

## Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast

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Hernández, C. E., Moreno, R. A. and Rozbaczylo, N. 2005. Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. – *Ecography* 28: 363–373.

Recently three biogeographical units were identified along the Chilean coast (the Magellanic Province, an Intermediate Area, and the Peruvian Province), however few studies have focused on the factors and dynamic processes that formed these spatial units (e.g. Rapoport's rule and its causal mechanisms). In this study we used benthic polychaetes of the Chilean coast to evaluate patterns of latitudinal distribution and species richness, and the existence of the three main biogeographical provinces described for the Chilean coast. Additionally, we evaluated the latitudinal Rapoport effects and geometric constraint as a null hypothesis explaining the species richness distribution.

We found that benthic polychaete diversity increased towards southern latitudes. The cluster and ordination (non-metric MultiDimensional Scaling, nMDS) analyses of the distribution data, presented only two statistically significant (bootstrapping techniques) biogeographic provinces along the Chilean coast, with a break occurring between 41° and 42°S. While, our results did not support a latitudinal Rapoport effect, they did support the view that latitudinal Rapoport effects are a local phenomenon, occurring only for the Northeastern Pacific marine taxa. The relationship between latitudinal range extent and mean latitude indicated the existence of two hard boundaries at either extreme of the Chilean coast, limiting the geographical ranges of the species. However, geometric constraints tested using a Monte Carlo simulation approach showed a weak level of mid-domain effect on species richness. Finally, we propose that geometric constraint together with the geomorphology and historical characteristics of the Chilean coast explain the biogeographical patterns of benthic polychaete taxa in Chile.

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The southeastern Pacific coast of Chile (18°20'S–56°S) has traditionally been divided into two principal zoogeographic provinces: the Peruvian Province north of 30°S, which is under subtropical influence, and the Magellanic Province south of 41°S, which is under subantarctic influence (Dahl 1960, Brattström and Johanssen 1983). Between these zones (30°–41°S) researchers distinguish a transition zone (Balech 1954, Dell 1971, Viviani 1979,

Brattström and Johanssen 1983). Lancellotti and Vásquez (1999) proposed new limits for this zone ranging from 35°S to 48°S, and corresponding to an area with a gradual change in species composition, including a conventional biogeographical break around 41°S–42°S. Recently, Camus (2001) reviewed 27 biogeographic classifications proposed for the Chilean coast. Based on this review, Camus (2001) identified three

Accepted 19 October 2004

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ISSN 0906-7590

principal spatial units: a Northern Area (18°–30°S) containing a warm temperate biota (i.e. the Peruvian Province), a Southern Area (41°–56°S) with an austral biota (i.e. the Magellanic Province), and an extensive Intermediate Area (30°–41°S) lacking transitional elements, and containing a mixed biota without a distinguishing character or biogeographic range. In spite of the numerous efforts made to describe macroscale patterns on the Chilean coast, there are few studies focused on understanding the factors that generate these species distribution patterns (Fernández et al. 2000) (e.g. Rapoport's Rule and its associated causal mechanisms, Santelices and Marquet 1998).

The zoogeographic study of polychaetes on the southeastern Pacific coast of Chile has historically received little attention. However, during the last few years there has been a progressive increase in studies attempting to establish the faunistic affinities of this group between distinct geographic areas. Recent comparative studies of faunistic affinities between polychaetes in the Magellanic and Antarctic Provinces (Gambi and Mariani 1999, Cañete et al. 1999), for the entire coast of Chile (Lancellotti and Vásquez 2000), indicate two essential faunistic units for the polychaete group: 1) taxa occurring from Valparaíso (33°S) towards the north, which is under subtropical influence; and 2) taxa occurring from Concepción (36°S) towards the south, showing greater similarity to the subantarctic fauna, and a latitudinal pattern of progressive increase in diversity from low latitudes to more southern latitudes. This biodiversity trend is contrary to that suggested by the general biogeographical principle, Rapoport's rule (Stevens 1989, 1992, 1996). Given that the number of polychaete records on the southeastern Pacific coast has increased considerably during the last few years (see Carrasco and Palma 2000, 2003, Rozbaczylo and Quiroga 2000, Hernández et al. 2001, Moreno et al. 2002), it is necessary to conduct a new analysis of biogeographical patterns and an assessment of Rapoport's rule for this taxa.

Rapoport's rule was originally stated as a correlation between the latitudinal extent of species' geographical range sizes and latitude, suggesting that the geographical extent of species' ranges increases towards one end of a physical gradient; this is observed as a positive relationship between latitudinal range extent and range midpoint (Stevens 1989). Subsequently, it was suggested that this rule also holds over elevational and bathymetric gradients (Stevens 1992, 1996). Research on several North American taxa supports the latitudinal relationship, and bathymetric Rapoport effects have been documented in northeastern Pacific taxa (Stevens 1996, Smith and Brown 2002, Smith and Gaines 2003). Nevertheless, the generality of this latitudinal pattern has been questioned by studies of some Pacific and Atlantic taxa (Rohde and Heap 1996, Santelices and Marquet 1998).

Stevens (1989, 1992, 1996) suggested seasonal variation as a causal mechanism of Rapoport's rule. This author hypothesizes that the geographical extent of species' ranges declines in more stable environments (i.e. towards low latitudes), because this kind of environment promotes specialization, and consequently, the coexistence of more species with smaller ranges. However, for many marine species water masses are relatively stable throughout the year, and, thus, the distribution patterns of these species may not be determined by seasonal variation. In this sense, Rapoport's rule may not apply to marine species that do not experience marked seasonal environmental variation. Recently, it has been suggested that in the absence of environmental gradients, patterns of species richness and distribution may depend on geometric constraints of the species' spatial distributions (Colwell and Hurtt 1994, Willig and Lyons 1998, Colwell and Lees 2000, Jetz and Rahbek 2001, 2002, Bokma et al. 2001, Grytnes and Vetaas 2002, Grytnes 2003). Geometric constraints are geographical features that limit the geographical ranges of species by acting as barriers to dispersal (see Grytnes 2003). This constraint produce the mid-domain effect, which refers to the random placement of species' geographical ranges along a geographical gradient with hard boundaries (i.e. a domain). This produces a hump-shaped pattern of species richness, such that local species richness peaks at the midpoint of the domain (Pineda 1993, Colwell and Hurtt 1994, Willig and Lyons 1998, Lees et al. 1999, Colwell and Lees 2000, McCain 2003, 2004, see Grytnes 2003).

In this study we assessed the biogeographical patterns, and the generality of Rapoport's rule, for southeastern Pacific benthic polychaete taxa. We first established patterns of latitudinal distribution and species richness. Next, we evaluated the consistency of the three main biogeographical provinces described for the Pacific coast of Chile by Camus (2001). Then, we evaluated whether the extent of latitudinal range of southeastern Pacific polychaetes shows a positive correlation with the range midpoint, as predicted by Rapoport's rule. Finally, we evaluated geometric constraint as a null hypothesis explaining the species richness distribution.

## Methods

### Data base and patterns of latitudinal distribution

The database used in this study consists of a list of 467 species of benthic polychaetes obtained from sampling conducted in littoral and sublittoral benthic habitats on the continental shelf (<200 m depth), compiled by Rozbaczylo (1985), and unpubl. The species list includes polychaete taxa from the southeastern Pacific coast of Chile ranging from 18°S (Arica) to 56°S (Cape Horn). A total of 29 species were omitted from the original

database (504 species) because their distributional range was beyond the continental shelf, and another eight species were omitted because their reported geographic distributions were imprecise. The database compiled for this study is the most current and complete database for this region of the world, and is based on an exhaustive literature search, reviews of museum collections and field expeditions.

Maps of species' distributions were created using data with a spatial resolution of 1° of latitude, and ranges were assumed to be continuous between points. To describe latitudinal patterns and compare species' distributions with the biogeographical units described by Camus (2001) we categorized species' distribution ranges into four groups: a) species recorded within only 1° of latitude; b) species with medium-small ranges of distribution from 2° to 14° of latitude; c) species with medium-large distributions ranging from 15° to 26° of latitude; and d) species with large distributions ranging from 27° to 37° of latitude. To evaluate latitudinal patterns of distribution in benthic polychaete taxa, we divided the coast of Chile into 3° bands of latitude, registering the presence or absence of each taxa in each 3° segment of the coast. Species richness (alpha diversity) was calculated as the sum of all species within each latitudinal band along the coast of Chile. To describe the latitudinal trend in species richness, we estimated the relationship between the lower latitudinal limit of the 3° bands versus species richness, and evaluated the significance of this relationship in EcoSim 7.68 software (Gotelli and Entsminger 2004). In this software we fit a standard linear regression to the data and then used the randomization approach (50 000 random matrices, random number seed = 12 345) to test the null hypothesis that the slope was equal to 0 (a significance level of  $p < 0.05$  was assumed in this study).

### Evaluation of biogeographical provinces

The degree of faunistic similarity between 3° latitudinal bands was calculated using the Jaccard coefficient of similarity based on presence/absence records of the benthic polychaete taxa. To evaluate the existence of biogeographical units (i.e. provinces) we conducted a cluster analysis using the Jaccard similarity values. For this analysis we utilized the unweighted pair/group method with arithmetic averages (UPGMA) as the agglomeration algorithm (Sokal and Rohlf 1995). We determined the significance level ( $p = 0.05$ ) of the resulting clusters by calculating the 95th percentile of the pseudovalues of similitude. These pseudovalues were obtained using the bootstrapping technique (Manly 1997) with 10 000 iterations, implemented in SYSTAT 9.0 software for Windows (SPS, Chicago, IL, USA). To confirm the existence of biogeographic patterns

we performed non-metric MultiDimensional Scaling (nMDS) ordination (Field et al. 1982, Clarke 1993) on the Jaccard similarity matrix.

### Rapoport's rule: latitudinal range extent vs range midpoint relationships

We registered the latitudinal range extent of a species as the difference between the maximum and minimum latitude in its range of distribution. The range midpoint was calculated as the average latitude between the maximum and minimum latitude the distribution. The relationship between latitudinal range extent and range midpoint was evaluated using simple regression analyses, as well as polynomial models to the second degree, implemented in JMP-IN ver. 4.0.3 (SAS Inst. 2001). When the relationship between both variables was positive, we concluded the existence of a latitudinal Rapoport effect. Additionally, we assessed the geometric shape (e.g. left triangle, right triangle, pyramid, or inverted pyramid) that best explained the distribution of data points between both axes, using EcoSim 7.68 software (Gotelli and Entsminger 2004). In this software we used the macroecology options to generate 50 000 random matrices of data (random number seed = 12 345). Next we evaluated: a) the dispersion index (DI) of points, by dividing the bivariate space into four quadrants; b) the number of points within the shape; c) the number of points falling outside the boundary of the shape (i.e. upper left and upper right boundaries); and d) only for the points falling beyond the boundary (i.e. beyond the upper left or upper right boundaries), we calculated the deviation of the points from the boundary (i.e. sum of squares, SS).

### Geometric constraint and species richness

We tested for the existence of geometric constraints using the Monte Carlo simulation program, Mid-Domain Null (McCain 2003, 2004), implemented in Excel software. The species richness data for each 3° latitude band were compared with null model predictions using a Monte Carlo simulation of species richness curves. The simulated curves were based on empirical range sizes within a bounded domain, using the analytical stochastic models of Colwell and Hurtt (1994) and Colwell (1999). We used 50 000 Monte Carlo simulations sampled with replacement (i.e. the bootstrap method) and without replacement (i.e. the randomization procedure) from empirical range sizes, to calculate the amplitude of the 95% confidence simulation prediction curves (Manly 1997, McCain 2004). As stated by Manly (1997), in randomization procedures "the hypothesis under investigation suggests that there will be a tendency for a certain type of pattern to appear in data, whereas the

null hypothesis says that if this pattern is present then this is a purely chance effect of observations in a random order". This situation (the randomization procedure) corresponds precisely to the mid-domain and geometric constraints model (McCain 2004).

## Results

### Patterns of latitudinal distribution

Of the 467 species analyzed in this study, 180 (38.5% of total species) presented recorded within only 1° of latitude, of which 24 were distributed in the Peruvian Province (PP), 50 in the Intermediate Area (IA) and 106 in the Magellanic Province (MP) (Fig. 1A). On the other hand, 157 species (33.6%) presented medium-small ranges of distribution, with 7 species restricted to PP, 27 in IA, and 73 in MP (Fig. 1B). The rest of the species with medium- small ranges ( $n=50$ , 31.8%) was shared between two or three provinces (Fig. 1B). The species group with medium-large ranges included 97 species (20.7%) (Fig. 1C), of which 15 species were restricted to the MP (15.5%), a large proportion overlapped between the PP and the IA (60.8%), and a lesser number were shared with the MP (23.7%). The most widely distributed species group included 33 species (7%) extending over all three provinces (Fig. 1D).

The latitudinal pattern of diversity shows two zones with a greater number of species along the Chilean coast (Fig. 2): 1) the latitudinal band corresponding to 39°–41°S (215 species, 12.1%), and 2) the area between 51° and 53°S (187 species, 10%). On the other hand, the zones with least species richness occurred at the geographic extremes of the Chilean coast. In the northern extreme the lowest richness was found in the first three latitudinal bands (18°20'S–20°S,  $n=82$  species, 4.6%; 21°–23°S,  $n=94$  species, 5.3%; 24°–26°S,  $n=96$  species, 5.4%), and in the southern extreme the lowest richness occurred in the most southern latitudinal band (54°–56°S,  $n=107$  species, 6%) (Fig. 2). The relationship between the lower latitudinal limit of 3° bands of latitude versus species richness indicated that species richness increased towards southern latitudes, however this relationship was marginally non-significant ( $p=0.0567$ ,  $R^2=0.214$ ) (Fig. 2).

### Evaluation of the biogeographical provinces

Cluster analysis of benthic polychaete distributions indicated only two statistically significant biogeographic units (bootstrap analysis: 95th percentile = 28.4% similarity) (Fig. 3), of the three biogeographical units proposed by Camus (2001). The first unit includes the latitudinal bands between 18° and 41°S, coinciding the biogeographic units described by Camus (2001) as

the PP and the IA. The second unit includes the latitudinal bands between 42° and 56°S, coinciding with the MP described by Camus (2001). The nMDS ordination analysis supported the existence of these two major biogeographic units along the Chilean coast (stress = 0.004) (Fig. 4).

### Rapoport's rule: latitudinal range extent vs range midpoint relationships

The simple regression analysis of the relationship between latitudinal range extent and range midpoint showed a significant negative slope ( $p<0.0001$ ) and a low  $R^2$  value ( $R^2=0.07$ , Fig. 5). A second degree polynomial model showed the maximum latitudinal ranges at middle latitudes, with minimum range size at extreme latitudes ( $p<0.0001$ ;  $R^2=0.17$ ; Fig. 5). These analyses do not support a latitudinal Rapoport's effect. On the other hand, the our assessment of geometric shapes indicated that an asymmetric pyramid was the most appropriate model to describe this data set (Fig. 5). The observed dispersion (DI = 287.42) was significantly greater than the average dispersion of the simulated data sets (mean of simulated DI = 126.29, variance = 1851.60; number of times observed DI > simulated DI = 49 345;  $p=0.0131$ ). The dispersion index demonstrated that the points were unusually concentrated in some corners of the shape space. The observed number of points that fell within the shape ( $n=385$ ) was significantly greater than the number found in most of the simulated data sets (mean of simulated number of points = 367.23, variance = 29.87; number of times observed number of points > simulated number of points = 49 968;  $p=0.0006$ ), indicating that the points are unusually clustered within the shape. The observed number of points that fell outside of the upper right boundary of the shape ( $n=0$ ) was significantly smaller than the number found in most of the simulated data sets (mean of simulated number of points = 54.40, variance = 25.17; number of times observed number of points < simulated number of points = 50 000;  $p<0.0001$ ), indicating that the points were unusually sparse beyond this boundary. The observed number of points that fell outside of the upper left boundary of the shape ( $n=67$ ) was significantly greater than the number found in most of the simulated data sets (mean of simulated number of points = 27.93, variance = 15.80; number of times observed number of points > simulated number of points = 50 000;  $p<0.0001$ ), indicating that the points were usually sparse beyond the boundary. The points that fell beyond the upper left boundary showed a deviation of the points from the boundary, or observed sum of squares (SS = 568.15) significantly smaller than the sum of squares found in most of the simulated data sets (mean of simulated SS = 3362.35, variance = 1 084 725.0;

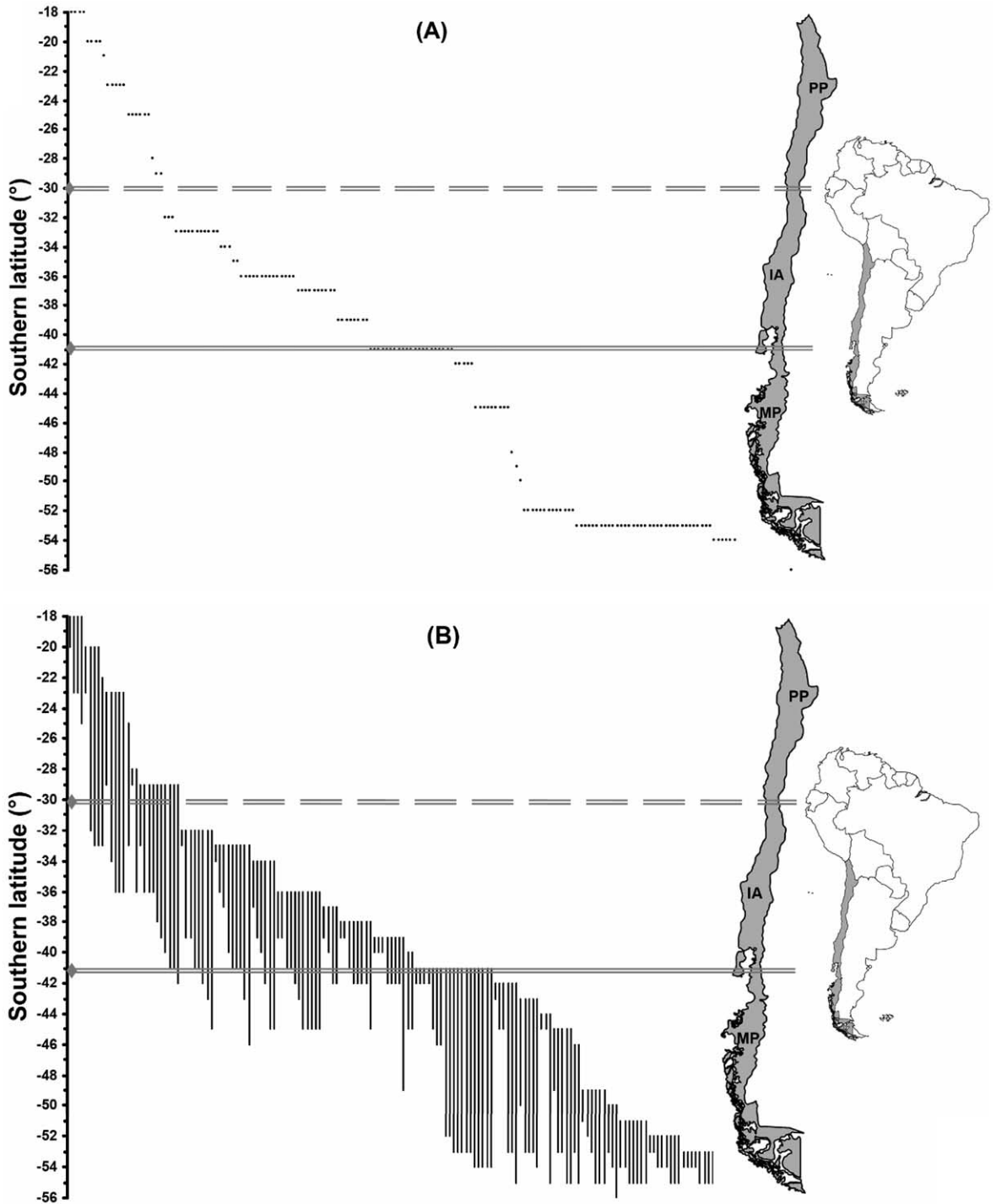


Figure 1. (Continued)

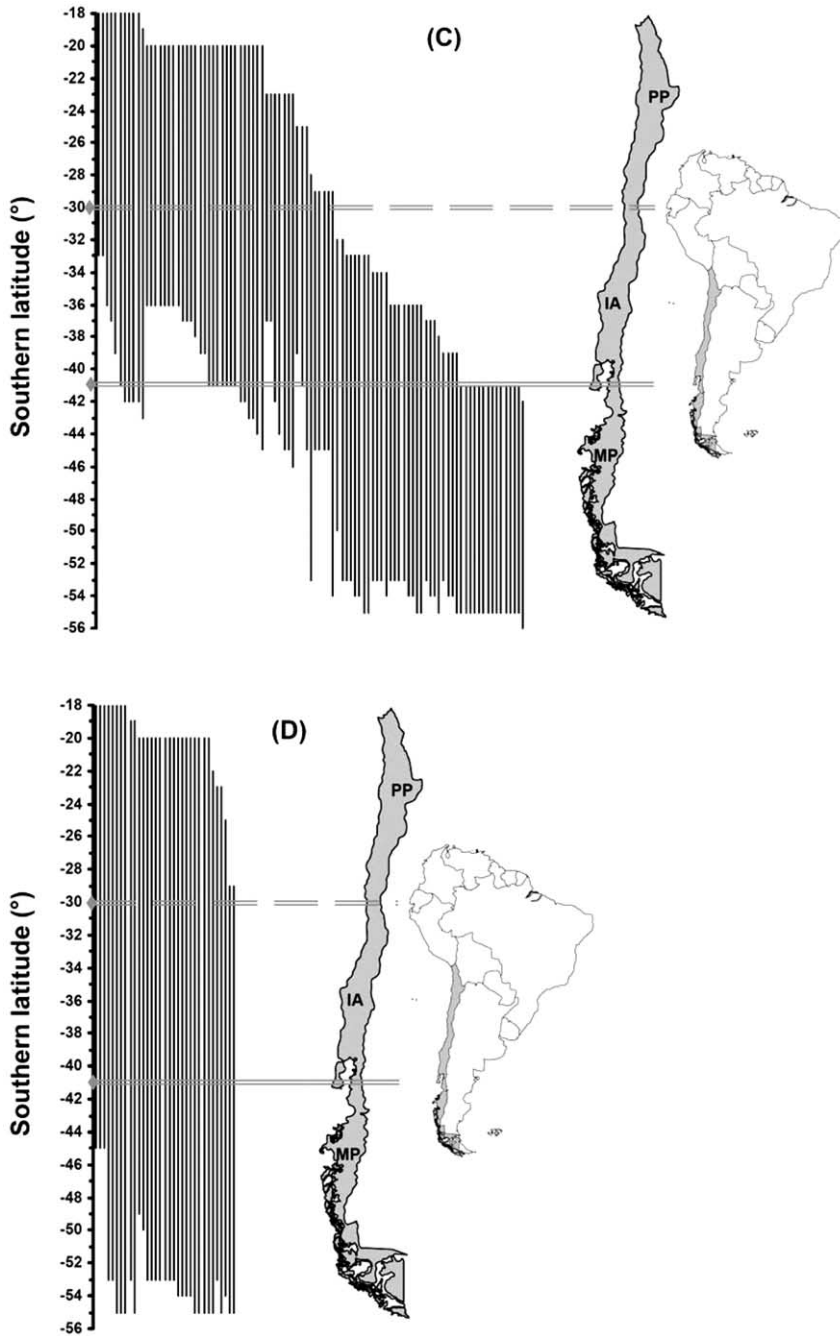


Fig. 1. The latitudinal extent of benthic polychaete species found along the Chilean coast. (A) 180 species recorded within only 1° of latitude; (B) 157 species with medium-small ranges of distribution from 2° to 14°; (C) 97 species with medium-large distributions ranging from 15° to 26°; and (D) 33 species with large distributions ranging from 27° to 37°. Each vertical bar represents the distribution of a single species. The horizontal gray lines show the limits of the three major biogeographical units described by Camus (2001): Peruvian Province (PP), Intermediate Area (IA), and Magellanic Province (MP).

number of times observed  $SS < \text{simulated } SS = 49\,999$ ;  $p = 0.0001$ ), indicating that the sum of squares was unusually low, and that the points that fell beyond the upper left boundary were clustered near to the boundary.

### Geometric constraint and species richness

The species-richness curves of each 3° band of latitude showed a weak mid-domain effect (Fig. 2). A compar-

ison of the empirical data with the prediction curves from the 95% simulation without replacement (i.e. randomization procedures) showed that 39% of empirical diversity points (5 of 13 points) occurred within the predicted range of the analytical–stochastic null model (Fig. 2). These points include one northern band of latitude (21°–23°S), one central band of latitude (36°–38°S), and three southern bands of latitude (42°–50°S). A comparison of the empirical data with the prediction curves from the 95% simulation with replace-

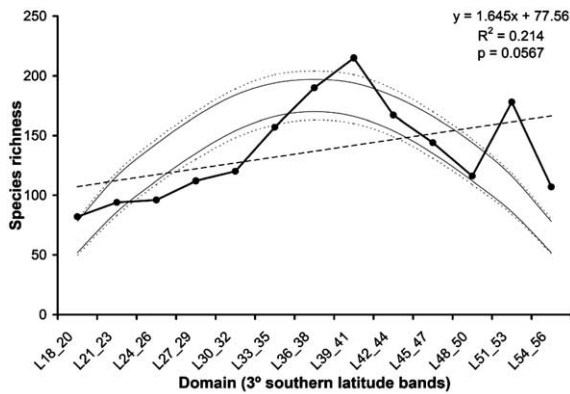


Fig. 2. Total number of benthic polychaete species found along the Chilean coast at each 3° band of latitude (black lines with data points). The dotted black line shows the standard linear regression fit to the data. The p-value is the result of randomization analysis (50 000 random matrices, random number seed = 12 345) to test the null hypothesis that the slope equals 0. The gray lines show the 95% prediction curves sampled without replacement (solid gray lines) and with replacement (dotted gray lines) using the program “Mid-Domain Null” (50 000 simulations).

ment (i.e. bootstrap method) showed that 46% of empirical diversity points (6 of 13 points) occurred within the predicted range of the analytical–stochastic null model (Fig. 2). This analysis included the same points as the prior analysis, but with one additional central band of latitude (33°–35°S). The two maximum points of species richness (39°–41°S and 51°–53°S) were in disagreement with the mid-domain peak in species richness.

## Discussion

### Patterns of latitudinal distribution

The analysis of distribution patterns of benthic polychaetes showed a progressive increase in diversity (alpha) from low latitudes towards more southern latitudes along the Chilean coast (Fig. 2). This pattern is in accordance with patterns of mollusk diversity in the southern Pacific (Valdovinos et al. 2003), as well as with the proposed pattern for polychaetes on the Chilean coast described by Lancellotti and Vásquez (2000). Nevertheless, of the four zones of maximum diversity registered by Lancellotti and Vásquez (2000) only that located in the zone of the Chiloé Archipelago corresponds to one of the two bands of maximum diversity registered in our analysis (i.e. 39°–41°S). In this band of maximum diversity the final points of distribution of various benthic polychaete species from the north and the south converge (Fig. 1B and C), whatsmore there are also various species with single records ( $n = 21$ , Fig. 1A). This situation suggests the existence of an ecotone

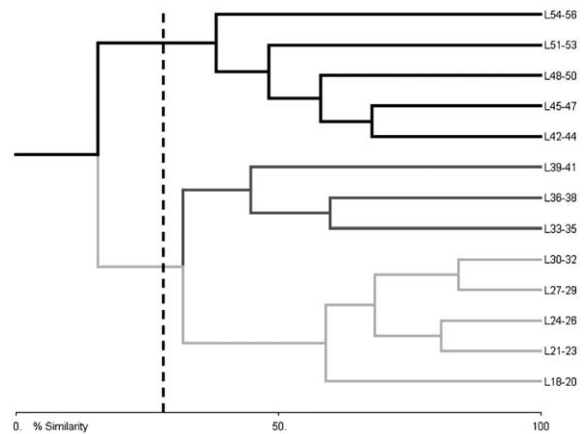


Fig. 3. Latitudinal similarity phenogram based on the presence or absence of benthic polychaete species found in 3° latitudinal sections along the Chilean coast. The dotted line indicates the level of similarity between pairs of latitudinal sections for which significant biogeographic units could be recognized in the phenograms after the application of a bootstrapping procedure. The different line tones in the phenogram indicate the three major biogeographical units described by Camus (2001): Magellanic Province (black lines), Intermediate Area (dark gray lines), and Peruvian Province (bright gray lines).

located at the Chiloé Archipelago, likely due to the great divergence of the oceanic current system around 41°S (corresponding to the Subtropical Convergence), which provokes a spatial differentiation of great magnitude along the coast (Castilla et al. 1993, Ahumada et al. 2000, Camus 2001). Around 41°S the West Wind Drift Current divides before reaching the coast, splitting into the north flowing Humboldt Current and the south flowing Cape Horn Current, from which the Fjord Current arises. This ecotonal boarder (i.e. the Chiloé Archipelago) between two coastal zones, could limit the patterns of distribution of various benthic polychaete taxa (Fig. 1B and C), which are not able extend their ranges of distribution due to tolerance limits to environmental variations (Camus 2001). This pattern has been reported for Porifera Demospongiae, Decapod Crustaceans, Bryozoans and Echinoderms (see Moyano 1991 and references therein). The zone south of 41°S has historically experienced the combined effects of climatic processes, tectonic activity and glaciers, provoking the formation of a great system of archipelagos with an abundance of golfs, fjords, and canals (Camus 2001). This has been associated with changes in local conditions (i.e. substrate types, tidal amplitude, temperature, and salinity) (Santelices and Meneses 2000), which would generate a highly diversified mosaic of different biotopes (Mariani et al. 1996), which would act as refuges during repeated glacial advances over the last 40 million years (Crame 1997). The sum of these factors would favor local radiation of the taxa, leading to the current area of high taxonomic diversity between 41° and 56°S (140 species with restricted distribution south of 41°S,

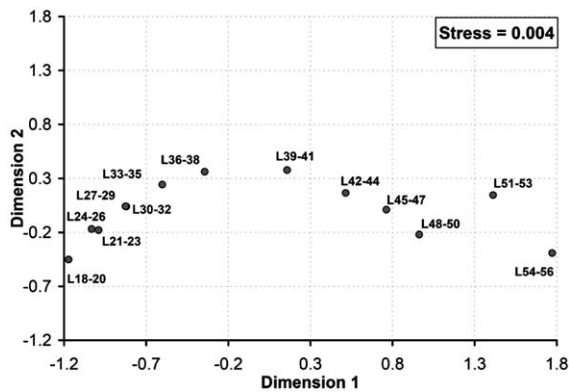


Fig. 4. The ordination analysis (nMDS) and Kruskal stress value for the nMDS configuration based on the presence or absence of benthic polychaete species found in 3° latitudinal sections along the Chilean coast.

Fig. 1 and 2), first affecting the presence of the second zone of maximum diversity, reported in our study for the subantarctic latitudinal band between 51° and 53°S, and secondarily causing a low faunistic affinity with the benthic polychaete taxa of the Antarctic Peninsula (Cañete et al. 1999).

In the northern zone, the bands of lowest diversity (18°–26°S) are characterized as being strongly influenced by the large-scale of low frequency spatial disturbances called El Niño/Southern Oscillation (ENSO), a phenomenon which provokes a series of alterations in the structure of the current system, and thus the coastal biota of the region, with regional scale influences up to 30°–36°S (Camus 1990, Gutiérrez et al. 2000). Since the appearance of ENSO ca 5000 yr ago (Rollins et al. 1986), the Southeastern Pacific biota has experienced a continuing disturbing influence, now ENSO is a critical component of the regional dynamic, which has played an important role in defining the current biogeography of the area (Fernández et al. 2000). According to Camus (1990), the characteristics of ENSO likely submitted local populations to frequent bottlenecks, and non-selective extinctions, which could generate high interpopulational variability and even provoke founder effects. These population level processes, together with ENSO should have produced increases in local diversity, however, our results did not support this hypothesis, although they did support the ENSO hypothesis as a cause of extinctions and low diversity in the zone. The low diversity of benthic polychaetes observed in the northern zone can probably also be attributed to a low speciation rate, due to the low differentiation of niches (i.e. low diversity of microhabitats) observed in this zone with respect to the zone south of 41°S, which would function as a biological mechanism determining local scale diversity (Shmida and Wilson 1985).

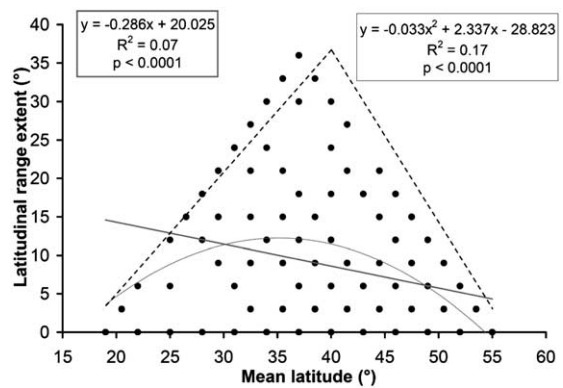


Fig. 5. Relationship between latitudinal range extent and range midpoint. The straight gray line shows the simple regression analysis, and the curved gray line shows the second degree polynomial model. The two dotted lines show the geometric shapes (pyramid) that best explained the data point distribution between both axes. Results of the linear regression fit are shown in the upper lefthand box and results from the second degree polynomial fit are shown in the upper righthand box.

### Evaluation of the biogeographical provinces

The results of the degree of faunistic similarity analyses between 3° latitudinal bands suggests the existence of two biogeographical units along the Chilean coast, the first occurring between 18° and 41°S, and the second between 42° and 56°S. These biogeographical units are in agreement with those previously described at the level of biogeographic provinces (i.e. the warm temperate zone and a cold temperate zone), based on the patterns of distribution of various benthic marine invertebrate taxa (see Dall 1909, Ekman 1953, Fernández et al. 2000). Nevertheless, our results do not concur with studies that recognize an extensive transition zone between both biogeographical units (Dahl 1960, Knox 1960, Brattström and Johanssen 1983, Thiel 2002) or an extensive (but not transitional) Intermediate Area, which includes mixed components of biota lacking a defined character and biogeographic range (Camus 2001). With respect to the polychaete fauna of the Chilean coast, the only previous extensive biogeographic study (Lancellotti and Vásquez 2000) also recognizes only two faunistic units, although, these units did not coincide with those proposed in our study. This discrepancy is probably due to the fact that in the study by Lancellotti and Vásquez (2000) the authors analyzed fewer species ( $n = 403$ ), fewer latitudinal bands ( $n = 10$ ), and did not use robust statistical analyses to determine the faunistic units (e.g. bootstrapping and nMDS analysis). In this sense, our results provide the first evaluation of the biogeographic limits of benthic polychaetes on the southeastern Pacific coast using robust statistical tests, and the second study where two statistically significant biogeographical units are recognized with a limit at the



zone of Chiloé (40°–41°S; see the study conducted by Ojeda et al. (2000) for littoral fish).

Finally, the general biogeographical model proposed by Camus (2001) for the Chilean coast at the level of biota (i.e. flora and fauna), only coincides with the latitudinal distribution of benthic polychaetes in the MP, in our study. The other two biogeographical units proposed in the model by this author do not agree with the results from our analysis of benthic polychaete taxa, which indicate that the PP and the IA constitute a single biogeographic unit (Figs 3 and 4). Nevertheless, it should be considered that the hypothesis proposed by Camus (2001) includes a review of distinct methodological focuses (the majority of which are qualitative), distinct types and quantities of data used, and distinct selection criteria of the study units, which potentially limit the recognition of general biogeographic patterns.

### Rapoport's rule and geometric constraint

Our results do not support a latitudinal Rapoport effect in the southeastern Pacific benthic polychaetes of the Chilean coast, as previously suggested for IndoPacific and Atlantic taxa (Rohde et al. 1993, Rohde and Heap 1996, Santelices and Marquet 1998, but see Macpherson and Duarte 1994). However, our data do support the view that latitudinal Rapoport effects are a local phenomenon (see Rohde 1996, 1999, Gaston and Chown 1999), occurring only for Northeastern Pacific marine taxa (Stevens 1996, Smith and Brown 2002, Smith and Gaines 2003). This means that southeastern Pacific benthic polychaetes may not experience marked seasonal environmental variation which Stevens (1989, 1992, 1996) suggested as a causal mechanism of Rapoport's rule. Specifically, for polychaete taxa found in the southeastern Pacific, the relationship of latitudinal range extent versus mean latitude can be explained by the geomorphology and historical characteristics of the Chilean coast (see discussion above in Patterns of latitudinal distribution, and Evaluation of the biogeographical provinces). However, since the polychaete species along the Chilean coast that occur in the lowest and highest mean latitudes tend not to have large geographic range extensions, and only species in middle latitudes have large geographic range extensions (Fig. 5), an alternative and complementary explanation for the observed pattern is the random placement of species' geographical ranges along a geographical gradient, like the mid-domain effect. This explanation is also supported by the idea that in the absence of environmental gradients, species' distributions may form patterns that depend on the geometric constraints of species' spatial distributions (Colwell and Hurtt 1994, Colwell and Lees 2000, Grytnes 2003). Nevertheless, our results only showed a weak level of mid-domain effect on species

richness (Fig. 2), where the relationship between latitudinal range extent and mean latitude indicates the existence of two hard boundaries at both extremes of the Chilean coast, limiting the geographical ranges of the species (Fig. 5). In the northern latitudes (18°S) this boundary is the result of the intense influence of the cold water of the Humboldt Current and the appearance of the warm water of the Peru Current. At southern latitudes (56°S) the boundary is formed by the end of the Cape Horn Current and the edge of continental shelf. Finally, we propose that geometric constraint together with the geomorphology and historical characteristics of the Chilean coast explain the biogeographical patterns of benthic polychaete taxa in Chile.

*Acknowledgements* – The authors are very grateful to Paula E. Neill for comments and suggestions that greatly improved the manuscript. This study was partially funded by grants awarded by IDEA WILD and FONDAP-FONDECYT 1501-0001 Programs 4 and 5 to the Center for Advanced Studies in Ecology and Biodiversity. C. E. Hernández was supported by a CONICYT Doctoral Fellowships.

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*Subject Editor: John Spence.*