

LETTER

Deconstructing latitudinal species richness patterns in the ocean: does larval development hold the clue?

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Abstract

The consistent decrease in species richness with latitude shows several exceptions among marine organisms. We hypothesize that contrasting latitudinal diversity gradients can be explained by differences in critical life-history attributes, such as mode of larval development (MLD). We deconstructed latitudinal species richness patterns of marine benthic invertebrates according to MLD to elucidate differences in patterns of species richness and to reveal underlying processes. The patterns of species richness were remarkably similar across taxa within MLD but differed between MLD. Species richness decreased polewards in planktotrophic species and increased in direct developers. Temperature explained most of the variation in species richness. Low temperature at high latitudes may generally favour direct developing species, but, together with low chlorophyll-*a* concentration, limit the distribution of planktotrophic species. The contrasting influence of temperature on different MLDs might be explained by its effect on the length of planktonic life and on brooding costs.

Keywords

Diversity patterns, larval development, primary production, temperature.

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INTRODUCTION

The sharp systematic change in species richness with latitude, altitude and depth is one of the most intriguing patterns in nature (Hillebrand 2004). However, the typical decrease in species richness towards high latitudes observed in most taxonomic groups and environments (Roy *et al.* 1998, 2000; Macpherson 2002; Hillebrand 2004) exhibits several exceptions among benthic marine organisms (Myers 1996; Clarke & Crame 1997; Valdovinos *et al.* 2003). In the south-eastern Pacific the classic decline in species richness reverses south of 40 °S, where the number of species of molluscs, echinoderms and polychaetes doubles the counts observed equatorwards of 40 °S (Lancellotti & Vásquez 2000; Valdovinos *et al.* 2003; Hernández *et al.* 2005). The causal factors proposed to explain the classic and reverse latitudinal patterns of species richness also differ among

regions, further complicating the problem of identifying the general processes behind these patterns (Blackburn & Gaston 2003). For instance, the tight covariation between sea surface temperature (SST) and mollusc species richness along the Pacific and Atlantic coasts of North America was not found in the south-eastern Pacific (Roy *et al.* 1998, 2000; Valdovinos *et al.* 2003). Thus, the energy input hypothesis, which explains mollusc diversity in the Northern Hemisphere (Roy *et al.* 1998, 2000), does not apply to south-eastern Pacific molluscs where coastal geomorphological complexity and shelf area are better predictors of total mollusc species richness (Valdovinos *et al.* 2003). It is remarkable that in the same region, in the Southern Hemisphere, SST is an excellent predictor of the decrease in species richness of anomuran and brachyuran crabs towards high latitudes (Macpherson 2002; Astorga *et al.* 2003).

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Marquet *et al.* (2004) hypothesized that the opposing patterns of species richness, and the contrasting causal factors identified to explain them, might be related to the coarse way species richness is usually quantified. The deconstructive approach proposed by Marquet *et al.* (2004) is based on the observation that, in general, species assemblages are not symmetric or homogeneous in the biological attributes of their constituent species, and that the prevalent approach of simply counting numbers neglects among-species biological differences that might be fundamental for understanding ecological patterns in general, and latitudinal ones in particular. Deconstructing species richness according to biological attributes may thus help to understand differences in patterns of species richness and also to reveal underlying processes. From this perspective, different patterns of species richness can be expected between taxa or regions as a result of the interaction between species' attributes and the environmental context in which they are embedded. We used this general approach to test the hypothesis that the disparate latitudinal patterns of species richness of marine invertebrates reflect differences in species' life-history attributes, namely larval developmental modes, which in turn determine contrasting responses to environmental variables.

Larval developmental mode has been shown to be a critical life-history attribute of marine species with deep ecological, biogeographical and evolutionary consequences because it affects population dynamics, potential for dispersal, speciation and extinction rates, as well as range size distribution (Jackson 1974; Shuto 1974; Hansen 1980; Burton & Feldman 1982; Jablonski & Lutz 1983). Moreover, some of the taxa failing to conform to the classic latitudinal diversity pattern exhibit non-feeding larvae (Protobranch Bivalves; Roy *et al.* 2000) or lack a larval phase (Valentine & Jablonski 1983). Marine invertebrates show an enormous diversity of larval development modes, which according to their feeding strategy can be broadly classified into feeding (planktotrophic) or non-feeding (lecithotrophic; Poulin 2001). Species showing non-feeding larvae can develop in the plankton (planktonic development) or lack a planktonic stage (direct development; Poulin 2001). The larvae of planktotrophic species develop in the water column which confer them high dispersal potential, leading to higher gene flow among populations and also to lower potential for isolation and speciation (Jablonski & Lutz 1983). In contrast, species with direct development show restricted dispersal, lower connectivity and higher potential for isolation. Due to these biological differences, the effect of temperature is expected to differ between species with different modes of larval development. Cold water temperatures decrease developmental rate (Gillooly *et al.* 2002) which in turn increases the residence time of larvae in the plankton (O'Connor *et al.* 2007). Long larval residence time

increases the distance that larvae can be passively dispersed, thus reducing opportunities for isolation and speciation. Although temperature also affects development rates of direct developers, its effect on early stage survival cannot be easily anticipated because in these species larvae develop inside protective structures. However, direct developers might face lower reproductive costs and, therefore, potentially greater ecological success towards higher latitudes as lower water temperatures support higher oxygen concentration, and dissolved oxygen is a limiting factor affecting the capacity to aggregate embryos and larvae as well as the cost of brooding (Brante *et al.* 2003).

Thorson's (1950) broad and comprehensive study reports a decrease in the frequency of planktotrophic species towards the poles, which was attributed to the lack of food throughout the extended length of larval development at low temperatures. Productivity, or energy availability, is usually identified as an important driver of species richness in terrestrial ecosystems through two general mechanisms (e.g. Hawkins *et al.* 2003; Evans *et al.* 2005, 2008). The individual mechanism suggests that higher productivity will on average allow species to achieve higher local abundance, increasing population persistence and potentially species diversity by reducing extinction. On the other hand, the sampling mechanism suggests that productivity enhances diversity by increasing the total number of individuals at regional scales (i.e. regional assemblage), whose random allocation to local areas generates a positive species–energy relationship (Evans *et al.* 2008). We hypothesized that the sampling mechanism is most likely to apply to planktotrophic species with high dispersal capability, while the more individual mechanism may hold for the species with direct development. Considering in addition the effect of temperature, our hypothesis leads us to predict the following: (1) a strong positive species–energy relationship for planktotrophic and direct developers, although for different reasons; (2) a strong positive association between richness of planktotrophic species and SST; (3) a weak or negative association between SST and richness of direct developing species, and (4) strong positive association between species richness of direct developing species and shelf area as a consequence of their restricted dispersal and the heterogeneity and opportunities for isolation that characterized the Fjord region in southern Chile (Valdovinos *et al.* 2003). No clear pattern is expected for planktotrophic species.

MATERIALS AND METHODS

To test our hypotheses we studied latitudinal patterns of species richness of marine benthic invertebrates along the Chilean continental shelf, which encompasses 36 degrees of latitude and little variation in longitude (70–75 °W),

comparing species exhibiting only planktotrophic development against species with direct development. Two taxa, crustaceans and molluscs, with markedly different evolutionary histories but exhibiting planktotrophic and direct developmental modes were included in the analysis to make a more powerful and general comparison. As spatial variation in species richness may result from the direct effects of environmental variables, from a shared spatial structure between species richness and the environmental variables, or from spatial autocorrelation of species richness itself (i.e. other biotic or abiotic processes that produce a given spatial structure in species richness; Legendre & Legendre 1998), our analysis evaluated the relationships between diversity and each environmental variable considering their spatial structure. This is the first study that explicitly deconstructs patterns of species richness considering relevant life-history attributes of marine species, while at the same time assesses the effect of the spatial structure of environmental variables.

Database

The database includes benthic shallow water crustacean and mollusc species inhabiting the continental shelf (< 200 m depth) from 18 °S to 54 °S in the south-eastern Pacific. Data were obtained through an exhaustive search of the primary literature, as well as from museum collections and records of scientific expeditions. Molluscs and crustaceans have been extensively sampled by individual taxonomists and major research expeditions since the late 1800s in Chile (Valdovinos 1999; Boschi 2000 and references therein). The database contains information on the distribution of 859 species; 564 molluscs (374 Gastropoda, 139 Bivalvia and 51 Polyplacophora) and 295 species of crustaceans (47 Anomura, 88 Brachyura, 69 Isopoda and 91 Amphipoda). Both databases have already been used in recent studies (Astorga *et al.* 2003; Valdovinos *et al.* 2003). Single reports were excluded. Data on larval developmental mode were available for all crustaceans as each clade is locked to a single mode of larval development (MLD). Anomura and Brachyura exhibit planktotrophic development (except for two anomuran species with planktonic lecithotrophic development reported for southern Chile), whereas all species of Isopoda and Amphipoda exhibit exclusively direct development. In the case of molluscs, information on modes of larval development was obtained from intensive literature searches and interviews with expert scientists on invertebrate zoology, taxonomy, ecology or aquaculture at 11 major universities in Chile. The data obtained from the interviews were based on observation or unpublished data and in no case did we use expert judgement or assign the species to a larval development category based on information from related species. We gathered information

on larval development modes for 35% of the species, a level of information that is comparable to other geographical areas (e.g. Pacific Northwest, Strathmann 1987). However, as our goal was to compare molluscs and crustaceans, we excluded species with planktonic lecithotrophic larvae from the analysis because only two crustacean species of our database exhibit this MLD. Therefore, only 74 mollusc species were finally included (13.12%). The subset of the data for which we had information on developmental modes (planktotrophic or direct) includes 30 families out of 108 families of the whole mollusc assemblage (27.8%) and 51 genera out of 246 (20.7%). The average and median range size of the 74 species used in this study was within the 95% confidence interval of random samples taken from the entire database of 564 molluscs (CI = 16.34–20.72; bootstrap analysis of 10 000 random samples of 200 species each).

Three environmental variables were evaluated: mean SST, minimum surface chlorophyll-*a* concentration (chl-*a*) and continental shelf area. Mean SST was obtained as weekly averages for the past 17 years over 1° of latitude and 1° of longitude alongshore, and is publicly available through the FERRET server of the National Centers for Environmental Prediction (<http://ferret.wrc.noaa.gov/Ferret/las>). Temperature at depths of 50, 100 and 150 m are well correlated with SST, therefore mean SST can be used as an environmental correlate for benthic taxa inhabiting the continental shelf. Minimum chl-*a* concentration was obtained as 8-day averages from SeaWiFs satellite images for 4 years (1997–2000), averaged alongshore for the first 12 km cross-shore per degree of latitude. Chlorophyll-*a* concentrates mainly near the coast, showing lower concentrations beyond this 12 km cross-section (Thomas 1999). Minimum chl-*a* was used as it could better represent limiting food conditions for feeding invertebrate larvae in the water column. In fact, minimum chl-*a* showed better correlations with species richness than any of the other chl-*a* measurements (mean, maximum, range of chl-*a*). Although we recognize that available chl-*a* is a crude estimate of food availability for feeding larvae (Vargas *et al.* 2006), at this point there is no other source of information over the spatial scales involved in this study. Continental shelf area was calculated by digitizing a 1 : 10⁶ scale Lambert Zenithal Azimuthal equal area projection map down to the 200 m isobath (continental shelf). Given the coarse scale of this map and the measurement error, the values should be considered relative rather than absolute measures of area. As our study comprised such a large extent, we obtained environmental data (SST and chl-*a*) mainly from available satellite information on the web, and therefore it was difficult to obtain exact matching data in terms of temporal and spatial scales (number of years or km from the coast). However, both SST and chl-*a* were measured within the

continental shelf (area for which we had species richness data) and within a one-degree longitudinal band cross shore (area where the species included in our analyses concentrate), therefore they provide a good representation of large-scale patterns within the continental shelf. Similar environmental data have been used in studies assessing large-scale patterns of species richness (Roy *et al.* 1998, 2000; Macpherson 2002; Valdovinos *et al.* 2003).

Data analyses

All the analyses were performed separately for each larval developmental mode and each taxonomic group. Species richness was determined as the sum of all species whose along-shore ranges crossed a one-degree latitudinal band. We assumed continuous distributions between the northern and southernmost collection sites. First we explored the relationships between species richness and each of the environmental variables included in our analysis. As correlations were found among the environmental variables, squared semi-partial correlation coefficients (r^2) in a standard multiple regression model (Tabachnik & Fidell 1989; Freckleton 2002) allowed us to estimate the unique contribution of each environmental variable to the total variance in species richness for each larval developmental mode.

The squared semi-partial correlation analysis allows for statistical control of variation in other co-variables, but does not account for patterns of spatial structure in the data. To test for the effect of the spatial structure of the data (Legendre & Legendre 1998; Lichstein *et al.* 2002; Diniz Filho *et al.* 2003), we used partial regression to partition the variance explained by the environmental variables and that explained by the spatial structure alone. The environmental model was built including all the three variables and manually selecting the significant ones. The contribution of spatial structure to variation in species richness, was modelled using a third-order polynomial equation ($f(x,y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$), where x and y represent the centred longitude and latitude respectively. For the environmental and spatial models, Akaike Information Criterion was used to select the best model (Burnham & Anderson 2002). Using partial regression we obtained three coefficients of determination for the three general linear models: one combining significant environmental variables and spatial variables, one including only significant spatial variables and the third including only significant environmental variables. By comparing these three coefficients of determination we were able to obtain the unique contributions of each component for each taxonomic group and developmental mode. Thus, species richness of crustaceans and molluscs was partitioned into four components: (a) pure environmental (local effects of the environmental variables on

species richness), (b) spatially structured environmental (shared spatial pattern between species richness and the environmental variables), (c) pure spatial (biotic or abiotic factors not evaluated in the analysis that are causing variation in species richness) and (d) unexplained (residual) variation (Legendre & Legendre 1998). Variance partitioning was done using the *vegan* package in R program (Oksanen *et al.* 2008). This analysis had two primary aims: (i) to avoid false correlations between species and environmental variables that may arise when unmeasured environmental factors show the same spatial structure than the environmental variables considered in the model, and (ii) to determine if there is a substantial amount of broad-scale spatially structured variation in species richness unexplained by the measured environmental variables (Lichstein *et al.* 2002).

RESULTS

Latitudinal patterns

The overall latitudinal trend of mollusc and crustacean species richness showed contrasting patterns (Fig. 1a,b). Mollusc species richness was nearly constant from 20 °S to 40 °S increasing steeply towards higher latitudes (Fig. 1a). Similar patterns of increasing species richness towards higher latitudes were found when the different orders of molluscs (bivalves, gastropods and chitons) were plotted individually (see Valdovinos *et al.* 2003). In contrast, crustaceans showed a smooth increase in species richness from 18 °S to 30 °S remaining relatively constant towards the south (Fig. 1b). In this case, different patterns of species richness were observed among the different orders of crustaceans (amphipods, isopods and decapods; Fig. 1d,f).

When overall species richness was deconstructed by larval developmental mode, similar and clear patterns were found within each MLD for both phyla (Fig. 1c–f). Monotonic increases in species richness towards high latitudes were found for species with direct development (Fig. 1c, d), whereas richness of species with planktonic development remained relatively constant between 18 °S and 35 °S, and then decreased polewards (Fig. 1e,f). The trends were remarkably similar in both phyla in spite of the contrasting patterns of overall species richness (Fig. 1a,b) and differences in sample size. The parallel patterns within major crustacean taxa are also noteworthy. Within direct developing (amphipods and isopods; Fig. 1d) and planktonic decapod crustaceans (brachyuran and anomuran crabs; Fig. 1f), the species richness of different taxonomic groups showed similar relationships with latitude. We did not explore patterns within major taxa of molluscs given the small number of mollusc species included in our analysis.

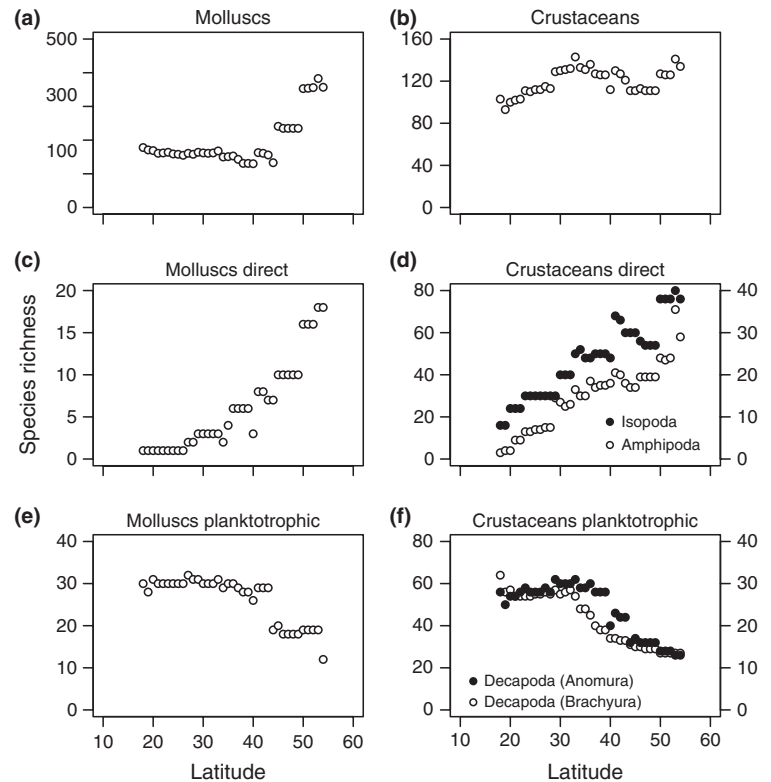


Figure 1 The overall latitudinal patterns of species richness for molluscs (a) and crustaceans (b) along the coast of Chile was deconstructed by larval developmental mode between species exhibiting direct development of molluscs (c) and crustaceans (d) and species showing planktotrophic larvae of molluscs (e) and crustaceans (f). For crustaceans we plotted separately amphipods and isopods (d) and decapods (anomuran and brachyuran crabs; (f). In Fig. 1d, the y-axis on the right corresponds to anomura and on the left to brachyura. Similarly in Fig. 1f, the y-axis on the right corresponds to isopods and on the left to amphipods.

Relationship between species richness and environmental variables

SST was the environmental variable that showed the most clear and consistent relationship with species richness for each MLD. A negative relationship between species richness and SST was found for direct developing species in both phyla (Fig. 2a), while the opposite trend was observed for planktotrophic species (Fig. 2b). In fact, the unique contribution of SST to the total variance in mollusc and crustacean species richness along the entire coast of Chile was always significant and the highest explanatory variable in semi-partial correlation analyses (Table 1).

Contrasting patterns were also found between larval development types for the relationships between species richness and shelf area or species richness and chl-*a* (Fig. 2 and Table 1). In general, a negative relationship between species richness and chl-*a* was observed for direct developing species in both phyla (Fig. 2a), and the opposite pattern for planktotrophic species (Fig. 2b). However, the unique contribution of chl-*a* concentration to the total variance in species richness was only significant for crustaceans with direct development, for anomuran crabs and for molluscs with planktotrophic development (Table 1). It is important to point out that species richness showed high variance within 0.1 and 0.2 mg m⁻³ of

chlorophyll-*a* in both phyla within the geographical region encompassed between 18 °S and 32 °S. In general, chl-*a* explained a small fraction of the variance in species richness, but about three times as much among planktotrophic than direct developing species.

Shelf area explained a small but significant fraction of the total variance in crustacean species richness for both modes of larval development (Table 1). In spite of the similar trends between shelf area and species richness within MLD in both phyla (Fig. 2a,b), the unique contribution of shelf area did not explain a significant fraction of the total variance in mollusc species richness (Table 1).

Variance partitioning

The environmental variables that had a significant unique contribution in the semi-partial correlation analysis (see Table 1) were also selected in the environmental model, for each taxa and mode of development (Table 2). Different arrangements of environmental and spatial variables were significant for each group and developmental mode (Table 2). The spatial models always retained different combinations of spatial variables (latitude and longitude), which generally explained high percentage of species richness variation (Table 2). The

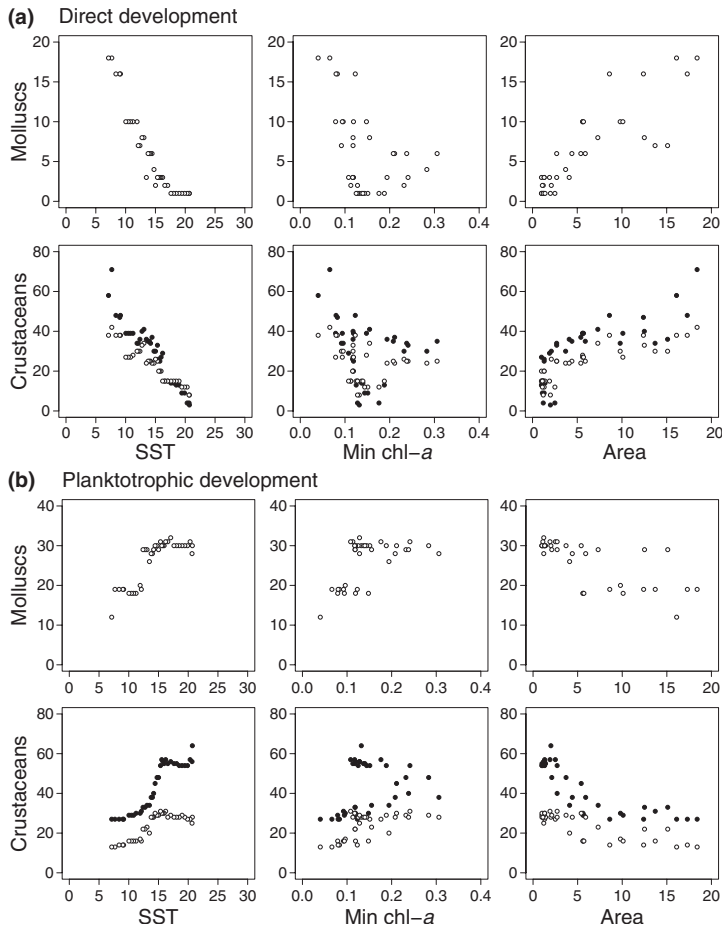


Figure 2 Relationship between environmental variables and species richness for both modes of larval development and taxonomic group: (a) direct development and (b) planktotrophic development. Crustaceans are shown individually for Decapods (Anomura and Brachyura), Amphipoda and Isopoda. Environmental variables included here are: sea surface temperature (°C; SST), minimum chlorophyll-*a* concentration (mg m⁻³; min chl-*a*) and continental shelf area (km² × 1000; Area).

Taxonomic group per mode of development	SST	chl- <i>a</i>	Area	Shared	Total
Direct molluscs	0.1650	0.0081	0.0162	0.7176	0.9069
Direct crustaceans	0.2643	0.0220	0.0075	0.6683	0.9621
Planktotrophic molluscs	0.1884	0.0637	0.0004	0.4983	0.7508
Planktotrophic crustaceans	0.1528	0.0007	0.0220	0.5753	0.8632
Amphipoda (direct)	0.2740	0.0159	0.0036	0.6312	0.9247
Isopoda (direct)	0.1844	0.0207	0.0287	0.7427	0.9351
Decapods; Brachyura (planktotrophic)	0.1773	0.0076	0.0213	0.6620	0.8682
Decapods; Anomura (planktotrophic)	0.0822	0.0653	0.0209	0.6260	0.7870

Values with $P < 0.05$ are indicated in bold. Area, continental shelf area; chl-*a*, minimum chlorophyll-*a* concentration; SST, sea surface temperature.

main component explaining variation in species richness in both phyla and larval developmental modes was the spatially structured environmental component (always > 73%; Fig. 3). The pure spatial component explained a larger fraction of the variation of both planktotrophic groups (11–17%) than of direct developers (< 6%; Fig. 3). The pure environmental component accounted for a very small proportion of variation in species richness in all cases (Fig. 3).

DISCUSSION

Our results demonstrate the importance of considering life-history attributes to investigate the nature of the processes driving latitudinal trends of species richness. By deconstructing the latitudinal pattern of species richness by the MLD, the formerly opposing trends of species richness reported along the coast of Chile became remarkably similar. Richness of species exhibiting exclusively planktotrophic

Table 2 Adjusted R^2 for the environmental, spatial and mixed models

Taxonomic group per mode of development	Env+			Significant variables
	Environmental	Spatial	Spatial	
Direct molluscs	0.8928	0.9530	0.9598	SST*** Area* x, y, x^2, xy, xy^2, x^3
Direct crustaceans	0.9586	0.9555	0.9637	SST*** chl- <i>a</i> ** Area* x, y, y^2, x^2y, x^3
Planktotrophic molluscs	0.7358	0.9605	0.9651	SST*** chl- <i>a</i> ** $x, y, x^2, xy, y^2, x^2y, xy^2$
Planktotrophic crustaceans	0.8544	0.9605	0.9651	SST*** Area* x, xy, x^2y, y^2, y^3

Significant spatial and environmental variables are indicated. Area, continental shelf area; chl-*a*, minimum chlorophyll-*a* concentration; SST, sea surface temperature; x , longitude; y , latitude.

* $P \leq 0.05$; ** $P \leq 0.001$; *** $P \leq 0.0001$.

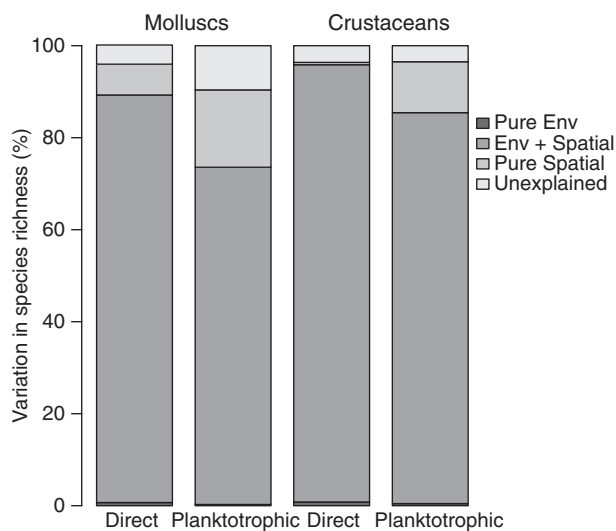


Figure 3 Percentage of variation in species richness of planktotrophic and direct developing molluscs and crustaceans along the coast of Chile. Variation in species richness was partitioned into four components, pure environmental variation (Pure Env), spatially structured environmental variation (Env+Spatial), pure spatial variation (Pure Spatial) and unexplained variation.

development decreases towards the pole, following the typical species richness gradient. In contrast, species richness of direct developing species increased monotonically with increasing latitude in all the cases. The pattern was clear even though the analysis was based on a sample of the mollusc species on the one hand, and the complete set of the reported crustacean species on the other. The sparse

evidence in the literature also shows a consistent decrease in species richness towards high latitudes in the Southern and Northern hemispheres for all benthic taxa exhibiting exclusively planktotrophic development or pelagic life (Table 3; Thorson 1950; this study). Inverse patterns of species richness in different hemispheres and oceans come from benthic taxa showing exclusively non-planktotrophic development (Table 3; this study). In the north-western Atlantic, where molluscs exhibit the typical latitudinal decrease in species richness towards higher latitudes, the only exception is Protobranch Bivalves, a group of molluscs exhibiting non-feeding larvae (Roy *et al.* 2000). Finally, Articulate Brachiopods, a group lacking a larval phase also fail to conform to the decreasing latitudinal species richness trend towards high latitudes (Valentine & Jablonski 1983).

The increases in total species richness of extra-tropical bivalves, echinoderms, gastropods, polychaetes and polyp-lacophora reported south of 40°S clearly oppose the common decrease in species richness from low to high latitudes (Brattström & Johanssen 1983; Lancellotti & Vásquez 2000; Valdovinos *et al.* 2003; Hernández *et al.* 2005). Although the patterns reported for the south-eastern Pacific can be influenced by the Antarctic fauna (Clarke & Crame 1997), it is important to point out that similar patterns have been reported for predatory Protobranch gastropods north of 40°N in the north-eastern Atlantic (Taylor & Taylor 1977). We think that the inverse trend of overall diversity in these groups, when compared with molluscs studies on both coasts of North America (Roy *et al.* 1998, 2000), might be related to a higher frequency of direct developing species in some regions (Taylor & Taylor 1977; Gallardo & Penchaszadeh 2001) as clades locked to a

Table 3 Summary of existing evidence on latitudinal patterns of species richness following the normal (decrease towards the poles) and reverse trends for benthic biota

Taxonomic group	Developmental mode	Latitudinal gradient	Source
Brachyura and Anomura	Planktotrophic	Normal	Macpherson (2002) Astorga <i>et al.</i> (2003)
Brachipoda Inarticulata	Planktotrophic	Normal	Valentine & Jablonski (1983)
Gastropods	Direct	Inverse	Gallardo & Penchazadeh (2001)
Isopoda	Direct	Inverse	Lancellotti & Vásquez (2000) López Gappa <i>et al.</i> (2006)
Amphipoda	Direct	Inverse	Myers <i>et al.</i> (1996) Lancellotti & Vásquez (2000)
Protobranch Bivalves	Non-feeding larvae, low fecundity	Inverse	Roy <i>et al.</i> (2000)
Polyplacophora	Primarily non-planktotrophic	Inverse	Valentine & Jablonski (1983)
Modern Articulata	Non-planktotrophic	Inverse	Valentine & Jablonski (1983)

single MLD, such as anomuran and brachyuran crabs, consistently exhibit the typical decrease in species richness with latitude in all oceans (Macpherson 2002; Astorga *et al.* 2003). Although our study clearly shows the influence of larval developmental modes on latitudinal patterns of diversity, it is still necessary to reach a deeper understanding of the historical and environmental conditions that determine the distribution of the different modes of development in the different oceans and hemispheres.

Considering the purported interaction between temperature, productivity, area and development mode we predicted a positive relationship between temperature and species richness for planktotrophic species, and a weak or negative relationship for direct developers. Our results support these predictions. SST is the most consistent and important environmental variable for both taxa and also for both larval developmental modes, although species with direct development show a strongly negative relationship with SST. Large-scale patterns of SST are not only an indicator of solar radiation and potential energy, but also a critical factor affecting rates of development (Wear 1974; Gillooly *et al.* 2002) and physiological processes (Pörtner 2002). The slower metabolic and developmental rates in the colder water temperature characteristic of high latitudes (Wear 1974; Vermeij 1978; Morgan 1995) might indirectly contribute to increasing larval mortality by prolonging the duration of exposure to predation in the plankton (O'Connor *et al.* 2007; Pechenik & Levine 2007). The prediction from these, admittedly simple relationships, is that species with planktonic larvae would not perform well at high latitudes (Thorson 1950), which could explain the decline in species richness of these species towards the poles and the prevalence of species without planktonic larvae. Temperature may also reduce the opportunities for isolation and speciation of planktotrophic species. On the other hand, low temperature at high latitudes might generally favour

direct developers as the cost of brooding increases with temperature (e.g. oxygen provision; Brante *et al.* 2003). Our results and the high prevalence of brooding species in Antarctica support this contention (Thorson 1950; Clarke & Crame 1997; Gallardo & Penchazadeh 2001). As the cost of brooding decreases polewards, more energy invested in reproduction can be devoted to egg production (Brante *et al.* 2003; Fernández *et al.* 2007) fostering higher local abundance, increasing population persistence and probably species diversity by reducing extinction. Some level of reproductive isolation and habitat heterogeneity generated by the fiord topography and recurrent glaciations (Valdovinos *et al.* 2003) might be needed to translate increased reproductive efficiency into higher speciation rates.

Our second prediction entailed a positive relationship between productivity, measured as chl-*a* concentration, and species richness of planktotrophic and direct development species. Results suggest that chl-*a* plays a role in the distribution of both phyla, but the amount of variance in species richness explained by chl-*a* was much lower (more than 1 order of magnitude) than that explained by SST. As expected if chl-*a* concentration represents food availability for larvae, chl-*a* was positively related only to richness of species exhibiting feeding larvae and it explained a higher proportion of the variance in diversity of planktotrophic than of direct developing species. Both planktotrophic molluscs and anomura species showed a significant and positive association between species richness and chl-*a*, which is consistent with the prediction that reduced availability of chl-*a* levels may limit the development of planktotrophic larvae over extended periods and thus the distribution of planktotrophic taxa at higher latitudes (Thorson 1950). The lack of association in the case of brachyuran crabs might be related to the high species richness of Brachyura in a region of comparatively low chl-*a* minimum (0.1 and 0.2 mg m⁻³) in northern Chile

(18–32 °S), which suggest that the influence of chl-*a* on species diversity might be weaker and more complex than the effect of SST. The predicted pattern was observed only in planktotrophic groups and most taxa with direct development exhibited a significant negative association with chl-*a*. The trend reported here for planktotrophic species is compatible with the individual as well as the sampling mechanisms (e.g. Hawkins *et al.* 2003; Evans *et al.* 2005, 2008).

Shelf area was not significant in most cases and did not show a consistent pattern within region or larval developmental mode (see also Roy *et al.* 1998), which provides only partial support to our predictions. Valdovinos *et al.* (2003) showed a distinctly different result, where shelf area was the main causal factor behind species richness of benthic molluscs along the Chilean coast. However, they pooled all species together, regardless of the larval developmental mode. These authors hypothesized that the high heterogeneity of the southernmost fjord area created a highly vicariant landscape that fostered isolation and speciation, which is reflected in a high ratio of species per genera when compared with northern areas. If this were so, direct development species would be expected to be especially sensitive to area effects given their restricted dispersal. As direct developing crustacean fit this prediction, the lack of consistent support in the case of molluscs may be related to the reduced sample size.

The strong relationship between SST and species richness for both taxa and larval developmental modes was also revealed by the variance partitioning analysis. Although the environmental model shows that the three environmental variables studied here explain together a large fraction of the variation in species richness, SST was by far the best predictor and also the only variable consistently selected among the different components of the model in both phyla and developmental modes. Moreover, the spatially structured environmental component, which reflects mainly the SST gradient but also the spatial variation of area and chl-*a*, explains the largest fraction of species richness variation. Non-spatial variation in the environmental variables contributed little to species richness, suggesting that local variation of environmental variables appears to be irrelevant in explaining species richness variation at the spatial scale of our analysis. Interestingly, the pure spatial component explained a larger fraction of variation of planktotrophic groups than direct developers, which suggests that unmeasured biotic or abiotic variables with a precise spatial structure affect differently the variation in species richness between both modes of larval development. Two possible factors are upwelling regimes and the oxygen minimum layer, which are spatially structured across the coast of Chile (Correa-Ramírez *et al.* 2007) and can influence larval survival and primary production (Thomas 1999).

It is important to bear in mind that macro-scale analyses are always correlative in nature and can only suggest potential explanations; they are not strict inferential tests of causality. However, the strong relationships and contrasting patterns that we report suggest that SST is a driving factor behind species diversity gradients, but with opposite effects on different groups. We suggest that this variation in the response of species richness to temperature depends largely on larval developmental modes. Although the analyses are not directly comparable between phyla, due to differences in numbers of species, the striking parallel patterns suggest the relevance of MLD and the interaction between this fundamental attribute of marine benthic invertebrates and the environmental context in which they are embedded.

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