dissolved oxygen. Surface deposit-feeders (52.5%) and burrowers (12.5%) were frequent in muddy sediments with high contents of organic matter and were well represented by ampharetids and maldanids, respectively. Carnivores (20%), represented mainly by phyllodocids, were frequent in coarser sediments with low organic content. Omnivores (6%) comprised the families Nereididae, Onuphidae, Eunicidae, Lumbrineridae and Oeonidae, and were better represented by the onuphid *Nothria abyssalis* in wide ranges of depth, temperature and oxygen, and in enriched muddy sediments. The analyses of the trophic categories allowed the establishment of general patterns related to the distribution of the deep-sea epibenthic polychaete community, whose biology has been poorly studied in the Gulf of California.

Key words: polychaeta, epifauna, trophic categories, environmental variables, continental slope

Resumen. Distribución de categorías tróficas de poliquetos epibentónicos en fondos blandos del mar profundo del sureste del golfo de California, México. Ejemplares de poliquetos epibentónicos de aguas profundas del sureste del golfo de California se recolectaron con un trineo bentónico entre 360 y 2309 m de profundidad. El material procedente de cuatro cruceros oceanográficos (2000 y 2001) incluyó 52 taxa de poliquetos epibentónicos representados en 21 familias. Se identificaron 35 especies y cinco géneros. A pesar de que no se observaron correlaciones de Spearman significativas de las variables ambientales con la densidad y con las categorías tróficas, se observaron ciertas tendencias de acuerdo con las estrategias de alimentación y las diferentes condiciones ambientales: el tamaño de grano y materia orgánica del sedimento presentaron mayor influencia que la profundidad, la temperatura y el oxígeno disuelto. Los consumidores de depósito de superficie (52.5%) y los excavadores (12.5%) fueron frecuentes en sedimentos lodosos con altos contenidos de materia orgánica y estuvieron bien representados por los anfarétidos y maldánidos, respectivamente. Los carnívoros (20%), representados principalmente por filodócidos, fueron frecuentes en sedimentos más gruesos con poco contenido orgánico. Los omnívoros (6%) comprendieron las familias Nereididae, Onuphidae, Eunicidae, Lumbrineridae y Oeonidae y estuvieron mejor representados por el onúfido *Nothria abyssalis* en rangos amplios de profundidad, temperatura y oxígeno y en sedimentos enriquecidos. Los análisis de las categorías tróficas permitieron el establecimiento de patrones generales relacionados con la distribución de la comunidad de poliquetos epibentónicos de mar profundo, cuya biología estaba pobremente estudiada en el golfo de California.

Palabras clave: polychaeta, epifauna, categorías tróficas, variables ambientales, talud continental

Introduction

The class Polychaeta is the largest group of marine invertebrates, with more than 16000 known species. It represents the highest component (about 70%) of the marine benthic fauna inhabiting coastal and abyssal zones (Blake 1994). Polychaetes have different feeding guilds which are normally associated to the mode of locomotion, their feeding structures and the presence or absence of tubes (Fauchald & Jumars 1979, Gambi & Giangrande 1985, Blake 1994). Thus, free living species are usually carnivores, scavengers, detritivores or omnivores, while filter feeders and some detritivores tend to be sedentary with tubes. Also, a wide variety of structures (i.e. tubes, proboscis, tentacles, jaws) are present in the different groups depending on their diet. For instance, burrowers and surface deposit feeders with soft pharynx, swallow bulk particles, surface deposit-feeders conduct food to the mouth through their grooved palpi or tentacular crowns, or some detritivores and carnivores have soft proboscis to take muddy sediments (Pagliosa 2005). In general terms, each family has a specific feeding guild, but some families have more than one, which proves that the selection of a guild for a particular species can be arbitrary (Dauer 1984). According to Mattos *et al.* (2013), the number of trophic groups and feeding guilds can be associated with the environmental characteristics, the latitudinal variation and the sampling effort (species/family richness).

It has been reported that the distribution patterns of trophic groups of polychaetes are sensitive to multiple factors, including environmental disturbance, food supply, sediment types, hydrodynamic conditions and anthropogenic effects. Thus, the use of feeding guilds is a suitable tool to analyze polychaete assemblage patterns, due to their dependence on the environmental variables. Several authors have concluded that the analysis of the faunal distribution patterns based on feeding guilds produce similar results to those found with the composition and abundance of species (Gaston 1987; Muniz & Pires 1999; Pagliosa 2005; Domínguez-Castanedo *et al.* 2012). Recently, Mattos *et al.* (2013) have stated that an analysis of the trophic structure of a community may provide indirect information about the physical characteristics of the environment, which have a strong influence on feeding of benthic animals.

Several authors have observed strong relationships between polychaete feeding guilds with environmental factors, being granulometry of sediments probably the most important (Maurer & Leathern 1981, Pagliosa 2005, Carrasco & Carbajal

1998, Muniz & Pires 1999, Mattos *et al.* 2013). In contrast, Domínguez-Castanedo *et al.* (2012) found that sediment composition was not the main factor that determined the distribution of the polychaete feeding guilds in shallow bottoms in the Gulf of Mexico. Muniz & Pires (1999) concluded that organic matter in sediments also has a strong influence on feeding guilds of polychaetes, while Carrasco & Carbajal (1998) found no relationship with this variable, but a strong influence of depth. According to Paiva (1993), depth acts on sediment stabilization and consequently increases the feeding guild variety. Domínguez-Castanedo *et al.* (2012) observed that depth determined the distribution of the feeding guilds of polychaetes even though their range analyzed was only 15–49 m. Salinity has shown to be also an important factor for the changes in trophic structure (Maurer & Leathern 1981, Domínguez-Castanedo *et al.* 2012, Mattos *et al.* 2013), as well as oxygen (Maurer & Leathern 1981, Domínguez-Castanedo *et al.* 2012) and temperature (Domínguez-Castanedo *et al.* 2012).

Studies related to the deep-sea polychaetes from the Gulf of California and adjacent areas have been previously performed by some research groups (see Méndez 2006, 2007). Based on the revision of material from four (IV-VII) cruises of the TALUD project (Unidad Académica Mazatlán, ICMYL, UNAM), a list of infaunal and epibenthic polychaetes inhabiting soft-bottoms from the southeastern Gulf of California was elaborated (Méndez 2006), showing that the polychaete fauna of this zone is very similar to that previously recorded in adjacent areas by Hartman (1960, 1963) and Fauchald (1972). The first characterization of the deep-sea infaunal polychaetes in the southeastern Gulf of California was based on samples collected with a Karling dredge during the TALUD IV-VII cruises, in a depth range of 732-2110 m, and included an analysis of the relationship between the infaunal polychaete community and the environmental parameters (Méndez 2007).

Recently, a comparison between the infaunal and epifaunal benthic polychaetes collected with a Karling dredge and a benthic sledge respectively (TALUD IV-VII cruises) was performed based on their density, diversity, number of species, and selected environmental variables where they were found (Méndez 2012). Also, new information related with the tubes where worms were found was provided. Nevertheless, the characterization of the polychaete assemblages belonging to the epifauna was not provided by Méndez (2007, 2012). Thus, the aim of this study was to analyze the spatial distribution of the trophic categories of epibenthic

deep-sea polychaetes in relation with the environmental variables.

Materials and methods

Benthic organisms associated with soft bottoms from 360 to 2309 m depth were collected aboard the R/V "El Puma" (Universidad Nacional Autónoma de México) during four oceanographic cruises in the southeastern Gulf of California: TALUD IV in August 2000 (seven stations), TALUD V during December 2000 (four stations), TALUD VI in March 2001 (four stations), and TALUD VII in June 2001 (seven stations) (Table I).

Epifauna was collected with a 2.35 m wide by 0.95 m high benthic sledge, with a collecting net of ca 5.5 cm (2 1/4") stretch mesh lined with a ca 2 cm (3/4") mesh net in the mouth area, towed during 30 min in each station. Polychaetes retained in the net were collected with forceps and fixed on board with a 10% formaldehyde solution. In the case of the thick muddy polychaete tubes, a 10% formaldehyde solution was added manually through one of the tube openings using a syringe. In the laboratory, specimens were washed with fresh-water repeatedly, preserved in 70% ethanol, and identified following specific literature for the polychaetes.

Table I. Positions of the sampling stations visited during the TALUD IV-VII cruises, southeastern Gulf of California.

Cruises	Stations	Latitude N	Longitude W
TALUD IV	13	23°17'30"	107°29'51"
	14	23°13'24"	107°41'48"
	20	24°27'24"	108°35'16"
	25	24°53'12"	108°59'24"
	33	25°45'54"	109°48'06"
	34	25°40'42"	109°54'24"
	35	25°53'59"	110°11'17"
TALUD V	3	21°59'14"	106°28'30"
	11	23°14'00"	107°00'00"
	18	24°15'12"	108°17'09"
	25	24°51'46"	108°57'59"
TALUD VI	3	22°00'01"	106°28'06"
	18	24°14'56"	108°16'17"
	25	24°51'41"	108°57'54"
	34	25°43'50"	109°53'59"
TALUD VII	3	22°13'18"	106°31'36"
	4	22°03'18"	106°34'42"
	11	23°16'54"	106°59'48"
	13B	23°30'18"	107°44'00"
	18	24°14'30"	108°16'24"
	25	24°52'48"	108°58'00"
	32B	26°03'00"	109°55'24"

Samples of sediments (200-250 g) for granulometric and organic matter content analyses were collected with a 110 cm x 40 cm x 20 cm modified Karling dredge attached behind the benthic sledge allowing the collection of a maximal volume of 85 l of sediment when it is full. This dredge has two 7-cm wedges, and since it is a heavy apparatus, it can be assumed that it can collect the top 7 cm layer of sediment, but depending on the nature of the

bottom, the total sediment volume may be variable. Percentage of organic matter was obtained by loss of ignition at 550°C for 1 h (Dean 1974). According to conventional methods (i.e., Folk 1965), samples of about 200 g were sieved through a 2-mm mesh to separate gravel from sand and through a 0.0625-mm mesh to separate sand from mud (the latter considered as a mixture of silt and clay). Grain size was expressed as percentages of mud (<0.0625 mm),

sand (0.0626-2.00 mm) and gravel (> 2.01 mm). Sampling depth was estimated with an analogical Edo Western echo sounder. Temperature was measured ca 10 m above the bottom level with a CTD. Opening-closing bottles were used to obtain near-bottom water samples and oxygen concentrations were determined by the Winkler method (Strickland & Parsons 1972) using a Metrohm Herisau (Mod. E-415) burette with an estimated precision of 2.34% and with a lower limit of 0.01 ml/l.

Abundance of the identified species and genera was expressed in terms of density in order to compare results after statistical analyses. Approximate density values (expressed as number of individuals/100 m²) were estimated through the relationship between the abundance divided by 3701 m², which represented the swept area for a 30 minutes trawl. This area was estimated considering an average trawling speed of 1.75 knots, the trawl time (30 minutes = 0.5 hours) and the width of the mouth of the benthic sledge (2.35 m). Then, considering that 1 knot = 1 nautical mile/hour = 1.8 Km/hour, the swept distance was calculated as:

Swept distance = (1.75 nautical miles) x (1.8 Km/h) x (0.5 hours) = 1.575 Km

Finally, the swept area was calculated considering the swept distance and the width of the mouth of the sledge, as 1575 m x 2.35 m = 3701 m² (Méndez & Hendrickx 2012).

Dominant identified species and genera were determined according to the mean dominance index $Dm = (n_i/N) \times 100$, where Dm = mean dominance index for species i ; n_i = number of individuals belonging to species i ; N = total number of individuals belonging to all the species (Picard 1965). Due to the high density of *M. gracilis* recorded in station 25 from TALUD IV (mean dominance of 98.4% in the benthic sledge; Méndez 2009), this species was excluded from the dominance analysis to avoid biased data. Frequent identified species and genera were obtained through the Glémarec (1964) index as $F = (m_i \times 100)/M$, where m_i = number of samples in which species i appeared and M = total number of samples containing polychaetes (20 stations out of 22 stations sampled). The most important epibenthic polychaete species were considered those which mean dominance was $\geq 1\%$ and the frequency was ≥ 10 .

The trophic categories for the study area were established based on the feeding guilds for polychaete families proposed by Fauchald & Jumars (1979) and Gambi & Giangrande (1985). This attribution was made considering the most common feeding guild reported for each family. Analyses

were performed based only on trophic categories of each family, without considering feeding structures and motility, as suggested by Gaston (1987). Four trophic groups were established: surface deposit-feeders (generally discrete motile or sessile, tentaculate, with tubes), burrowers (equivalent to the subsurface deposit-feeders, with not-jawed proboscis), carnivores (with a considerable motility and usually armed with jaws), omnivores (eat a wide variety of food, with jaws, with or without tubes), and filter-feeders (sessile, with tentacles and tubes). For simplicity, the combination of the two first groups was catalogued here as detritivores.

In order to know if the environmental variables influence the distribution of epibenthic polychaetes, the non-parametric Spearman correlation (Statistica 10 program) between mean density and the measured abiotic variables was performed due to the Kolmogorov-Smirnov test indicated that data were not normal. A second Spearman correlation analysis was performed between the established trophic categories and the environmental variables.

Results

From the 22 sampled stations during the four TALUD cruises, 20 presented polychaetes. Fifty two epibenthic polychaete taxa included in 21 families were found, from which 35 species and five genera (*Eumida*, *Pareurythoe*, *Amage*, *Samytha* and *Thelepus*) were identified (Table II). The rest of the taxa belonging to the families Spionidae, Maldanidae, Phyllodocidae, Polynoidae, Lumbrineridae, Sabellidae and Serpulidae, were damaged and lack important diagnostic structures, thus they were catalogued as "indeterminable". Some species names registered in Méndez (2006) have been updated due to changes in recent literature. The families better represented in the study area in terms of the number of taxa were Ampharetidae (ten taxa, from which eight species and two genera were identified), Maldanidae (six taxa from which only one species could be identified), and Phyllodocidae (five taxa with three species, one genus and an indeterminable taxon). Density range (whenever a taxon was observed in more than one sample expressed as individuals/100 m²), frequency (%), and mean dominance (%) calculated for each identified species and genus are shown in Table II.

From the 40 taxa identified at species or genus levels, 52.5% were surface deposit-feeders (21 taxa, from which 10 were ampharetids), 20% were carnivorous (8 taxa), 12.5% were burrowers (5 taxa), and 15% were omnivores (6 taxa). The only

filter-feeder taxa corresponded to an indeterminable serpulid. Table III contains a compilation of feeding guilds information (according to Fauchald & Jumars 1979, and Gambi & Giangrande 1985) of the

families collected in this study. The trophic categories established here for the study area were also included.

Table II. Epibenthic polychaete taxa collected during the TALUD IV-VII cruises, density range, frequency and mean dominance (roman numbers= cruises; arabic numbers= stations; families in bold letters; - = not calculated).

Taxa	Cruises and stations	Density (Ind/100 m ²)	Frequency (%)	Dominance (%)
Orbiniidae				
<i>Califia calida</i> Hartman, 1957	VI-25, VII-18	0.08-0.7	10.00	3.00
Spionidae				
Spionidae indeterminable	IV-33	-	-	-
Chaetopteridae				
<i>Phyllochaetopterus limicolus</i> Hartman, 1960	VI-25, VII-18	0.03-0.08	10.00	0.41
Cirratulidae				
<i>Aphelochaeta monilaris</i> Hartman, 1960	VI-3	0.05	5.00	0.21
<i>Cirratulus sinicolens</i> Chamberlin, 1919	VII-3, VII-11	0.03-0.19	15.00	1.04
<i>Cirratulus cf sinicolens</i> Chamberlin, 1919	IV-25, V-3, V-11	0.22-0.81	15.00	5.28
Capitellidae				
<i>Neoheteromastus lineus</i> Hartman, 1960	IV-20	0.11	5.00	0.41
Maldanidae				
<i>Maldane cristata</i> Treadwell, 1923	V-18, VI-25, VII-18	0.03-3.0	15.00	11.70
Maldanidae indeterminable sp 1	IV-34	-	-	-
Maldanidae indeterminable sp 4	IV-20	-	-	-
Maldanidae indeterminable sp 5	VI-34	-	-	-
Maldanidae indeterminable sp 8	VII-18	-	-	-
Maldanidae indeterminable	V-25, VI-25	-	-	-
Phyllodocidae				
<i>Eumida sanguinea</i> (Oersted, 1843)	IV-35	0.03	5.00	0.10
<i>Eumida</i> sp	IV-34	0.03	5.00	0.10
<i>Paranaitis polynoides</i> (Moore, 1909)	VI-34	0.03	5.00	0.10
<i>Steggoa gracilior</i> Chamberlin, 1919	IV-34	0.03	5.00	0.10
Phyllodocidae indeterminable	VI-25	-	-	-
Aphroditidae				
<i>Aphrodita parva</i> Moore, 1905	IV-25, V-11, V18, V-25, VI-18, VII-32B	0.03-0.76	25.00	3.83
<i>Laetmonice pellucida</i> Moore, 1903	VII-13B	0.03	5.00	0.10
Polynoidae				
Polynoidae indeterminable 1	IV-25	-	-	-
Polynoidae indeterminable 3	IV-35	-	-	-
Nereididae				
<i>Nereis anoculopsis</i> Fauchald, 1972	IV-33	0.03	5.00	0.10
Amphinomidae				
<i>Pareurythoe</i> sp	IV-25	0.08	5.00	0.31
<i>Pseudeurythoe cf ambigua</i>	VII-18	0.03	5.00	0.10

Onuphidae				
<i>Anchinothria fissurata</i> Fauchald, 1972	IV-14	0.27	5.00	1.04
<i>Nothria abyssalis</i> Fauchald, 1968	IV-35, VI-25	0.03-0.62	10.00	2.48
Eunicidae				
<i>Eunice megabranhia</i> Fauchald, 1970	IV-25, V-18, VII-11, VII-18	0.03-0.11	20.00	0.83
Lumbrineridae				
<i>Ninnoe fuscooides</i> Fauchald, 1972	IV-25, V-3	0.03	10.00	0.21
Lumbrineridae indeterminable	IV-35, VI-25	-	-	-
Oeonidae				
<i>Drilonereis falcata</i> Moore, 1911	VI-34	0.03	5.00	0.10
Sternaspidae				
<i>Sternaspis fossor</i> Stimpson, 1854	V-18	0.03	5.00	0.10
Flabelligeridae				
<i>Brada pluribranchiata</i> (Moore, 1923)	V-3, VI-25, VI-34	0.03-1.24	20.00	5.49
Fauveliopsidae				
<i>Fauveliopsis rugosa</i> Fauchald, 1972	IV-25, V-11, VI-34	0.03-8.05	15.00	36.33
Ampharetidae				
<i>Amage</i> sp	VI-25	0.14	5.00	0.52
<i>Ampharete acutifrons</i> (Grube, 1860)	IV-25	0.57	5.00	2.17
<i>Ampharete arctica</i> Malmgren, 1866	IV-35, V-3	0.03-0.97	10.00	3.83
<i>Amphicteis scaphobranchia</i> Moore, 1906	VII-25	0.35	5.00	1.35
<i>Egamella quadribranchiata</i> Fauchald, 1972	IV-35	0.95	5.00	3.62
<i>Melinna exilia</i> Fauchald, 1972	V-25, VI-25, VI-34, VI-18	0.03-1.08	20.00	4.87
<i>Melinnampharete gracilis</i> Hartman, 1969	IV-25, V-11, VI-25, VII-18, VII-25	0.03-416.84	25.00	NC
<i>Paramage scutata</i> Moore, 1923	VI-34	0.57	5.00	2.17
<i>Samytha</i> sp	V-11	0.38	5.00	1.45
<i>Schistocomus hiltoni</i> Chamberlin, 1919	V-18, VII-18	0.05-0.33	10.00	1.35
Terebellidae				
<i>Thelepus hamatus</i> Moore, 1905	V-18, VI-25, VII-25	0.03	15.00	0.31
<i>Thelepus setosus</i> (Quatrefages, 1865)	V-11, VII-11	0.03-0.05	10.00	0.31
<i>Thelepus</i> sp	VII-11	0.03	5.00	0.10
<i>Streblosoma crassibranchia</i> Treadwell, 1914	VII-25	0.03	5.00	0.10
Sabellidae				
<i>Chone gracilis</i> Moore, 1906	VII-18	0.03	5.00	0.10
<i>Pseudopotamilla intermedia</i> Moore, 1905	VI-34	0.03	5.00	0.10
Sabellidae indeterminable	V-11	-	-	-
Serpulidae				
Serpulidae indeterminable	IV-34	-	-	-

Values measured for each environmental variable (depth, temperature, dissolved oxygen, granulometry and organic matter content) were provided for each identified species and genus, including the range whenever a taxon was found in more than one sample (Table IV). Density values

ranged from a minimum of 0.03 ind/100 m² (a single specimen per sample) to 416.84 ind/100 m², the later value corresponding to *Melinnampharete gracilis* in station 25 of the TALUD IV cruise. Second in density was *Fauveliopsis rugosa* (8.05 ind/100 m²). Density for the rest of the species was always lower than 1.24 ind/100 m² (Table II). Excluding the surface deposit-feeder *M. gracilis*, the 11 dominant (>1%) and frequent (>10%) species were the surface deposit-feeders *Ampharete arctica*, *Brada pluribranchiata*, *Cirratulus sinicolens*, *Cirratulus*

cf. *sinicolens*, *Melinna exilia*, and *Schistocomus hiltoni*, the burrowers *Califia calida*, *Fauveliopsis rugosa* and *Maldane cristata*, the carnivore *Aphrodita parva*, and the omnivore *Nothria abyssalis* (Table II), which were considered as the most important epibenthic species of the southeastern Gulf of California in terms of dominance ($\geq 1\%$) and frequency ($\geq 10\%$), although such parameters were relatively close to the lower limits.

Table III. Feeding guilds, motility, feeding structures, presence/absence of tubes of the families found in this study (sources: Fauchald & Jumars (1979) and Gambi & Giangrande (1985); *mostly carnivores; NR= not recorded), number of taxa recorded in each family, and trophic categories established for each family (Burr=burrowers, Carn= carnivores; Fil= filter-feeders; Omn= omnivores; SDF= Surface deposit-feeders).

Family	Feeding	Motility	Feeding structures	Tubes	Number of taxa	Trophic categories
Orbiniidae	Subsurface deposit-feeder	Burrower	Not-jawed proboscis	No	1	Burr
Spionidae	Surface deposit-feeder	Discretely motile	Tentacules	Yes	1	SDF
Chaetopteridae	Surface deposit-feeder	Sessile	Tentacules	Yes	1	SDF
Cirratulidae	Surface deposit-feeder	Discretely motile	Tentacules	Yes	3	SDF
Capitellidae	Subsurface deposit-feeder	Burrower	Not-jawed proboscis	Yes	1	Burr
Maldanidae	Subsurface deposit-feeder	Burrower	NR	Yes	6	Burr
Phyllodocidae	Carnivorous+detritivorous	Motile	Not-jawed proboscis	No	5	Carn
Aphroditidae	Carnivorous	Motile	Jaws	No	2	Carn
Polynoidae	Carnivorous	Motile	Jaws	No	2	Carn
Nereididae	Omnivorous *	Motile	Jaws	Yes	1	Omn
Amphinomidae	Carnivorous	Motile	Not-jawed proboscis	No	2	Carn
Onuphidae	Omnivorous *	NR	Jaws	Yes	2	Omn
Eunicidae	Omnivorous *	NR	Jaws	Yes	1	Omn
Lumbrineridae	Omnivorous *	NR	Jaws	No	2	Omn
Arabellidae	Omnivorous *	NR	Jaws	No	1	Omn
Sternaspidae	Subsurface deposit-feeder	Motile	NR	No	1	Burr
Flabelligeridae	Surface deposit-feeder	Discretely motile	Tentacules	No	1	SDF
Fauveliopsidae	Subsurface deposit-feeder	Sessile	NR	Yes	1	Burr
Ampharetidae	Surface deposit-feeder	Sessile	Tentacules	Yes	10	SDF
Terebellidae	Surface deposit-feeder	Sessile	Tentacules	Yes	4	SDF
Sabellidae	Surface deposit-feeder	Sessile	Tentacules	Yes	3	SDF
Serpulidae	Filter-feeder	Sessile	Tentacules	Yes	1	Fil

The identified genera and species were collected in depths ranging from 732 to 2050 m, temperatures from 2.5 to 6.2°C, dissolved oxygen from 0.04 to 1.68 ml/l, 8.3 to 17.47% organic matter, 20.6 to 100% mud, 0 to 79.4% sand and 0.38.7% gravel. The highest sand and gravel percentages

corresponded to a single station each (Table IV). The Spearman correlation analysis between mean density and the environmental parameters showed no significant correlations except for gravel ($R = -0.49$; $N = 44$; $p < 0.05$).

Correlation (Spearman) between the trophic categories and the environmental variables indicated that only carnivores had a significant negative correlation with organic matter ($R=-0.648$; $N=18$; $p<0.05$). Table V contains the percentages recorded by each trophic category in the different

environmental variables (gravel was not included because only one station presented gravel). All the trophic categories (especially the omnivores) were found in wide ranges of the environmental variables. No trends were observed for depth, temperature and oxygen.

Table IV. Values of the environmental variables where the identified species and genera were found (names in alphabetical order; ND= no data due to logistic problems).

Taxa	Mean depth (m)	Temperature (°C)	Oxygen (ml/l)	Organic matter (%)	Mud (%)	Sand (%)	Gravel (%)
<i>Amage</i> sp.	840	5.6	0.22	10.9	97.3	2.7	0.0
<i>Ampharete acutifrons</i>	789	5.1	0.29	9.9	99.1	0.9	0.0
<i>Ampharete arctica</i>	732-2050	2.5-5.5	0.12-1.68	10.27-17.23	93.5-100.0	0.0-6.5	0.0
<i>Amphicteis scaphobranchia</i>	815	4.7	0.04	12.2	99.7	0.3	0.0
<i>Anchinothria fissurata</i>	ND	ND	ND	ND	ND	ND	ND
<i>Aphelocheta multifilis</i>	775	5.8	0.21	19.9	98.8	1.2	0.0
<i>Aphrodita parva</i>	789-965	5.0-5.9	0.10-0.29	9.86-14.74	98.1-100.0	0.0-1.5	0.0-0.4
<i>Brada pluribranchiata</i>	732-980	5.2-6.2	0.12-0.77	10.90-17.42	60.3-100.0	0.0-2.7	0.0-38.7
<i>Califia calida</i>	840-980	5.2-5.6	0.13-0.22	10.9-13.12	97.3-100.0	0.0-2.7	0.0
<i>Chone gracilis</i>	980	5.2	0.13	13.1	100.0	0.0	0.0
<i>Cirratulus</i> cf. <i>sinicolens</i>	732-789	5.1-5.5	0.12-0.29	9.86-17.23	99.1-100.0	0.0-0.90	0.0-0.0
<i>Cirratulus sinicolens</i>	745-865	5.6-6.2	0.10-0.77	14.74-17.42	60.3-100.0	0.0-1.0	0.0-38.7
<i>Drilonereis falcata</i>	1200	3.5	0.87	14.4	99.6	0.4	0.0
<i>Egamella quadribranchiata</i>	2050	2.5	1.68	10.3	93.5	6.5	0.0
<i>Eumida sanguinea</i>	2050	2.5	1.68	10.3	93.5	6.5	0.0
<i>Eumida</i> sp.	1220	3.5	0.79	8.3	20.6	79.4	0.0
<i>Eunice megabranhia</i>	785-980	5.0-5.6	0.13-0.29	9.86-17.47	99.1-100	0.0-0.9	0.0
<i>Fauveliopsis rugosa</i>	789-1200	3.5-5.1	0.29-0.87	9.86-14.41	99.1-99.6	0.4-0.9	0.0
<i>Laetmonice pellucida</i>	1425	3.0	1.04	10.6	88.4	10.4	1.2
<i>Maldane cristata</i>	840-980	5.0-5.6	0.13-0.22	10.9-13.74	97.3-100.0	0.0-2.7	0.0
<i>Melinna exilia</i>	830-1200	3.5-5.6	0.13-0.87	10.87-14.41	97.3-100.0	0.0-2.7	0.0-0.4
<i>Melinnampharete gracilis</i>	789-980	4.7-5.2	0.04-0.29	9.86-13.12	98.1-100.0	0.0-1.5	0.0-0.4
<i>Neoheteromastus lineus</i>	1510	3.1	1.26	15.5	98.1	1.9	0.0
<i>Nereis anoculopsis</i>	1075	4.3	0.51	13.9	99.9	0.1	0.0
<i>Ninoe fuscooides</i>	732-789	5.1-5.5	0.12-0.29	99.86-17.23	99.1-100.0	0.0-0.9	0.0
<i>Nothria abyssalis</i>	840-2050	2.5-5.6	0.22-1.68	10.27-10.90	93.5-97.3	2.7-6.5	0.0

<i>Paramage scutata</i>	1200	3.5	0.87	14.4	99.6	0.4	0.0
<i>Paranaitis polynoides</i>	1200	3.5	0.87	14.4	99.6	0.4	0.0
<i>Pareurythoe</i> sp.	789	5.1	0.29	9.9	99.1	0.9	0.0
<i>Phyllochaetopterus limicolus</i>	840-980	5.2-5.6	0.13-0.22	10.9-13.12	97.3-100.0	0.0-2.7	0.0
<i>Pseudeurythoe ambigua</i>	980	5.2	0.13	13.1	100.0	0.0	0.0
<i>Pseudopotamilla intermedia</i>	1200	3.5	0.87	14.4	99.6	0.4	0.0
<i>Samytha</i> sp.	ND	ND	ND	ND	ND	ND	ND
<i>Schistocomus hiltoni</i>	965-9.80	5.0-5.2	0.13-0.15	13.12-13.74	100.0	0.0	0.0
<i>Steggoa gracilior</i>	1220	3.5	0.79	8.3	20.6	79.4	0.0
<i>Sternaspis fossor</i>	965	5.0	0.15	13.7	100.0	0.0	0.0
<i>Streblosoma crassibranchia</i>	815	4.7	0.04	12.2	99.7	0.3	0.0
<i>Thelepus hamatus</i>	815-965	4.7-5.6	0.04-0.22	10.90-13.74	97.3-100.0	0.0-2.7	0.0
<i>Thelepus setosus</i>	785	5.6	0.15	17.5	100.0	0.0	0.0
<i>Thelepus</i> sp.	785	5.6	0.15	17.5	100.0	0.0	0.0

Discussion

Méndez (2007) reported that deep-sea infaunal polychaetes from the TALUD IV to VII cruises had significant correlation between density and the environmental variables, especially depth, dissolved oxygen and temperature. In contrast, in this study no correlation between epibenthic polychaetes density and the environmental variables was observed. This lack of correlation can be mainly attributed to methodological problems. Due to the large mesh aperture of the net, only the larger specimens were retained with the rest of the capture and eventually brought to deck. The loss of small specimens was also induced by washing when the gear was being hauled through the water column to surface, as discussed by Méndez & Hendrickx (2012). In spite of these difficulties, the results presented here were useful to know some spatial distribution aspects, including the environmental variables and feeding of deep-sea epibenthic polychaetes from the southeastern Gulf of California that were not previously studied.

Except for the significant negative correlation between carnivores with organic matter that resulted by the Spearman correlation analysis, the studied trophic groups were not significantly correlated with the environmental variables, but it was suggested that such trophic groups were more sensitive to environmental changes than density. Although it has widely been demonstrated a strong relationship between polychaete feeding guilds with

environmental factors, such as granulometry, organic matter, depth, salinity, temperature and oxygen (Maurer & Leathern 1981, Paiva 1993, Carrasco & Carbajal 1998, Muniz & Pires 1999, Pagliosa 2005, Domínguez-Castanedo *et al.* 2012; Mattos *et al.* 2013), results from this study indicate no preference for specific depths, temperatures and dissolved oxygen values. In contrast, the highest percentages recorded for the trophic categories could give the guideline for certain distribution trends, especially for the sediment characteristics (i.e., detritivores in muddy sediments with high organic matter content and carnivores in sediments with low percentages of mud and organic matter), which suggests that the distribution of the trophic groups of epibenthic polychaetes was mainly governed by grain size and organic matter contents. This was demonstrated by the high percentage of detritivorous (65%), represented by surface deposit-feeders and burrowers, which were dominant in muddy sediments with high contents of organic matter.

According to Jumars (1976) and Maurer & Leathern (1981), large detritivore organisms can live in the deep-sea, where organic matter content in sediments is high. The most frequent and dominant species from the epibenthic community of the study area were mostly surface deposit-feeders (*C. sinincolens*, *C. cf. sinincolens*, *B. pluribranchiata*, *A. arctica*, *M. exilia*, *M. gracilis*, *S. hiltoni*), and burrowers (*C. calida*, *M. cristata*, and *F. rugosa*). Fine grain and organic matter in sediments were the

main responsible of the spatial distribution of such species, which were collected in muddy sediments reaching 17% organic matter. This suggests that the detritivorous epibenthic polychaete community was not food limited. According to Gambi & Giangrande (1985), Muniz & Pires (1999) and Mattos *et al.* (2013), detritivores are frequently associated with environments of low hydrodynamism, and consequently with high concentrations of organic matter. It has been also demonstrated that

detritivores are common in soft muddy sediments (Carrasco & Carbajal 1998, Mattos *et al.* 2013, Maurer & Leathern 1981). Moreover, detritivores have been shown to be tolerant to environmental changes, especially in sediments, and thus, able to explore more habitats (Muniz & Pires 1999). All these characteristics explain the dominance of detritivore polychaetes in the studied deep-sea soft bottoms.

Table V. Percentages recorded by the trophic categories in the established ranges of each environmental variable.

Depth ranges (m)	Burrowers	Carnivores	Omnivores	Surface deposit-feeders
500-1000	14.8	11.1	11.1	63.0
1000-1500	9.1	36.4	18.2	36.4
1500-2000	100.0	0.0	0.0	0.0
2000-2500	0.0	20.0	20.0	40.0
Temperature ranges (°C)				
2-3	0.0	20.0	20.0	60.0
3-4	20.0	40.0	10.0	30.0
4-5	0.0	0.0	20.0	80.0
5-6	16.0	12.0	12.0	60.0
6-7	0.0	0.0	0.0	100.0
Oxygen ranges (ml/l)				
0.01-0.5	14.3	10.7	14.3	60.7
0.5-1.0	10.0	30.0	10.0	50.0
1.0 -1.5	50.0	50.0	0.0	0.0
1.5- 2.0	0.0	25.0	25.0	50.0
Organic matter ranges (%)				
8-10	9.1	36.4	18.2	36.4
10 -12	15.4	23.1	7.7	53.8
12 -14	20.0	13.3	13.3	53.3
14 -16	22.2	22.2	11.1	44.4
16 -18	0.0	0.0	25.0	75.0
18-20	0.0	0.0	0.0	100.0
Mud ranges (%)				
20-40	0.0	100.0	0.0	0.0
40-60	0.0	0.0	0.0	0.0
60-80	0.0	0.0	0.0	100.0
80-100	13.9	16.7	13.9	55.6
Sand ranges (%)				
0-20	13.9	16.7	13.9	55.6
20-40	0.0	0.0	0.0	0.0
40-60	0.0	0.0	0.0	0.0
60-80	50.0	50.0	0.0	0.0

According to Gaston (1987), surface deposit-feeders are regulated mainly by food resources (i.e. plankton), and are generally tubicolous. In their study off Southern California, Jumars & Fauchald (1977) showed a positive correlation between depth and the proportion of sessile polychaetes because sediment stability increases with water depth and flux of organic matter, which is in agreement with findings from Maurer & Leathern (1981), Gaston (1987) and Domínguez-Castanedo *et al.* (2012). These arguments explain the success of the families Spionidae, Chaetopteridae, Cirratulidae, Ampharetidae, Terebellidae and Sabellidae in deep-sea waters of the southeastern Gulf of California studied here.

Twenty-one taxa of surface deposit-feeders (52.2%) were found, ten of which were ampharetids. The family Ampharetidae was the best represented in terms of number of taxa and density. It is well known that ampharetids density increases with depth and that they dominate abyssal sediments (Fauchald & Jumars 1979, Hernández-Alcántara & Solís-Weiss 1993). All ampharetids make mucus-lined tubes covered with sediment particles and, compared with body-length, most species of this family build very long tubes. Deep-sea polychaetes make ventilating tubes to withstand low oxygen conditions, and especially ampharetids build tubes continuously, which may represent an efficient form of locomotion (Fauchald & Jumars 1979). Most of the ampharetid tubes found over the study were long (more than 30 cm), wide (more than 1 cm diameter) and robust, which explains the success of this family in the study area and other deep sea zones (i.e. stable areas).

Most ampharetids are surface deposit-feeders, using their retractable and ciliated tentacles to pick up food particles (Fauchald & Jumars 1979). Gambi & Giangrande (1985) catalogued the family Ampharetidae as surface detritivorous and sessile. During feeding, the tube of many species projects obliquely above the substratum and is distally curved towards the mud. The worm stretches out of the tube, spreading the tentacles over the substratum, keeping the branchiae up in the water. Some species like *Melinna cristata* (Sars 1851), have vertically orientated tubes that form a turf binding up the soft sediments (Fauchald & Jumars 1979), which favour the collection of very high numbers of specimens with a benthic sledge.

It has been stated that burrowers increase significantly with depth and fine sediments because topographic depressions act as sediment sinks that

accumulate sediment and subsequently bury detritus (Gaston 1987). Burrowers are frequently associated with environments of low hydrodynamics and consequently with high concentrations of organic matter (Maurer & Leathern 1981, Bianchi & Morri 1985, Gambi & Giangrande 1985, Muniz & Pires 1999), as shown by *C. calida*, *F. rugosa*, *M. cristata*, *N. lineus* and *S. fossor* found here. Burrowers were represented by only five taxa (12.5%) and thus their presence in epifaunal samples could be accidental. Benthic sledges are designed to collect mostly epifaunal species, but some burrowing species, including polychaetes with protruding tubes, are occasionally caught when a large portion of their tube emerge from the sediment and is vertically oriented. In this study, the muddy nature of the substrate in most of the stations provoked the sinking of the basis of the sledge in the sediment, thus facilitating the capture of the protruding tubes and infaunal species represented mainly by burrowers.

The family Maldanidae was also important in terms of the number of taxa. According to Gambi & Giangrande (1985), most maldanids are tubicolous and are generally represented by burrowers. The high content of organic matter in the sediments and the dominance of muddy bottoms explain the success of the family in the study area comprising both, infauna (Méndez 2007) and epifauna (this study).

On the other hand, 20% of the epibenthic polychaetes corresponded to the group of the carnivores, which were more common in coarse sediments with low amount of organic matter, as demonstrated by the significant negative correlation found between this trophic group and organic matter. It is well known that carnivorous polychaetes are more frequent in coarser sediments that have greater pore space enhancing movement of their interstitial preys, and greater pore space also enhances oxygen penetration (Gaston 1987, Maurer & Leathern 1981, Carrasco & Carbajal 1998, Paiva 1994, Muniz & Pires 1999, Pagliosa 2005). This was confirmed with results presented here, since high percentages of carnivores were found in coarser sediments and relatively high oxygen values. Gaston (1987) found that the proportion of carnivores decreased significantly with depth, which is consistent with data found here, since the highest proportions of carnivores were found in the lower depth ranges (500 to 1500 m).

The family Phyllodocidae was also well represented in the epibenthic community in terms of number of taxa. Most filodocids are considered as

carnivores that catch preys with the muscular pharynx (Fauchald & Jumars 1979). Gambi & Giangrande (1985) placed this family in the group of carnivores, motile, with pharynx usually lacking jaws or hard structures. The life style of members belonging to this family explains their success in the surface of the sediment, where they can easily find and hunt other animals.

According to Fauchald & Jumars (1979) jawed species are better adapted to ingest variable prey sizes than non-jawed species. The families Nereididae, Onuphidae, Eunicidae, Lumbrineridae and Oeonidae were classified as omnivores and all of them have jaws useful to trap different sizes and kinds of food. The onuphid *N. abyssalis*, the only omnivore important due to its dominance and frequency, was found in wide ranges of depth, temperature and dissolved oxygen, while its distribution in predominantly muddy sediments with high organic matter content indicates that this species followed a similar trend as detritivores. This confirms that this species can feed in a high variety of food, including detritus.

The wide variety of trophic groups exhibited by the epibenthic community inhabiting deep-sea of the southeastern Gulf of California can be explained by the stability of the water-sediment interface found at greater depths, as suggested by Paiva (1993) and Domínguez-Castanedo *et al.* (2012). The environmental variables values observed in this study were not clearly associated with density of species and trophic categories, making difficult the establishment of assemblages based on a single or more abiotic variable. Nevertheless, general spatial distribution patterns of the deep-sea epibenthic polychaete community could be observed based on the trophic categories of each family, which represents a new contribution to the knowledge of their biology, which has been poorly studied.

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