



Spatial and bathymetric trends in composition and taxonomic diversity of Polychaeta (Annelida) assemblages from the deep southern Gulf of California

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ABSTRACT.—The deepsea fauna from the southern Gulf of California is currently poorly known, with only 193 species reported to date. The aim of this study was to analyze the composition, density, species richness, and taxonomic diversity (Δ) of the deepsea polychaetes of this region. Fifteen stations (238–2900 m depth) were sampled in 2012 and 2013. Eighty-four species from 58 genera and 26 families were identified. Density ranged from 4.76 to 42.86 ind 0.1 m⁻² and was not significantly correlated with depth; species richness ranged from 2 to 17 species per station, the lowest (2–6 species) occurring between depths of 651 and 915 m. Four assemblages were identified associated with depth ($R_{\text{ANOSIM}} = 0.43$, $P = 0.002$) and geographic position ($R_{\text{ANOSIM}} = 0.56$, $P = 0.001$): *Prionospio elhersi*–*Subadyte mexicana*–*Syllis alternata* (<350 m depth) and *Aricidea* sp. A–*Ninoe jessicae* (600–1000 m) in the western gulf; and *Onuphis similis*–*Aricidea (Acmira) simplex* (1300–1600 m) and *Aglaophamus paucilamellata*–*Sthenolepis spargens* (>1200 m) in the middle gulf. Stations 14A and 2A, sharing only their position at the far eastern gulf, remained isolated from any other assemblage. The highest diversity was found at 1300–1600 m ($\Delta = 86.1$) and at >2000 m ($\Delta = 83$ –98) but decreased to $\Delta = 61.85$ at 600–1000 m. The assemblage structure based on genera and family levels were similar to those based on species ($\text{Rho} > 0.6$), suggesting that either of the former two could be suitable surrogates for monitoring changes at the studied depths.

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The extensive deepsea benthic environment (i.e., deeper than 200 m) shows physical, chemical, and sedimentological factors that are characteristically more homogeneous and stable over larger areas than the corresponding shallower ones (Sanders 1968, Solís-Weiss et al. 2014). Under high pressure and low light conditions, the salinity, temperature, and dissolved oxygen in the sediment and in the water immediately above remain virtually constant or vary only slightly over long distances (Gage and Tyler 1991). Although deepsea communities have been considered more diverse than shallow water communities (Hessler and Sanders 1967), the real magnitude

of deepsea diversity is still the subject of constant debate (Costello and Chaudhary 2017).

Food sources are not as abundant or easily available in the deepsea compared to most shallow environments, which may largely control the development, evolution, and persistence of deepsea communities. Their composition and distribution depend on organic material falling from the ocean surface as metabolic products or “rain of corpses”—also known as “marine snow” (Sanders 1969, Sokolova 1977, Grassle and Maciolek 1992)—or transported down from adjacent coastal shallow waters (Sokolova 1977, Danovaro 2003). Therefore, surface primary productivity, together with sedimentation rates and eutrophy, determine the levels of deepsea diversity and biomass (Sanders 1969, Sokolova 1977, Grassle and Maciolek, 1992, Lutz et al. 2007).

The Gulf of California is one of the most productive marine regions of the world. Primary productivity rates here are as high as those of the Bay of Bengal and the upwelling of the western coasts of Baja California or North Africa (Zeitzschel 1969). It is also extremely diverse, supporting almost 5000 macroinvertebrate species (Brusca and Findley 2005). However, its deepsea oceanographic and biological characteristics are still less well known than those of the corresponding adjacent shallow waters, and this is particularly true for annelid polychaetes.

Polychaetes are an important component of macrobenthic assemblages worldwide—both in terms of abundance and diversity—and account for roughly 35% to 65% of the species, mainly in soft bottoms (Blake and Hilbig 1994) but also in most known deepsea areas (Grassle and Maciolek 1992, Wei et al. 2020). They play key roles in processing and transforming organic matter, nutrient recycling, and bioturbation (Grémare et al. 2003). However, their taxonomic composition and distribution patterns, as well as any other information about their occurrence below the shelf break, are poorly understood (Méndez 2006, Schüller et al. 2009), and the Gulf of California is no exception.

The first polychaete was reported from the Gulf of California by Gravier (1901): a heteronereidid, probably *Platynereis polyscalma* Chamberlin, 1919. Since then, around 860 species have been reported (Cuéllar-Mercado et al. 2019), but only 193 species in 41 families from the deepsea (Solís-Weiss et al. 2014). Chamberlin (1919) was the first to describe the numerous local deepsea species and was followed particularly by Fauchald (1972), who reported 227 species (including 66 new) along western Mexico and adjacent eastern Pacific areas collected during the oceanographic expeditions “Albatross” (1886–1891 and 1911), “Velero” (1967, 1970), and “Allan Hancock Pacific Expeditions” (1932 and 1942). Later, Méndez (2006, 2007, 2012, 2013) recorded 106 species from 34 families from the continental slope of the eastern gulf and, in 2013, she found that environmental variables were not clearly related to species density or their trophic categories, making it difficult to determine faunal assemblages. Since then, no other studies have provided data on the ecological roles of deepsea polychaetes in the gulf.

The structure of deepsea marine assemblages has often been related to bathymetric differences in oceanographic characteristics (Tolimieri and Levin 2006, Anderson et al. 2013, Papiol et al. 2017). Thus, the aims of the present study were to analyze: (1) the distribution, composition, density, species richness, and taxonomic diversity of deepsea polychaete assemblages along a bathymetric gradient in the southern Gulf of California, (2) the relationships between these assemblage descriptors and water mass distributions, and (3) the feasibility of using family and gender levels as surrogates for monitoring changes in assemblage structure at the studied depths.

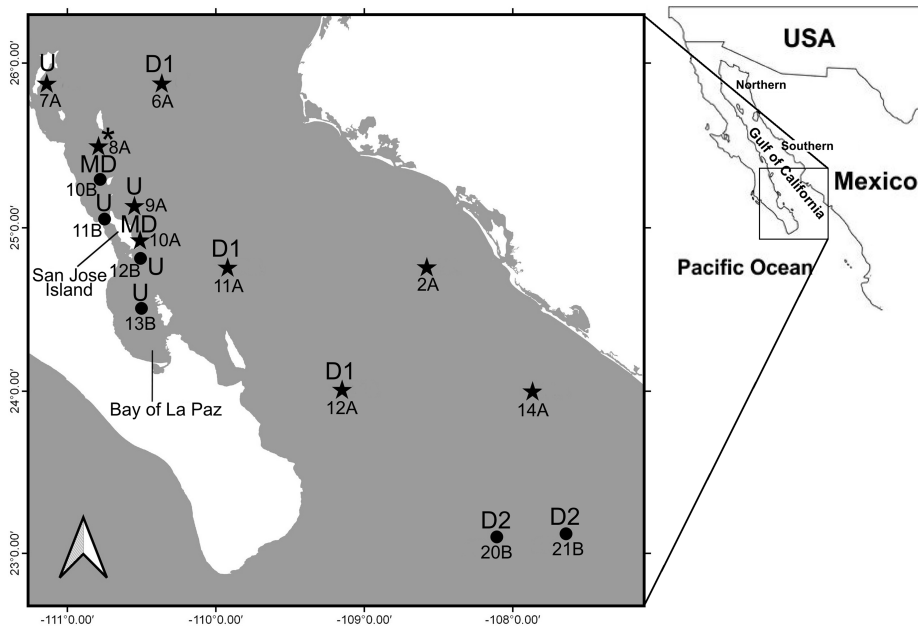


Figure 1. Location of sampling stations in the southern Gulf of California, showing the oceanographic expeditions (stars = ECOGOCA–2012; circles = COSURGC–2013) and faunal assemblages (U = *Prionospio elhersi*–*Subadyte mexicana*–*Syllis alternata*, <350 m; MD = *Aricidea* sp. A–*Ninoe jessicae*, 600–1000 m; D1 = *Onuphis similis*–*Aricidea (Acmira) simplex*, 1300–1600 m; D2 = *Aglaophamus paucilamellata*–*Sthenolepis spargens*, >2000 m).

METHODS

STUDY AREA.—The Gulf of California is a narrow, elongated basin (about 1100 km long and 200 km wide) located in the northeastern Pacific Ocean (23°N–31°N, 105°W–107°W) and well-known for its high primary productivity (1–4 gr C m⁻² d⁻¹; Álvarez-Borrego and Lara-Lara 1991). An archipelago in the central gulf, mainly formed by Ángel de la Guardia, Tiburón, San Esteban, and San Lorenzo islands, affects its hydrography and separates the gulf into two main oceanographic regions: the shallower northern gulf and the deeper southern gulf. Surface water circulation through the gulf produces a net surface outflow through the archipelago, balanced by a permanent near-bottom inflow along the western coast (Lavín et al. 1997). The southern gulf has a series of progressively deeper basins (2000–3500 m depth). Its southern end opens into the Pacific Ocean (Fig. 1), which controls its climatic and oceanographic features. The deep gulf is characterized by water masses with distinct physical and chemical characteristics: Pacific Deep Water (PDW; salinity > 34.5, temperature < 4 °C) from the bottom to the 4 °C isotherm at a depth of about 1200 m and Pacific Intermediate Water (PIW; salinity = 34.5–34.8, temperature = 4–9 °C) from about 1200 m to the 9 °C isotherm at 500 m depth, both of which are relatively stable and comprise most of the gulf's volume (41% and 33%, respectively). The rest of the gulf is occupied by Subtropical Subsurface Water (StSsW) from 500 to 150 m just above the PIW (characterized by salinity of 34.5–35.0 and temperature of 9–18 °C) and by Gulf of California Water (GCW) at less than 150 m, which is more

Table 1. Location and depth of the sampling stations in the southern Gulf of California. Station: A = ECOGOCA–2012 expedition; B = COSURGC–2013 expedition.

Station	Latitude (N)	Longitude (W)	Depth (m)
2A	24°45'09"	108°34'46"	915
6A	25°52'12"	110°21'52"	1604
7A	25°52'09"	111°08'23"	260
8A	25°29'21"	110°47'28"	651
9A	25°07'33"	110°32'56"	262
10A	24°55'01"	110°30'39"	736
11A	24°45'01"	109°55'16"	1335
12A	24°00'06"	109°09'00"	1423
14A	23°59'30"	107°52'01"	300
10B	25°17'33"	110°46'46"	798
11B	25°03'04"	110°45'00"	314
12B	24°48'41"	110°30'28"	348
13B	24°30'21"	110°30'05"	238
20B	23°05'57"	108°06'28"	2900
21B	23°07'07"	107°38'29"	2184

saline (≥ 35) and warmer (≥ 12 °C). This last water mass is mainly located in the northern gulf but reaches the Guaymas basin in summer; it is formed by evaporation of Eastern Tropical Pacific Surface Water (ETPSW), the other surface water mass in the southern gulf (salinity < 35 , temperature ≥ 18 °C; Torres-Orozco 1993, Lavín et al. 1997). All of these water masses create a complex thermohaline structure and a constant presence of fronts, whirlpools, and intrusions (Torres-Orozco 1993).

SAMPLING DESIGN AND FIELD METHODS.—Samples were collected during two oceanographic expeditions carried out on the R/V EL PUMA from the Universidad Nacional Autónoma de México (UNAM): ECOGOCA–2012 (“Comparative study of the Gulf of California”) and COSURGC–2013 (“Oceanographic characterization of the Southern Gulf of California”). Both were conducted in April–May 2012 and 2013 to control interannual environmental variability. A Reineck boxcore (0.042 m²) was used to collect sediment samples from 238 to 2900 m for biological and sedimentological analyses. Fifteen stations were selected along the western margin of the gulf (Table 1, Fig. 1), where the deepsea polychaete fauna was practically unknown. Stations were georeferenced on-board; depth was measured with a Kongsberg (SIMRAD ES60) echosounder and salinity and temperature with a Niels Brown CTD. Water samples were collected using Niskin bottles to measure dissolved oxygen concentration using the Winkler method (Strickland and Parsons 1977). Additional box core samples were taken to analyze sediment textural characteristics using the sieving method (Folk 1980).

Biological samples were washed on board through a 0.5-mm mesh sieve and immediately fixed with 10% formalin/seawater solution. In the laboratory, the fixed material was washed to eliminate the formalin, and the specimens were sorted under a stereomicroscope and preserved in 70% ethanol. The polychaetes were initially identified to family level, quantified, and then identified to genus and species levels following Chamberlin (1919), Fauchald (1972), Blake and Hilbig (1994), and the most recent systematic reviews of genera and species (e.g., Jirkov 2011, Schüller and Hutchings

2013, Jimi et al. 2018, Blake 2020). The validity of all scientific names was verified with the World Polychaeta Database (Read and Fauchald 2021). The identified material was catalogued and deposited in the Colección Nacional de Anélidos Poliquetos of the Instituto de Ciencias del Mar y Limnología (ICML), UNAM (CNAP-ICML, UNAM: DFE.IN.061.0598).

DATA ANALYSES.—All analyses were conducted using the software Plymouth Routines in Multi-Variate Ecological Research (PRIMER v.7; Clarke and Gorley 2015). Annual environmental variability was analyzed by a one-way similarity analysis (ANOSIM) on normalized data (Clarke and Gorley 2015). The bathymetric trends of the abiotic factors were examined with linear regression models. The environmental factors defining the stations' structure were assessed by principal components analysis (PCA) based on a normalized data matrix (Clarke et al. 2014, Clarke and Gorley 2015). The visualization and interpretation of environmental and faunal distributions along the shelf were facilitated by labelling the stations according to bathymetry and, thus, to the dominant water mass: Upper (<350 m) in StSsW, Mid-depth (600–1000 m) in PIW, and Deeper (>1300 m) in PDW.

A matrix of species density (ind 0.1 m^{-2}) by station was built to examine the structure of the faunal assemblages. Polychaete diversity was expressed as taxonomic diversity (Δ), which is based on sample phylogenetic structure (Warwick and Clarke 1995, Clarke et al. 2014). Δ represents the average taxonomic distance between each pair of individuals (or the expected taxonomic distance between any two individuals chosen at random) in a given sample (Clarke et al. 2014). Δ ranges from 0 to 100 and is a "distance" representing the length of the path connecting these two organisms, traced through a Linnean or phylogenetic classification of the full set of species involved. Δ is considered as a natural extension of Simpson's index that incorporates taxonomic (or phylogenetic) information.

The assemblage structure was analyzed by nonmetric multidimensional scaling (nMDS) using the Bray–Curtis similarity index on fourth root-transformed data (Clarke et al. 2014, Clarke and Gorley 2015). The significance of differences in assemblage structure was tested with a one-way analysis of similarity (ANOSIM; Clarke et al. 2014, Clarke and Gorley 2015). Station 8A was excluded from the nMDS to avoid biases caused by its exceptionally low density ($4.76 \text{ ind } 0.1 \text{ m}^{-1}$) and richness (two species). The similarity percentage analysis (SIMPER) was used to measure the contribution of a given species to the within-assemblage similarity and the between-assemblage dissimilarity (Clarke and Gorley 2015). The relationships between faunal structure and environmental factors were analyzed by multiple Pearson's correlations, and the resulting vectors of each abiotic variable were projected onto an nMDS ordination plot.

To assess whether genus or family levels could be suitable surrogates for species in analyzing assemblage structure, which is at the basis of taxonomic sufficiency (Ellis 1985, Domínguez-Castanedo et al. 2007), the PRIMER RELATE routine was used to search for the genera and family subsets best matching the structure based on species. To measure how closely related two sets of multivariate data are, through their respective resemblance matrices, the Spearman's rank correlation coefficient (Rho) was used, with Rho = 0 indicating no relationship and Rho = 1 indicating total agreement (Clarke and Gorley 2015). The respective contributions were represented in nMDS plots which allowed us to visually interpret the respective genus- or family-level contributions to the overall structure.

Table 2. Mean, range, and standard deviation (SD) of the environmental factors per bathymetric level.

Variables	Upper			Mid-depth			Deeper		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
Depth (m)	287.0	238–350	40.9	775.0	651–915	111.1	1,889.3	1,335–2,900	654.8
Temperature (°C)	11.8	10–15.2	1.9	5.3	5–6.1	0.6	3.4	1.3–5	1.8
Salinity (psu)	34.7	34.5–35.1	0.2	34.6	34.5–34.7	0.1	34.5	34.5–34.6	0.2
Dissolved oxygen (ml L ⁻¹)	0.3	0.1–0.9	0.3	0.3	0.1–0.6	0.2	1.1	0.2–2.4	1.0
Mud (%)	72.8	43–94	23.1	72.5	60–84	10.1	78.6	48–98	20.3

RESULTS

ENVIRONMENTAL DESCRIPTORS.—The environmental conditions in Spring 2012 and 2013 did not differ significantly ($R_{ANOSIM} = 0.203$, $P = 0.062$). Therefore, the data from both years were analyzed together.

Overall, the widest ranges were found in depth (238–2900 m) and mud content (43%–98%; Table 2). Depth variability progressively increased towards deeper zones (Table 2). Mud content was always higher than 70% on average (Table 2) and was not related to depth ($R^2 = 0.11$, $P = 0.22$; Fig. 2).

Salinity slightly decreased with depth ($R^2 = 0.41$, $P < 0.05$), but small differences between bathymetric levels were observed (Table 2). Dissolved oxygen increased significantly with depth ($R^2 = 0.66$, $P < 0.05$) mainly due to the two deepest stations (20B at 2900 m = 2.08 ml L⁻¹; 21B at 2184 m = 2.4 ml L⁻¹), both located at the southern-most gulf. However, these oxygen concentrations were high relative to most of the southern gulf, where they were close to the minima (0.1–0.8 ml L⁻¹). Temperature gradually decreased with depth ($R^2 = 0.67$, $P < 0.05$), with low variations within each bathymetric level (Table 2, Fig. 2).

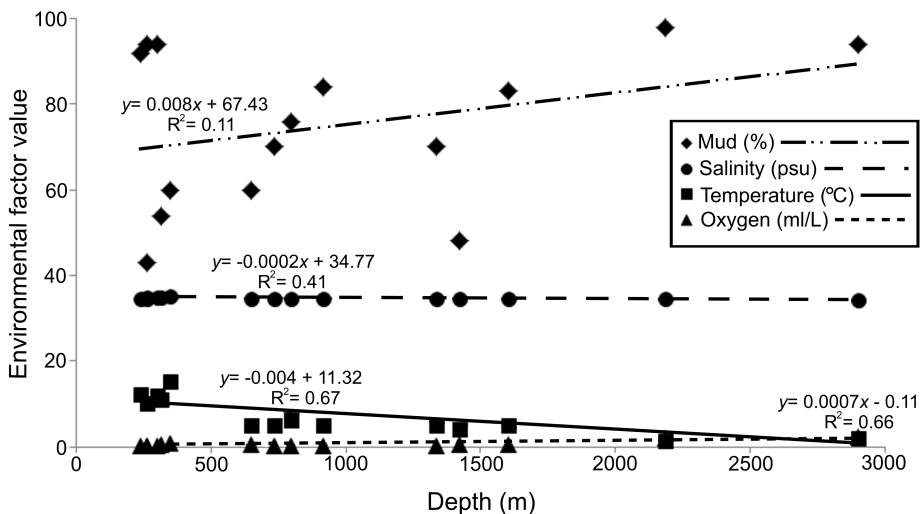


Figure 2. Bathymetric distribution of the environmental factors showing their linear relationships with depth.

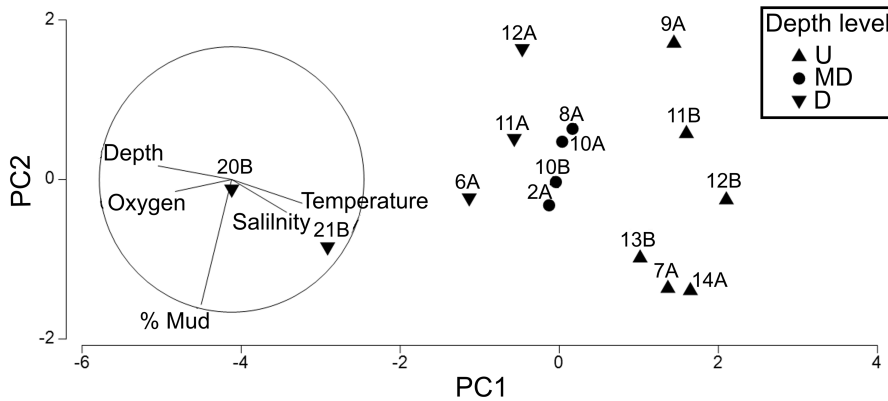


Figure 3. Two-dimensional PCA ordination based on environmental characteristics. Sampling stations labelled according to bathymetric levels (U = Upper; MD = Mid-depth; D = Deeper).

The first two PCA components explained 77.9% of the total environmental variation (PC1 = 60%; PC2 = 17.9%; Fig. 3). PC1 was defined by depth (eigenvector = -0.56) and temperature (eigenvector = 0.53), while PC2 was mainly explained by mud content (eigenvector = -0.94). Three main groups of stations directly associated with the bathymetric levels may be identified (Fig. 3). Group 1 included Upper stations (7A, 9A, 14A, 11B, 12B, 13B; <350 m) with higher temperature (mean = 11.77 °C) and salinity (mean = 34.74). Group 2 included Mid-depth stations (2A, 8A, 10A and 10B; 600 – 1000 m) with intermediate temperature (mean = 5.3 °C) and salinity (mean = 34.6). Group 3 included the Deeper stations (6A, 11A, 12A, 20B, 21B; >1300 m), which were the coldest (mean = 3.43 °C) and least saline (mean = 34.49) stations.

SPECIES COMPOSITION AND DIVERSITY PATTERNS.—A total of 277 individuals from 84 species belonging to 58 genera and 26 families were identified (Table 3). The dominant families were Paraonidae (119.05 ind 0.1 m $^{-2}$), Spionidae (88.10 ind 0.1 m $^{-2}$), Lumbrineridae (73.81 ind 0.1 m $^{-2}$), Pilargidae (66.67 ind 0.1 m $^{-2}$), and Onuphidae (57.14 ind 0.1 m $^{-2}$), accounting for 61.6% of the total density. The most diverse families (number of species in parenthesis) were Onuphidae (11), Spionidae (8), Cirratulidae (8), and Paraonidae (6), representing 39.3% of the species identified.

The average density was 43.33 ind 0.1 m $^{-2}$ and ranged from 4.76 ind 0.1 m $^{-2}$ at 651 m (Station 8A) to 126.19 ind 0.1 m $^{-2}$ at 798 m (Station 10B). Density was irregularly distributed along the Upper and Mid-depth levels ($y = 0.023x + 29.05$; $R^2 = 0.03$, $P = 0.83$), then decreased with increasing depth from 61.90 – 73.81 ind 0.1 m $^{-2}$ at around 1500 m to 30.95 ind 0.1 m $^{-2}$ at 2900 m ($y = 0.022x + 91.69$, $R^2 = 0.60$, $P < 0.05$; Fig. 4). The number of species per station ranged from 2 (station 8A) to 17 (stations 6A and 11A), the first two located to the north of San José Island and the latter in front of the Bay of La Paz. Species number was overall positively correlated with density (Pearson correlation = 0.7) and showed irregular bathymetric variations (Fig. 4). The Upper-level stations had an average of 8 species compared to an average of 4 species in the Mid-depth level and 13 species in the Deeper level. However, there was no significant correlation between species richness and depth until 1000 m ($R^2 = 0.29$, $P > 0.05$),

Table 3. List of deep-sea polychaete species collected in the southern Gulf of California (* species collected only at station 14A; ** species collected only at station 2A).

Species	Species
Family Ampharetidae	Family Paraonidae (<i>Continued</i>)
<i>Ampharete finnarchica</i> (M. Sars, 1865)	<i>Paradoneis forticirrata</i> (Strelzov, 1973)
<i>Ecamphicteis</i> sp. A	Family Phyllodocidae
<i>Samytha californiensis</i> Hartman, 1969	<i>Eteone</i> cf. <i>californica</i> Hartman, 1936
Family Amphinomidae	Family Pilargidae
<i>Benthoscolex</i> sp. A **	<i>Ancistrosyllis groenlandica</i> McIntosh, 1878
<i>Linopherus abyssalis</i> (Fauchald, 1972)	<i>Sigambra setosa</i> Fauchald, 1972
Family Capitellidae	<i>Sigambra</i> sp. A
<i>Capitella</i> sp.	Family Poecilochaetidae
<i>Leiochrides hemipodus</i> Hartman, 1960	<i>Poecilochaetus johnsoni</i> Hartman, 1939 *
<i>Notomastus hemipodus</i> Hartman, 1945	Family Polynoidae
Family Cirratulidae	<i>Subadyte mexicana</i> Fauchald, 1972
<i>Aphelochaeta elongata</i> Blake, 1996	<i>Lepidasthenia curta</i> Chamberlin, 1919
<i>Aphelochaeta glandaria</i> Blake, 1996	Family Sigalionidae
<i>Aphelochaeta monilaris</i> (Hartman, 1960)	<i>Sthenolepis spargens</i> Fauchald, 1972
<i>Aphelochaeta multifilis</i> (Moore, 1909)	Family Spionidae
<i>Aphelochaeta phillipsi</i> Blake, 1996	<i>Dispio uncinata</i> Hartman, 1951 *
<i>Aphelochaeta williamsae</i> Blake, 1996	Family Maldanidae
<i>Chaetozone hedgpathi</i> Blake, 1996	<i>Asychis lobata</i> Fauchald, 1972
<i>Chaetozone</i> cf. <i>lunula</i> Blake, 1996	<i>Lumbriclymene</i> sp. **
Family Dorvilleidae	<i>Petaloproctus</i> sp.
<i>Meiodorvillea apapalpata</i> Jumars, 1974	<i>Sonatsa meridionalis</i> Chamberlin, 1919
Family Glyceridae	Family Nephtyidae
<i>Hemipodia simplex</i> (Grube, 1857)	<i>Aglaothamum erectans</i> Hartman, 1950
Family Goniadidae	<i>Aglaothamum paucilamellata</i> Fauchald, 1972
<i>Bathylglycine mexicana</i> Fauchald, 1972	<i>Nephtys californiensis</i> Hartman, 1938 *
<i>Glycine armigera</i> Moore, 1911 *	<i>Nephtys punctata</i> Hartman, 1938
<i>Goniada brunnea</i> Treadwell, 1906	Family Nereididae
Family Lumbrineridae	<i>Nereis imajima</i> de León-González and Díaz-Castañeda, 1998
<i>Eranno lagunae</i> (Fauchald, 1970)	<i>Profundilycastis</i> sp. A
<i>Lumbrineris index</i> Moore, 1911	Family Onuphidae
<i>Lumbrineris latreilli</i> Audouin and Milne-Edwards, 1833	<i>Diopatra splendidissima</i> Kinberg, 1865
<i>Lumbrineris</i> sp. A	<i>Kinbergonuphis cedroensis</i> (Fauchald, 1968)
<i>Ninoe jessicae</i> Hernández-Alcántara, Pérez-Mendoza and Solís-Weiss, 2006	<i>Kinbergonuphis microcephala</i> Hartman, 1944 *
Family Magelonidae	<i>Kinbergonuphis proalopus</i> (Chamberlin, 1919)
<i>Magelona marianae</i> Hernández-Alcántara and Solís-Weiss, 2000 *	<i>Kinbergonuphis</i> sp. A
<i>Onuphis elegans</i> (Johnson, 1901) *	<i>Parapriospio pinnata</i> (Ehlers, 1901) *
<i>Onuphis geophiliformis</i> (Moore, 1903)	<i>Prionospio dubia</i> Day, 1961
<i>Onuphis iridescens</i> (Johnson, 1901)	<i>Prionospio ehlersi</i> Fauvel, 1928
<i>Onuphis similis</i> Fauchald, 1968	<i>Spiophanes anoculata</i> Hartman, 1960 *
<i>Onuphis vibex</i> (Fauchald, 1972)	<i>Spiophanes berkeleyorum</i> Pettibone, 1962
<i>Paradiopatra multibranchiata</i> Hernández-Alcántara, Mercado-Santiago and Solís-Weiss, 2017	<i>Spiophanes duplex</i> (Chamberlin, 1919) *
Family Orbinidae	<i>Spiophanes kroyeri</i> Grube, 1860
<i>Califia calida</i> Hartman, 1957	Family Syllidae
<i>Leitoscoloplos mexicanus</i> (Fauchald, 1972)	<i>Exogone</i> sp. A
<i>Leitoscoloplos</i> sp. A	<i>Syllis alternata</i> Moore, 1908
<i>Leodamas cirratus</i> (Ehlers, 1897) *	Family Terebellidae
<i>Orbinia</i> sp. A *	<i>Loimia medusa</i> (Savigny, 1822)
Family Paralacydoniidae	<i>Pista wui</i> Safronova, 1988
<i>Paralacydonia paradoxa</i> Fauvel, 1913	<i>Scionides</i> sp. A
Family Paraonidae	Family Traviidae
<i>Aricidea</i> (<i>Acmira</i>) <i>simplex</i> Day, 1963	<i>Travisa brevis</i> Moore, 1923
<i>Aricidea</i> (<i>Strelzovia</i>) <i>ramosa</i> Annekova, 1934	Family Trichobranchidae
<i>Aricidea</i> sp. A	<i>Terebellides horikoshii</i> Imajima and Williams, 1985
<i>Aricidea</i> sp. B	<i>Terebellides</i> sp. A
<i>Levinsenia oculata</i> (Hartman, 1957)	

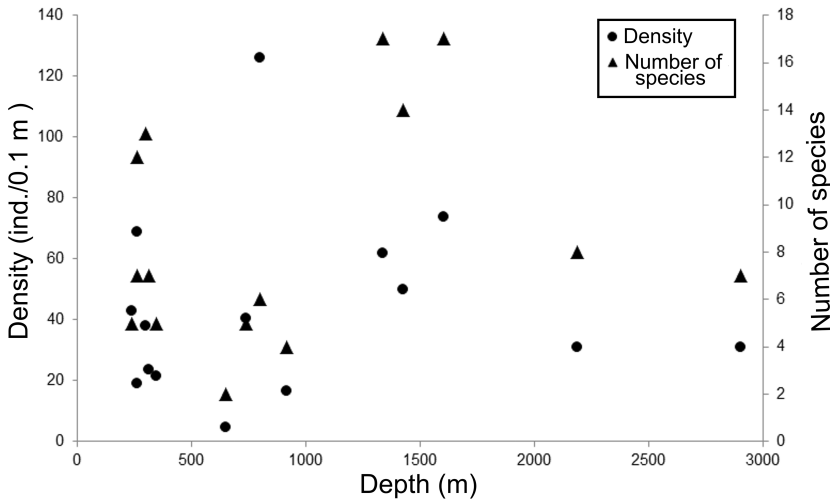


Figure 4. Bathymetric distribution of density (ind 0.1 m⁻²) and number of species per station.

below which there was a significant decrease down to 1300 m ($y = -0.007x + 25.12$, $R^2 = 0.81$, $P < 0.05$), from 17 (1335 m) to 7 (2900 m) species (Fig. 4).

The families Dorvilleidae, Glyceridae, Magelonidae, Traviidae, Paralacydoniidae, Phyllodocidae, Poecilochaetidae, and Sigalionidae (i.e., 30.8% of the families) were represented by one species each, while only 13 out of the 58 identified genera (i.e., 22%) included more than two species (Fig. 5). Accordingly, the species dataset was positively correlated with the family ($R^2 = 0.84$, $P < 0.05$) and genus ($R^2 = 0.94$, $P < 0.05$) datasets.

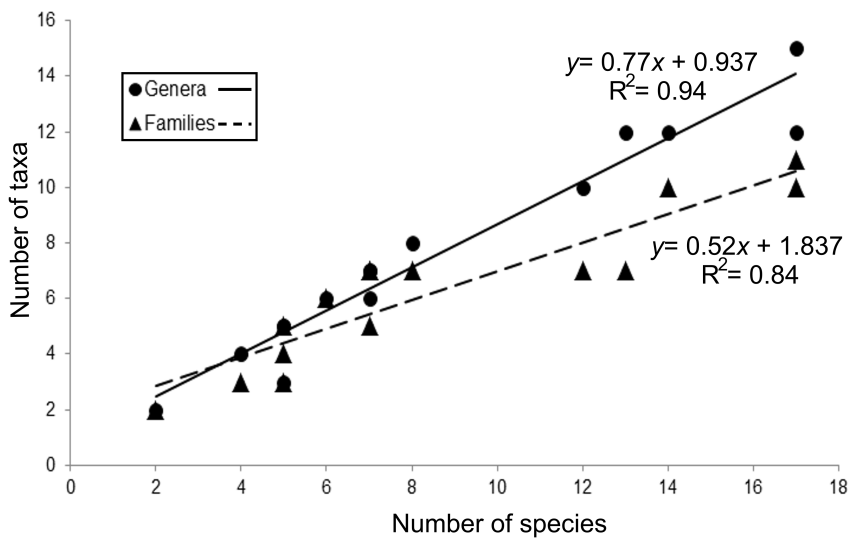


Figure 5. Relationships between number of species and number of genera and families of polychaetes.

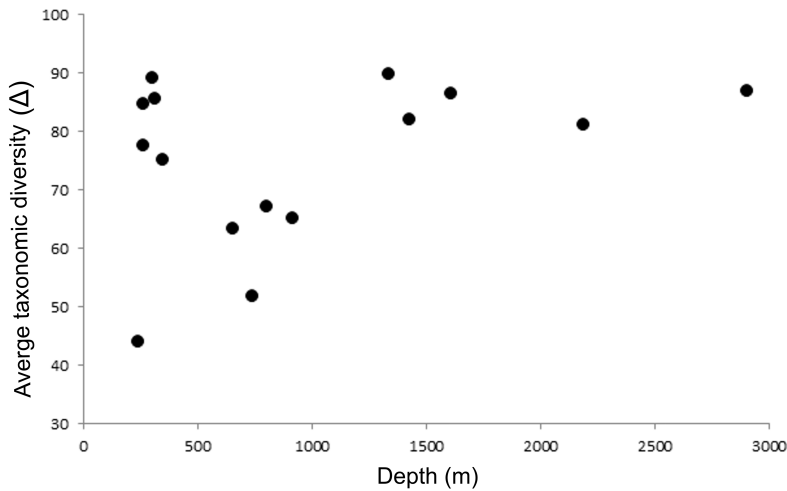


Figure 6. Bathymetric distribution of average taxonomic diversity (Δ).

The Δ bathymetric distribution was heterogeneous [mean (SD) = 75.32 (14.09)], being higher in the Deeper level [85.25 (3.61), range = 81.12–89.78] and decreasing with greater variability [76.02 (16.51)] in the Upper level. This was mainly due to the lowest Δ (44.03) at station 13B (inside the Bay of La Paz at 238.2 m), which differed from the other western stations (Δ = 75.11–89.06; Fig. 6). The Mid-depth level showed the lowest Δ [61.85 (6.89)], essentially because there were just 2–6 species per station. Δ was positively correlated with the number of species ($R^2 = 0.42$, $P < 0.05$), genera ($R^2 = 0.50$, $P < 0.05$), and families ($R^2 = 0.54$, $P < 0.05$; Fig. 7), but these regressions did not differ significantly from each other ($F_{(2,42)} = 1.38$, $P = 0.26$).

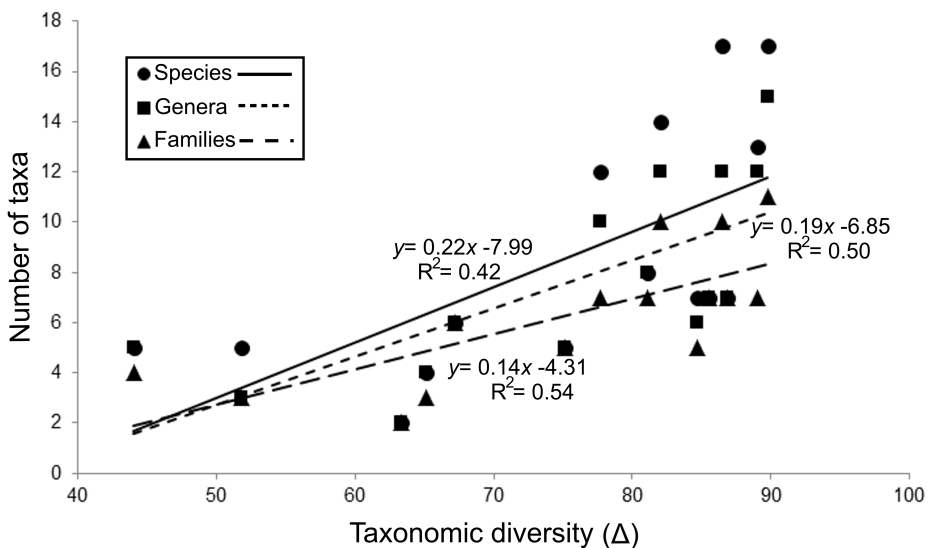


Figure 7. Relationships among taxonomic diversity (Δ) and number of polychaete species, genera, and families.

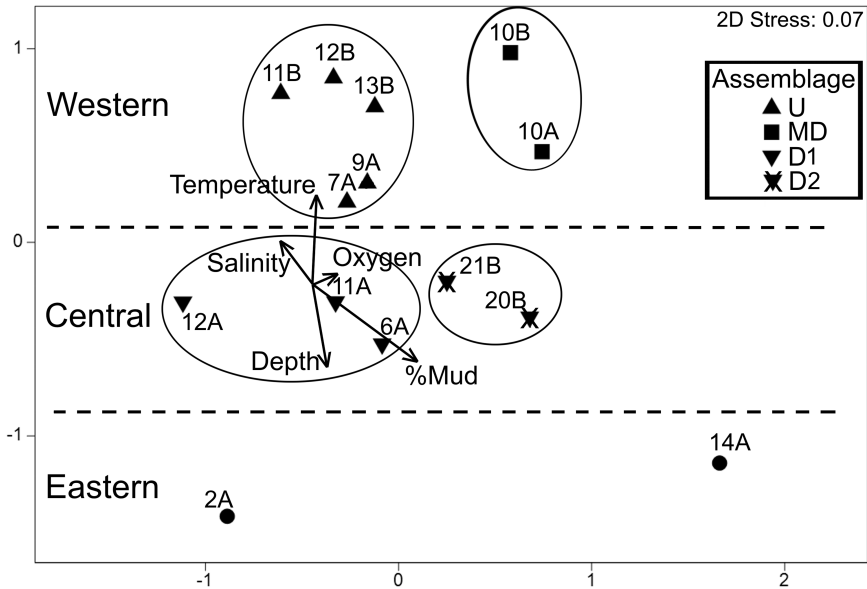


Figure 8. Nonmetric multidimensional scaling (nMDS) ordination plot of the sampling stations based on species composition and density. Ovals show the faunal assemblages linked to bathymetric levels (U = Upper; MD = Mid-depth; D1 and D2 = Deeper). Dotted lines separate gulf regions. Vectors show the influence of environmental variables on the spatial arrangement.

Four faunal assemblages were distinguished (Fig. 8) and correlated significantly with bathymetry ($R_{\text{ANOSIM}} = 0.43$, $P < 0.05$) and geographic location ($R_{\text{ANOSIM}} = 0.56$, $P < 0.05$). The deepest stations (>1300 m) from the central region of the gulf formed assemblages D1 and D2 (Fig. 8). D1 (stations 6A, 11A, 12A; 1300–1600 m) showed the highest density (mean = 61.9 ind 0.1 m^{-2}), species richness (mean = 16 species per station) and Δ (mean = 86.1). The most representative species were *Onuphis similis* (14%) and *Aricidea (Acmira) simplex* (12.6%). D2 (stations 20B, 21B; >2000 m) showed very low densities (mean = 30.9 ind 0.1 m^{-2}) and species richness (mean = 7 per station), but a high Δ (mean = 83.98); the only common species were *Aglaophamus paucilamellata* (50%) and *Sthenolepis spargens* (50%).

Western stations shallower than 1000 m formed the assemblages MD and U. MD stations (10A and 10B; 600–1000 m) showed a high density (mean = 83.34 ind 0.1 m^{-2}) but the lowest number of species (mean = 5 per station) and Δ (mean = 61.85); the most representative species were *Aricidea* sp. A (55.3%) and *Ninoe jessicae* (44.7%). U stations (7A, 9A, 11B, 12B, 13B; <350 m) showed the lowest density (mean = 35.24 ind 0.1 m^{-2}), intermediate species richness (mean = 7 per station), and low Δ (mean = 76.02), and the most representative species were *Prionospio elhersi* (33.8%), *Subadyte mexicana* (26.4%), and *Syllis alternata* (16.8%).

Stations 14A (300 m) and 2A (915 m) remained isolated in the nMDS because they harbored a completely distinct fauna lacking emblematic (or characteristic and shared) species and sharing only their position at the far eastern gulf. Station 14A showed 12 exclusive species out of 13 present, while that proportion was two of four at station 2A (see Table 3).

Prionospio ehlersi, *S. mexicana*, *S. alternata*, *N. jessicae*, *Aricidea* sp. A, and *Aglaophamus erectans* Hartman, 1950 were present only in the western gulf. *Ancistrosyllis groenlandica*, *S. spargens*, and *O. similis* were found only in the central gulf. *Lumbriclymene* sp., *Benthoscolex* sp. A, and *Califia calida* Hartman, 1957 were only present on the eastern margin. The overall assemblage structure was mainly correlated with mud content ($R^2 = 0.57$), depth ($R^2 = 0.32$), and temperature ($R^2 = -0.30$; Fig. 8). However, D1 and D2 assemblages were associated with high mud content and low temperature; those from U and MD were linked to low mud content and higher temperatures (Fig. 8).

The assemblage structure based on species was significantly correlated with that based on genera (Rho = 0.73, $P = 0.001$) and families (Rho = 0.64, $P = 0.001$). The main differences were chiefly related to faunal structure of stations 14A and 20B (Fig. 9A–C). When based on genera (Fig. 9B) and especially on families (Fig. 9C), unexpectedly both stations were related to other faunal groups. First, station 14A (located at 300 m in the far eastern gulf) was moved closer to those from assemblage D1 (1300–1600 m). This displacement was associated with its higher density (38.1 ind 0.1 m^{-2}) and number of species (13), but also because >92% of its species belonged to different genera and >53% to distinct families, similar faunal characteristics to those observed in D1 stations: >50 ind 0.1 m^{-2} , >14 species per station, and >70% of their species belonging to different genera and >58% to distinct families.

On the other hand, station 20B (2900 m) from the southernmost gulf (with 30.9 ind 0.1 m^{-2} and 7 species) was also moved closer to stations from assemblage U (<350 m), which had similar densities of 35.24 ind 0.1 m^{-2} and 7 species per station, on average. Nevertheless, station 20B and those comprising group U were mainly related because practically all their species belonged to different genera and families.

DISCUSSION

The physical-chemical complexity of marine ecosystems plays an important role in structuring the spatial distribution of their associated faunal communities (Tolimieri and Levin 2006, Anderson et al. 2013, Papiol et al. 2017, Cruz-Acevedo et al. 2018). Bathymetry-related factors (e.g., temperature, salinity, pressure) most often drive deepsea biological and environmental processes (Carney 2005). The deep Gulf of California shows a highly stable hydrological structure (i.e., water mass distribution) that does not differ from most deepsea water bodies worldwide. In fact, the Upper, Mid-depth, and Deeper slope levels reported here resemble those from the northern Atlantic (Haedrich and Merrett 1988), northeastern New Zealand (Zintzen et al. 2012), Mediterranean Sea (D'Onghia et al. 2004), and eastern Pacific (Tolimieri and Levin 2006, Anderson et al. 2013, Cruz-Acevedo et al. 2018).

Bathymetric variability in the Gulf of California mainly correlates with water mass distributions, which are expressed by differences in temperature, salinity, and oxygen concentrations (Torres-Orozco 1993, Lavín et al. 1997). Accordingly, all examined samples showed temperature and salinity matching those of the dominant water masses, while oxygen concentration was typically very low (0.13–0.85 ml L^{-1}) except in the deepest southern gulf end (around 2 ml L^{-1}). However, this was somewhat expected, since the east Pacific is the largest area in the world's oceans with severe hypoxia, roughly from southern Canada to central Chile, including most of the Gulf of California (Diaz and Rosenberg 1995, Lluch-Cota et al. 2007). Inside the gulf,

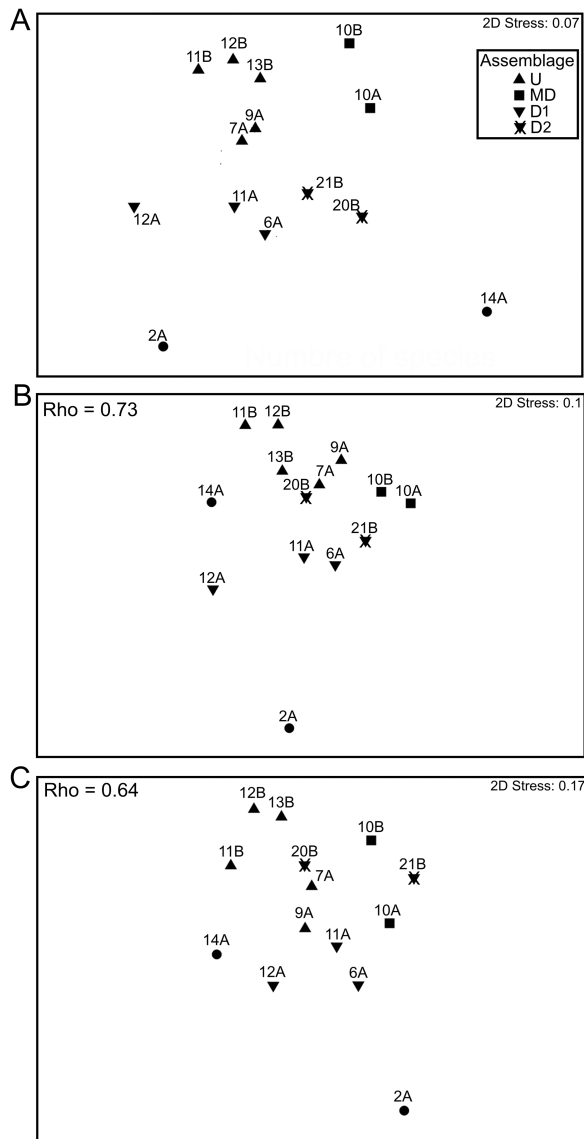


Figure 9. Nonmetric nMDS ordination diagram of polychaete assemblages based on (A) species, (B) genera, and (C) families. Spearman's rank coefficient (Rho) corresponds to correlations best matching the ordination generated by the species set.

oxygen concentrations lower than 0.5 ml L^{-1} are usually found between 74 and 1269 m depth, while a concentration of 0.2 ml L^{-1} has been reported between 89 and 2021 m (Hendrickx and Serrano 2010). Such low oxygen concentrations prevent the establishment and maintenance of species that cannot tolerate hypoxia but permit species that tolerate almost anoxic conditions. However, polychaetes appear to be better adapted than crustaceans, echinoderms, or even molluscs (Diaz and Rosenberg 1995, Lamont and Gage 2000, Hendrickx and Serrano 2010), with some spionids even able to permanently live in hypoxic environments (Levin et al. 2000).

Table 4. Number of polychaete families and species reported from American marine regions. SE = southeastern.

No. Expeditions	No. Stations	Depth range (m)	No. Species	No. Families	Marine region	Source
2	15	238–2,900	84	26	Southern Gulf of California	Present study
4	158	200–3,456	227	43	Western Mexico	Fauchald (1972)
---	47	600–3,000	142	36	Off Central Oregon	Fauchald and Hancock (1981)
2	14	745–3,353	82	31	Eastern Pacific	Levin et al. (1991)
4	46	732–2,250	73	33	SE Gulf of California	Méndez (2006)
4	46	732–2,110	84	32	SE Gulf of California	Méndez (2007)
4	66	730–2,110	106	34	SE Gulf of California	Méndez (2012)
4	20	360–2,309	35	21	SE Gulf of California	Méndez (2013)
1	13	200–3,760	65	21	Sigsbee Basin, Gulf of Mexico	Pérez-Mendoza et al. (2003)
3	51	200–3,700	532	---	Northern Gulf of Mexico	Carvalho et al. (2013)

Deepsea faunal bathymetric trends, including changes in species distributions and diversity, are mainly regulated by temperature, pressure, and food availability (Wei et al. 2010, 2012). However, precise causes are still poorly understood (Carney 2005, Rex and Etter 2010, Wei et al. 2020). In the gulf, the bathymetric distribution of water masses contributes to the observed differences in abundance and diversity, and favors the presence and distribution of distinctive polychaete assemblages.

The few studies on deepsea polychaete diversity, bathymetric zonation, and other depth-related trends in the Mexican Pacific (Solís-Weiss et al. 2014), together with the lack of sampling and taxonomic consistency, limit possible comparisons. The number of species and families from the southern Gulf of California resemble those from the eastern Pacific, the southeastern Gulf of California, and the Sigsbee Basin (Gulf of Mexico; Table 4). By contrast, they clearly differ from those off western Mexico, off Central Oregon, or the northern Gulf of Mexico, where the sampling stations were markedly more numerous (Table 4).

Most of the 193 species known from the deep Gulf of California (Solís-Weiss et al. 2014) also occur in the eastern Pacific. For instance, 35 of the 106 species recorded from the eastern margin of the gulf (Méndez 2006, 2007, 2012, 2013) had already been recorded in deeper adjacent areas off southern California by Hartman (1960) or off western Mexico by Fauchald (1972). Although the fauna in our samples also resembled that from the adjacent eastern Pacific, only seven species were coincident (Méndez 2006, 2007, 2012, 2013). This points out the singularity of the polychaete fauna from the deep Gulf of California, also highlighting its high diversity, which has now reached a total of 160 species.

Deepsea species diversity usually follows parabolic bathymetric distributions, with a maximum on the continental rise around 1500–2500 m, followed by a decrease towards the abyssal plain (Rex 1981, 1983, Carney 2005, Hernández-Alcántara et al. 2014). This agrees with the maximum around 1500 m found in the present study. This pattern has been associated with abiotic stability (Sanders 1969), biological disturbance and anthropic deposition (Román et al 2016), or predation and productivity-mediated competition (Rex 1976). Nevertheless, in most cases, how these processes give rise to a mid-depth maximum in diversity remains unsolved (Wei et al. 2020), and this is also unclear in the Gulf of California.

Density in deepsea communities usually tends to decrease with depth (Wei et al. 2010, 2020, Carvalho et al. 2013, Román et al. 2016), a trend not observed in this study. Primary productivity in the Gulf of California is 2–3 times higher than those

of water masses at similar Atlantic and Pacific latitudes due to phytoplankton blooms associated with nutrient-enrichment caused by upwelling (Álvarez-Borrego and Lara-Lara 1991). It is suggested that phytodetritus derived from these blooms (supplemented by small particulate macrophyte detritus, fecal pellets, and marine snow) could help explain the observed low bathymetric variability in polychaete density.

Bathymetric faunal zonation is often characterized by homogeneous areas parallel to isobaths, separated by transition areas with a gradual species turnover, with all (or some) species having constrained ranges of distribution (Rex 1981, Carney 2005, Wei et al. 2010) and responding to bathymetric environmental gradients (Wei et al. 2012). In the Gulf of California, the observed Mid-depth peak in species number and density of the D1 assemblage could be linked to the environmental stability offered by the low variations in salinity (about 34.5) and temperature (about 4 °C) of the PDW (Torres-Orozco 1993). A similar richness peak with a distinct taxonomic composition was previously reported in the eastern gulf between 1100 and 1600 m, followed by a marked decrease at depths greater than 1900 m (Méndez 2007).

Beyond 2000 m, where PDW also dominates, the number of species and density clearly decreased. The only common species were the nephtyid *A. paucilamellata* and the sigalionid *S. spargens*, both originally described from deep western Mexico (Fauchald 1972). In the relatively warm and saline Upper level, where StSsW prevails, the polychaetes were not abundant, but showed an intermediate richness and a composition entirely different from those in deeper zones. In the Mid-depth zone, density increased again, but the number of species drastically decreased, particularly between 600 and 1000 m. This trend had not been previously reported and merits further studies.

Density and faunal composition at each bathymetric zone of the gulf clearly differed, with the representative species belonging to different families. Moreover, their distribution patterns were directly related to bathymetric changes in Δ . Between depths of 1300 and 1600 m and above 2000 m, Δ was similar (about 85), with most species belonging to different genera and families, although the deepest sites recorded fewer species. In the Upper level, Δ slightly diminished (about 76), since each genus and family was represented by more species. Between 651 and 915 m, Δ clearly decreased (about 61) due to a striking reduction in species richness to only 2–6 species per station.

These diversity variations respond to the presence of distinct taxonomic pools along the bathymetric gradient, which in most cases correspond to families represented by a single genus and to genera represented by only one species. Accordingly, identifying polychaetes at levels higher than species could allow for the detection of faunal changes without significant loss of information, as postulated by the “taxonomic sufficiency” approach (Ellis 1985, Domínguez-Castanedo et al. 2007). This approach satisfactorily detected faunal changes mainly in shallow waters and on the continental shelf, particularly in disturbed environments. However, both our data and those from polluted or extreme environments share a relatively low number of species per family or genus which allows for an adequate representation based on taxonomic sufficiency as, for instance, in shallow water benthos along pollution gradients (Narayanaswamy et al. 2003, Domínguez-Castanedo et al. 2007). The overall lack of information led us to highlight the need for new studies to validate the use of higher taxa as surrogates in deep-sea communities, as well as to compare them with those from other environments.

The faunal assemblages and their spatial distribution in the deep gulf were comparable regardless of whether species, genera, or families were used, and the loss of information with the progressively higher taxa was relatively low. Thus, in these conditions the use of surrogates seems sufficient to characterize diversity patterns. However, one cannot discard masking some relevant information perceptible only when using species, as occurred between 150 and 1000 m in the northeastern Atlantic (Narayanaswamy et al. 2003). Therefore, the appropriateness of applying a taxonomic sufficiency approach depends on the specific questions to be answered as well as the context. Moreover, one should not forget that using satisfactorily accurate surrogates may also contribute to reduced work time and, thus, costs.

Species-level identifications have the intrinsic interest of increasing knowledge on biodiversity. However bathymetric variations in faunal assemblages and diversity patterns could be recognized using surrogates with similar results as those revealed by species. Therefore, when time and financing constraints may interfere with project aims, as in a monitoring study and particularly in the deepsea, using surrogates may be adequate. Although the final decision may depend on project aims and priorities, the importance of increasing taxonomic knowledge of deepsea diversity must always be taken into consideration, particularly for sediment dwelling species which are still poorly known throughout the world's oceans.

CONCLUSIONS

The deepsea polychaete fauna of the southern Gulf of California included 160 species, of which 84 species were identified here from 58 genera and 26 families.

The faunal assemblages were directly related to bathymetry and the associated water masses, and identified according to the most characteristic species: <350 m with StSsW (*P. elhersi*–*S. mexicana*–*S. alternata* assemblage) and 600–1000 m with PIW (*Aricidea* sp. A–*N. jessicae* assemblage) in the western gulf; 1300–1600 m with PDW (*O. similis*–*A. (A.) simplex* assemblage) and >1200 m with PDW (*A. paucilamellata*–*S. spargens* assemblage) in the middle gulf. Stations 14A and 2A—sharing only their position at the far eastern gulf—remained isolated from any other assemblage.

The highest Δ and species number at 1300–1600 m could be explained by the environmental stability offered by PDW that exhibits low variations in salinity (about 34.5) and temperature (about 4 °C).

Most genera and families were monotypic, allowing their use as surrogates to assess the faunal assemblage structure with similar results to those obtained by using species. Thus, at least in this study area and depths, surrogates may be used to shorten identification time (and, thus, costs) in future monitoring projects. However, more studies are needed to further support the regular use of surrogates.

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