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Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral

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Abstract

Aim To use new collections and taxonomic reviews of the Chilean coastal biota, and studies on biodiversity on a reappraisal of Southeastern Pacific littoral biogeography.

Location The temperate coastline of the Southeastern Pacific, extending over 6000 km from northern Peru to the southern tip of Chile.

Methods Records of coastal macroinvertebrates were assigned to ten geographic zones along the Chilean coast. The Spearman rank correlation coefficient, ρ, was used to establish the relationship between the total number of species and the number of single records for each zone. Regions and underlying faunal gradient were verified via an unweighted paired group method using arithmetic averages (UPGMA), and ordination non-metric multidimensional scaling (nMDS) analysis based on a disagreement distance matrix of presence/absence data. Abundance down-weighting was preferred to rare species down-weighting, owing to the nature of the records, where a larger number of references for a given taxon did not necessarily indicate a greater abundance or commonness. The dissimilarity matrices between the different zones were used to establish the degree of agreement between the different levels of analysis, using a weighted Spearman rank correlation coefficient ρ_w. Statistical significance was established using a randomization (permutation) test.

Main conclusions Analysis of new macroinvertebrate data and taxonomic reviews of the Chilean coastal fauna indicates a Transitional-Temperate Region for the Southeastern Pacific littoral, located between 35°S and 48°S where a gradual mixing and replacement of species negates previous hypotheses on the existence of a marked distributional break at 42°S.

Keywords
Chile, marine macroinvertebrates, littoral zone, Transitional-Temperate region, zoogeography.

Resumen

Los estudios biogeográficos de la fauna de invertebrados litorales del Pacífico Sud-Oriental sugieren la presencia de una Región Templada Cálida al norte de los 42°S y una Región Templada Fría al sur de esta latitud. El análisis de una nueva serie de datos de las distribuciones de macroinvertebrados litorales y de revisiones taxonómicas realizadas para la costa Chilena, permiten definir una Región Templada Transicional para el litoral del Pacífico Sud-Oriental. Localizada entre los 35°S y 48°S, el reemplazo y la mezcla gradual de especies observados en la Región descarta la hipótesis de la existencia de un marcado quiebre distribucional a los 42°S. Los componentes al nivel Específico y Genérico de la Región Templada Transicional muestra una mayor afinidad con la fauna subtropical, mientras que a nivel de Familia y Orden esta presenta una mayor afinidad con la fauna sub-Antártica.

Palabras claves
Chile, macroinvertebrados marinos, Región Templada Transicional, zoogeografia.

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INTRODUCTION

Biodiversity and distributional patterns of littoral marine invertebrates provide a qualitative and quantitative understanding of regional zoogeography. The temperate coastline of the Southeastern Pacific, extending over 6000 km from northern Perú to the southern tip of Chile, provides a formidable challenge in this arena. Two previous studies have summarized available data on the zoogeography and controlling oceanographic processes of the Peru–Chile littoral (Viviani, 1979; Brattström & Johanssen, 1983), but were restricted in both collection sites and species. Distribution of 201 (Viviani, 1979) and 240 (Brattström & Johanssen, 1983) marine invertebrate species, collected by the Lund University Chile Expedition (LUCE) and other expeditions prior to the 1970s formed the basis for early conclusions. Brattström & Johanssen (1983) divided the area into a warm-temperate region (6° to 42°S) and a cold-temperate region (42° to 56°S), with a transitional area southward from 30°–33°S. These authors, however, recognized that a limited regional knowledge of the fauna may have produced distributions with marked species breaks along the N–S latitudinal gradient, which could not be corroborated by major intervening oceanographic or topographical features other than the fjordland region south of 42°S. This latter feature has been considered a warm- and cold-temperate regional boundary (Briggs, 1974, 1995). Some pre-1950 collection taxonomic deficiencies within the regions inherent in the studies have since been modified by new collections and taxonomic reviews of the Chilean coastal biota and studies on biodiversity at lesser studied northern latitudes.

This new information on the distribution of benthic macroinvertebrates permits a reappraisal of the Southeastern Pacific littoral biogeography.

METHODS

Criteria for species selection and definition of geographical zones

The extensive data sets from benthic macroinvertebrate distributions produced by more recent studies during the last two decades (Jaramillo, 1981; Osorio, 1981; Ramírez, 1981, 1987, 1990; McLean, 1984; Rozbaczylo, 1985; Desqueyroux-Faúndez & Moyano, 1987; González, 1991; Knight-Jones & Knight-Jones, 1991; Ponder & Worsfold, 1994; Retamal, 1994; Desqueyroux-Faúndez & Van Soest, 1996; Schrödl, 1996; Coan, 1997; Wehrtmann & Carvacho, 1997; Vásquez *et al*., 1998; Vásquez *et al*., in press) were added to the data set used by Brattström & Johanssen (1983). Only benthic taxa from the intertidal to 100 m were considered, excluding parasites, plankton and pelagic species and imprecise collection data. Porifera, Anthozoa, Polychaeta, Mollusca, Crustacea, Echinodermata and Ascidiacea are the principal taxa, of which Porifera, Polychaeta, Isopoda and Amphipoda have not been included in previous studies. Records were assigned to ten geographical zones along the Chilean coast: (1) Arica (18°–21°S), (2) Antofagasta (21°–26°S), (3) Coquimbo (26°–31°S), (4) Valparaíso (31°–35°S), (5) Concepción (35°–38°S), (6) Valdivia (38°–41°S), (7) Chiloé Archipelago (41°–44°S), (8) Los Chonos Archipelago (44°–48°S), (9) Magellan Strait (48°–54°S) and (10) Cape Horn (54°–56°S) (Fig. 1).

Biogeographic analysis

The Spearman rank correlation coefficient, ρ, was used to establish the relation between the total number of species and the number of single records for each zone (Zar, 1996). Regions and underlying faunal gradient were verified using the unweighted paired group method using arithmetic averages (UPGMA) (Sneath & Sokal, 1973) and the ordination nonmetric multi-dimensional scaling (nMDS) analysis (Kruskal & Wish, 1978) based on disagreement distance matrix of presence/absence data, where:

Distance(Zone X, Zone Y) = (Number of entities (Zone X ≠ Zone Y))/Total number of entities under analysis.

Abundance down-weighting was preferred rather than rare species down-weighting, owing to the nature of the records, where a larger number of references for a given taxon did not necessarily indicate a greater abundance or commonness. The (rank) disimilarity matrices between the different zones were used to establish the degree of agreement between the different levels of analysis, using a weighted Spearman rank correlation coefficient ρ_w. Statistical significance was established using a randomization (permutation) test at a $\alpha = 0.05$ (Clarke & Ainsworth, 1993).

RESULTS

Of the total 1597, more than one-third (38.2%) of the benthic macroinvertebrate species inhabiting the Chilean coast initially considered by this study are represented by single records (very few individuals at a single locality). Distributional pattern of total fauna showed that major variations between zones were associated with the presence of this single records component ($r = 0.769$; $F_{1,8} = 11.570$, $P < 0.01$) (Fig. 1), which was excluded from all subsequent analyses. The zones classically visited by expeditions correspond to the best studied and exhibit greater single records, namely: Arica (zone 1), Valparaíso (zone 4), Chiloé Archipelago (zone 7) and the Magellan Strait (zone 9). Thus, the South-eastern Pacific local macroinvertebrate fauna remains poorly known.

We evaluated the agreement between zoogeographic patterns at four taxonomic levels: specific, generic, familial and ordinal levels. UPGMA analysis of species and genus showed three consistent faunistic components over the latitudinal gradient ($\rho_w = 0.986$, $P < 0.05$): (1) zones between 18° and 35°S, (2) between 35°S and 48°S and (3) south of 48°S (Fig. 2ai,bi). This was shown in the nMDS ordinations as opposing faunal gradients connected by one of transitional character with a major affinity for northernmost fauna (Fig. 2aii,bii). The three components persisted at familial level ($\rho_w = 0.942$, $P < 0.05$), although the faunistic transitional assemblage showed more affinity with southernmost fauna (Fig. 2ci,cii), inverting the aforementioned faunistic relationship. At the ordinal level, the association of northernmost fauna was maintained, but not the relationships within the other zones ($\rho_w = 0.765$, $P > 0.05$)

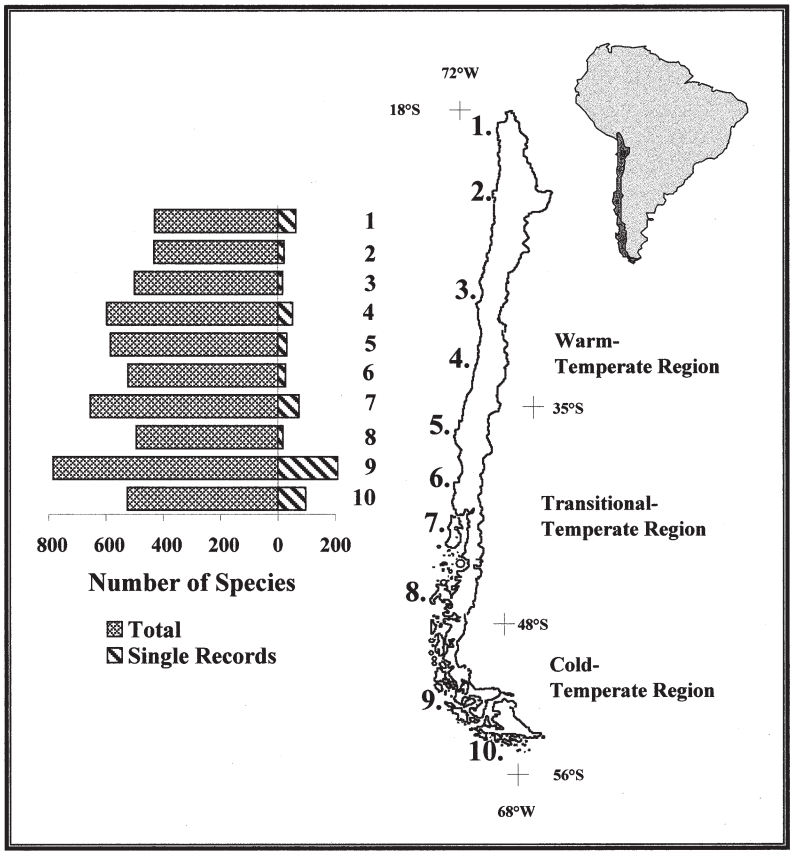

Figure 1 Number of species and total single records on the latitudinal gradient. The zones are: 1, Arica; 2, Antofagasta; 3, Coquimbo; 4. Valparaíso; 5, Concepción; 6. Valdivia; 7, Chiloé Archipelago; 8, Los Chonos Archipelago; 9, Magellan Strait; 10, Cape Horn. The new proposed region and boundaries are indicated.

(Fig. 2di). The transitional assemblage, now localized at 35°–41°S [Concepción (zone 5) to Valdivia (zone 6)] showed more of a southern fauna affinity, with strong sub-Antarctic influence (Fig. 2dii). Analysis on each of the seven taxonomic groups (Table 1), showed high consistency with the patterns observed which was less evident in poorly represented superior taxonomic levels.

DISCUSSION

In contrast to previous studies (Knox, 1960; Hartmann-Schröder & Hartmann, 1962; Dell, 1971; Briggs, 1974; Sebens & Paine, 1978; Viviani, 1979; Brattström & Johanssen, 1983) we demonstrate a loosely recognized transitional area (southward from 30°–33°S) formed part of a well-defined faunal aggregate located between 35° and 48°S [Concepción (zone 5) to Los Chonos Archipelago (zone 8)]. Classically, the boundary between this transitional area, warm-temperate and cold-temperate regions, at about 42°S, has been associated with the topographical breakup of the coastline by fjords where large amounts of fresh water enter the sea. South of 42°S including Chiloé and Los Chonos archipelagos (zones 7 and 8), inshore waters (< 20 m depth) are characterized by low-salinity fjords compared with high salinity at deeper waters and on the open coast for the same latitudes (Viviani, 1979). Such contrasting systems also occur between the Concepción (zone 5) and 42°S where large rivers enter the sea (Viviani, 1979). This extent, 35° to 48°S [Concepción (zone 5) to Los Chonos Archipielago (zone 8)], coincides with winter–summer oscillation in the Humboldt current system (Brattström & Johanssen, 1983), producing a discrete biotic/abiotic macro-zone. It is limited, to the north, by the warm Peru counter-current, the effect of which is felt as far south as Valparaíso (zone 4), is coincident with the southermost effect of El Niño events (Jaksic, 1998), and to the south by the Cape Horn current, which directly affects in the Magellan Strait (zone 9) and Cape Horn (zone 10) (Bernal *et al.*, 1982). Within this macro-zone, our results indicate gradual species replacement rather than major distributional breaks, but inhabiting similar estuarine communities (Viviani, 1979). Thus, the classical hypotheses for a faunal break related to the topographic breakup at 42°S are negated. Summarizing, the Chilean coastal fauna shows a clear separation of three faunistic entities: (1) a warm-temperate region north of 35°S (2) a cold-temperate region south of 48°S and (3) a transitional-temperate region between 35°S and 48°S. The divergent faunistic affinities observed within this latter region, subtropical at specific and generic levels, but subantarctic at familial and ordinal levels, suggests coexistence between the recent influences and the past history of the region, respectively.

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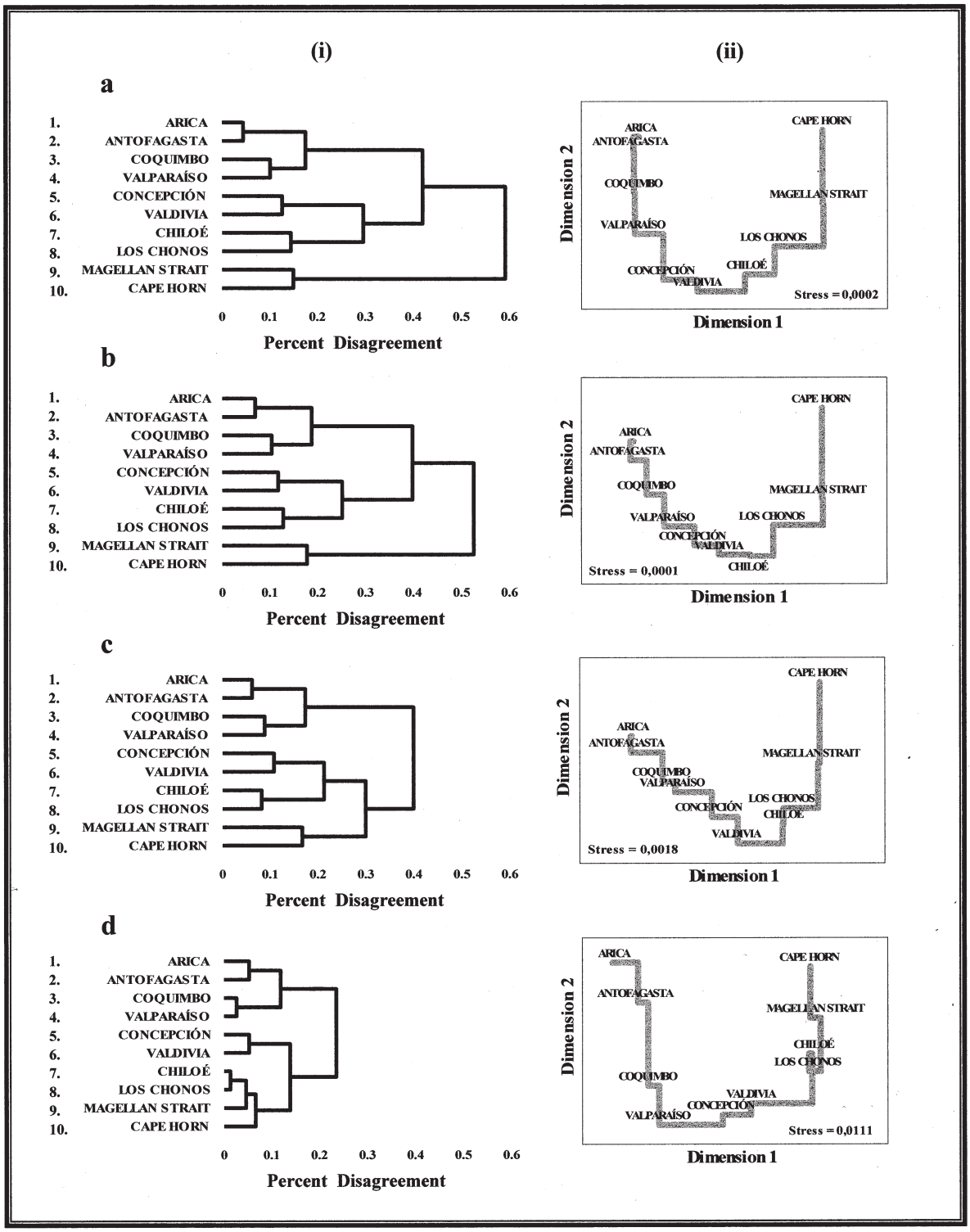

Figure 2 UPGMA classification (i) and nMDS ordination (ii) resolved at different taxonomic levels, excluding the single records. a, Species level (986 entities). b, Genus level (659 entities). c, Family level (300 entities). d, Order level (seventy entities).

Table 1 Concordance, ρ_w, for each taxon between each taxonomic level and the zoogeographic pattern of the respective level. *n* is the number of entities of each taxon, and NS indicates a not significative relation at $P=0.05$ (ρ_w was calculated excluding single records).

Taxonomic levels	Porifera	Anthozoa	Polychaeta	Mollusca	Crustacea	Echinodermata	Ascidiacea
Species	0.867	0.821	0.960	0.987	0.979	0.912	0.879
	$n=53$	$n=23$	$n=251$	$n=334$	$n=245$	$n=58$	$n=22$
Genus	0.720	0.809	0.938	0.971	0.990	0.884	0.930
	$n=33$	$n=20$	$n=149$	$n=209$	$n=180$	$n=51$	$n=17$
Family	0.734	0.665NS	0.841	0.955	0.960	0.897	0.869
	$n=25$	$n=8$	$n=41$	$n=115$	$n=72$	$n=29$	$n=10$
Order	0.772	0.168NS	0.762	0.819	0.417NS	0.879	0.417NS
	$n=10$	$n=2$	$n=14$	$n=21$	$n=5$	$n=15$	$n=3$

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