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Do Rapoport's rule, the mid-domain effect or the source–sink hypotheses predict bathymetric patterns of polychaete richness on the Pacific coast of South America?

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ABSTRACT

Aim We evaluated the bathymetric gradient of benthic polychaete species richness from the Chilean coast, as well as its possible underlying causes. We tested three possible hypotheses to explain the richness gradient: (1) Rapoport's effect; (2) the mid-domain effect (MDE); and (c) the source–sink hypothesis.

Location South-eastern Pacific coast of Chile.

Methods The bathymetric gradient in richness was evaluated using the reported ranges of bathymetric distribution of 498 polychaete species, from the intertidal to abyssal zone (c. 4700 m). Rapoport's effect was evaluated by examining the relationship between bathymetric mid-point and bathymetric range extent, and species richness and depth. The MDE was tested using the Monte Carlo simulation program. The source–sink hypothesis was tested through nestedness analysis.

Results Species richness shows significant exponential decay across the bathymetric gradient. The pattern is characterized by a high presence of short-ranged species on the continental shelf area; while only a few species reach abyssal depths, and they tend to show extremely wide bathymetric ranges. Our simulation analyses showed that, in general, the pattern is robust to sampling artefacts. This pattern cannot be reproduced by the MDE, which predicts a parabolic richness gradient. Rather, results agree with the predictions of Rapoport's effect. Additionally, the data set is significantly nested at species, genus and family levels, supporting the source–sink hypothesis.

Main conclusions The sharp exponential decay in benthic polychaete richness across the bathymetric gradient supports the general idea that abyssal environments should harbour fewer species than shallower zones. This pattern may be the result of colonization–extinction dynamics, characterized by abyssal assemblages acting as 'sinks' maintained mainly by shallower 'sources'. The source–sink hypothesis provides a conceptual and methodological framework that may shed light on the search for general patterns of diversity across large spatial scales.

Keywords

Biogeography, macroecology, mid-domain effect, nestedness, Rapoport's bathymetric rule, source–sink hypothesis, South America, species richness.

INTRODUCTION

Bathymetric gradients of species diversity are among the most well-documented biogeographical patterns in the benthic marine realm (Vinogradova, 1959, 1962, 1979; Sanders &

Hessler, 1969; Rex, 1973; Pineda, 1993; Pineda & Caswell, 1998; Rex *et al.*, 2006). Yet, in spite of the numerous studies carried out during more than five decades, to date there is no consensus about the real shape of the species–richness pattern and its possible underlying causes (Gray, 2001; Levin *et al.*, 2001; Rex *et al.*, 2005b).

Perhaps the most commonly reported pattern of bathymetric benthic richness is the existence of a parabolic trend, where richness peaks at intermediate depths and declines towards shallower and deeper areas (Rex, 1973, 1981; Etter & Grassle, 1992; Paterson & Lamshead, 1995; Pineda & Caswell, 1998; Stuart *et al.*, 2003). Explanations for this parabolic pattern are many, including biotic interactions, speciation rates, food availability, productivity, habitat heterogeneity and boundary constraints (see Ricklefs & Schluter, 1993; Gray, 2001; Levin *et al.*, 2001; Rex *et al.*, 2005b). Among these, boundary constraints appear as a null model, offering a simple non-biological explanation for the parabolic pattern, just as proposed for the existence of a latitudinal gradient in species richness (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell *et al.*, 2004). Here, the parabolic pattern arises simply due to geometric constraints that limit the geographical ranges of species by acting as barriers to dispersal (see Grytnes, 2003). These constraints produce the mid-domain effect (MDE), which refers to the random placement of species geographical ranges along a geographical gradient with hard boundaries (i.e. a domain), imposing a massive overlapping of most of the species bathymetric ranges at intermediate depths. In the case of marine systems, these hard boundaries are the surface and the bottom of the ocean. The few evaluations of this non-biological hypothesis, however, have shown significant departures from the null model (see Pineda & Caswell, 1998; McClain & Etter, 2005), suggesting that other non-random factors may be acting to create the parabolic pattern.

Peaks of species richness across large spatial scales are often associated with the prevalence of short-ranged species, a pattern dubbed as 'Rapoport's rule' (Stevens, 1989, 1996), which 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 (Stevens, 1989). Although originally proposed to explain latitudinal gradients of richness, Rapoport's rule is also applicable to altitudinal and bathymetric gradients (Stevens, 1992, 1996). According to this rule, in a bathymetric context, there should be a correlation between species bathymetric ranges and the mid-point of their distributions, and zones with higher richness should contain species with shorter ranges (see Stevens, 1996 for details). Although its validity as a 'rule' has been heavily criticized (Gaston *et al.*, 1998; Hernández *et al.*, 2005; Kendall & Haedrich, 2006), studies on several marine taxa have reported the validity of the Rapoport effect (Stevens, 1996; Smith & Brown, 2002; Harley *et al.*, 2003; Smith & Gaines, 2003, but see Pineda, 1993; Pineda & Caswell, 1998; Kendall & Haedrich, 2006). These studies supporting the Rapoport effect show a strong monotonic decline in richness across the bathymetric gradient (i.e. maximum richness is observed in shallow zones). This fact immediately rules out the specific mechanism proposed by the original Rapoport effect, that short-ranged species should be associated with environments exhibiting little climatic variability (as in the case of tropical areas for the latitudinal gradient of richness; Stevens, 1989). Indeed, shallower marine environments are quite variable and dynamic, as opposed to highly stable abyssal zones (Levin *et al.*, 2001). Therefore, if valid, Rapoport's effect

requires another mechanism to explain the high richness observed in shallower zones (see also Smith & Brown, 2002; Kendall & Haedrich, 2006).

Recently, Rex *et al.* (2005a) proposed a novel hypothesis, the so-called source-sink hypothesis, suggesting that the bathymetric gradient of richness could be explained by some sort of source-sink dynamics. In this hypothesis, the species-depauperated abyssal zones are constituted by non-viable populations maintained only by the permanent migration of larvae from the richer bathyal areas, where populations are actively growing and reproducing. This hypothesis is supported by the fact that most abyssal species that have large bathymetric ranges are also present at shallower depths, and tend to have higher dispersal capabilities. In addition, abyssal zones tend to show extremely low abundances and biomasses (Rex *et al.*, 2005a,b, 2006), generated by the existence of a bathymetric gradient in productivity, which supports the idea that deep-sea assemblages are not self-sustained. Although Rex *et al.* (2005a,b) did use the source-sink hypothesis to explain the decline in diversity towards abyssal depths, not the whole parabolic pattern of benthic richness, the hypothesis is perfectly compatible with a monotonic decline in richness, and hence with the existence of Rapoport's effect.

In this study, we evaluated the bathymetric gradient of species richness in marine benthic polychaetes from the south-eastern Pacific Ocean of the Chilean coast, one of the most well-studied marine taxa in the region (e.g. Hernández *et al.*, 2005; Moreno *et al.*, 2006; Rozbaczylo & Moreno, in press). Most of the debate about the real shape of the bathymetric gradient, and its possible causes, has been conducted for species in the Northern Hemisphere; this the first study analysing the topic in this region of the world. Our specific goals were: (1) to evaluate the shape of the bathymetric gradient of richness, from intertidal to abyssal zones (0–4700 m); and (2) to test different hypotheses explaining the gradient, including Rapoport's effect, the mid-domain effect and the source-sink hypothesis.

MATERIALS AND METHODS

Data base

The data base utilized in this study consists of 498 species of benthic polychaetes, encompassing 241 genera and 47 families which are present on the south-eastern Pacific coast, ranging from 18° S (Arica) to 56° S (Cape Horn). This exhaustive data base was originally compiled by Rozbaczylo (1985) and was recently updated by Rozbaczylo and Moreno (in press), and is based on a comprehensive literature search, reviews of museum collections and field expeditions. This data base summarizes knowledge gathered during the last 158 years for the south-eastern Pacific coast, and is currently the most complete data set for polychaete taxa in this region of the world. All the information will be freely available in the aforementioned electronic catalogue.

For each species, we recorded the minimum and maximum depth of its distribution from the intertidal zone to *c.* 4700 m. The bathymetric range of each species was estimated as the

difference between the maximum and minimum depth recorded, and the bathymetric mid-point was calculated as the average of maximum and minimum depth. The bathymetric gradient of richness was estimated grouping species into 100-m depth bands, assuming a continuous presence of species across their bathymetric ranges.

Evaluation of sampling artefacts

Two types of analyses were performed in order to rule out possible artefacts. First, analyses were redone using species inhabiting the continental shelf zone (the upper 200 m of the gradient). Historically this zone has been the subject of most of the sampling effort, and hence by restricting the analysis to this area we avoid the sampling incompleteness which affects deeper areas. If sampling artefacts are not operating, then similar results should be expected. An analysis of the total number of occurrences (across all species) versus depth (using 100-m bins) showed a significant decline in the number of occurrences towards deeper zones ($r = -0.34$, $P < 0.019$, $n = 47$ bins). Indeed, as the bathymetric range estimated for each species is dependent on the number of occurrences used ($r = 0.35$, $P < 0.001$, $n = 498$ species), declines in richness may be generated simply as a result of incomplete sampling. In order to test this possible effect we performed simulation analyses, sequentially removing species with a given number of occurrences, and then recalculating the median (across species) of the bathymetric range and slope of the species richness–depth relationship (assuming an exponential decline, see Fig. 1) of the remaining species. The observed values were compared with expected values generated by simply bootstrapping the same number of species from the original data set. Observed values above the 95th and below the 5th expected percentiles indicated departures from the null model.

Analyses

We contrasted the bathymetric pattern of polychaete richness with the predictions of three hypotheses: (1) Rapoport's effect; (2) the MDE; and (c) the source–sink hypothesis. First, Rapoport's effect was evaluated by examining the relationship between median bathymetric range (across species) and depth, using 100-m depth bins. Rapoport's effect is expected if the relationship between both variables is positive, and species richness is negatively correlated with depth. Second, to test the MDE we compared the observed bathymetric pattern of species richness with a null model built by reshuffling species bathymetric ranges of distribution. The analyses were performed using a Monte Carlo algorithm simulation, implemented in the module Mid-Domain Null (McCain, 2003, 2004, 2005). Species-richness data (i.e. the number of benthic polychaete species) for each 100-m depth bathymetric range were compared with null model predictions using a Monte Carlo simulation of species-richness curves. Simulated curves were based on empirical range sizes within a bounded domain, using the analytical stochastic models of Colwell and Hurtt (1994) and Colwell (2006). We used 50,000 Monte Carlo simulations of empirical range sizes sampled

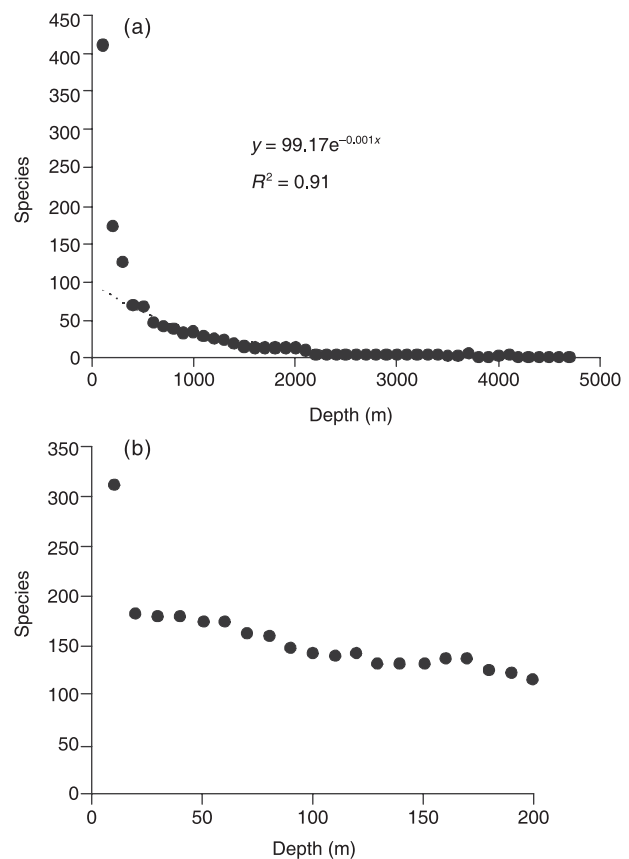


Figure 1 (a) Bathymetric gradient of polychaete richness using 100-m depth bands and (b) bathymetric gradient of polychaete richness for the upper 200 m, in 10-m depth bins.

without replacement (i.e. the randomization procedure) to calculate the amplitude of the 95% confidence simulation prediction curves (Manly, 1997; McCain, 2003, 2004, 2005; Hernández *et al.*, 2005; Moreno *et al.*, 2006). Third, we evaluated the source–sink hypothesis of Rex *et al.* (2005a). These authors have suggested a series of analyses to test this hypothesis (e.g. bathymetric patterns of resource availability, species relative abundance, body size, reproductive state and larval dispersal), but here we used a different and simpler methodological approach. Given that this hypothesis predicts that species in depauperated (abyssal) areas should be a subset of richer (bathyal) zones (Rex *et al.*, 2005a) we proposed that nestedness analysis would provide a robust way to test this idea. Nestedness analysis evaluates the degree of ‘order’ in a species assemblage through a simple presence–absence species–site matrix (Atmar & Patterson, 1993; Wright *et al.*, 1998). Nested assemblages are evident when impoverished sites tend to be simple subsets of the richest ones, suggesting a highly ordered system in which colonization/extinction dynamics may be actively shaping species occurrences across sites (Cutler, 1998). Indeed, the existence of colonization–extinction dynamics is core to the source–sink hypothesis. Briefly, the nestedness analysis evaluated the degree of disorder in the system as estimated by the ‘temperature’ (T) of the matrix, where $T = 0^\circ$ indicated perfect nestedness and

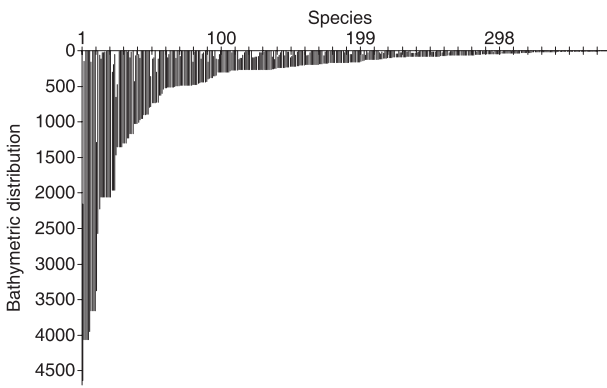


Figure 2 Bathymetric ranges of distribution of 498 polychaete species, from the intertidal zone to 4700 m in the south-eastern Pacific of the Chilean coast.

$T = 100^\circ$ indicated complete randomness. This method had been previously used by Smith and Brown (2002) to analyse the ‘orderliness’ in the bathymetric gradient of pelagic fishes, but not in the context of the source–sink hypothesis. Analyses were conducted at species, genus and family levels, where nestedness patterns above the species level have may been an indication of possible evolutionary processes. Calculations were performed using the BINMATNEST (binary matrix nestedness temperature calculator) program developed by Rodríguez-Gironés and Santamaría (2006).

RESULTS

Species richness showed a significant exponential decline across the bathymetric gradient (Fig. 1). Maximum richness occurred on the shallowest areas of the continental shelf (i.e. at a depth of less than 100 m), where 296 species were recorded. The intertidal zone was particularly diverse, with more than 300 species recorded for this fringe (Fig. 2). Richness declined quickly across the gradient where fewer than 70 species were found at 500 m depth. At zones deeper than *c.* 2000 m, fewer than 10 species were found. The abyssal area was considerably impoverished in species richness. The same trends were detected when analysis was restricted to species present in the upper 200 m of the gradient (Fig. 1b).

The simulation analyses showed that median bathymetric range calculated across species was strongly affected by the number of occurrences used (Fig. 3a). Median range was much larger for better-sampled species, and variation was above that expected by the null model. Nonetheless, the slope of the species–depth regression remained notably invariant and negative irrespective of the inclusion of less-sampled species, and small variations were within the natural variation expected by the null model (Fig. 3b).

We observed that a power equation model with two parameters presented the best regression coefficient (R^2) and a significant fit to the bathymetric range extent vs. range mid-point relationship (Fig. 4a). In parallel with the species–richness

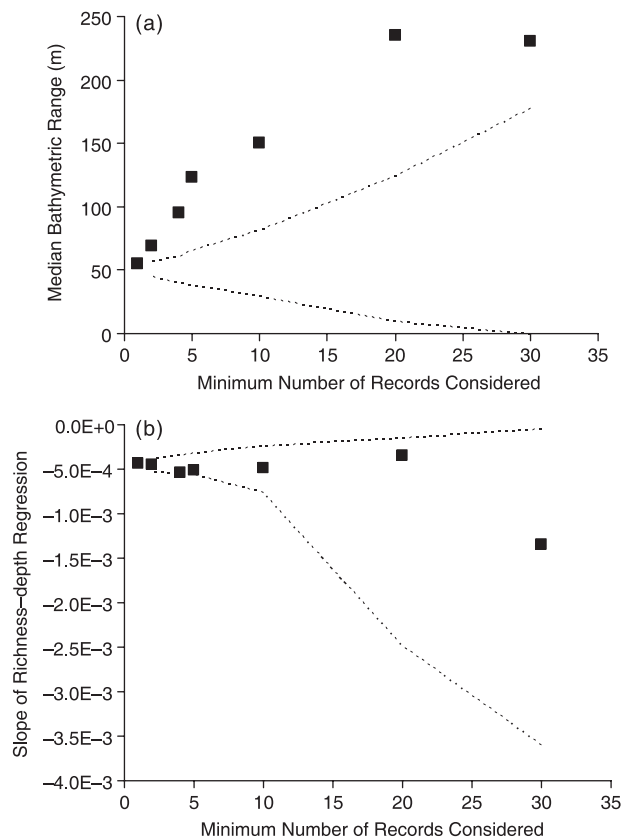


Figure 3 Changes in bathymetric patterns using different subsets of species with different numbers of depth records: (a) median bathymetric range and (b) slope of the richness–depth exponential regression. Dotted lines show the expectation under a null model based on resampling of the original data base.

gradient (Fig. 1a), this result showed an increase of bathymetric range extent towards greater depth (Fig. 4b). Species present within the upper 100 m have a median bathymetric range of only 60 m. In contrast, species inhabiting deeper areas tend to have bathymetric ranges of thousands of metres. These analyses support a bathymetric Rapoport effect.

The species–richness curves of each 100-m depth band did not show empirical support for the MDE (Fig. 5). A comparison of the empirical data with the prediction curve from the 95% simulation performed without replacement (i.e. randomization procedures) showed that only 10% of empirical diversity points (5 of 47 points) occurred within the predicted range of the analytical–stochastic null model (Fig. 5). This situation was notably different from the observed exponential decline pattern (Fig. 1a), with no significant fit to the empirical pattern (Fig. 5).

Species distribution across the bathymetric gradient was significantly nested, showing a high degree of order ($T = 0.29^\circ$, $P < 0.0001$). The same significant nestedness pattern with an extreme degree of order was also observed at both the genus ($T = 0.45^\circ$, $P < 0.0001$) and family ($T = 1.28^\circ$, $P < 0.0001$) levels. The high degree of nestedness above the species level was also corroborated by the fact that 85% of genera (203 out of 241) and

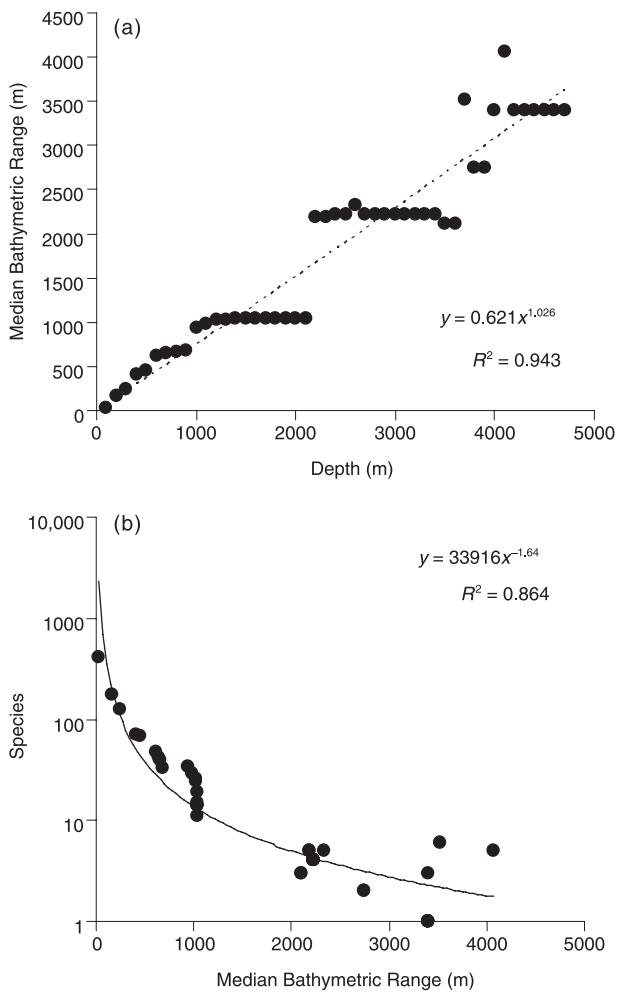


Figure 4 Evaluation of Rapoport's bathymetric effect: (a) bathymetric increase in the median bathymetric range and (b) relationship between species richness and median bathymetric range.

98% of families (46 out of 47) had a minimum bathymetric range of less than 100 m.

DISCUSSION

Our results showed the existence of a sharp bathymetric gradient in polychaete richness on the south-eastern Pacific coast of Chile, characterized by an exponential decline in richness from shallow to abyssal depths. Our pattern corresponds with some studies that show declining richness with depth (Schopf, 1969; Pineda & Caswell, 1998; Smith & Brown, 2002; Pérez-Mendoza *et al.*, 2003). In addition, although the absolute bathymetric pattern may be sensitive to sampling effort, the overall bathymetric trend (slope of the richness–depth regression) is notably insensitive to sampling bias, reinforcing the validity of our findings. Besides, when analyses were restricted to the upper 200 m (i.e. the coastal shelf), which traditionally corresponds to the best-sampled zone of the benthic realm, the same exponential decline was evident.

However, this very well-defined gradient does not correspond with other studies, which show a mosaic of different

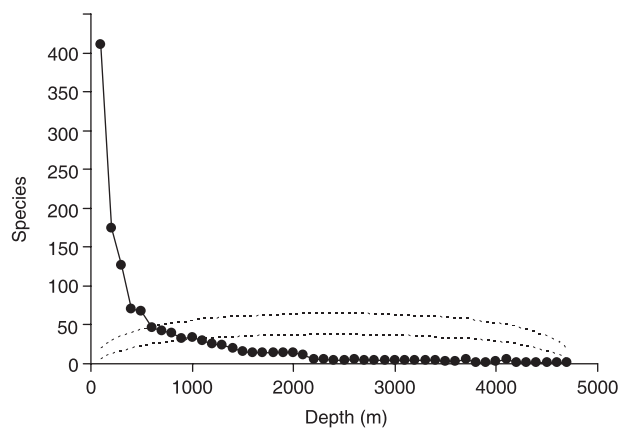


Figure 5 Total number of benthic polychaete species found along the Chilean coast in each 100-m depth band (black lines with data points). The dotted lines show the 95% prediction curves sampled without replacement using the program 'Mid-Domain Null' (50,000 simulations).

patterns (Sanders, 1968; Rex, 1973; Pineda, 1993; Paterson & Lambhead, 1995; Cosson-Sarradin *et al.*, 1998; Gray, 2001; Rex *et al.*, 2005a,b; McClain & Etter, 2005; Narayanaswamy *et al.*, 2005). Differences are mainly attributed to taxonomic or geographical variations (Dauvin *et al.*, 1994; Rex *et al.*, 2005b) or simply because there are not enough studies to make general statements (Gray, 2001). However, the kind of methodology used to evaluate the pattern should also be a concern. Traditionally, bathymetric gradients of richness have been analysed using local estimates, standardized through rarefaction procedures (Gray, 2001; Levin *et al.*, 2001; Rex *et al.*, 2005a,b), but this approach is not free of bias, particularly the unwarranted assumption of a similar distribution of species abundances across the gradient (e.g. see Gotelli & Graves, 1996). The classical approach used by terrestrial and coastal marine biogeographers (i.e. the use of the geographical ranges of species distribution to construct gradients of richness) circumvents the statistical problems of rarefaction, and provides a measure of gamma diversity. Nonetheless, its application to bathymetric questions is very recent (e.g. Rex *et al.*, 2005a,b; but see Schopf, 1969). However, even after restricting comparisons only to those studies following this approach a general pattern is still elusive. On the one hand, the existence of a sharp decline in richness towards deeper zones has been observed in a number of taxa (Schopf, 1969; Pineda & Caswell, 1998; Smith & Brown, 2002), in agreement with our results. On the other hand, a parabolic pattern of richness has also been described in several taxa from the northern Atlantic (Rex *et al.*, 2005a,b). Although all studies conclude the existence of impoverished abyssal zones, it is unclear whether maximum richness should be observed at shallower or intermediate zones of the slope. This lack of generality may simply be due to the notable paucity of studies. More comparative analyses are needed in order to establish whether the shape of the bathymetric gradient of diversity is universal or idiosyncratic.

The ultimate causes of the observed pattern are much more elusive, and several mechanisms have been proposed, with no

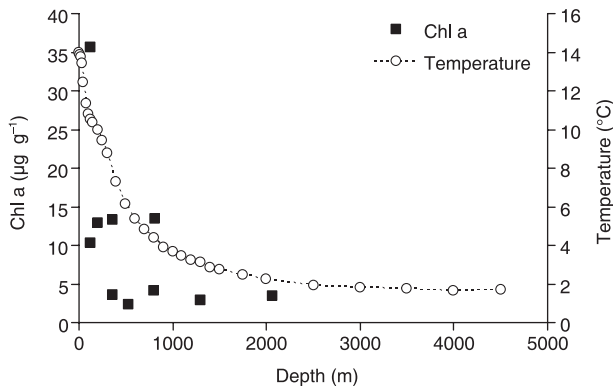


Figure 6 Bathymetric variation in sea temperature, and chlorophyll *a* concentration (Chl *a*) off central Chile. Sea temperature corresponds to an offshore point obtained from the World Ocean Atlas 2005 (37.125° S, 74.375° W). Chl *a* concentration corresponds to two sites sampled in the area of Concepción (c. 37° S), and was extracted from Quiroga *et al.* (2005).

definitive evidence supporting any particular hypothesis (Gray, 2001; Levin *et al.*, 2001; Rex *et al.*, 2005b). Of course, this lack of consensus is also tied to the multiplicity of reported patterns. A number of physical and ecological factors, including temperature, productivity, habitat heterogeneity, population density and biomass, also varied along the depth gradient, and they could be linked in a phenomenological way with the richness gradient (Cosson-Sarradin *et al.*, 1998; Gray, 2001; Levin *et al.*, 2001; Rex *et al.*, 2005a,b; Narayanaswamy *et al.*, 2005).

During the last decade, a geometric constraint has been increasingly considered as the null hypothesis against which to test spatial patterns of richness. However, our results contrasted markedly with expectations of the null model. Indeed, two previous evaluations showed that even the parabolic gradient of richness is not well explained by the null model (Pineda & Caswell, 1998; McClain & Etter, 2005), hence invoking the existence of non-random factors generating the gradient. In contrast, our results support another pattern, i.e. the existence of Rapoport's effect (Stevens, 1989, 1996), where the highly diverse shallower zone is composed mainly of short-ranged species. However, the original mechanism proposed to explain this pattern, the existence of a highly variable environment in the depauperate zones, clearly does not apply in our system, given that deep-sea environments are comparatively more stable than shallower ones (Levin *et al.*, 2001; Smith & Brown, 2002).

Productivity is a common oceanographic variable linked to the structure of benthic assemblages (Cosson-Sarradin *et al.*, 1998; Paterson *et al.*, 1998; Palma *et al.*, 2005), and therefore authors have tried to explain bathymetric gradients of richness in terms of some sort of diversity–productivity hypothesis (Gray, 2001; Rex *et al.*, 2005b). Although we do not have enough information to test this idea, our preliminary analyses show that sea temperature and a productivity proxy (chlorophyll *a*) decline in a similar way on the south-eastern Pacific coast (Quiroga *et al.*, 2005) (Fig. 6). This may be used to claim some

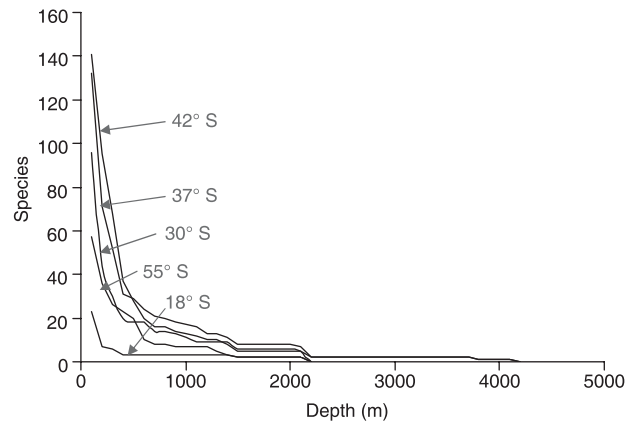


Figure 7 Bathymetric gradient of polychaete richness at different one degree latitudinal bins along the Pacific coast of South America.

support for a diversity–productivity hypothesis (e.g. Smith & Brown, 2002).

Another possibility is that the extremely shallow oxygen minimum zone (OMZ) characterizing the Humboldt Current System (Levin, 2002, 2003; Helly & Levin, 2004), a well-know factor depressing the diversity of local benthic assemblages in the region (Gallardo, 1963; Levin *et al.*, 2002; Levin, 2003; Gallardo *et al.*, 2004; Palma *et al.*, 2005; Quiroga *et al.*, 2005), could be also operating at a regional scale constraining the diversity at mid-depths. Therefore, the OMZ could be ‘pruning’ the ‘canonical’ parabolic gradient of diversity, creating the monotonic gradient. However, this explanation seems very unlikely. If the OMZ hypothesis is correct, south of 37° S, where the OMZ is weak or non-existent (Helly & Levin, 2004), the gradient of diversity should exhibit the classic parabolic pattern. This is not the case (Fig. 7), and the monotonic decline in diversity is evident across the entire region, even in the absence of a sharp OMZ.

All previous hypotheses are merely correlational and offer little insight into the real processes and mechanisms accounting for the phenomenon. Recently, Rex *et al.* (2005a) proposed a different and novel hypothesis, providing a conceptual framework for the phenomenon. They proposed that the bathymetric gradient of richness is governed by a source–sink dynamics, where depauperate deep zones (sinks) are constituted by non-viable populations maintained via dispersal from the more active shallow areas (sources). We should note, however, that in its original formulation, the source–sink hypothesis was only intended to explain the decline in richness from bathyal to abyssal depths (Rex *et al.*, 2005a). Nonetheless, there is no a priori reason to restrict the hypothesis to only bathyal to abyssal depths. Moreover, the hypothesis offers a much more general and parsimonious explanation for monotonic gradients of diversity (as showed by our analysis), in opposition to parabolic gradients observed in Rex *et al.* (2005a), since it can be applied to the whole bathymetric range of analysis.

Source–sink dynamics were originally proposed by Pulliam (1988) to highlight the role of differential colonization/extinction dynamics across the space, and its impact on patterns at population

and community levels, and the concept is closely related to rescue and mass effects (Brown & Kodric-Brown, 1977; Shmida & Wilson, 1985). Indeed, Lomolino (2001) suggested the importance of rescue and mass effects shaping altitudinal gradients of diversity. Our results provide strong support for the source–sink hypothesis, based on the existence of a bathymetric Rapoport effect, and the existence of significantly nested assemblages, as previously observed in pelagic fishes (Smith & Brown, 2002). In addition, other lines of evidence could also be used to evaluate the hypothesis (e.g. bathymetric patterns of body size, morphological disparity, larval types; McClain, 2005; McClain *et al.*, 2005; Rex *et al.*, 2005a). The elevated richness in shallow water is associated with a greater number of species with restricted bathymetric ranges, but at the same time, the more depauperate deeper assemblages emerge simply by the penetration of a few shallow water forms with wider bathymetric ranges. In other words, deep-water species are essentially an impoverished subset of the shallow-water assemblage. Furthermore, the abundance and biomass of deeper faunas is notably lower in comparison with shallow-water assemblages of Pacific South America (Quiroga *et al.*, 2005), in agreement with that observed in regional and global scale compilations (Rex *et al.*, 2005b, 2006) and with the preliminary correlation between richness and productivity (see above).

This integrated picture suggests that colonization–extinction dynamics should be crucial for shaping the bathymetric gradient of richness, according to the source–sink hypothesis. These dynamics may be taking place not only on an ecological time-scale but also on evolutionary time-scales. Our analyses demonstrate that the vast majority of genera and families (> 85%) inhabit very shallow-water zones (< 100 m), hence corroborating the existence of a nested pattern evident above the species level. This pattern suggests that evolutionary novelties would appear in shallow-water zones, then disperse towards deeper zones, similar to palaeontological evidence reported for several benthic groups (Jablonski *et al.*, 1983; Jablonski & Bottjer, 1991). Shallow-water zones would act as both ‘nests’ and ‘cradles’ of diversity, promoting the appearance of new forms, further dispersing towards deeper zones, like the ‘out of the Tropics’ hypothesis explains the existence and maintenance of the latitudinal gradients of richness (Jablonski *et al.*, 2006). Although the polychaete fossil record is very poor, further analyses of dispersal modes (e.g. Rex *et al.*, 2005a) as well as phylogenetic analyses could be used to verify this hypothesis.

We have shown that the richness of benthic polychaete species declines exponentially across a 4700-m depth gradient in the Pacific South America region. Our results are in agreement with predictions for the source–sink hypothesis, suggesting that some kind of processes involving colonization–extinction dynamics may be responsible for the gradient. If correct, the source–sink hypothesis highlights the importance of shallow areas for overall marine biodiversity. Hence, the varied human impacts over coastal ecosystems may have a profound impact on the evolutionary history of the taxa. The source–sink hypothesis provides not only testable predictions about underlying processes, but also, more importantly, it provides a conceptual scheme for

improving our understanding of the bathymetric richness gradient phenomenon.

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