

## Mollusk species diversity in the Southeastern Pacific: why are there more species towards the pole?

Claudio Valdovinos, Sergio A. Navarrete and Pablo A. Marquet

Valdovinos, C., Navarrete, S. A. and Marquet, P. A. 2003. Mollusk species diversity in the Southeastern Pacific: why are there more species towards the pole? – *Ecography* 26: 139–144.

The most ubiquitous and well recognized diversity pattern at large spatial scales is the latitudinal increase in species richness near the equator and decline towards the poles. Although several exceptions to this pattern have been documented, shallow water mollusks, the most speciose group of marine invertebrates, are the epitome of the monotonic decline in species diversity toward higher latitudes along the Pacific and Atlantic coasts of North America. Here we analyze the geographic diversity of 629 mollusk species along the Pacific South American shelf. Our analyses are based on the most complete database of invertebrates assembled for this region of the world, consisting of latitudinal ranges of over 95% of all described mollusks between 10° and 55°S. Along this coast, mollusk diversity did not follow the typical latitudinal trend. The number of species remained constant and relatively low at intermediate latitudes and sharply increased toward higher latitudes, south of 42°S. This trend was explained by changes in shelf area, but not by sea surface temperature, unlike the pattern documented for Northern Hemisphere mollusks. Direct sampling of soft bottom communities along the gradient suggests that regional trends in species richness are produced by increased alpha diversity, and not only by artifacts produced by the increase in sampling area. We hypothesize that increased shelf area south of 42°S, geographic isolation produced by divergence of major oceanic currents, and the existence of refugia during glaciations, enabled species diversification. Radiation could have been limited by narrow continental shelves between 10°–42°. Asymmetries in latitudinal diversity trends between hemispheres show that there is not a single general factor determining large-scale diversity patterns.

*C. Valdovinos, Unidad Sistemas Acuáticos, Centro EULA Chile, Univ. de Concepción, Casilla 160-C, Concepción, Chile. – S. A. Navarrete (snavarre@genes.bio.puc.cl) and P. A. Marquet, Centro de Estudios Avanzados en Ecología, Biodiversidad, Dept Ecología and Estación Costera de Investigaciones Marinas, Pontificia Univ. Católica de Chile, Casilla 114-D, Santiago, Chile.*

The impinging human alteration of earth's ecosystems through increased habitat destruction and overexploitation of resources has heighten the need to quantify the levels and distribution of biodiversity, and to improve our understanding of the processes that limit or favor diversification of species over large scales (Vitousek et al. 1997). The most ubiquitous and well recognized diversity pattern at large spatial scales is the latitudinal increase in species richness near the equator and decline toward the poles. This latitudinal diversity gradient has

been documented in both terrestrial and marine ecosystems (Rosenzweig 1995, Brown and Lomolino 1998). The shape of the diversity pattern has important practical implications for identifying priorities for the conservation of the world's biodiversity, as well as for the allocation of economic resources directed at the preservation of different ecoregions. Explanations of the latitudinal pattern remain highly controversial (Clarke 1992, Rohde 1992, 1998, 1999, Rosenzweig 1995, Rosenzweig and Sandlin 1997, Lyons and Willig 1999,

Accepted 20 June 2002

Copyright © ECOGRAPHY 2003  
ISSN 0906-7590

Taylor and Gaines 1999, Waide et al. 1999, Colwell and Lees 2000). Uncertainty about causal processes is due in part to differences in the spatial scale of the different studies (Clarke 1992, Rosenzweig 1995, Gaston et al. 1995, Santelices and Marquet 1998, Lyons and Willig 1999), and in part to the difficulty of controlling for other variables that may also produce this pattern, such as available area or geometric restrictions on species geographic ranges (Lyons and Willig 1999, Colwell and Lees 2000). Thus, without corroborative evidence of latitudinal trends on different continents, it becomes difficult to advance general explanations and to evaluate the effects of unique attributes of different regions of the world. Yet, it is these regional characteristics that should be born in mind when designing conservation policies.

In this study we compiled an extensive dataset of marine mollusks diversity along the Pacific South American shelf. Mollusks are the most diverse group of shelf macrobenthos for which good comparative taxonomic data are available. We quantify latitudinal diversity gradients of Prosobranchia, Bivalvia and Placophora, from northern Peru (10°S) to Cape Horn (55°S) and their relationship to temperature and shelf-area, comparing our results with the trends documented for both, the north-western Atlantic and north-eastern Pacific Oceans.

## Methods

We analyze the diversity and distribution of 629 shelled mollusk species along the Pacific South American shelf, from 10°S to 55°S, including only those known to live in waters shallower than 200 m. Our database represents the most complete and updated database assembled for this region of the world, corresponding approximately to 95% of all described mollusk species for the continental shelf (Valdovinos 1999). Data were obtained through an exhaustive search of the primary literature, as well as from inspection of major museum collections. The mollusks in the region encompassed by this study have been extensively sampled by individual taxonomists as well as major research expeditions since the late 1800's (Valdovinos 1999). The database includes the records of 407 species of Prosobranchia, 166 Bivalvia and 56 Placophora. Species of *Opisthobranchia*, *Gymnomorpha* and *Pulmonata* were not considered in this study because their taxonomy and distribution are not well known.

Latitudinal patterns of diversity were analyzed considering the number of all species occurring in every 5° latitudinal band (Roy et al. 1998, Colwell and Lees 2000). The range of a species was assumed to be continuous between its range endpoints, so diversity at any given latitudinal band was defined as the number of

species whose ranges crossed that band. To analyze the effect of solar-energy input on species diversity (species-energy hypothesis, see Currie 1991, Roy et al. 1998, 2000), we calculated the annual mean SST (Sea Surface Temperature) in every five degrees of latitude along the west coast of South America from NOAA's annual mean SST database publicly available on the web (< [http://ferret.wrc.noaa.gov/fbin/climate\\_server](http://ferret.wrc.noaa.gov/fbin/climate_server) >). To evaluate the effects of available habitat on species diversity (species-area effects. See Rosenzweig 1995, Rohde 1999), we calculated shelf areas every 5° latitudinal segments from 0° to 55°S by digitizing a 1:10<sup>6</sup> scale Lambert Zenithal Azimutal equal area projection map for the eastern Pacific coast, down to the 200 m depth contour. Given the coarse scale of these maps and the associated measurement error, the area values should be taken as relative along the coast and not as absolute measures.

To determine whether the patterns observed are the result of changes in total available area alone, or whether they reflect changes in alpha (local) diversity, we compiled additional data from studies conducted at eight sites between Ancón (11°45'S) and the Magellan Strait (53°30'S). These studies directly sampled shallow soft bottoms using the same methods and reported the number of species and the area sampled with similar resolution.

## Results

Strong latitudinal changes in mollusk species diversity were evident along the Peru-Chilean shelf (Fig. 1a), for all major mollusk taxa studied and especially for Prosobranchia, the most diverse group within mollusks. However, the change in species diversity was not monotonic across latitudes. Diversity of prosobranch species remained relatively low and constant around a value of 100 species/latitudinal band between 10 and 40°S, and then sharply increased to the south, reaching ca 300 species/band around the area of Cape Horn (Fig. 1b). This general pattern was similar for all taxonomic groups, but stronger for shelled species inhabiting mostly hard bottoms (Prosobranchia and Placophora), than for Bivalvia, which inhabit mostly soft bottom habitats (Figs 1b–d). There was also a clear correspondence in the location of the diversity break among groups. The latitude at which the break in diversity was observed (40–45°S), coincided with an area of high species turnover, as evidenced by the frequency distribution of species range endpoints (Fig. 2). The high percentage of endpoints occurring at ca 45°S is indicative of a transition between two different biogeographic provinces (Chile-Peruvian and Magellanic Provinces, Brattström and Johanssen 1983, Castilla et al. 1993). The percentage of endpoints, rep-

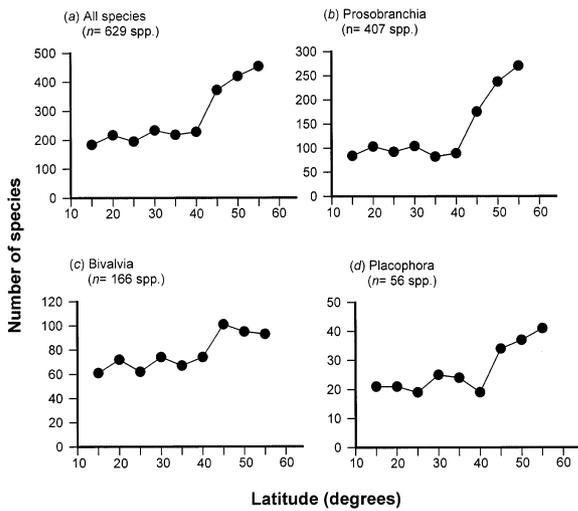


Fig. 1. Latitudinal diversity gradient of marine mollusks on the southeastern Pacific shelf, in bands of five degrees latitude. The values were calculated considering the number of all species occurring within 5° latitudinal bands. The range of a species was assumed to be continuous between its range endpoints. (a) All species (Prosobranchia, Bivalvia and Placophora), (b) Prosobranchia, (c) Bivalvia and (d) Placophora.

resents the ratio of the number of species ranges that end at that latitude to the total number of species present at that latitude. A weaker peak in species range

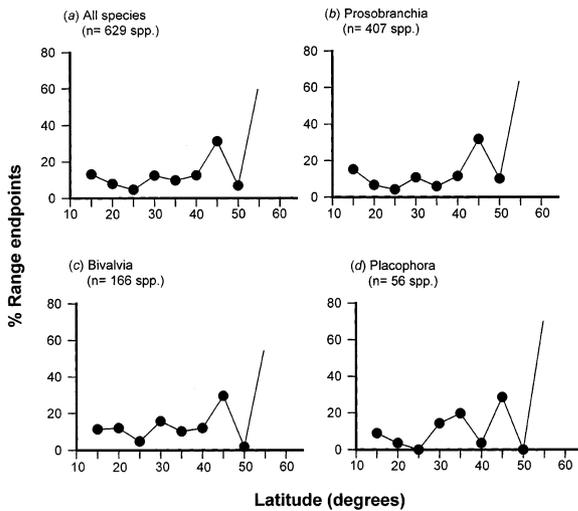


Fig. 2. Latitudinal distribution of the range endpoints of marine mollusks on the southeastern Pacific shelves in bands of five degrees latitude. The values are the percentage of species range endpoints occurring within a given 5° latitudinal band, in proportion to the total number of all species in that band. Latitudes with a high proportion of range endpoints represent biogeographical boundaries. (a) all species (Prosobranchia, Bivalvia and Placophora), (b) Prosobranchia, (c) Bivalvia and (d) Placophora. The peak observed at the end of the continent.

endpoints was also observed at ca 30°S, which corresponds well with a previously described area of lesser compositional change (Brattström and Johanssen 1983).

To test for the potential direct or indirect effects of impinging solar energy on mollusk diversity, we examined the relationship between species richness and SST. This regression was statistically not significant and weakly negative (Fig. 3a,  $r^2 = 0.24$ ,  $p = 0.1517$ ). Removing the potentially confounding effect of latitude did not improve the relationship, as we did not observe a significant relationship between mean SST and the residuals of the regression of the number of species versus latitude.

Unlike temperature, shelf area explained a significant portion of the variance (59%) in species diversity south of the equator (Fig. 3b). This significant relationship was produced by the large increase in area south of

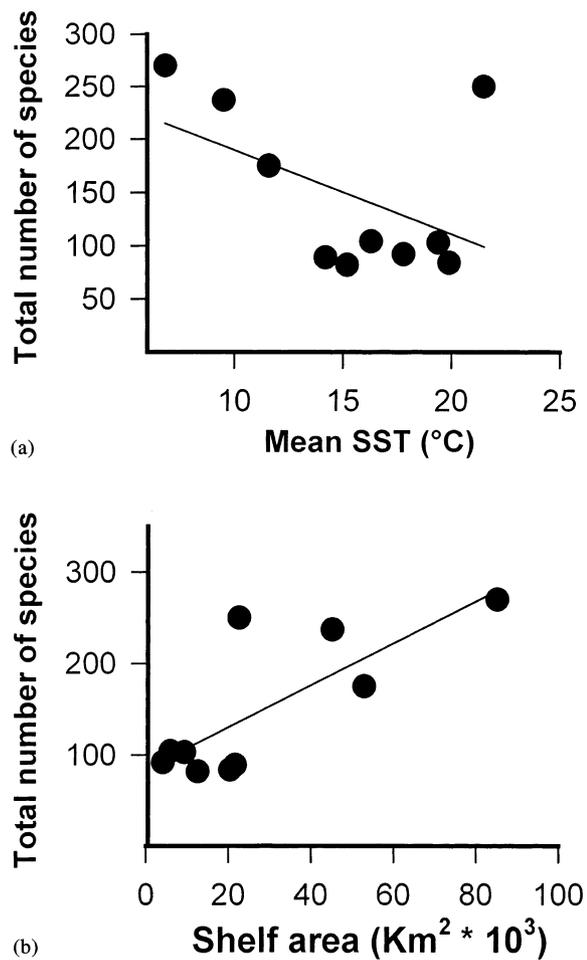


Fig. 3. Relationship between the number of prosobranch species in the southeastern Pacific and: (a) mean annual SST ( $r^2 = 0.24$ ,  $p = 0.1517$ ) for the Southern Hemisphere and (b) shelf area ( $r^2 = 0.59$ ,  $p = 0.0093$ ).

about 42–45°S, a region dominated by large archipelagoes, fjords, and convoluted interconnected channels (see Castilla et al. 1993). A linear multiple regression including shelf area and SST showed that area and not temperature was significantly and positively correlated with species diversity ( $p = 0.0254$  and  $p = 0.3382$ , for area and temperature, respectively).

Data from eight separate studies conducted along the region, which directly sampled shallow soft-bottom communities, showed a clear increase in alpha diversity of Prosobranchia and Bivalvia south of 42°S, changing from 0.5–2.0 species  $m^{-2}$  in the northern region to 6.7–85.0 species  $m^{-2}$ , in the south (Fig. 4). These results suggest that the regional changes in diversity are matched by an increase in alpha diversity.

## Discussion

In a series of recent studies, Roy et al. (1998, 2000) have shown that the prosobranch and bivalve mollusk fauna exhibit the typical latitudinal diversity gradient along both coasts of North America: diversity reaches maxima at the tropics and tails off monotonically toward higher latitudes. Moreover, along the Pacific and Atlantic coasts, there was a tight correlation ( $r^2 = 0.92$ ) between diversity and mean sea surface temperature, which suggested that solar radiation at the surface directly or indirectly controls the diversity of mollusk species. Since the Pacific coasts of North and South America are influenced by roughly similar east-margin

oceanographic conditions (Longhurst 1998, Strub et al. 1998) and show remarkably similar trends in terms of mean SST, similar patterns of mollusk diversity should be expected. Our results show that this is not the case. To better appreciate inter-hemispheric differences along the eastern Pacific shelves, from north Alaska (70°N) to Cape Horn (55°S), we combined our data with the information presented by Roy et al. (1998), selecting points every 5° of latitude. The global pattern shows important asymmetries between hemispheres, despite the roughly similar trends in SST (Fig. 5). First, as pointed out before, there is a strong peak in diversity located at tropical and subtropical latitudes, but displaced about ten to twenty degrees to the north (Fig. 5 segment b). Second, the peak in diversity steadily decreases towards high latitudes in the Northern Hemisphere (Fig. 5 segment a), but remains constant at intermediate latitudes along the Chile-Peruvian Province (Fig. 5 segment c). Third, species diversity increases towards higher latitudes in the Southern Hemisphere, a pattern not seen in its northern counterpart (Fig. 5 segment d). Thus, while the solar-energy input hypothesis (Currie 1991) does seem to be a good explanation for diversity patterns in the Northern Hemisphere, it clearly does not affect mollusk diversity in the same manner in the Southern Hemisphere. This suggests that towards high latitudes along the southeastern Pacific, there may be a shift in the relative importance of the factors controlling diversity, with available shelf area playing a more prominent role. Indeed, Roy et al. (1998) showed that there is no significant relationship between shelf area and Prosobranch diversity along the northeastern Pacific, while a significant relationship was found in our study.

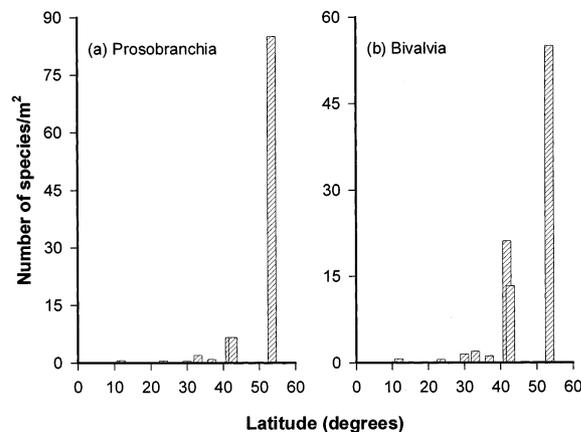


Fig. 4. Local (alpha) diversity of Prosobranchia (a) and Bivalvia (b) in shallow soft bottom habitats. Samples were obtained using a Van Veen grab at the following localities (north–south): Ancón-11°45'S (number of samples ( $n$ ) = 288; Tarazona et al. 1988), Antofagasta-23°28'S ( $n$  = 72; Palma 1999), Coquimbo-29°57'S ( $n$  = 40; Palma 1999), Valparaíso-32°59'S ( $n$  = 20; Andrade et al. 1986), Arauco-36°50'S ( $n$  = 76; Valdovinos 1998), Calbuco-41°45'S ( $n$  = 9; our data, obtained in July 2001), Chonchi-42°40'S ( $n$  = 9; our data, obtained in July 2001), Magallanes-53°30'S ( $n$  = 4; our data, obtained during the Italian Expedition R/V “OGS Explora” in 1991).

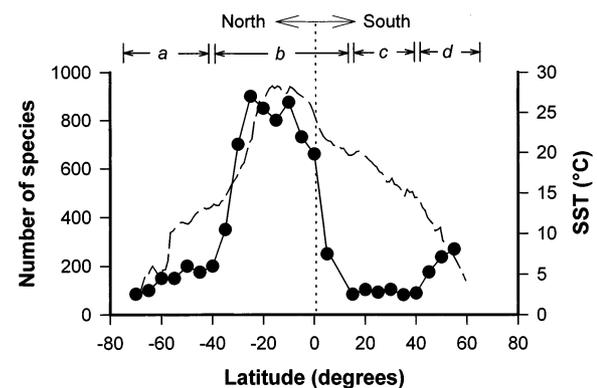


Fig. 5. North–south view of the latitudinal diversity gradient of marine gastropod prosobranchs along the north and south eastern Pacific shelves, between north Alaska to the Cap Horn. Information for the Northern Hemisphere comes from Roy et al. (1998), selecting points in bands of five degrees latitude. The segments a through d denote the major tendencies observed in the inter-hemispheric comparison (see text). Mean SST along the continental margin is also shown (segmented line).

The strong positive relationship between shelf area and number of species in southeastern Pacific suggests that available habitat has played an important role in shaping the mollusk biota along the south Pacific. As suggested by Rosenzweig (1995) and Rosenzweig and Sandlin (1997), larger areas could harbor more species because of an increase in speciation rate and/or a decrease in extinction. The weak palaeontological record available for the Southeastern Pacific precludes us from assessing extinction rates along the latitudinal gradient. However, available data allow us to hypothesize that the trend in mollusks diversity has been the results of higher diversification of mollusks at higher latitudes, south of 42°S. The use of discrete refugia may have enabled taxa to survive repeated glacial advances over the past 40 million years, and the consequent fragmentation and isolation of mollusk distributional areas, could have actually favored the diversification of species in the Magellan fjords (Crame 1997), conforming a pocket of high taxonomic diversity at these latitudes. As expected by this model explanation, there is a higher proportion of congeneric species south of 42°S (3.3 species per genus) than in the central coast of Chile (1.6 species per genus), suggesting that the increased diversity was produced by local radiation and not by recent colonization of species from other areas, such as New Zealand or the Antarctic peninsula (Powell 1973, Dell 1990, Crame 1997). In addition, at ca 42°S there is a divergence of major oceanic currents (Castilla et al. 1993), which apparently leads to the relative isolation of the marine fauna within the Magellan fjords. Similar regional trends in species diversity north and south of 42°S are observed among other invertebrate groups, such as Demospongiae (Desqueyroux and Moyano 1987) and Bryozoa (Moyano 1991).

It must be noted that the observed relationship between area and number of species could be the result of sampling area effects (Rosenzweig 1995) or from increased alpha (local) diversity towards the south. Data compiled from species ranges (e.g. Roy et al. 1998, data presented here), give no information about the diversity of species within local habitats and therefore it is difficult to separate between these alternatives. Moreover, standardization of the number of species per unit of area requires information of species-area or rarefaction curves along the region (Lyons and Willig 1999, Rohde 1999), which are not currently available for these taxonomic groups. However, results from the compilation of available community sampling data collected by eight different studies along the gradient, give strong support to the claim that regional changes in diversity are indeed produced by an increase in alpha diversity, and not solely by sampling artifacts. More studies sampling soft and hard bottom communities in similar manner along the region are needed to further determine the influence of area and habitat heterogeneity on mollusk diversity.

An implicit assumption of our explanation is that available area, and correlated factors, such as habitat complexity, have limited the number of species of mollusks along the open coast of Chile, from the subtropics to ca 42°S. Certainly, the total number of species found at these latitudes is less than half the numbers observed in the Northern Hemisphere (see Fig. 5), where no correlation between diversity and shelf area was observed (Roy et al. 1998), and it is suggestive that this part of the Peru-Chilean coast is characterized by a much narrower continental shelf than similar latitudes in the Northern Hemisphere (Longhurst 1998). The characteristic presence of a sharp and shallow oxygen minima (Arntz et al. 1991) could further reduce available habitat for mollusks on the continental shelf. It is important to note that this is also one of the most productive areas of the world (Bernal et al. 1982, Strub 1998), suggesting that comparatively low diversity is not a consequence of energy limitation. Further evaluation of the effects of available area on mollusk diversity should incorporate a measure of habitat composition and heterogeneity, as their proportions could change along the Chilean coastal shelf.

The observed latitudinal patterns are not an artifact of the quality of the data. The analysis of the frequency of singletons, the rate of description of new species, and the sampling effort along the Chilean coast over the last 200 yr, suggest that the species diversity of shelled mollusks are well known (see Lozada and Osorio 1995, Linse 1999, Valdovinos 1999, Reid and Osorio 2000, Fernández et al. 2000). Thus, while future revisions could change the status of some species included in our analyses, we do not expect significant changes in the diversity patterns reported here.

Our results show the importance of comparative inter-hemispheric analyses to examine biogeographic gradients. In particular, asymmetries in latitudinal diversity patterns for marine mollusks allowed us to show that there is not a single general factor determining large-scale diversity. There is strong evidence suggesting that SST directly or indirectly affect mollusk diversity along the Pacific and Atlantic coasts of North America (Roy et al. 1998), but the relationship breaks down in the Southern Hemisphere, where shelf area restrictions acquire increased relevance, underscoring the importance of regional processes in affecting global biogeographic patterns. Our preliminary data support the idea that the increased regional geomorphological heterogeneity has lead to increased local diversity of mollusks. Greater spatial resolution and more comparative studies on other taxonomic groups are needed to further resolve the causes of latitudinal trends. Yet, the patterns reported here should be strongly weighed when designing conservation plans for the World's biodiversity.

*Acknowledgements* – We thank B. Broitman, M. Fernandez, K. Nielsen, F. Smith and E. Wieters for comments and cogent criticisms on the manuscript. We are in debt to I. Di Geronimo of Catania Univ., Italy, for making samples from Magellan Strait available to us. Data compilation, analyses and preparation of this manuscript were possible thanks to a grant by FONDAP O. & B. M., no. 3 in Ecology and Conservation and FONDAP-Fondecyt 1501-0001. S.A.N. also appreciates a grant by the Andrew Mellon Foundation for continuous support.

## References

- Andrade, H., Gutiérrez, S. and Salinas, A. 1986. Efectos del vertimiento de desechos orgánicos no tratados sobre la macrofauna bentónica de un sector de la Bahía de Valparaíso (Chile). – *Ciencia y Tecnología del Mar, CONA* 10: 21–49.
- Arntz, W. E. et al. 1991. Benthic communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean coast, and changes caused by El Niño. – In: Tyson, R. V. and Pearson, T. H. (eds), *Modern and ancient continental shelf anoxia*. Geological Society, pp. 131–154.
- Bernal, P. A., Robles, F. L. and Rojas, O. 1982. Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú. – In: Castilla, J. C. (ed.), *Bases Biológicas para el Uso y Manejo de Recursos Naturales Renovables: Recursos Biológicos Marinos*, Monografías Biológicas 2. P. Univ. Católica de Chile, Santiago, Chile, pp. 75–102.
- Brattström, H. and Johannsen, A. 1983. Ecological and regional zoogeography of the marine benthic fauna of Chile. – *Sarsia* 68: 289–339.
- Brown, J. H. and Lomolino, M. V. 1998. *Biogeography*. – Sinauer, 2nd ed.
- Castilla, J. C., Navarrete, S. A. and Lubchenco, J. 1993. Southeastern Pacific coastal environments: main features, large-scale perturbations, and global climate change. – In: Mooney, H. A., Fuentes, E. R. and Kronberg, B. I. (eds), *Earth system responses to global change. Contrasts between North and South America*. Academic Press, pp. 167–188.
- Clarke, A. 1992. Is there a latitudinal diversity cline in the sea. – *Trends Ecol. Evol.* 7: 286–287.
- Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – *Trends Ecol. Evol.* 15: 70–76.
- Crame, J. A. 1997. An evolutionary framework for the polar regions. – *J. Biogeogr.* 24: 1–9.
- Currie, D. J. 1991. Energy and large scale patterns of animal and plant-species richness. – *Am. Nat.* 137: 27–49.
- Dell, R. K. 1990. Antarctic mollusca: with special reference to the fauna of the Ross Sea. – *Roy. Soc. New Zealand* 27: 1–297.
- Desqueyroux, R. and Moyano, H. 1987. Zoogeografía de demospongias chilenas. – *Boletín de la Sociedad de Biología de Concepción (Chile)* 58: 39–66.
- Fernández, M. et al. 2000. Diversity, ecology and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. – *Revista Chilena de Historia Natural* 73: 797–830.
- Gaston, K. J. et al. 1995. Large scale patterns of biodiversity: spatial variation in family richness. – *Proc. R. Soc. Lond. B* 260: 149–154.
- Linse, K. 1999. Abundance and diversity of Mollusca in the Beagle Channel. – *Scientia Marina* 63: 391–397.
- Longhurst, A. 1998. *Ecological geography of the sea*. – Academic Press.
- Lozada, E. and Osorio, C. 1995. Moluscos. – In: Simonetti, J. A. et al. (eds), *Diversidad Biológica de Chile, CONYCYT. Artograma*, Santiago, pp. 148–155.
- Lyons, S. K. and Willig, M. R. 1999. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. – *Ecology* 80: 2483–2491.
- Moyano, H. I. 1991. Bryozoa marinos chilenos VIII: Una síntesis zoogeográfica con consideraciones sistemáticas y la descripción de diez especies y dos géneros nuevos. – *Gayana Zool. (Chile)* 55: 305–389.
- Palma, M. 1999. Composición taxonómica, abundancia y diversidad de la macrofauna bentónica del norte de Chile, Antofagasta-Coquimbo. – Tesis Magister, Univ. de Concepción, Chile.
- Powell, A. W. 1973. The patellid limpets of the world (Patellidae). – *Indo-Pacific Mollusca* 3: 75–206.
- Reid, D. and Osorio, C. 2000. The shallow-water marine Mollusca of the Estero Elefantes and Laguna San Rafael, southern Chile. – *Bull. Nat. Hist. Mus. Lond. (Zool.)* 66: 109–146.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. – *Oikos* 65: 514–527.
- Rohde, K. 1998. Latitudinal gradients in species diversity. Area matters, but how much? – *Oikos* 82: 184–190.
- Rohde, K. 1999. Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? – *Ecography* 22: 593–613.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. – Cambridge Univ. Press.
- Rosenzweig, M. L. and Sandlin, E. A. 1997. Species diversity and latitudes: listening to the area's signal. – *Oikos* 80: 172–176.
- Roy, K. et al. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. – *Proc. Natl. Acad. Sci. USA* 95: 3699–3702.
- Roy, K., Jablonski, D. and Valentine, J.W. 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. – *Proc. R. Soc. Lond. B* 267: 293–299.
- Santelices, B. and Marquet, P. A. 1998. Seaweeds, latitudinal patterns, and Rapoport's rule. – *Div. Distribut.* 4: 71–75.
- Strub, P. T. et al. 1998. Coastal ocean circulation off western South America. – *The Sea* 11: 273–313.
- Tarazona, J., Salzwedel, H. and Arntz, W. 1988. Oscillations of macrobenthos in shallow waters of the Peruvian central coast induced by El Niño 1982–83. – *J. Mar. Res.* 46: 593–611.
- Taylor, P. H. and Gaines, S. D. 1999. Can Rapoport's rule be rescued? Modeling causes of the latitudinal gradient in species richness. – *Ecology* 80: 2474–2482.
- Valdovinos, C. R. 1998. Patrones de distribución geográfica de la macrofauna bentónica sublitoral en el Golfo de Arauco (Chile Central). – Tesis Doctorado, Univ. de Concepción, Chile.
- Valdovinos, C. R. 1999. Biodiversidad de moluscos chilenos: Base de datos taxonómica y distribucional. – *Gayana Zool. (Chile)* 63: 59–112.
- Vitousek, P. M. et al. 1997. Human domination of Earth's ecosystems. – *Science* 277: 494–499.
- Waide, R. B. et al. 1999. The relationship between productivity and species richness. – *Annu. Rev. Ecol. Syst.* 30: 257–300.