ORIGINAL ARTICLE

Geographical patterns in species richness of the benthic polychaetes in the continental shelf of the Gulf of California, Mexican Pacific

Pablo Hernández-Alcántara · David Alberto Salas-de León · Vivianne Solís-Weiss · María Adela Monreal-Gómez

Abstract The present study is the first attempt to describe meso-scale patterns in the species richness of polychaetes along the Gulf of California, which stretches from about 23°N to 31°N. We examine herein the spatial changes in species distribution and explore the overlapping of species' ranges towards the centre of the Gulf, to test whether the mid-domain effect (MDE) could explain an expected mid-domain peak in species richness. The faunal composition and the latitudinal range of 244 species of polychaetes recorded along the continental shelf of the Gulf of California were analysed in latitude bands of 1°. The species composition changes around the Gulf's archipelago (∼29°N), and the highest values of species richness are found at the 25° (197 species) and 26° (193 species) of latitude. Although the species richness pattern could be described by a parabolic shape, the regional trend was not strongly consistent with the peak of diversity at 27°N (176–191 species) predicted by the mid-domain effect: the random sorting of species' ranges within spatial domain does not explain satisfactorily the geographical patterns of diversity. Nevertheless, a partial contribution of MDE to these natural patterns of diversity could be detected, and the increase in species richness towards middle latitudes was basically determined by species with distribution ranges larger than 6°. The low level of significance between the empirical species richness pattern and the mid-domain model prediction for polychaetes in the Gulf does not restrict their use as a model for exploring the randomness of the diversity patterns.

Keywords Polychaeta · Species richness · Geographical patterns · Mid-domain effect · Gulf of California

Introduction

Geographical gradients in species richness have always attracted the interest of ecologists and biogeographers because of their remarkable importance to understand ecological and evolutionary processes (Colwell et al. 2004). Although we are still far from having a detailed list of the distribution of given organisms in all areas at the global scale, many patterns of spatial variation in diversity have been documented, the latitudinal gradient of taxonomic richness (LGTR) being one of the most conspicuous patterns of global diversity. Indeed, the decreasing number of species from low (equator) to high (poles) latitudes has been well documented for terrestrial taxa. However, this latitudinal gradient appears to be less consistent with the marine biota (Gray 1997, 2002; Roy et al. 2000; Willig et al. 2003; Giangrande and Licciano 2004; Currie and Kerr 2008). The polar-equatorial cline in species richness has been recognized for some groups of gastropods, coastal fishes and in some benthic communities (Sanders 1968; Roy et al. 1994, 2000), but in several groups, the species richness does not consistently adjust to this latitudinal trend, for example, turtles and marine mammals show inverse latitudinal gradients (Proches 2001; Stephens and

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Wiens 2003), whereas diversity of planktonic taxa such as foraminifera (Rutherford et al. 1999) or euphausiids (Reid et al. 1978) peaks at some distance away from the Equator, and molluscs appear to be distributed in hot spots rather than in latitudinal clines of diversity (Crame and Clarke 1997).

Different interpretations about the factors that could regulate these spatial patterns have been subjected to constant debate, and at least 30 hypotheses have been put forward to explain the latitudinal gradients in species richness (Rhode 1992; Kerr 2001). Many of these hypotheses are closely related and interdependent, since several environmental and biotic factors influencing the diversity trends covary with latitude (Jetz and Rahbek 2001; McClain and Etter 2005).

Recently, a renewed interest in the distribution patterns of species studied at global and regional scales has produced new hypotheses to explain the latitudinal variations in species richness (Gray 2001; Rodriguero and Gorla 2004). In nature, a substantial signature of parabolic latitudinal trends of species richness in a large variety of taxonomic groups and habitats has been observed, since the number of species peaks at the middle of the analysed region and the diversity patterns can be described as unimodal (Willig and Lyons 1998; Lees et al. 1999; Hillebrand 2004). However, these parabolic distributions of diversity may be also generated stochastically in the absence of environmental gradients and even in the absence of biological and evolutionary processes (Colwell and Hurtt 1994): a random arrangement of species distribution within a bounded domain can theoretically produce a peak of diversity in the middle of the domain, similar to those spatial patterns observed in nature (Colwell and Hurtt 1994; Colwell and Lees 2000; Jetz and Rahbek 2001; Colwell et al. 2004, 2005; Currie and Kerr 2008). The accumulation of distribution ranges in the central zone of the domain is the result of the dubbed "mid-domain effect" (MDE). The mid-domain effect theory is associated with a null model that only considers the geometry of spatial gradients and species' ranges excluding any assumptions of environmental, biological or historical causes and predicts that when the species' ranges are randomly arranged within a constraint domain, more ranges will overlap in the middle of the domain producing a unimodal curve (Colwell and Lees 2000).

Like any idea driving for a new way to explain an old problem, the mid-domain theory has been subjected to strong debates (Zapata et al. 2003, 2005; Hawkins et al. 2005). It is obvious that environmental gradients play an important role in determining the distribution range of species, but the effect of such gradients in overlapping the species' ranges towards the middle of a bounded geographical domain is less clear (Colwell et al. 2009). Of

course, the model predictions in regards to species richness showing a parabolic shape declining symmetrically from the centre towards the borders of the domain can operate in complex ways in accordance or not with other causes from the spatial pattern, such as area (Romdal et al. 2005), or climate and/or productivity (Jetz and Rahbek 2002; Kerr et al. 2006).

In the tropical seas, invertebrate communities include thousands of species that play important roles in the establishment of diversity patterns and in the ecological processes that happen, for example, in the benthic systems. Paradoxically, macro- and meso-scale studies of diversity are rarely carried out in marine tropical areas, and the quantitative information available concerning species richness variations in tropical coastal environments is relatively scarce (Gray 2002). The Gulf of California, in the eastern Pacific, is not an exception, and regional distribution patterns of invertebrates, specially the polychaetes, are poorly documented (Brusca 1980; Hernández-Alcántara and Solís-Weiss 1999, 2005, 2008).

The study of polychaetes in the Gulf of California started during the twentieth century when Gravier (1901) reported a heteronereidid, maybe *Platynereis integer fide* Monro (1931), at its south-west sector. Now, about 90 publications have been carried out in the Gulf to expand the knowledge of the taxonomy of these invertebrates. However, so far, no efforts have been made to compile and summarize the information about the local species' distribution and to understand the factors that generate current diversity patterns. In this sense, the present study is the first attempt to describe meso-scale trends in species richness of the polychaetes in the Gulf of California and to examine spatial changes in composition and distribution of those species. Our general hypothesis is that a peak of diversity emerges around the middle latitudes of the Gulf, and we explore an expected overlapping of species' ranges towards the centre of the study area to test whether this pattern of species richness is consistent with the mid-domain effect (MDE) predictions.

The mid-domain effect on latitudinal gradients in benthic marine environments has only been tested for corals and demersal fishes from the Indo-Pacific (Connolly et al. 2003; Bellwood et al. 2005), littoral fishes from the tropical eastern Pacific (Mora and Robertson 2005) and polychaetes from Chilean coasts (Hernández et al. 2005; Moreno et al. 2006). So, it is evident that the agreement between observed patterns of species richness and MDE predictions at meso-scale level in the benthic realm is practically unknown. The Gulf of California, chosen for this study, is a long (1,100 km) and narrow (150–200 km) semi-closed sea with a hard constraint in the north and a southern communication with the Pacific Ocean, where the oceanographic processes and the associated environmental

features vary with the latitude. Of course, these oceanographic patterns have a direct influence on the biota inhabiting the Gulf, and several species, basically those recorded in its southern half, are tropical in distribution (Hendrickx et al. 2002). In this sense, these physiographic and faunal peculiarities suggest that the Gulf of California could be used to examine the geographical patterns of diversity and to test whether the MDE principle potentially operating at the large scale could also operate at the meso-scale level ($\sim 9°$ latitude).

Methods

Study area

The Gulf of California is located in the north-eastern Pacific Ocean (23°–31°38′N; 105°–107°W). It is a large basin (283,000 km^2) north-west–south-east oriented, more than 1,100 km long (approximately 9° of latitude) and about 200 km wide in average (Fig. 1). The southern end of the Gulf has an open communication with the Pacific Ocean that largely controls its climatic and oceanographic characteristics (Salas-de León et al. 2003). Around its central region, there is an archipelago, or islands zone, which alters the hydrographic structure between the upper and lower Gulf; this happens because of the many sills and narrow channels present in this area and the consequent extensive and strong tidal mixing both by bottom friction and by internal instabilities (Salas-de León et al. 2011). The northern zone, with an average depth of 200 m, is dominated by the Colorado River Delta, while to the south, there are a series of basins which become progressively deeper (2,000 to >3,500 m). The Gulf is characterized by a strong seasonality in circulation and thermohaline structure as a response to the seasonality of the main forcing agents, including the geostrophic circulation of the eastern tropical Pacific, the wind system and the fluxes of heat and moisture. As a consequence of these temporal patterns on the fields of temperature, salinity, water masses, stored heat, among others, two main hydrodynamic seasons can be distinguished, winter–spring and summer–autumn (Lavín et al. 1997). The surface circulation in the entire Gulf shows an anticyclonic gyre in winter and a cyclonic circulation in summer and a net surface outflow from the north through the archipelago, which is compensated by a permanent inflow close to the bottom on the western coasts (Lavín and Marinone 2003).

Data analysis

A database was built with information from polychaetes collected in the continental shelf of the Gulf of California (<200 m depth) and kept in the "Colección Nacional de Anélidos Poliquetos de México" from the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (CNP-ICML, UNAM: DFE.IN.061.0598). Because the hydrodynamic variations in the Gulf are linked to two main climatic periods, and in order to control the influence of environmental factors on the species richness pattern, in this study, only the data associated with samples taken in the winter-spring season were analysed. The seasonal changes in distribution of polychaetes in the Gulf of California have been poorly explored; however, the study on one of the most abundant and diverse polychaete groups, the Spionidae, showed that the distribution of species varied seasonally, basically as a response to temperature changes (Hernández-Alcántara and Solís-Weiss 2005). The information of the database includes the scientific names of all identified species, and each species entry is associated with the spatial distribution data of the species within the Gulf. Information about the dispersal potential of polychaete species is included, in accordance with the estimations made by Carson and Hentschel (2006), who grouped the dispersal potential into three categories: high, medium and low, based on known life history (fertilization and dispersal methods, feeding behaviour of the larvae, average time before settlement, motility of adults, presence or absence of epitokous reproduction) or inferred life history from closely related species. The "high" rate includes species that can potentially disperse tens of kilometres, exchanging larvae with far away populations; the "medium" category is associated with dispersal on the scale of kilometres; the "low" potential implies dispersal to less than 1 km.

The geographical information contained in the database was transformed into latitudinal ranges for each polychaete species. The geographical range was defined as the latitudinal endpoints of its distribution in the continental shelf of the Gulf of California. So, the *latitudinal range* of a species (L_r) is the difference (in degrees of latitude) between the northernmost (l_{mx}) and southernmost (l_{mn}) points included in its geographical range ($L_r = l_{mx} - l_{mn}$), and the *latitudinal midpoint* (M_l) was estimated as the mean of the latitudinal extremes of distribution ($M_l = (l_{mx} + l_{mn})/2$) (Pineda and Caswell 1998).

Initially, using the Plymouth Routines in Multi-variate Ecological Research (PRIMER v6) software (Clark and Gorley 2006), the latitudinal changes in the species composition were evaluated along latitude bands of 1° by means of non-metric multidimensional scaling ordination (MDS). The MDS was run on the θ^+ (theta$^+$) taxonomic dissimilarity index, which is a presence/absence-based "beta-diversity" coefficient (Clarke and Warwick 2001). This is a natural extension of the index of taxonomic distinctness Δ^+ (Clarke and Warwick 1998), defined as the mean path length through a taxonomic tree between every pair of species in a sample. Linked to this analysis, the

Fig. 1 Location and
bathymetry (m) of the Gulf of
California
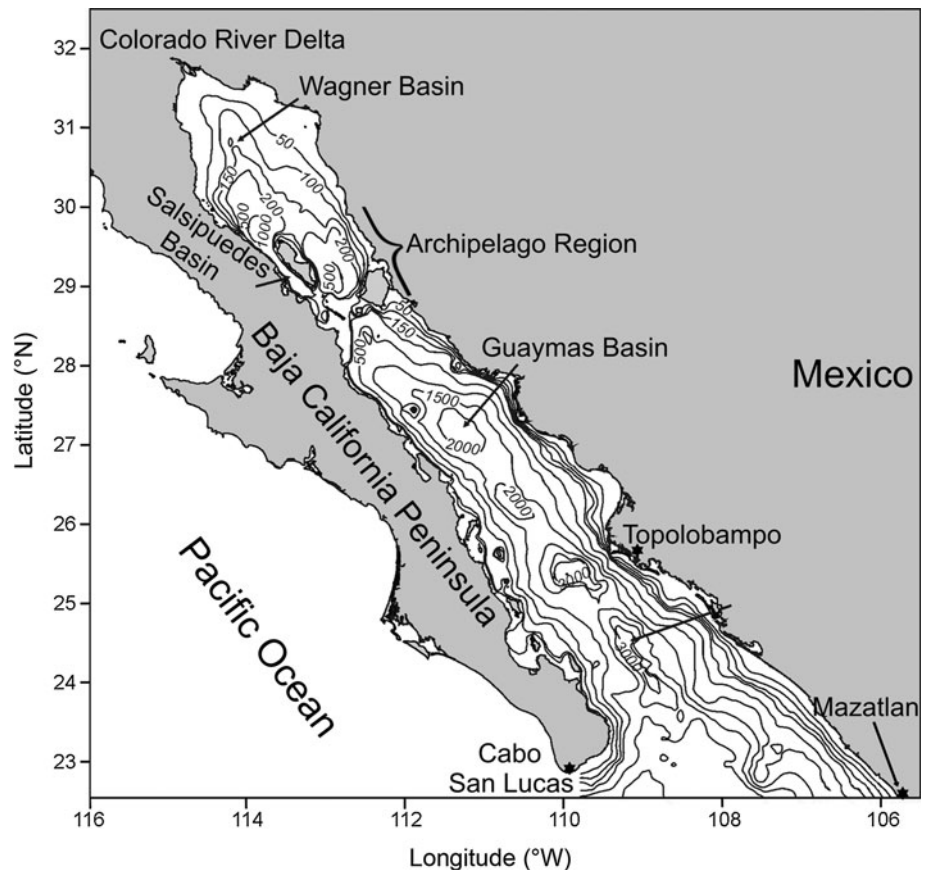
Index of Multivariate Seriation (IMS) was used to evaluate the latitudinal breakdown in faunal composition (seriation) between different latitudes, which measures the rank to which the latitudinal faunal changes conform to a linear standardized sequence (Clarke and Warwick 2001).

The number of species in the Gulf was calculated to each latitude bands of 1°, going from south to north. The geographical trend of the total number of species and its theoretical unimodal pattern was evaluated using a polynomial model to the second degree. Size and spatial distribution of the ranges of species and the relationship between the latitudinal range (L_r) and the latitudinal midpoint (M_l) for all species were analysed to show the dispersion of data on the continental shelf of the Gulf.

Mid-domain effect and species richness

The geometric effect on the latitudinal distribution of the number of species in the Gulf of California was tested comparing the observed values with the species richness prediction of the mid-domain hypothesis. To examine the overlapping of the species' ranges towards the centre of the geographical domain, and the mid-domain peak of species predicted by the null model, distribution curves of species richness were generated using the Monte Carlo simulation program Mid-Domain Null (McCain 2004). Species

richness curves were constructed dividing the gradient in latitude bands of 1°, and 50,000 Monte Carlo simulations were used based on empirical range sizes, to calculate the amplitude of the 95 % confidence for prediction curves (McCain 2004).

To test the relationship between the observed data and the species richness pattern predicted by the geometric constraint model, randomization was used to generate both a predicted species richness curve and the expected distribution of a displacement statistic, D, which measures the extent to which any empiric species richness curve would be expected to deviate from the predicted curve by chance alone (Veech 2000); high values of D indicate big differences between the observed and null curves. Analyses in the Gulf were based on 10,000 randomizations, and the significance of D value is given as a p value, calculated from the proportion of null D values greater than the observed D value.

Results

Faunal composition and latitudinal trends

The distribution of 244 species of polychaetes, belonging to 41 families, along the continental shelf of the Gulf of California was compiled and analysed. The number of

species by family varies considerably, from 1 to 21 species (Table 1). Ten families made up for 50 % of the total number of species, of which the most diverse in decreasing order were Spionidae (21 species), Onuphidae (17 species), Lumbrineridae (14 species), Nereididae (12 species) and Terebellidae (12 species).

Polychaetes show an amazing morphological variability, but the process and mechanisms involved in their reproduction and development have been described for very few species. Using estimations from Carson and Hentschel (2006) to calculate the dispersal potential of the polychaete species of this study, we could obtain useful information for 86 % of them (Table 1): in the Gulf, the polychaetes are assembled into three roughly similar groups in terms of the number of species: 74 species belong to 15 families with high dispersal potential; 75 species to 7 families with medium dispersal potential and 60 species to 6 families with limited potential for dispersal.

Although differences are not significant, the dispersal potential of these species is related to the size of their distribution range. The polychaetes with high dispersal potential display a slightly wider latitudinal range (m: median) than those with lower dispersal possibilities, although they also display a higher variation (s: standard deviation): high dispersal: $m = 4.2°$, $s = 2.44°$ latitudinal range; medium dispersal: $m = 3.9°$, $s = 1.33°$ latitudinal range; low dispersal: $m = 3.2°$, $s = 1.98°$ latitudinal range. Regionally, the species with higher dispersal potential ($m = 26.4°$, $s = 1.05°$ latitude) also display the lowest regional variability and tend to be distributed slightly more northwards than the polychaetes with lower dispersal potential (medium dispersal: $m = 24.8°$, $s = 5.43°$ latitude; low dispersal: $m = 24.2°$, $s = 7.03°$ latitude).

At the species level, the MDS shows significant geographical differences (81 % dissimilarity) among the polychaete fauna distributed in the southern (23°–25°), central (26°–28°) or northern (29°–31°) Gulf zones (Fig. 2). In addition, the values of the Index of Multivariate Seriation (IMS) are high and have a significant correlation with a linear sequence ($\rho = 0.926$; $p < 0.001$): the species composition changed following a south–north trend, although with higher differences between the 28° and 29°, and between 30° and 31° degrees of latitude.

According to the ranges' width and their latitudinal distribution, the frequency of the polychaete species shows a bimodal trend (Fig. 3): 63 species (26 %) are distributed along 8° latitude, and 52 species (21 %) are only recorded in one latitudinal band. The classes' intervals show that the species with wide latitudinal ranges, (6, 9) degrees of latitude, are dominant in the Gulf (123 species = 50 %). On the other hand, 69 species of polychaetes (28 %) are distributed in short intervals, (0, 3) degrees of latitude, while 52 species (21 %) have an intermediate distribution in the Gulf, (3, 6) degrees of latitude.

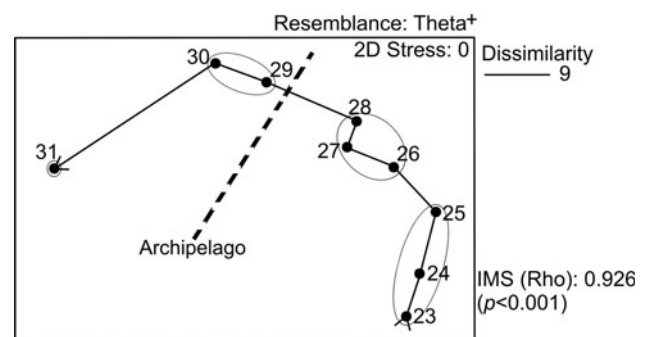The most widely distributed species group ($\geq 6°$) extends over practically all the study area, although a lower

Table 1 Number of species and dispersal potential (in parentheses) by family of polychaetes from the Gulf of California

Family	No. of species	Family	No. of species
Acoetidae (undet.)	4	Onuphidae (low)	17
Ampharetidae (low)	8	Opheliidae (high)	4
Amphinomidae (high)	3	Orbiniidae (medium)	8
Capitellidae (high)	10	Oweniidae (high)	1
Chaetopteridae (high)	1	Paraonidae (undet.)	11
Chrysopetalidae (undet.)	1	Phyllodocidae (high)	9
Cirratulidae (medium)	11	Pilargidae (undet.)	5
Cossuridae (undet.)	2	Pisionidae (undet.)	1
Dorvilleidae (medium)	2	Poecilochaetidae (high)	1
Eulepethidae (undet.)	1	Polynoidae (high)	7
Eunicidae (high)	6	Sabellidae (medium)	9
Euphrosinidae (undet.)	1	Serpulidae (high)	1
Flabelligeridae (undet.)	4	Sigalionidae (high)	6
Glyceridae (high)	6	Spionidae (medium)	21
Goniadidae (high)	4	Sternaspidae (undet.)	1
Hesionidae (high)	4	Syllidae (low)	7
Longosomatidae (undet.)	1	Terebellidae (medium)	12
Lumbrineridae (low)	14	Trichobranchidae (low)	6
Magelonidae (high)	5		
Maldanidae (low)	8		
Nephtyidae (high)	6	Total species	244
Nereididae (medium)	12	Total families	41
Oenonidae (undet.)	3		

Based on Carson and Hentschel (2006); Undet. = undetermined

Fig. 2 MDS plot of the latitude bands of 1° based on the taxonomic composition of the polychaete fauna with the θ^+ (theta$^+$) taxonomic dissimilarity index. The *lines* indicate the degree of seriation by linking consecutive points along the latitudinal gradient from southern to northern Gulf of California, and the numbers are the latitudinal bands
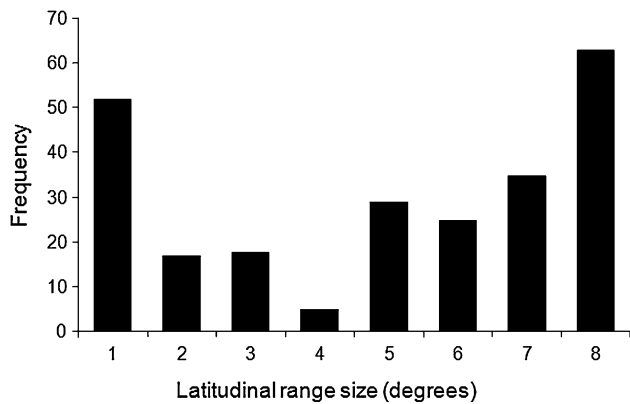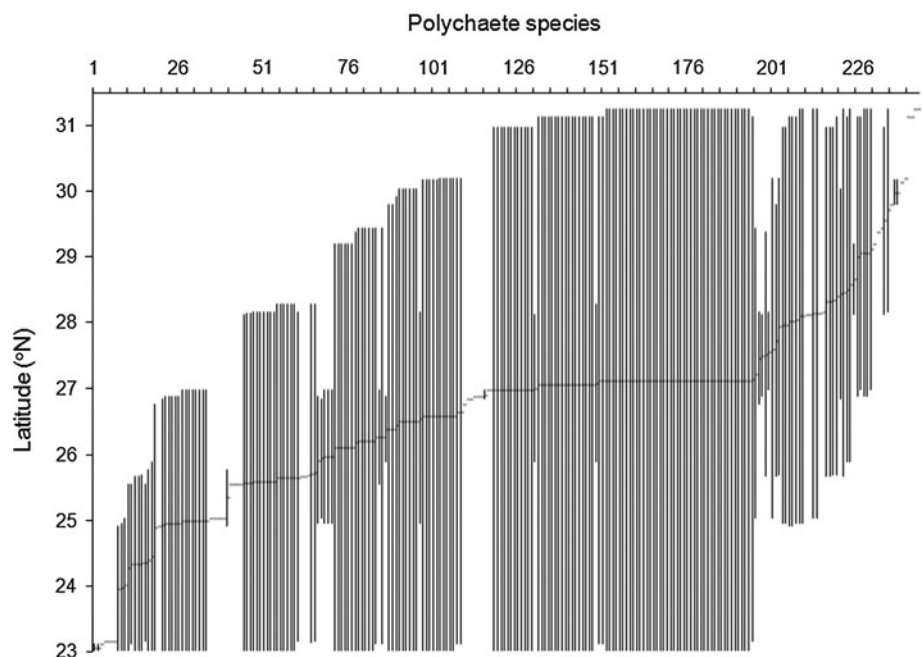
Fig. 3 Frequency of the latitudinal range sizes of the polychaete species

number of these kinds of species are observed towards the southernmost and northernmost end of the Gulf (Fig. 4). On the other hand, species located in only one latitudinal band are mostly distributed southwards of latitude 27°, while most of the species with intermediate ranges (3°–6°) are mainly brought southwards of latitude 28° (average 48 species/band).

Geographical distribution of species number

In the Gulf of California, the number of species at different latitudinal bands shows a large variation (84–197 species/band), but it is also evident that a peak of species richness emerges between the 25° and 26° latitudinal bands, with 197 and 193 species, respectively (Fig. 5). On the other hand, an evident decrease in the number of species towards the southern (162 species) and northern Gulf (84 species) is

observed. The lowest species richness is found in the latitudinal bands matching the northern Gulf region (≥29°), but a linear decline is also evident in the number of species in northward latitudes (29° = 146 spp.; 30° = 123 spp.; 31° = 84 spp.) (Fig. 5).

Given the maximum number of species at middle latitudes (25° = 197 species), and the lowest values observed at the northern (31° = 84 species) and at the Gulf's mouth surrounding area (23° = 162 species), the latitudinal distribution of the number of species fits a second-degree polynomial model (Fig. 5). Indeed, the nonlinear regression fit between the total number of species in each latitude band of 1° and the latitude is significant ($r^2 = 0.939$; $p < 0.05$), and the parabolic curve generated by this model explains 93 % of the latitudinal variance of the species richness in the continental shelf of the Gulf.

Mid-domain effect on the species richness pattern

The relationship between the latitudinal range and the mid-point for each species in the Gulf shows that the dispersion of data into the triangular shape is not homogeneous (Fig. 6), and three main groups of species stand out: a group characterized by species with mid-points located southwards from latitude 26°, which is dominated by species with 1–3 width range; a northern assemblage, with a few species whose distribution centres at latitudes higher than 28°; the more numerous group, with species widely distributed along the Gulf (mostly more than 6° of latitude), whose mid-points are assembled at middle latitudes (around 27°–28°N).

The maximum number of species observed at middle latitudes of the Gulf is consistent with the parabolic pattern

Fig. 4 Latitudinal extent of benthic polychaete species found along the Gulf of California. Each *vertical bar* represents the distribution of a single species

predicted by the mid-domain effect (Colwell and Hurtt 1994; Colwell and Lees 2000), although this humped shape has significant differences with the observed latitudinal pattern (Fig. 7). The empirical (197 species) and predicted (176–191 species) peaks of species richness are similar, but the empirical peak is found two degrees southwards (25°N) from the predicted values (27°N). Comparison between curves also shows that no empirical points of species richness are included within the predicted range (95 % of significance) (Fig. 7) and that the spatial distribution of the empirical points displays two main differences. First, in the southern Gulf (≤26°N), the observed data are clearly higher than the species richness generated by the model, particularly in the latitudinal bands close to the mouth of the Gulf (23°N); second, north of 27°N, the number of species decreases almost linearly with latitude, and the empirical species richness is distinctly lower than the values simulated by the analytical null model.
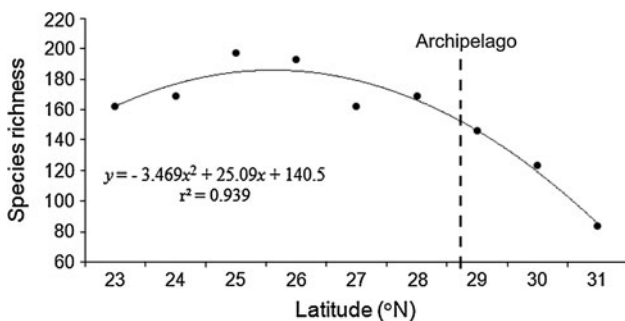
In the Gulf of California, the number of polychaetes (123 species) distributed on more than half of the area (range ≥6° latitude) is clearly more abundant than the species recorded on middle ([3,6]) degrees = 52 species) or narrow ([0,3]) degrees = 69 species) latitudinal ranges. To examine the influence of range size on the species richness pattern, a selective removal of species in observed and simulated data was performed (Fig. 7). When the geometric constraint model computes expected species richness based on large latitudinal ranges (≥6° latitude), the curve is clearly shifted up with respect to simulations corresponding to middle and short ranges, but if the analysis to generate the species richness distribution is only executed on species with ranges that cover at most 2° latitude, this parabolic trend nearly disappears. Differences between the observed and generated patterns of species richness cause that the mean displacement ($D = 121.17$) of the empiric curve from the predicted curve is significant ($p < 0.001$).

Discussion

Based on the large-scale data, the mid-domain effect (MDE) has shown that the random distribution of species' ranges into a geographical domain could generate appropriate predictions about the species richness distribution, since more ranges will overlap in the middle of the domain than at the edges (Colwell and Hurtt 1994; Colwell and Lees 2000). However, in the Gulf of California, the hypothesis assumed that MDE operating at the meso-scale level could also explain the latitudinal species richness

Fig. 5 Species richness of benthic polychaetes found in the Gulf of California at each latitude band of 1°. The *line* represents the second-degree polynomial fit data
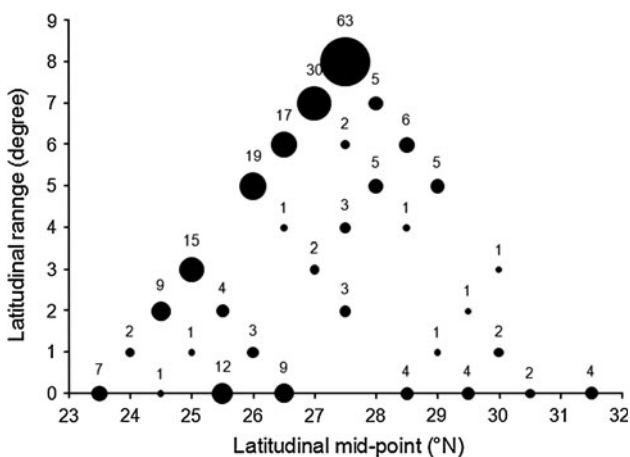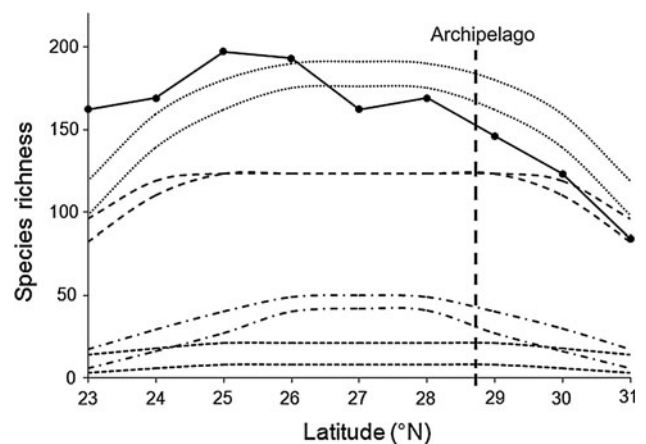

Fig. 6 Relationships between latitudinal range and the latitudinal mid-point of polychaete species. The *numbers* indicate the number of species, and the *circle size* is proportional to this number

Fig. 7 Observed species richness (*dots*) and simulated latitudinal distribution, the *top curve* represents all 244 species of polychaetes analysed (the *dotted lines* represent the limits of 95 % confidence level). *Downwards*, the computed curves (*dashed lines*) display results from 123 wide-ranging species (≥6° latitude), from 52 species with intermediate ranges (3,6) and from 69 species with ranges narrow that 3° latitude, respectively

pattern that cannot be entirely supported: the latitudinal distribution shows one peak of species richness at medium latitudes (25°N), but it is clearly different from the model's prediction (peaking at 27°N).

In the study area, the geographical changes in the species composition reveal clear geographical divergences: the species dwelling at the northern end and at the mouth of this semi-closed sea are different from each other, but they are also different from the fauna living in the central region. These northern–southern regional changes in the species composition had already been observed for Decapoda (Hendrickx 1992) or Mollusca (Hendrickx et al. 2007), since most of the fauna living in the Gulf could be eurythermic tropical species (Brusca 1980). The presence of many islands in the central region of the Gulf (~29°N) associated with shallow thresholds and narrow channels through which the circulation is disrupt (Lavín et al. 1997) could affect the dispersion of organisms (Salas-de León et al. 2011). That is why a limited genetic exchange would take place between the northern Gulf and the open Pacific regions (Brusca 1980; Hendrickx 1992), and the differences detected in species composition around 28°–29° latitude could be associated with a possible "confining effect" physiographically associated with the presence of this archipelago. In fact, higher dissimilarity in the polychaete composition occurs just in the proximities of this islands' group, leading to strong faunal differences in the northernmost latitudinal band.

Although the diversity patterns are widely known in polychaetes (Hutchings 1998; Arvanitidis et al. 2002; Giangrande and Licciano 2004; Hilbig et al. 2006), few studies have focused on testing the mid-domain effect on their distribution patterns. The mid-domain models have only been tested for latitude (Hernández et al. 2005; Moreno et al. 2006) and depth (Moreno et al. 2008) in the Chilean coasts and to depth in the western North Atlantic (Pineda and Caswell 1998; McClain and Etter 2005) and in the Gulf of Mexico (Haedrich et al. 2008). In general, the random sorting of species' ranges within spatial domains analysed in these studies does not sufficiently explain the latitudinal or bathymetric patterns of the polychaetes' species richness, but a partial contribution of MDE to these natural patterns can be detected.

The proportion of species with wide distribution ranges play an essential role to generate the unimodal species richness pattern. The species with large distribution ranges have more probabilities to overlap by chance the centre of the domain and determine the latitudinal trends of diversity (Lees et al. 1999; Colwell and Lees 2000; Grytnes 2003). In the Gulf of California, it is evident that the species with wide distribution ranges (≥6°) are the dominant ones (123 species) and hence contribute better to explain the mid-domain effect (Colwell et al. 2004). The residual latitudinal patterns,

once the large ranges have been removed from the data set, show that the simulated parabolic pattern gradually disappears: the frequency of the polychaetes with restricted distribution (≤2°) is similar in all latitudinal bands of the Gulf.

The life histories of marine invertebrates are linked with the potential to disperse far from the parental habitat (Carson and Hentschel 2006). Unfortunately, the scarce information about the diverse life histories of the polychaete species severely restricts the analysis of its correlations with the distribution patterns. However, the propositions of Carson and Hentschel (2006) that species having greater dispersal potential should have a wider distribution across the studied region than species with a lower dispersal potential could be applied to the polychaetes inhabiting the Gulf. Of course, there is no linear correlation between the dispersal potential and the current species distribution, due to several linked historical processes as vicariance; nevertheless, in the Gulf of California, the majority of the polychaete species have a high or medium potential for dispersion, and they are mainly distributed at 25°–26° of latitude, just where the maximum values of species richness were observed.

The latitudinal trend of species richness in polychaetes, increasing at medium latitudes and declining towards the northern and southern Gulf, looks different from those patterns reported in the Gulf for molluscs, crustaceans or stomatopods, among others (Hendrickx and Salgado-Barragán 1991; Hendrickx 1992; Hendrickx et al. 2007) where a progressive decline in the diversity towards the north is observed. However, north of the archipelago, the lineal drop in the polychaete species richness essentially displays the same pattern of those invertebrates, as a result of the reduction in the number of tropical species that are able to penetrate the northern sector (Brusca 1980). Although these studies have not focused on the dynamics of the processes producing those spatial patterns, the apparent lineal reduction in the number of species towards the north could be interpreted as the distribution trend suggested by the Rapoport's rule (Stevens 1992).

Although a substantial signal of the mid-domain effect on species richness patterns has been observed in nature (Willig and Lyons 1998; Lees et al. 1999; Hernández et al. 2005), significant deviations from the predictions of mid-domain models have also been found (Zapata et al. 2003; Currie and Kerr 2008). Some authors have even pointed out that when the empirical diversity is correlated with the data generated by the model, there are almost always stronger collinear environmental gradients (Currie and Kerr 2008). According to Currie and Kerr (2008), out of 53 studies that compare the empirical diversity and MDE predictions, 49 % display significant differences between the observed and the generated data or lack the mid-domain peak in species richness; 45 % of the studies also show differences

with the mid-domain hypothesis, although without reaching that conclusion.

Even though the distribution patterns that support the mid-domain effect have been questioned, Willig et al. (2003) maintain that observed data supporting the MDE predictions are increasing. In the Gulf of California, the greater diversity in the middle latitudes is a sign of the mid-domain effect, but the differences between the observed and predicted values are also evident. In this same sense, the few studies that have explicitly used the MDE model to explain the spatial variations in polychaete diversity have shown two trends: one related to the latitudinal variations (Hernández et al. 2005; Moreno et al. 2006), in which case the patterns of diversity are nearly consistent with the weakest prediction of the MDE, and the other related to bathymetric variations (Pineda and Caswell 1998; McClain and Etter 2005; Haedrich et al. 2008; Moreno et al. 2008), where the random re-arrangement of distribution ranges generates diversity patterns that differ substantially from null expectations.

Following the observed differences between the real and simulated curves, the latitudinal pattern of species richness in the Gulf of California is non-random to polychaetes, because of a significant departure from what would be expected when the species latitudinal ranges are randomly placed along the gradient. Of course, this deviation from the random predictions means that other processes need to be considered to explain that species richness pattern. So, now that the geographical distribution and the randomness of the species richness patterns of polychaetes in the Gulf of California have been explored, it is evident that additional factors should be taken into account to understand the diversity trends found in the polychaetes, including local and regional environmental features. The high environmental heterogeneity and the complex oceanographic dynamics, typical of the Gulf, can promote spatial changes in the faunal composition and the size of the distribution ranges displayed by the polychaete species along the Gulf, breaking the fit of the latitudinal variation of the species richness observed with the mid-point model predictions. Although the studies relating the distribution of species to oceanographic factors, specially to circulation processes, within the Gulf are scarce, it had been observed that the water movements could affect the dispersion potential of the species, specially on larval transport (Marinone et al. 2008; Salas-de León et al. 2011).

The circulation and thermohaline structures have effects on dispersal processes of species at a variety of spatial and temporal scales (Carson and Hentschel 2006). Particularly, the detailed effect of the archipelago on the distribution of polychaete species has not yet been analysed, but the faunal variations detected in this study constitute a first step to understand the mechanisms underlying the observed

species richness pattern. These islands group has an important role in the circulation patterns, since the strong tidal currents produce tidal mixing fronts, which disrupt the water flow between the upper and lower Gulf regions, but also modify the limits and distribution ranges of polychaetes. The polychaetes inhabiting the Gulf of California mainly show a medium or high potential for dispersal, but it is necessary to perform more research to determine whether the currents and coastal boundary layers in the Gulf significantly alter these mechanisms of settlement and distribution of polychaetes but also whether other benthic taxa.

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