Research Article

Species composition and biogeographical affinities of polychaetes (Annelida) from the southern Mexican Pacific shelf

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Abstract

Polychaetes from tropical ecosystems of the eastern Pacific have been poorly studied; thus, the aim of this study was to analyse their taxonomic composition in the southern Mexican Pacific shelf and to examine their biogeographic affinities. A total of 3741 specimens from 82 species, 52 genera, and 27 families were identified from 38 stations at 42–109 m depth. The Sedentaria group was more diverse (40 species, 48.8%) and abundant (1753 ind., 46.9%) compared to the Errantia (36 species, 43.9%; 346 ind., 9.2%) and the Basal Annelida groups (6 species, 7.3%; 1642 ind., 43.9%). The families Onuphidae (14 spp.), Spionidae (8 spp.), and Paraonidae (8 spp.) were the most diverse. The Amphinomidae and Spionidae accounted for 72.6% of the fauna; the remarkably high abundance of both families together is unusual in the tropical eastern Pacific. The polychaete species had high biogeographic affinities with the Mexican tropical Pacific ecoregion (45.1%), which has tropical conditions, and the Cortezian (29.3%), which has warm-temperate characteristics. Twelve amphiamerican species and ten with worldwide distribution were found. The tropical eastern Pacific is one of the world regions with the lowest number of polychaete records, thus underlining the importance of the taxonomic and biogeographic information provided here. The sampling effort should increase, since the non-parametric estimators indicated that 116–138 species were expected, instead of the 82 species actually found.

Introduction

The continental shelves of oceans cover about 7.5% of the surface of the world marine realm, playing an important role in coastal countries' economies, as sources of food and non-living resources (Hall, 2002). Their regional and local environmental variability leads to high habitat heterogeneity with considerable biodiversity and complex biotic interactions (Spalding *et al.*, 2007; Dauvin *et al.*, 2013; Martins *et al.*, 2013; Hernández-Alcántara *et al.*, 2014). However, their macrofaunal communities have been so far poorly studied in tropical regions compared to temperate zones. This is the case for polychaetes, which in most tropical regions, such as the Mexican eastern Pacific, remain practically unknown, so that our understanding of their biodiversity is limited due to insufficient spatial and bathymetric samplings.

Polychaetes include nearly 11,500 accepted nominal species (Pamungkas *et al.*, 2019), and are often the most abundant and diverse invertebrate group in macrobenthic communities worldwide in soft bottoms, both in terms of number of individuals and species (Grémare *et al.*, 1998; Hutchings, 1998; Brooks *et al.*, 2006). Their highly varied morphology, motility types, feeding guilds, and reproduction types make them ecologically important in the structure and functioning of benthic ecosystems (Mackie and Oliver, 1996; Jumars *et al.*, 2015). Currently, several polychaete databases are available worldwide in the Global Biodiversity Information Facility (GBIF) and in other local datasets (Pamungkas *et al.*, 2021). This has helped in the analysis of their biogeographical affinities in some marine regions such as the western Mediterranean (Bakalem *et al.*, 2020), Indonesia (Pamungkas, 2020), the Indian Ocean (Guillet, 1991), Antarctica (Gagaev *et al.*, 2022), or the Austral zones (Glasby and Alvarez, 1999). They have also been useful for the study of taxon-limited geographic patterns, such as that of Glasby (2005), who examined six families and ten clades of polychaetes in 24 global marine areas for endemism, or that of Garraffoni *et al.* (2006), who studied the distribution of Terebellidae from worldwide coastal and shelf zones. However, at a global scale, the only existing study was conducted by Pamungkas *et al.* (2021), based on datasets obtained from online biodiversity portals. They found that the north Atlantic (including the eastern and western Mediterranean), Australia, and Indonesia were the most species-rich biogeographic regions. Conversely, the tropical eastern Pacific was one of the regions with the lowest species records. That does not necessarily mean that the latter is poorer in diversity, but that the records are significantly less abundant.

In the southern Mexican Pacific, only 436 species have been recorded (Bastida-Zavala and Guevara-Cruz, 2012) in taxonomic publications and faunal inventories. Ecological issues in this group have only been analysed by González-Ortiz (1994), Rodríguez-Valencia (2004), Hernández-Alcántara *et al.* (1994), and González-Ortiz *et al.* (1997); in the latter two studies, however, only the Spionidae and Onuphidae families were studied. Solís-Weiss *et al.* (2000) have been, so far, the only ones to examine the biogeographic affinities of polychaetes collected in this region, particularly those from the Gulf of Tehuantepec shelf. Therefore, the aim of the present study was to analyse the taxonomic composition of polychaetes along the southern Mexican Pacific shelf and to compare their biogeographic affinities with other regions of the eastern Pacific. The abundance and species richness variations among the Errantia, Sedentaria, and Basal Annelida taxonomic groups were examined at the levels of order, family, and genera and the expected number of species for the region were estimated based on our data. The information of the present study will help to establish a much-needed baseline for future studies on the biodiversity and biogeography of polychaetes in this region, which are essential for future strategies of conservation and management of its natural resources, as well as for comparative studies with other regions of the world.

Materials and methods

Study area

The study area is located in the central region of the Mexican Pacific, between El Calvario and El Aguacoscla rivers (16°45′–17°14′N; 99°49′–101°2′W) (Figure 1). It is the most important seismic region of the Mexican Pacific, in the convergence zone of the continental North America and the oceanic Cocos plates (Yamamoto *et al.*, 2013). Its high tectonic activity, together with its subduction processes, produced a narrow continental shelf around 15 km wide on average (Karig *et al.*, 1978). Many rivers and coastal lagoons discharge in the southern Mexican Pacific and constitute its main sources of sediments. A highly variable topography includes soft bottoms, rocky shores, and two submarine canyons (Márquez-García and Morales, 1984; Marín-Guzmán, 2011) (Figure 1).

The marine circulation in the tropical eastern Pacific connects the Equatorial Countercurrent with the northern Equatorial Current moving from Panama towards north along the continental coasts of Central America and Mexico, where it is known as the Mexican Current. The superficial water masses converging there are the Tropical Superficial Water in the first 20–50 m depth, with temperatures higher than 25°C and salinities lower than 34 psu, and the Tropical Subsuperficial Water with an intense thermocline at 50–150 m depth and a salinity minimum of 34.55 psu (Badan, 1997). The eastern Pacific warm pool is located in front of Central America and southern Mexico, with high temperatures (>28°C), small annual thermal oscillations (<2°C), and a stable shallow thermocline (20–40 m) (Fiedler and Talley, 2006).

Sampling methods and taxonomic identification

As part of the 'Sedimento 4' oceanographic expedition, on board the R/V 'El Puma' of the Universidad Nacional Autónoma de México (UNAM), the biological material was collected in February 2008 at 38 stations in the continental shelf of the southern Mexican Pacific (Figure 1). The sediment was sampled using a Smith-McIntyre grab (0.1 m^2) between 42 and 109 m depth. Data of the geographic positions and depth of the sampling stations were harvested by the Caribbean OBIS Node and are available online through the GBIF portal at https://doi.org/10.15468/ha2uhn (Hernandez-Alcántara *et al.*, 2022). A 0.5 mm mesh was used to separate the macrofauna, which was fixed with a 10% formalin/seawater solution. Later, the fixed material was washed to eliminate the formalin, and the specimens were separated, the polychaetes were identified to the species level, and preserved in 70% ethanol. After quantification, they were catalogued and deposited in the Colección Nacional de Anélidos Poliquetos at the Instituto de Ciencias del Mar y Limnología, UNAM (CNAP-ICML, UNAM; DFE.IN.061.0598). The taxonomic identifications were made using specialized literature updated with the most recent systematic revisions of genera and species (see de León-González *et al.*, 2021). The validity of the polychaete species was verified chiefly with the World Polychaeta Database (Read and Fauchald, 2021), accessed through the World Register of Marine Species – WoRMS Database.

Data analyses

The information on abundance and distribution of the identified species and their related geographic records were organized in a database following the Darwin Core Archive format (Wieczorek *et al.*, 2012), which was harvested by the Biogeographic Information System (OBIS) Caribbean Node and is available through the GBIF portal at https://doi.org/10.15468/ha2uhn (Hernandez-Alcántara *et al.*, 2022). Initially, the polychaetes living in the southern Mexican Pacific were analysed at the level of order, family, and genera in the frame of the taxonomic groups now recognized: Errantia, Sedentaria, and Basal Annelida groups. The classification at higher taxonomic ranks, such as orders, was based on the phylogenomic studies of Weigert *et al.* (2014), Struck *et al.* (2011), and Struck *et al.* (2015), summarized by Weigert and Bleidorn (2016), and later also by Struck (2019). The spatial variations in the abundance and number of species of the Errantia, Sedentaria, and Basal Annelida groups along the study area are presented in maps, which include pie charts for each sampling station.

The taxonomic affinities between regions, transects, and bathymetry were assessed with the Sorensen coefficient: $S = 2a/(b + c)$, where a = number of species common to both samples of data; b = number of species unique in the first sample; c = number of species unique in the second sample; 0 indicates that the two samples of data have no species in common and 1 indicates that the two samples are identical in taxonomic composition (Sorensen, 1948). To estimate the completeness of the species inventory, we evaluated the expected species richness with sample based on the non-parametric estimators of richness Chao 2, Jackknife 1, and Jackknife 2, with 1000 randomizations without replacement (95% confidence intervals), which were computed with software Estimates v.9.1.0 (Colwell, 2013). These methods have demonstrated to be appropriate estimators of the number of species, including the marine taxa (Walther and Moore, 2005).

The geographic distribution of each species was reviewed with specialized bibliography, complemented and updated with supplementary references for the identified species (de León-González *et al.*, 2021; Read and Fauchald, 2021). The biogeographic affinities were determined following the bioregionalization proposed by Spalding *et al.* (2007), based on the benthic shelf and pelagic fauna. They largely match the biogeographic regions suggested by Pamungkas *et al.* (2021), which, as already mentioned, is the only study analysing the world distribution patterns of polychaetes. The faunal affinities among the ecoregions were assessed by means of a cluster analysis with the unweighted pair group method with arithmetic mean sorting strategy based on the presence/absence of Γ^+ dissimilarity
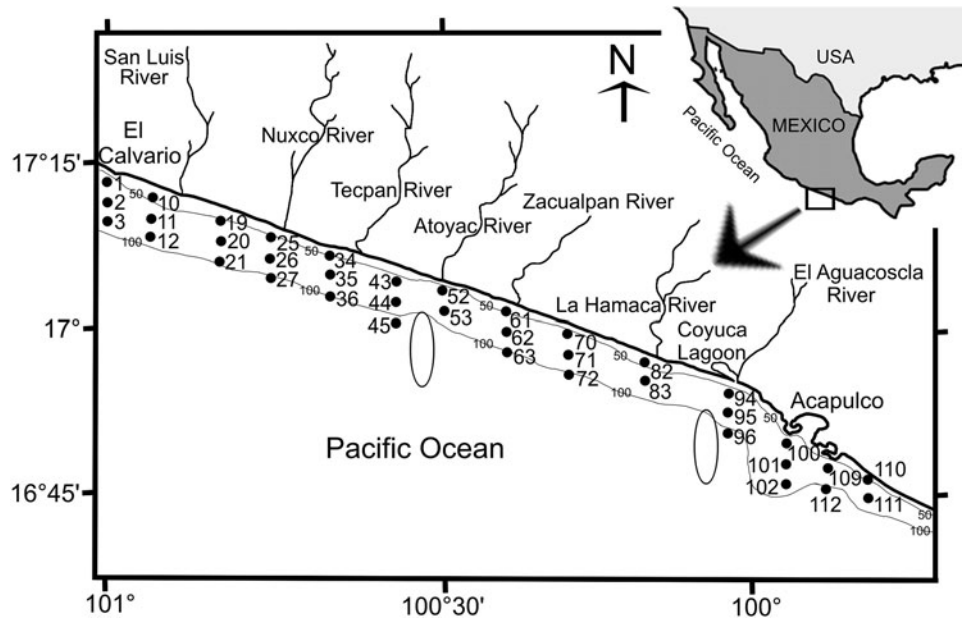
Figure 1. Study area and sampling stations in the continental shelf of the southern Mexican Pacific with isobaths in m; ellipses show the location of submarine canyons (modified from Marín-Guzmán, 2011).

coefficient, which is an extension of the Bray–Curtis dissimilarity on the presence/absence data. The Γ^+ coefficient is an adaptation to the concept of taxonomic distinctness, defined as the mean path length through a taxonomic tree between every pair of species in a sample (Clarke and Warwick, 1998). This analysis was carried out with the Plymouth Routines in Multivariate Ecological Research (PRIMER v7) software (Clarke and Gorley, 2015).

Results

A total of 3741 polychaetes from 82 species, 52 genera, 27 families, and 12 orders were identified. From these, 25 taxa (30.5% of fauna) possibly belong to new species and therefore are designated as undescribed species (*sp*'s). The recorded species belong to the large sets Errantia and Sedentaria, and the Basal Annelida group (Tables 1 and 2). The eight orders found in the group Sedentaria were more numerous compared to the two orders of Errantia, but their total number of families and species was similar: 13 families and 40 species in the Sedentaria, and 12 families and 36 species in the Errantia. The Sedentaria (1753 ind.) and the Basal Annelida groups (1642 ind.) were the most abundant groups, with 90.8% of the total fauna, whereas in the Errantia, only 346 individuals were recorded (Tables 1 and 2).

In the Errantia, the orders Eunicida (24 spp.) and Phyllodocida (9 spp.) were quite diverse, but only represented 4.8 and 4.4% of

Table 1. Number and percentage of orders, families, genera, and species, and abundance of the Basal Annelida, Errantia and Sedentaria polychaete groups found in the southern Mexican Pacific

Group	Order	No. of families	No. of genera	No. of species	Abundance
Basal Annelida	Amphinomida	1 (3.7%)	1 (1.9%)	1 (1.2%)	1359 (36.3%)
	Magelonida	1 (3.7%)	1 (1.9%)	5 (6.1%)	283 (7.6%)
Total		**2 (7.4%)**	**2 (3.8%)**	**6 (7.3%)**	**1642 (43.9%)**
Errantia	Eunicida	6 (22.2%)	11 (21.2%)	24 (29.3%)	180 (4.8%)
	Phyllodocida	6 (22.2%)	9 (17.3%)	12 (14.6%)	166 (4.4%)
Total		**12 (44.4%)**	**20 (38.5%)**	**36 (43.9%)**	**346 (9.2%)**
Sedentaria	Cirratulida	3 (11.1%)	8 (15.4%)	12 (14.6%)	190 (5.1%)
	Echiurida	1 (3.7%)	3 (5.8%)	3 (3.7%)	14 (0.4%)
	Opheliida	1 (3.7%)	1 (1.9%)	1 (1.2%)	1 (0.03%)
	Orbiniida	1 (3.7%)	2 (3.8%)	5 (6.1%)	26 (0.7%)
	Sabellida	1 (3.7%)	5 (9.6%)	5 (6.1%)	133 (3.6%)
	Spionida	2 (7.4%)	6 (11.5%)	9 (11.0%)	1361 (36.4%)
	Sternaspida	1 (3.7%)	1 (1.9%)	1 (1.2%)	2 (0.05%)
	Terebellida	3 (11.1%)	4 (7.7%)	4 (4.9%)	26 (0.7%)
Total		**13 (48.1%)**	**30 (57.7%)**	**40 (48.8%)**	**1753 (46.9%)**

Percentages are the proportion of the total value of the same taxonomic level.

Table 2. Abundance (*A*) and frequency (*F* (%)) of polychaete species in the southern Mexican Pacific

Group/Order	Family/Species	A	F	Group/Order	Family/Species	A	F
Basal Annelida				**Sedentaria**			
Amphinomida	**Amphinomidae**			Cirratulida	**Cirratulidae**		
	L. kristiani	1359	76.3		*Aphelochaeta multifilis*	4	7.9
Magelonida	**Magelonidae**				*Chaetozone corona*	1	2.6
	Magelona californica	1	2.6		*Kirkegaardia tesselata*	1	2.6
	Magelona marianae	239	39.5		**Cossuridae**		
	M. pacifica	29	10.5		*Cossura brunnea*	28	34.2
	Magelona spinifera	3	5.3		**Paraonidae**		
	Magelona tehuanensis	11	13.2		*Aricidea (Acmira) simplex*	5	7.9
Errantia					*Aricidea (Aricidea)* sp.	4	5.3
Eunicida	**Dorvilleidae**				*Aricidea (Acmira) lopezi*	48	21.1
	Genus A	20	15.8		*Aricidea (Aedicira)* sp.	7	13.2
	Lumbrineridae				*Aricidea (Aedicira)* sp. 1	7	13.2
	Cenogenus eliae	1	2.6		*Cirrophorus branchiatus*	5	7.9
	Ninoe foliosa	15	5.3		*Levinsenia gracilis*	75	39.5
	Scoletoma erecta	1	2.6		*Paradoneis* sp.	5	7.9
	Scoletoma monroi	1	2.6	Echiurida	**Capitellidae**		
	Scoletoma zonata	11	15.8		*Decamastus* sp.	1	2.6
	Oenonidae				*Mediomastus californiensis*	5	2.6
	Arabella iricolor	1	2.6		*Notomastus hemipodus*	8	13.2
	Driloneris longa	1	2.6	Opheliida	**Travisiidae**		
	Onuphidae				*Travisia brevis*	1	2.6
	Diopatra neotridens	11	5.3	Orbiniida	**Orbiniidae**		
	Diopatra obliqua	12	23.7		*Leitoscoloplos multipapillatus*	1	2.6
	Diopatra rhizophorae	2	2.6		*Leitoscoloplos panamensis*	1	2.6
	Diopatra splendidissima	1	2.6		*Scoloplos* sp. 1	9	7.9
	Diopatra tridentata	8	10.5		*Scoloplos* sp. 2	7	7.9
	Diopatra sp. 1	11	5.3		*Scoloplos* sp. 3	8	7.9
	Diopatra sp. 2	3	5.3	Sabellida	**Sabellidae**		
	Diopatra sp. 3	7	2.6		*A. modestum*	1	2.6
	Kinbergonuphis cedroensis	42	23.7		*Chone* sp.	109	26.3
	Kinbergonuphis microcephala	2	2.6		*Euchone incolor*	19	2.6
	Kinbergonuphis cf. pulchra	20	10.5		*Panousea* sp.	3	2.6
	Kinbergonuphis vermillionensis	5	10.5		*Parasabella* sp.	1	2.6
	Kinbergonuphis vexillaria	1	2.6	Spionida	**Spionidae**		
	Mooreonuphis sp. 1	1	2.6		*Malacoceros indicus*	1	2.6
Phyllodocida	**Glyceridae**				*Malacoceros* sp. 1	1	2.6
	Glycera branchiopoda	2	2.6		*Malacoceros* sp. 2	3	2.6
	Glycera prosobranchia	11	7.9		*P. pinnata*	1338	71.1
	Goniadidae				*Prionospio ehlersi*	2	2.6
	Goniada acicula	1	2.6		*Prionospio lighti*	4	5.3
	Nephtyidae				*Scolelepis cf. squamata*	7	2.6
	Aglaophamus verrilli	44	23.7		*Spiophanes kroeyeri*	1	2.6
	Nereididae				**Longosomatidae**		
	Neanthes sp.	4	5.3		*Heterospio* sp.	4	5.3
	Pilargidae			Sternaspida	**Sternaspidae**		

(*Continued*)

Table 2. (Continued.)

Group/Order	Family/Species	A	F	Group/Order	Family/Species	A	F
	Ancistrosyllis sp.	1	2.6		*S. maior*	2	5.3
	Hermundura bennei	4	10.5	Terebellida	**Ampharetidae**		
	Hermundura riojai	68	57.9		*Amphicteis cf. glabra*	1	2.6
	Hermundura salazarvallejoi	6	10.5		**Terebellidae**		
	Sigambra tentaculata	21	26.3		Genus B	22	10.5
	Polynoidae				*Pista* sp.	1	2.6
	Malmgreniella macginitiei	1	2.6		**Trichobranchidae**		
	Sigalionidae				*Terebellides californica*	2	5.3
	Sthenelanella uniformis	2	5.3				
	Syllidae						
	Paraehlersia sp.	1	2.6				
	Syllis sp.	3	7.9				

the total abundance, respectively. In the Sedentaria, the orders Cirratulida (12 species) and Spionida (9 species) were also diverse but, while in the former only 190 individuals were present, the Spionida were very abundant with 1361 organisms. The Basal Annelida group was represented by the orders Amphinomida and Magelonida, with only one family each, but while the Amphinomidae included 1359 individuals, in the Magelonidae only 283 organisms were present (Table 2). The other orders comprised only one family, Opheliida and Sternaspida (Sedentaria), so they were hardly represented in the study area, with one species each and one and two individuals, respectively.

The most diverse families were Onuphidae (14 species), and Spionidae and Paraonidae (8 species each). The spionids were also very abundant (1357 ind.), whereas the onuphids (126 ind.) and paraonids (156 ind.) had significantly fewer individuals. The Amphinomidae, the most abundant family (1359 ind.), together with the Spionidae represented 72.6% of the total fauna; the following abundant family, Magelonidae, had 283 individuals (7.6%). Conversely, 11 families, 40.7% of fauna, were only

represented by one–two species and less than five individuals each (Figure 2).

In the eastern zone, the fauna was less abundant (mean = 7.6 ind./sta.), while the western (mean = 44.2 ind./sta.) and central (mean = 37.5 ind./sta.) zones had the highest number of individuals. In the western zone, the highest abundance was found in the Basal Annelida (mean = 62.5 ind./sta.) and Sedentaria groups (mean = 60.61 ind./sta.), while in the central zone they were also the most abundant but with fewer numbers: mean = 57.4 ind./sta. in Sedentaria and mean = 46.1 ind./sta. in the Basal Annelida groups. In general, the Errantia were less abundant along the whole study area (mean = 9.1 ind./sta.; SD = 11.3) (Figure 3).

On average, 8.5 species per station were collected, but in several stations along the study area, more than 12 spp./sta. were found (Figure 4). The Sedentaria were more diverse in the central zone (mean = 4.3 spp./sta.); in the western and eastern zones, a similar number of species was recorded: 3.6 and 3.4 spp./sta., respectively. The highest number of species in the Errantia was mainly recorded in the western (mean = 3.5 ind./sta.) and eastern (mean = 3.3 ind./sta.) zones. The Basal Annelida group had the
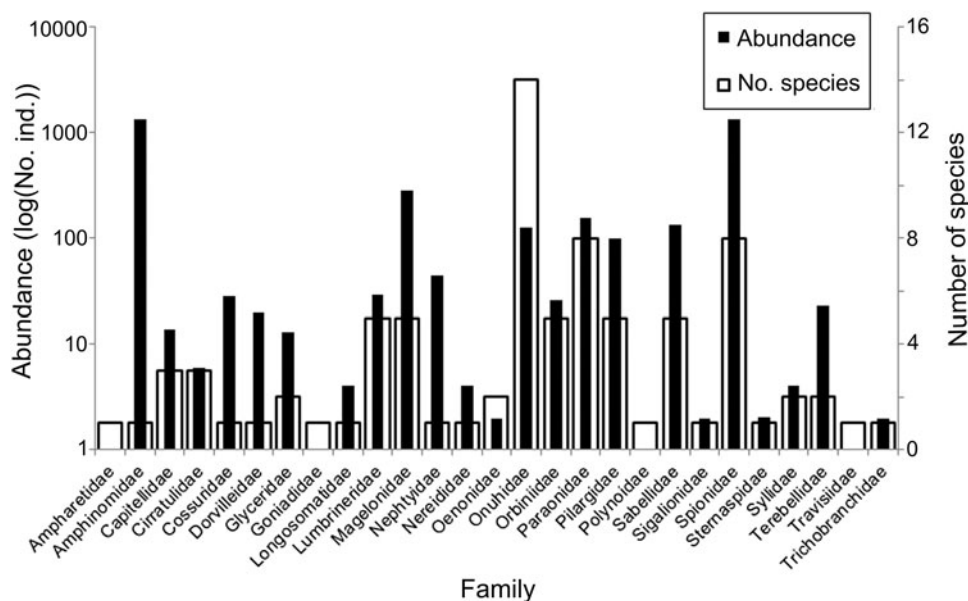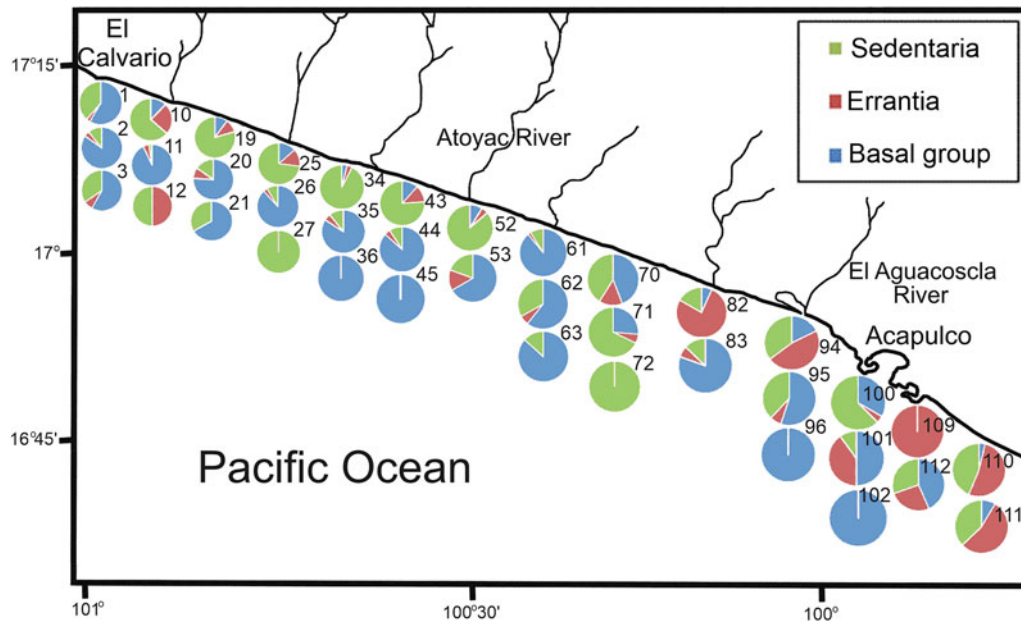

Figure 2. Number of individuals and species of polychaetes by family in the southern Mexican Pacific shelf.

Figure 3. Spatial variation in abundance (%) of Sedentaria, Errantia, and Basal Annelida groups by sampling station.

lowest species richness in all stations (mean = 1.5 spp./sta.; SD = 0.8), but was better represented in the central and eastern zones (mean = 1.7 and 1.6 ind./sta., respectively) (Figure 4).

The western and central zones shared the largest number of common species ($S = 0.62$), whereas the eastern zone had the lowest number of shared species, or taxonomic affinities, with the other zones ($S = 0.47$ with the central zone and $S = 0.48$ with the western one). Bathymetrically, faunal affinities decreased with depth. The highest number of common species was found between the inner (42–66 m) and middle (72–90 m) shelves ($S = 0.45$), decreasing between the middle and outer shelves (94–109 m) ($S = 0.33$); very few species were shared between the inner and outer shelves ($S = 0.29$). Among the transects, the taxonomic affinities of those located in the western zone gradually decreased towards the western Pacific, from $S = 0.65$ to 0.29 (Figure 5). On the contrary, in transects of the central zone, the

common species diminished eastwards, achieving the lowest affinity ($S = 0.23$) precisely in the boundary with the eastern zone. Although the shared species slightly increased among the transects of the eastern zone, no spatial trends were observed.

The non-parametric estimators of species richness showed an increase in the number of species with the number of sampling stations, indicating that the representativity of the species richness in the southern Mexican Pacific shelf is far from the asymptote. Those estimators indicated that between 116 and 138 species should be expected instead of the 82 actually recorded in the present study (Figure 6). That is, a completeness of 62.1% (Chao 2), 70.7% (Jackknife 1), and 59.4% (Jackknife 2) was estimated, showing that the less-frequent polychaete species, either unique or duplicate, dominated the fauna: 43.9 and 14.6% of the species were found only in one or two stations, respectively. The families with the higher species richness, Onuphidae, Spionidae, and
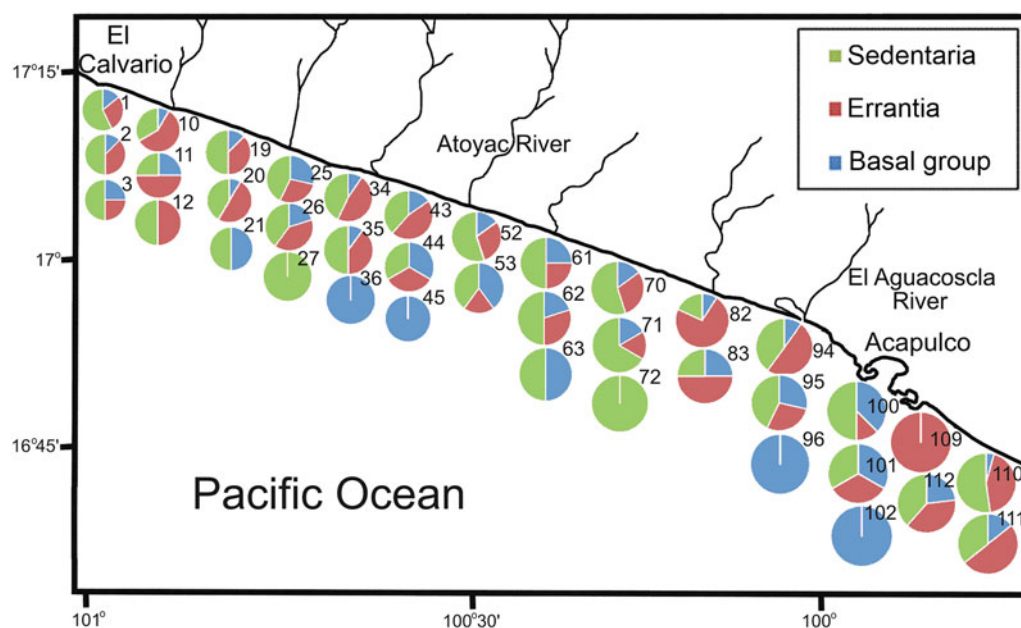
Figure 4. Spatial variation in percentage of species (%) of Sedentaria, Errantia, and Basal Annelida groups by sampling station.
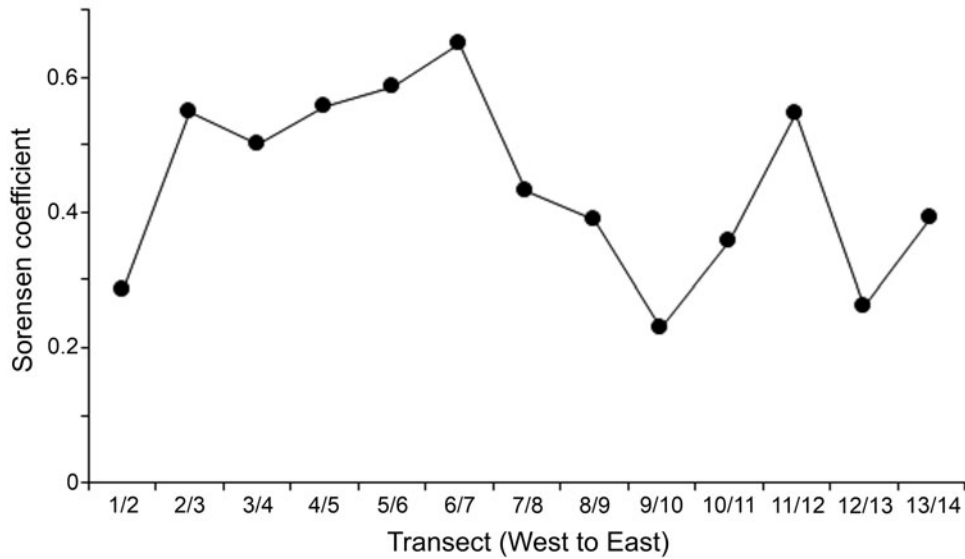
Figure 5. Spatial variation in the Sorensen coefficient values along the sampled transects, ordered from west to east.

Sabellidae, had the largest number of unique and duplicate species: nine, six, and four species, respectively, which contributed to 33.3% of the total rarity. Only in six families there were no unique or duplicate species.

The biogeographic affinities showed that the identified species had also previously been recorded in four biogeographic realms, but more often in the tropical eastern Pacific realm, and particularly in its Mexican tropical Pacific ecoregion. There, 37 of the collected species (45.1%) had already been recorded, and eight others had also been previously found in the southern adjacent ecoregions (Table 3). Twelve species (14.6%) were reported from both coasts of America and ten species (12.2%) had a wide distribution. In addition, two species, *Acromegalomma modestum* and *Paraprionospio pinnata*, had also been reported from the warm temperate southeastern Pacific province, in its Peru and central Chile ecoregions, respectively.

This fauna also presented important biogeographic affinities with the warm temperate northeast Pacific province: 24 species (29.3%) from the Cortezian ecoregion, 11 species (13.4%) from the southern California Bight ecoregion, and one species (1.2%) from the Magdalena transition ecoregion. Eight species widely distributed in the eastern Pacific, from the cold temperate northeast Pacific province to southern California or the Gulf of California, also occurred in the study area.

The affinities among ecoregions, based on the taxonomic relatedness of the identified species within the geographic units, gave rise to the integration of two large clusters (Dissim = 89.9) (Figure 7): group A, represented by ecoregions with the highest number of species, including the study area; and group B with ecoregions having only one or two species, revealing the low affinity of the collected fauna with that ecoregion's group. The Panama Bight ecoregion was noticeably separated from the other
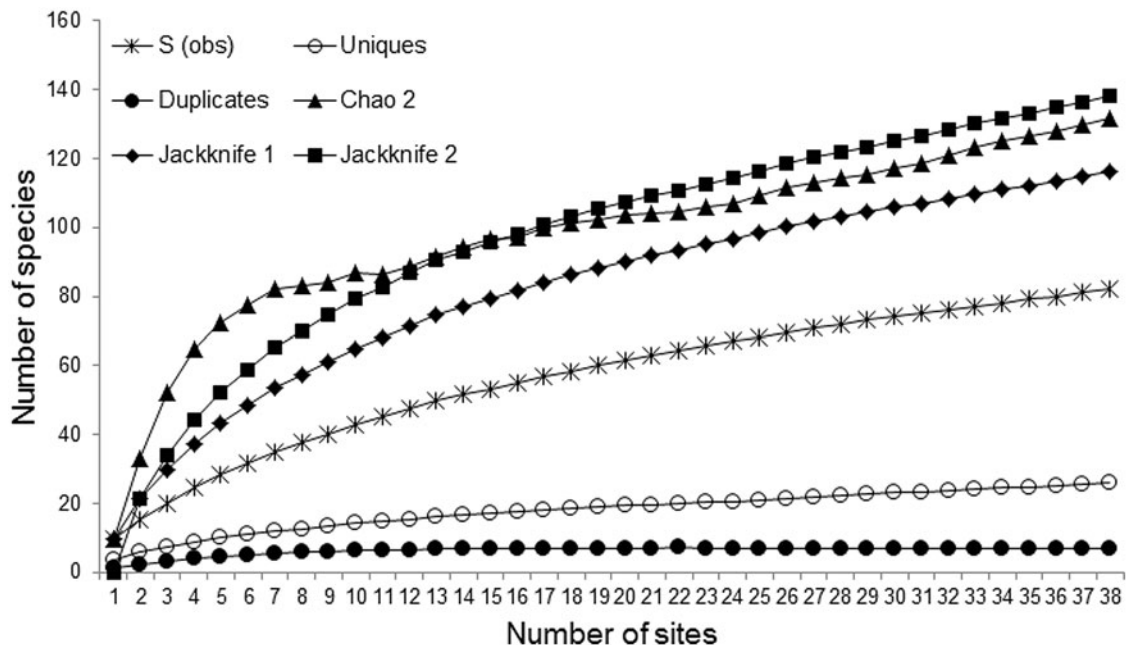

Figure 6. Observed (*S*) and expected polychaete number of species based on sample rarefaction curves, with non-parametric indices, unique and duplicate species in the southern Mexican Pacific shelf.

Table 3. Biogeographic affinities of the polychaete species from the southern Mexican Pacific, according to the bio-regionalization proposed by Spalding *et al.* (2007)

Biogeographic region	Number of species
Temperate northern Pacific realm (TeNP)	32 (39.0%)
Cold temperate northeast Pacific province	8 (9.8%)
Gulf of Alaska ecoregion (Ala)	2 (2.4%)
Oregon, Washington, Vancouver coast and shelf ecoregion (Ore)	7 (8.5%)
Warm temperate northeast Pacific province	32 (39.0%)
Southern California Bight ecoregion (SCal)	11 (13.4%)
Magdalena transition ecoregion (Mag)	1 (1.2%)
Cortezian ecoregion (Cor)	24 (29.3%)
Warm temperate northwestern Pacific province	1 (1.2%)
East China Sea ecoregion (Ech)	1 (1.2%)
Tropical eastern Pacific realm (TrEP)	42 (51.2%)
Tropical East Pacific province	42 (51.2%)
Mexican tropical Pacific ecoregion (Mex)	37 (45.1%)
Chiapas–Nicaragua ecoregion (ChNi)	2 (2.4%)
Nicoya ecoregion (Nico)	2 (2.4%)
Panama Bight ecoregion (Pan)	1 (1.2%)
Guayaquil ecoregion (Gua)	3 (3.7%)
Temperate South America realm (TeSA)	2 (2.4%)
Warm temperate southeastern Pacific province	2 (2.4%)
Central Peru ecoregion (Per)	1 (1.2%)
Central Chile ecoregion (Chil)	1 (1.2%)
Tropical Atlantic realm (TrA)	1 (1.2%)
Tropical northwestern Atlantic province	1 (1.2%)
Western Caribbean ecoregion (Car)	1 (1.2%)
Amphiamerican (AM)	12 (14.6%)
Wide distribution worldwide (Wd)	10 (12.2%)

Percentages for each region refer to the total number of species (82).

geographical zones (Dissim = 97.6) and its affinity was only due to the occurrence of *Magelona pacifica*.

Cluster A was divided into two subgroups (Dissim = 81.7), the assemblage 'NEPac' comprising the Mexican tropical Pacific ecoregion (Mex) and the groups of amphiamerican species (Am) as well as the species widely distributed (Wd) but, remarkably, also included the Cortezian (Cor), southern California (SCal), and Oregon (Ore) ecoregions, located in the temperate northern Pacific realm (Figure 7). On the contrary, the subgroup 'Trop' (Dissim = 47.5) included the Caribbean (Car), Chiapas–Nicaragua (ChNi), and Guayaquil (Gua) ecoregions, characterized by their tropical fauna which, unexpectedly, had less affinities with that found in the study area (Dissim = 73.5); the temperate Magdalena transition ecoregion is also comprised (Mag).

Despite the tropical characteristics of the study area, the collected fauna also presented higher biogeographic affinities with that distributed in the Gulf of California (Cortezian ecoregion) (Dissim = 31.2), and with that reported in the temperate ecoregions of Oregon (Ore) and southern California (SCal) (Dissim = 53.8). The fauna distributed in both coasts of America (Am; Dissim = 50.3) and that with wide distribution (Wd; Dissim =

59.1) were also importantly recorded in the southern Mexican Pacific (Figure 7).

Discussion

Polychaetes are frequently the dominant group in the macro-benthic communities of soft bottoms worldwide, both in the number of individuals and species (Grémare *et al.*, 1998; Hutchings, 1998; Brooks *et al.*, 2006), therefore, their ecological patterns could epitomize what happens in whole local benthic ecosystems (Mackie and Oliver, 1996; Glasby and Read, 1998; Hernández-Alcántara *et al.*, 2013, 2014). Particularly, in the Mexican Pacific, the polychaete fauna with around 1000 species reported, is considered quite diverse, but its spatial and bathymetric distribution is very heterogeneous, likely associated with the variety of environmental conditions present in their ecosystems (Hernández-Alcántara, 1992). In the Gulf of California, with warm-temperate features and a wide continental shelf up to 50 km wide, nearly 554 species have been recorded (Hernández-Alcántara *et al.*, 2014), but in the southern Mexican Pacific, with tropical characteristics and a narrow continental shelf (around 15 km wide) (Marín-Guzmán, 2011), only around 300 species have been reported. The distribution of marine species is mainly determined by temperature variations, but also by changes in the habitat characteristics (Briggs, 2007). These regional differences in species richness could be related to topographic particularities, sediment particle size, bathymetry, and other such environmental conditions that influence the polychaetes' distribution. However, in this case, the observed differences are mainly related to the poor sampling effort carried out in the study area, while the Gulf of California is, by far, the best studied region in the Mexican Pacific (Hernández-Alcántara, 1992).

Despite the limitations caused by the different sampling methods used and different sizes of the sampled areas, the 116–138 species assessed by the non-parametric estimators was higher than the richness reported in the continental shelf of other zones of the southern Mexican Pacific, such as the 96 species (González-Ortiz, 1994) and 84 species (Solís-Weiss *et al.*, 2000) recorded in the Gulf of Tehuantepec, or the 104 species reported from the Oaxaca shelf (Bastida-Zavala and Guevara-Cruz, 2012). In Petacalco Bay, Guerrero, 124 species were recorded (Rodríguez-Valencia, 2004), a number similar to the estimated richness of the present study; nevertheless, those samplings were restricted to the inner shelf (<23 m), so that the estimated richness could have been significantly higher if the sampling had been extended to 200 m depth.

Likewise, the estimation that 116–138 species are found between 40 and 109 m depth also shows that the number of polychaete species living in the whole continental shelf of the study area should be higher. Again, clearly insufficient sampling effort has been carried out in the study area, known for its spatial heterogeneity, and the recorded richness is almost certainly an underestimation of the real situation. In fact, the estimated completeness of 59.4–62.1% could indicate that the southern Mexican Pacific shelf harbours a more diverse fauna, and the number of species only collected in one (unique = 43.9%) or two (duplicate = 14.6%) stations would confirm that it is necessary to increase the sampling effort to recognize its true diversity levels.

At a global scale, each of the Errantia and Sedentaria groups comprise almost half of the known diversity of the marine annelids (Tilic *et al.*, 2022); this proportion was similar to the 36 and 40 species of Errantia and Sedentaria recorded in the present study, respectively. Almost all the families found here had already been reported in the tropical eastern Pacific (Hernández-Alcántara and
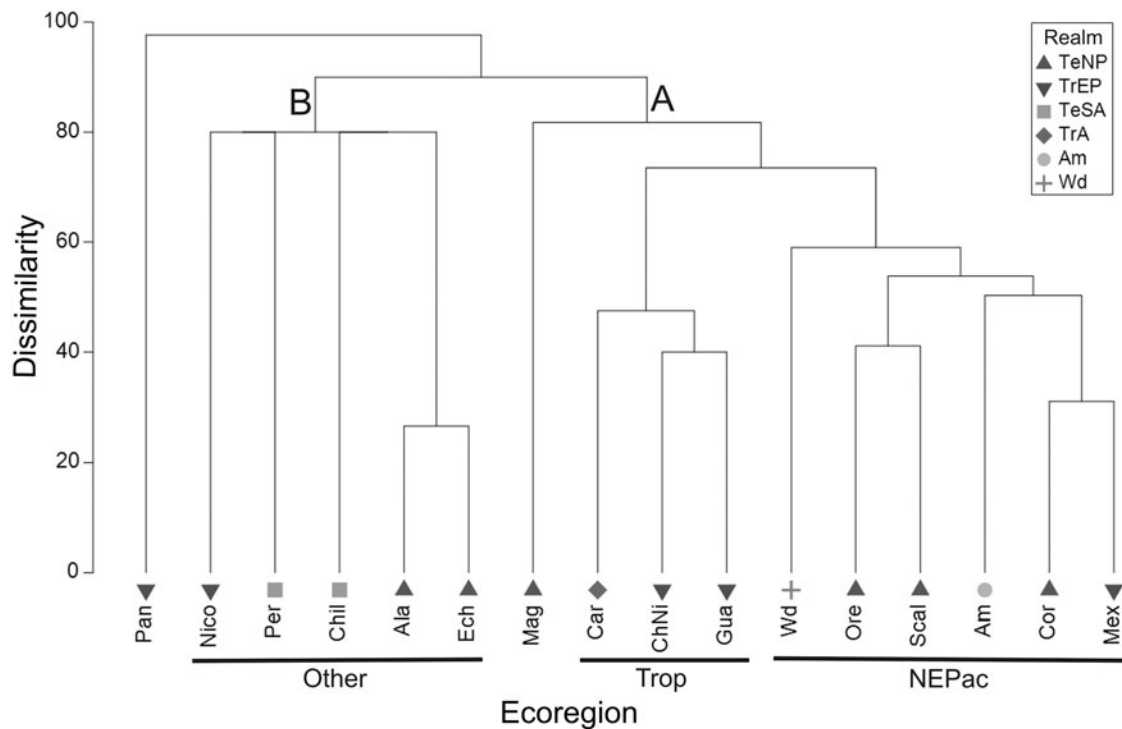
Figure 7. Cluster classification analysis of the biogeographic groups of polychaete species, based on the presence/absence of Γ⁺ dissimilarity coefficient. (Abbreviations to realms and ecoregions are indicated in Table 3. Assemblages: NEPac, Northeastern Pacific; Trop, tropical zones; Other, ecoregions from several zones.)

Solís-Weiss, 1999; Hernández-Alcántara, 2002), and only the family Sternaspidae was recorded here for the first time in the southern Mexican Pacific. Its species *Sternaspis maior* was already reported from the Gulf of California both at 180–1143 m (Chamberlin, 1919; Sendall and Salazar-Vallejo, 2013) and at 28.6–97 m depth (as *Sternaspis fossor*) (Hernández-Alcántara, 2002), a bathymetric range similar to that reported here (65–109 m).

The Errantia group was mainly represented by the Onuphidae and Lumbrineridae. As in other Pacific regions, both families are common in the Mexican Pacific shelf (Hernández-Alcántara, 2002). In the Gulf of Tehuantepec shelf, where 36 species of Errantia were recorded, the most diverse families were Lumbrineridae (8 species) and Onuphidae (6 species) (González-Ortiz, 1994), while Hernández-Alcántara and Solís-Weiss (1999) and Hernández-Alcántara (2002) also found that the Onuphidae (18 species) and Lumbrineridae (15 species), together with the Nereididae (13 species) were the families with the highest richness in the Gulf of California.

The Sedentaria, as in many soft-bottom environments, was the most abundant group, largely due to the family Spionidae, which, with eight species gathered 36.3% of the total abundance. In the world seas, the largest number of records (>62,000) belongs to the family Spionidae (Pamungkas *et al.*, 2021) and, in the soft bottoms of the Mexican Pacific, it is also one of the main components of the polychaete assemblages (González-Ortiz, 1994; Hernández-Alcántara *et al.*, 1994). In the Gulf of Tehuantepec, ten species accounted for 27% of the fauna (González-Ortiz, 1994), while in the Gulf of California, 27 species represented 41.3% of the polychaete fauna (Hernández-Alcántara *et al.*, 1994; Hernández-Alcántara and Solís-Weiss, 2005). In the Basal Annelida group, the other very abundant family Amphinomidae (36.3% of fauna) was included, but it was exclusively represented by *Linopherus kristiani*, a species widely recorded from the Gulf of California to the Gulf of Nicoya, Costa Rica, but with low abundances in other records (Salazar-Vallejo, 1987; Hernández-Alcántara and Solís-Weiss, 1991; Dean, 1996).

The number of species coexisting in an ecological assemblage must be the result of varied processes operating at local and regional scales, but in the tropical eastern Pacific little is known about these processes and their effects on the polychaete diversity and their distribution patterns (Witman *et al.*, 2004; Hernández-Alcántara *et al.*, 2013). In general, the biogeographic studies on polychaetes have shown that the information available online in biodiversity portals is often unsatisfactory, because several of the existing biogeographic regions have not been sufficiently covered (Pamungkas *et al.*, 2021). The eastern Pacific is precisely one of these regions, because it has the lowest polychaete records, only 574, compared with the more than 550,000 records compiled by Pamungkas *et al.* (2021) to analyse the biogeography of the world polychaetes. The shortage of available data in this marine region is thus demonstrated, and this also enhances the importance of the records provided in the present study for the knowledge of the polychaete biogeographic patterns in the Mexican Pacific. The sampling effort in the region should definitely increase, in the continental shelf as well as in deep waters, to get more complete inventories.

Temperature is the primary factor limiting the distribution of species in marine environments, since it influences their growth, reproduction, and physiology (Pamungkas *et al.*, 2021). However, in the eastern Pacific, the geological history is also an important factor on the evolution of the fauna and useful to determine related processes having affected their distribution patterns (Riddle *et al.*, 2000). Polychaete assemblages with a large variety of biogeographic affinities are not rare in the eastern Pacific. Their composition and distribution have been influenced by geological and ecological events, such as the formation of the Gulf of California (around 25 million years ago) (Holt *et al.*, 2000) or the rising of the Panama Isthmus (about 3.5 million years ago) (Leigh *et al.*, 2014). These events modified the topography and the environmental conditions along the eastern Pacific, but also disrupted the regional composition of species, due to extinctions, speciation

processes, or dispersions from the neighbouring marine regions to local sites (Robertson *et al.*, 2004).

The representation of a robust geographic regionalization based on empirical data is difficult due to the insufficient number of species distribution records (Costello *et al.*, 2017). However, the variations in taxonomic composition along the study area exhibited a trend comparable with that observed at a regional scale. The higher taxonomic affinities, found in the central zone, clearly decreased westwards, towards warm-temperate conditions, whereas eastwards the number of common species also gradually diminished. However, in the eastern zone, close to Coyuca Lagoon and Acapulco Bay, in a more tropical environment, the number of shared species between the samples increased again.

Thus, following these local taxonomic affinities at the regional scale, the polychaetes living in the southern Mexican Pacific, characterized by the presence of abundant coastal lagoons and rivers (Marín-Guzmán, 2011), revealed higher resemblances with those previously reported in the Mexican tropical Pacific ecoregion (45.1%), in the tropical eastern Pacific realm, and with that from the Cortezian ecoregion (29.3%), in the temperate northern Pacific realm.

The affinities between the studied fauna and that from the temperate northern Pacific realm could be related to the formation of the Gulf of California (about 25 million years ago). During the separation of the Baja California Peninsula from the Mexican mainland, it was probably fragmented into one or more islands, connecting the eastern Pacific with the Gulf of California on several occasions, thus allowing temperate species on both the Pacific and Gulf coasts (Riddle *et al.*, 2000). This has been previously observed in the polychaete fauna living in the Gulf, which resembles that found in the warm-temperate north-eastern Pacific (Kudenov, 1980; Bastida-Zavala, 1991; Hernández-Alcántara, 1992). In turn, it has been reported that the polychaete species from the temperate western Baja California Peninsula resemble those from the tropical eastern Pacific (de León-González, 1994). This is because their distribution mechanisms along the eastern Pacific are favoured by the topography and geographic orientation of the relatively straight shore, with a continuous continental shelf and few islands disrupting the coastline (Palacios-Salgado *et al.*, 2015).

Conversely, as in the present study, the polychaetes recorded in Panama's Pacific side (Fauchald, 1977), Colombia (Laverde-Castillo, 1986), or the Gulf of Tehuantepec, Mexico (Solís-Weiss *et al.*, 2000) display mostly tropical affinities, due to their similar environmental conditions, and also their similar local physiographic characteristics, with many lagoon–estuarine systems, discharges from rivers, predominance of soft bottoms, or large mangrove areas (Spalding *et al.*, 2007).

The rise of the Panama Isthmus interrupted the connectivity between the Pacific and Atlantic oceans, and thus favoured extinction and speciation processes, as well as the settling of distinct faunal assemblages (Knowlton and Weigt, 1998). It could help explain the higher affinities of the identified fauna with the tropical environments, but also the occurrence of amphiamerican species (14.6%), which would have been present before the formation of the isthmus, and the presence of possibly new species (30.5%), as a result of the speciation processes in environments different from those where they originally lived.

Biogeographically, the tropical eastern Pacific is the largest isolated tropical marine region, separated from the Atlantic by the Panama Isthmus and from the central and western Pacific by the world's broadest deep-water barrier (4000–7000 km), limiting the dispersion of shelf species (Robertson *et al.*, 2004). However, at a local scale, differences in the habitat characteristics also modify their settling and distribution (Costello *et al.*, 2017). In turn, the variations in abiotic factors such as food availability, sediment type, salinity, upwellings, nutrient inputs, currents, or bathymetric heterogeneity, among others, can modify their biogeographic patterns (Spalding *et al.*, 2007). The oceanographic data are scarce on the study area and the water current system (as a very important mechanism to the larval dispersion in polychaetes), is not well known either. Therefore, the higher affinity of the collected fauna with that distributed in the tropical eastern Pacific realm could also be explained by the movement of the eastern branch of the North Pacific subtropical gyre, through the North-Equatorial Countercurrent and the Costa Rica Current. These currents drift towards the eastern Pacific carrying tropical waters at more than 25°C and salinities lower than 34 psu (Badan, 1997). This could favour the establishment of polychaete species with warm-water adaptations in the study area.

The resemblance of the collected fauna with that distributed in the temperate northern Pacific realm, essentially with species recorded in the Cortezian ecoregion (29.3%), is also probably related to the ocean currents' flow (Stevenson *et al.*, 1998), which could favour the establishment of tropical species in the Cortezian ecoregion. In the Gulf of California, the Equatorial Superficial Water (ESW) and the Gulf of California Water (GCW) are present in the first 150 m depth (Lavín *et al.*, 1997). The ESW comes from the equatorial region, mainly in the summer–autumn season, moving warm waters (higher than 18°C) with salinities lower than 35 psu, while the GCW, though mainly located in the northern gulf, is water of equatorial origin transformed by superficial evaporation (temperature >12°C; salinity >35 psu) (Lavín *et al.*, 1997). In addition, the observed affinities between the identified polychaetes and those of the temperate regions could also be explained by the global climate warming, since the tropical region may already be too hot (Chaudhary *et al.*, 2016), so that some species can move to higher latitudes, as was observed in echinoderms and decapod crustaceans (O'Hara and Poore, 2000).

Understanding the biogeographic processes requires the faunal affinities to be sufficiently large to reflect the ecological or evolutionary mechanisms involved in the distribution patterns of species (Spalding *et al.*, 2007). However, the representation of a robust geographic regionalization based on empirical data of the species distributions is difficult (Costello *et al.*, 2017). It is necessary to create a complete and updated database on the species distributions, but also to incorporate an integrative taxonomy approach, including distinct information sources such as ecological, molecular, and morphological data, in order to understand better the evolutionary history and the relationships between the examined taxa. This approach, in the southern Mexican Pacific or even in the whole eastern Pacific, in their continental shelves as well as in their data-poor habitats, might generate more accurate patterns of species distributions and help in the recognition of the ecological and biogeographic processes that are occurring there.

Conclusions

In the southern Mexican Pacific shelf, the polychaetes with the highest number of species and individuals were members of the Sedentaria group, and although the Errantia were also diverse, few individuals were collected. Among the enigmatic taxa from the Basal Annelida group (Amphinomida and Magelonida) only six species were recorded, but they were remarkably abundant, which is rare in the continental shelf of the tropical Pacific. The 116–138 species expected by using the non-parametric estimators, compared with the 82 species actually recorded, confirm the need to increase the sampling effort to get more complete inventories in the continental shelf of this region. The higher biogeographic affinities of the polychaete species of this study with those of

the Mexican tropical Pacific (45.1%) and Cortezian (29.3%) ecoregions were associated with the geological and ecological events that occurred during the formation of the Gulf of California and the rise of the Panama Isthmus, and with the regional influence of the eastern Pacific Sea circulation along the straight shoreline, favouring extinction, speciation, and dispersion processes, and the settling of distinct faunal assemblages.

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