



RESEARCH ARTICLE

Geographic variation in diversity of wave exposed rocky intertidal communities along central Chile

Variación geográfica de la biodiversidad en hábitats intermareales rocosos de Chile central

BERNARDO R. BROITMAN^{1,2,*}, FREDY VÉLIZ², TATIANA MANZUR², EVIE A. WIETERS², G. RANDALL FINKE², PAULINA A. FORNES¹, NELSON VALDIVIA¹ & SERGIO A. NAVARRETE²

¹ Centro de Estudios Avanzados en Zonas Áridas, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

² Estación Costera de Investigaciones Marinas & Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

*Corresponding author: bernardo.broitman@ceaza.cl

ABSTRACT

Along the coast of central Chile, geographic trends of diversity have been inferred from literature compilations and museum collections based on species range limits for some taxonomic groups. However, spatially-intensive field-based assessments of macrobenthic species richness are largely missing. Over the course of a multiyear study (1998-2005), we characterized latitudinal patterns of rocky intertidal diversity at 18 sites along the coast of central Chile (29-36° S). At each site, the number of sessile and mobile macrobenthic species was quantified in 0.25 m² quadrats. Two estimators of local (alpha) diversity were used: observed local species richness, calculated from the asymptote of a species-rarefaction curve, and the Chao2 index, which takes into account the effect of rare species on estimates of local richness. We identified a total of 71 species belonging to 66 genera for a total of 86 taxa. The most diverse groups were herbivorous mollusks (27 taxa) and macroalgae (43 taxa). Diversity showed a complex spatial pattern with areas of high species richness interspersed with areas of low richness. In accordance with previous work, we found no trend in the number of herbivorous mollusks and an inverse and significant latitudinal gradient in the number of algal species. Our results highlight the need for taxonomically diverse assessments of biodiversity of the dominant taxa that conform intertidal communities.

Key words: biological diversity, intertidal ecology, latitudinal diversity gradient, species richness.

RESUMEN

A lo largo de la costa de Chile central, los patrones geográficos de diversidad han sido inferidos a partir de revisiones literarias y colecciones de museos para algunos grupos taxonómicos. Sin embargo, aun no contamos con una evaluación integral, y en terreno, de la riqueza de especies macrobentónicas intermareales. En un estudio de largo plazo conducido entre 1998 y 2005 caracterizamos los patrones latitudinales en la biodiversidad del intermareal rocoso en 18 sitios a lo largo de la costa de Chile central (29-36° S). En cada sitio, el número de especies sésiles y móviles fue cuantificado en cuadrantes de 0.25 m². Usamos dos estimadores de la riqueza de especies: la riqueza local observada, correspondiente a la asíntota de la curva de acumulación de especies, y el índice Chao2, el cual considera el efecto de especies raras en la estimación de la diversidad local. Identificamos 71 especies pertenecientes a 66 géneros y a un total de 86 taxa. Los grupos más diversos fueron moluscos (27 taxa) y macroalgas (43 taxa). La riqueza de especies mostró un patrón complejo en el cual áreas de alta riqueza específica aparecieron intercaladas con áreas de baja riqueza. Además, observamos una alta variabilidad espacial en el número de especies herbívoras y un patrón latitudinal inverso en el número de especies algales. Nuestros resultados apuntan a la necesidad de incorporar una variedad de grupos taxonómicos y un rango de escalas espaciales en estudios de biodiversidad.

Palabras clave: diversidad, ecología intermareal, gradientes latitudinales en diversidad, riqueza de especies.

INTRODUCTION

Spatial patterns of species richness across different locales and the quest for the mechanisms that generate these patterns are among the most interesting and inspiring problems in ecology and evolutionary biology

(Pianka 1966, Hillebrand 2004, Mittelbach et al. 2007). Among-site variation in the number of species in a given region and the pervasive large-scale diversity gradients occurring over global scales have been typically documented using different methodologies, namely through in situ sampling of different sites and through

literature or museum compilations and species range endpoints, respectively. In the latter case, the presence of a species at a given section of the coast is inferred from range limits and assumed constant through space. These broad assessments compromise taxonomic breadth and spatial grain, making it difficult to assess the generality of richness patterns from a few sites and the reality of global trends based on species ranges rather than actual occurrences. A recent global meta-analysis (Hillebrand 2004) of the rich literature examining geographic variation in diversity revealed complex patterns underlying latitude-diversity relationships. Gradients over regional-scales were significantly stronger and steeper than on local scales, with slopes changing with sampling grain, and the strength in the relationship increasing with trophic level (Hillebrand 2004). A simple lesson from these results is that studies attempting to understand spatial variation in biodiversity require taxonomically detailed, systematic, and spatially-intensive biodiversity assessments. Collection and literature-based assessments need to be coupled with field-based biodiversity assessments and are an unavoidable step towards informing conservation and management initiatives (Fernandez et al. 2000).

Latitudinal diversity patterns along the rocky shores of central Chile have received considerable attention during the last decade, and the region has been the subject of several studies that have compiled species range-endpoints for several taxonomic groups inhabiting these nearshore habitats (Santelices & Marquet 1998, Lancellotti & Vasquez 1999, Fernandez et al. 2000, Meneses & Santelices 2000, Camus 2001, Valdovinos et al. 2003, Hernandez et al. 2005). These studies have helped to identify a number of broad patterns in the spatial distribution of the number of species of certain taxonomic groups. More prominently, there is an inverse latitudinal gradient in the diversity of macroalgae along the southeastern Pacific (Santelices & Marquet 1998), while the diversity of mollusks exhibits no trend along the entire open coast of Chile (18-43° S) and then shows a large increase from around 43° S to the south (Valdovinos et al. 2003).

The studies outlined above suggest the presence of different latitudinal structures in

the number of species of different taxa along the coast of Chile and serve as useful starting points for evaluating spatial aspects of diversity within local communities where species of these taxa actually coexist. A major shortcoming to interpret geographical patterns of local diversity in a community context is that these studies have focused on very large spatial scales (1000's of km) and were based on literature reviews and museum collections. The few field studies carried-out in the region, in which the actual presence of coexisting species (alpha diversity) was recorded, considered a limited number of sites and were often restricted to particular microhabitats (e.g., mussel beds of *Perumytilus purpuratus* Lamarck; Thiel & Ullrich 2002, Prado & Castilla 2006; or red algae, Thiel 2002). The spatially most extensive published study of alpha diversity along the coast of Chile was conducted by Rivadeneira et al. (2002) at 53 study sites covering 2600 km. This study highlighted the disparity between regional scale diversity patterns predicted from literature compilation and local diversity, but it was restricted exclusively to intertidal grazers.

Here, we characterized spatial patterns of species richness of local intertidal communities at the wave-exposed rocky intertidal shores of central Chile. The objectives were twofold. Firstly, we aimed to establish through a field-intensive methodology among-site patterns of spatial variation in species richness throughout central Chile. Secondly, using information from the field-based assessment we examined the spatial structure of diversity among coexisting species and its consistency across different trophic levels and major taxa. As a simple test of hypothesis, we test whether spatial patterns in diversity conform to a linear, latitudinal, pattern and discuss our findings in light of current knowledge of environmental and ecological mechanisms shown to regulate the structure of rocky shore intertidal communities.

METHODS

Study region and sampling design

We surveyed a total of 18 sites along the coast of central Chile, from 29.5° S to 36.07° S (i.e. ~970 km of shoreline, Fig. 1, Table 1). These sites are located across a region that spans an important oceanographic

transition located around 30° S-32° S and involves a major change in the alongshore upwelling regimes (Hormazábal et al. 2004). Differences in wind patterns cause sites poleward of the transition zone to experience strong and variable coastal upwelling conditions during the spring-summer season, while sites located to the north experience weaker but persistent upwelling-favorable wind conditions (Navarrete et al. 2005). A previous extensive study of the intertidal communities of the region showed that 8-22 quadrats 0.25 m² in area were sufficient to capture local-scale patterns of community structure such as percentage cover of the dominant macrobenthic (i.e. > 5 mm) species and density of mobile species at all these sites (Broitman et al. 2001). That study, however, did not present patterns of species richness, which could be more dynamic than those of abundance of

functional groups. Since we wanted to have a good representation of species richness at the local community level (alpha diversity), we sampled all 18 sites in 1998, 2003, 2004, and 2005, and conducted an additional sampling of the three southernmost sites (Table 1) in 2000. During the austral spring-summer season (November to March), we surveyed each site by sampling 7 to 15 0.25 m² quadrats located haphazardly along 1 to 3 transects of 20-30 m long parallel to the shoreline in the mid and low intertidal zones during daytime low tide intervals. Variations in the sampling effort arose from logistical constraints, such as harsh ocean conditions that prevented access to some sites within a season, but in all cases the number of quadrats was sufficient to represent local diversity (see Results).

In order to minimize variability in species richness due to habitat differences, we focused all sampling effort on flat, gently sloping rocky benches, avoiding crevices and tide pools. Moreover, only macroscopic organisms (ca. > 5 mm) were considered. Thus, our biodiversity estimates represented a conservative estimate of the biodiversity at each site, but ensured that the species coexisted within the same habitat. The study was focused on intertidal organisms that could be accurately identified in the field, and for which appropriate taxonomic keys were available. Hence, we focused on a taxonomically diverse group of intertidal organisms composed mostly of gastropods, bivalves, barnacles, asteroids, and decapod crustaceans, as well as chlorophycean, rhodophycean, and phaeophycean macroalgae (Hoffmann & Santelices 1991, Oliva & Castilla 1992, Espoz et al. 2004). Taxonomy was resolved to the lowest possible level in the field and a few specimens were collected when necessary. This strategy allowed us to identify to species level most of the specimens that grow as single individuals. In several cases, such as some turf-forming algae (e.g., *Gelidium chilense* (Montagne) Santelices & Montalva and *Gelidium linguatum* Kützing) where it is not possible to classify species in the field when they grow in mixed stands, species were recorded to genera. We also checked all algal species with Algaebase (<http://www.algaebase.org>). We used therefore a mixture of taxonomic resolutions and defined species richness as the number of taxonomic identities. Nevertheless, previous work showed similar patterns in community structure whether fine, coarse, or mixed taxonomic resolution was used (e.g., Chapman 2002, Underwood & Chapman 2006). Further details of the sampling scheme are presented elsewhere (Broitman et al. 2001).

Data analysis

We used both the observed local species richness (S_{obs}) and Chao2 index as estimates of local biodiversity. Diversity estimates were based on species-accumulation curves (number of species as a function of number of quadrats) constructed from 200 randomized quadrats at each site (Gotelli & Colwell 2001). S_{obs} at each site was then estimated as the asymptote of the species-accumulation curve, where increased sampling does not add an appreciable number of new species. The Chao2 (Chao 1987) index estimates the asymptote of the species-accumulation curve by taking into account the effect of rare species on total richness:

$$\text{Chao2 estimate} = S_{obs} + (Q_1)^2 / 2 Q_2$$

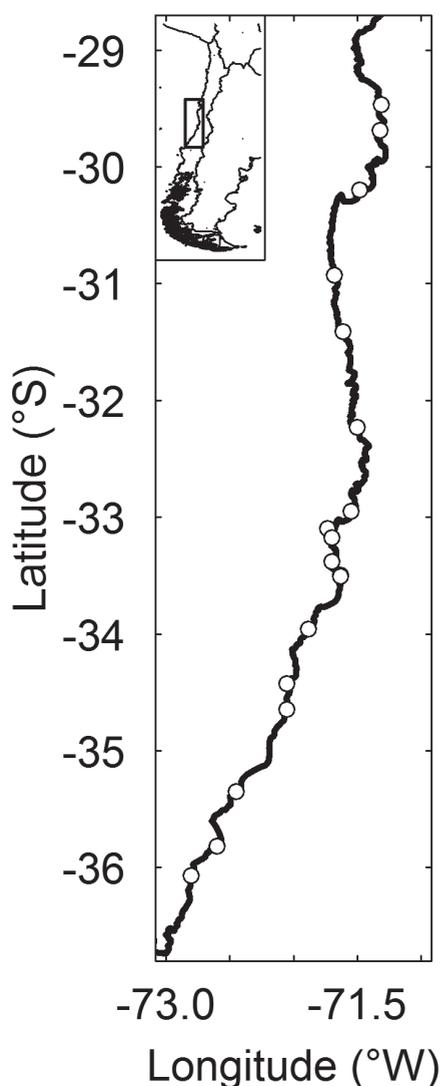


Fig. 1: Map of the coast of central Chile indicating the locations of the 18 study sites.

Mapa de la costa de Chile central indicando la ubicación de los 18 sitios de estudio.

where Q_1 and Q_2 are the frequencies of species with single and double records respectively. Non-parametric estimators, such as Chao2, perform better in terms of bias, precision, and accuracy than species-accumulation model (Walther & Martin 2001). Since Q_1 and Q_2 were always > 0 , no bias-correction was needed (Chao 1987).

We used linear regressions to explore the geographical patterns of diversity along the study region. All analyses were computed with the R environment version 2.9.1 (R Development Core Team 2009).

RESULTS

Across the 18 sites and over the course of the four-year study, we surveyed a total of 1863 quadrats, identifying 71 species belonging to 66 genera for a total of 86 identified taxa (Table 2). Species richness was partitioned evenly between macroalgae and invertebrates (Table 2). Across all sites, we found a total of 43 algal taxa belonging to 40 genera, while

invertebrates were represented by 43 taxa belonging to 25 genera. The more diverse taxonomic group were mollusks (chitons, gastropods, and bivalves; 32 taxa), followed by rhodophycean (25 taxa), phaeophycean (10 taxa), and chlorophycean macroalgae (8 taxa). In terms of functional groups, most of the species richness corresponded to 'herbivores' (chitons and all gastropods excluding *Concholepas* and *Acanthina*), 'filter-feeders' (mytilids and barnacles), and 'corticated algae' (sensu Steneck & Dethier 1994, see Broitman et al. 2001 for a functional classification), although many of the herbivores or grazers can be considered true omnivorous (Camus et al. 2008). The intensive sampling scheme resulted in reasonably good estimates of local community species richness for the wave exposed habitat. Species-accumulation curves generated after pooling all years showed asymptotic values after ca. 40 quadrats (Fig.

TABLE 1

List of all sampling localities shown in Fig. 1. Latitude and longitude are expressed as decimal degrees, N is the total number of quadrats surveyed in each site across all years, S_{obs} is the observed number of species, and Chao2 is the estimated asymptotic number of species at each site.

Lista de los sitios de muestreos mostrados en Fig. 1. Latitud y longitud están expresadas en grados decimales, N es el número total de cuadrantes muestreados en cada sitio a través de todos los años, S_{obs} es el número de especies observado, y Chao2 es el número de especies asintótico estimado en cada sitio.

	Site name	Code	Latitude (°S)	Longitude (°W)	N	S_{obs}	Chao2
1	El Temblador	TEM	29.50	71.32	67	48	58.08
2	El Arrayán	ARR	29.68	71.32	45	49	51.45
3	Guaqueros	GUA	30.18	71.47	95	60	75.12
4	Punta Talca	PTAL	30.92	71.50	91	66	74.16
5	Puerto Oscuro	POSC	31.42	71.60	77	58	62.00
6	Los Molles	MOLL	32.23	71.50	72	54	58.90
7	Montemar	MONT	32.95	71.55	96	52	55.60
8	Curaumilla	CUR	33.10	71.73	81	51	55.50
9	Quintay	QUN	33.18	71.70	70	50	54.16
10	El Quisco	ELQ	33.38	71.70	96	60	64.08
11	ECIM	ECIMN	33.50	71.63	116	63	73.28
12	Las Cruces	LCRU	33.51	71.63	103	66	67.78
13	Matanzas	MAZ	33.96	71.88	81	55	91.00
14	Punta de Lobos	PTL	34.43	72.05	97	67	70.00
15	Bucalemu	BUCA	34.65	72.05	63	64	67.60
16	Constitución	CON	35.35	72.45	124	60	70.00
17	Pelluhue	PELL	35.82	72.60	98	58	70.5
18	Buchupureo	BUP	36.07	72.80	99	60	64.08

TABLE 2

Taxa found across the four year study of macrobenthic diversity. % is the percentage of quadrats in which each species was found. Total number of quadrats was 1863.

Taxa encontradas a lo largo de los cuatro años de estudio de diversidad macrobentónica. % es el porcentaje de cuadrantes en las cuales cada especie fue encontrada. El número total de cuadrantes fue 1863.

Taxa	%
Rhodophyta	
1 <i>Ahnfeltiopsis</i> spp.	5.9
2 <i>Ahnfeltiopsis furcellata</i> (C. Agardh) P.C. Silva & DeCew	2.09
3 <i>Centroceras</i> spp.	0.27
4 <i>Ceramium</i> spp.	13.2
5 <i>Corallina officinalis</i> Linnaeus	38.22
6 <i>Gelidium rex</i> Santelices & I.A. Abbott	4.19
7 <i>Gelidium</i> spp.	36.77
8 <i>Grateloupia doryphora</i> (Montagne) M.A. Howe	3.65
9 <i>Hildenbrandia lecanellieri</i> Hariot	59.47
10 <i>Laurencia chilensis</i> De Toni, Forte & M.A. Howe	4.83
11 <i>Lithothamnion</i> spp.	54
12 <i>Mazzaella laminarioides</i> (Bory de Saint-Vincent) Fredericq	38.33
13 <i>Montemaria horridula</i> (Montagne) A.B. Joly & Alveal	0.54
14 <i>Nothogenia fastigiata</i> (Bory de Saint-Vincent) P.G. Parkinson	4.24
15 <i>Petroglossum pacificum</i> Hollenberg	3.49
16 <i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon	0.32
17 <i>Polysiphonia</i> spp.	25.34
18 <i>Porphyra columbina</i> Montagne	23.89
19 <i>Prionitis decipiens</i> (Montagne) J. Agardh	6.28
20 <i>Rhodomenia</i> spp.	4.62
21 <i>Sarcothalia crispata</i> (Bory de Saint-Vincent) Leister	3.44
22 <i>Schizymenia pacifica</i> (Kylin) Kylin	0.32
23 <i>Schottera nicaeënsis</i> (J.V. Lamouroux ex Duby) Guiry & Hollenberg	8.27
24 <i>Trematocarpus dichotomus</i> Kützing	3.86
25 <i>Chondrus canaliculatus</i> (C. Agardh) Greville	0.91
Phaeophyceae	
26 <i>Colpomenia phaeodactyla</i> M.J. Wynne & J.N. Norris	0.16
27 <i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier	0.32
28 <i>Dictyota kunthii</i> (C. Agardh) Greville	0.21
29 <i>Durvillaea antarctica</i> (Chamisso) Hariot	19.54
30 <i>Ectocarpus</i> spp.	0.64
31 <i>Halopteris funicularis</i> (Montagne) Sauvageau	0.27
32 <i>Lessonia nigrescens</i> Bory de Saint-Vincent	46.48
33 <i>Macrocystis pyrifera</i> (Linnaeus) C. Agardh	0.05
34 <i>Petalonia fascia</i> (O.F. Müller) Kuntze	5.42
35 <i>Scytosiphon lomentaria</i> (Lyngbye) Link	1.07
Chlorophyta	
36 <i>Bryopsis</i> spp.	0.21
37 <i>Chaetomorpha</i> spp.	5.21
38 <i>Cladophora</i> spp.	0.81
39 <i>Codium dimorphum</i> Svedelius	6.87
40 <i>Rama novae-zelandiae</i> (J. Agardh) Chapman	2.42
41 <i>Rhizoclonium</i> spp.	1.72
42 <i>Ulva</i> spp.	35.32
43 <i>Ulvella</i> spp.	4.72

(Table 2 Cont.)

Taxa	%
Polychaeta	
44 <i>Phragmatopoma</i> spp.	4.62
Gastropoda	
45 <i>Acanthina monodon</i> Pallas	10.09
46 <i>Concholepas concholepas</i> Brugière	21.47
47 <i>Fissurella costata</i> Lesson	1.77
48 <i>Fissurella crassa</i> Lamarck	12.67
49 <i>Fissurella cumingi</i> Reeve	0.86
50 <i>Fissurella limbata</i> Sowerby	11.43
51 <i>Fissurella maxima</i> Sowerby	0.54
52 <i>Fissurella picta</i> Gmelin	1.18
53 <i>Fissurella pulchra</i> Sowerby	0.7
54 <i>Lottia orbignyi</i> Dall	0.16
55 <i>Scurria araucana</i> Orbignyi	30.22
56 <i>Scurria ceciliana</i> Orbignyi	18.63
57 <i>Scurria fragilis</i>	2.31
58 <i>Scurria plana</i> Philippi	0.48
59 <i>Scurria scurra</i> Lesson	22.49
60 <i>Scurria variabilis</i> Sowerby	1.56
61 <i>Scurria viridula</i> Lamarck	2.58
62 <i>Scurria zebrina</i> Lesson	11.54
63 <i>Siphonaria lessoni</i> Blainville	0.64
64 <i>Tegula atra</i> Lesson	4.29
Polyplacophora	
65 <i>Acanthopleura echinata</i> Barnes	8.59
66 <i>Chaetopleura peruviana</i> Lamarck	1.02
67 <i>Chaetopleura benaventei</i> Plate	0.16
68 <i>Chiton cumingsii</i> Frembly	0.43
69 <i>Chiton granosus</i> Frembly	39.99
70 <i>Chiton latus</i> Sowerby	1.93
71 <i>Enoplochiton niger</i> Barnes	2.68
72 <i>Toncia chilensis</i> Frembly	6.87
73 <i>Toncia elegans</i> Fremblt	2.42
Bivalvia	
74 <i>Brachidontes granulata</i> Hanley	15.46
75 <i>Perumytilus purpuratus</i> Lamarck	8.64
76 <i>Semimytilus algosus</i> Gould	4.24
Cirripedia	
77 <i>Austromegabalanus psittacus</i> Molina	46.97
78 <i>Balanus laevis</i> Bruguière	31.62
79 <i>Jhelius cirratus</i> Darwin	7.03
80 <i>Nothobalanus flosculus</i> Darwin	10.74
81 <i>Nothochthamalus scabrosus</i> Darwin	10.84
Decapoda	
82 <i>Acanthocyclus gayi</i> Milne Edwards & Lucas	37.79
83 <i>Acanthocyclus hassleri</i> Rathbun	1.99
Asteroidea	
84 <i>Heliaster helianthus</i> Lamarck	61.51
85 <i>Stichaster striatus</i> Müller & Troschel	8.64
Tunicata	
86 <i>Pyura chilensis</i> Molina	9.29

2), less than half of our average local sampling effort (87.278 ± 4.608 quadrats). S_{obs} and Chao2 index were positively correlated across all sites (Fig. 3; $r^2 = 0.3022$, $F_{1, 15} = 6.49$, $P = 0.025$), with the Matanzas site (MAZ, open dot) showing a large departure from the trend due to large numbers of species with single or double records. When MAZ was excluded from the analysis, the relationship between S_{obs} and Chao2 was tighter ($r^2 = 0.7203$, $F_{1, 14} = 36.06$, $P < 0.001$). This statistical relationship was parallel to the 1:1 line, with the intercept indicating that S_{obs} was underestimating local richness by 6.39 species at each site (Fig. 3).

Geographic patterns of species richness across the latitudinal region encompassed by the study showed considerable spatial variability among sites, and neither S_{obs} nor Chao2 evidenced a clear linear trend with latitude (linear regressions: $P = 0.106$ and $P = 0.2061$ for S_{obs} and Chao respectively). Instead, we observed that centers of high species richness were present around 31° S and 34° S, alternated by areas of lower richness located around 30° S, 33° S, and 36° S (Figs. 4A and 4B). A similar trend is suggested by examining the latitudinal pattern of species richness in the more diverse algal groups, where the areas of

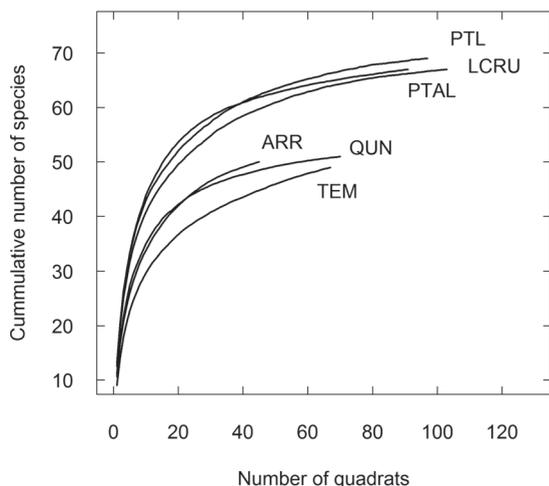


Fig. 2: Species-accumulation curves for the three sites with the largest (PTAL, LCRU, PTL) and the lowest (ARR, QUN, TEM) number of species. See Table 1 for site locations and abbreviations.

Curvas de acumulación de especies de los tres sitios con las mayores (PTAL, LCRU, PTL) y menores (ARR, QUN, TEM) riquezas de especies. Ver ubicaciones y abreviaciones de sitios en Tabla 1.

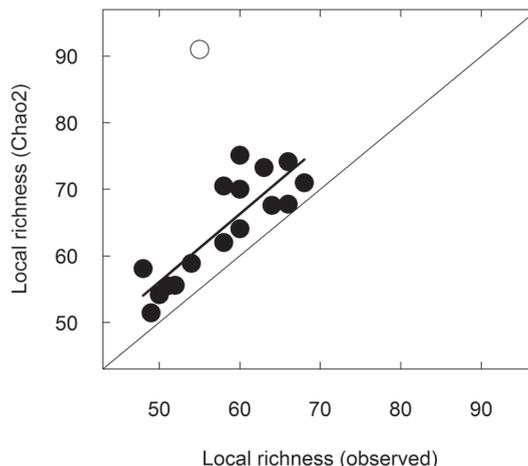


Fig. 3: Least-squares regression between the observed number of species at each location (S_{obs}) and the predicted species richness (Chao2) when MAZ (open dot) is excluded. $Chao2 = 6.39 + 0.993 S_{obs}$; $r^2 = 0.7203$, $F_{1, 14} = 36.056$, $P < 0.01$; the reference line indicates the 1:1 relationship.

Regresión de mínimos cuadrados entre el número observado de especies en cada sitio (S_{obs}) y la riqueza de especies predicha (Chao2) cuando MAZ (punto blanco) es excluido. $Chao2 = 6.39 + 0.993 S_{obs}$; $r^2 = 0.7203$, $F_{1, 14} = 36.056$, $P < 0.01$; la línea de referencia indica la relación 1:1.

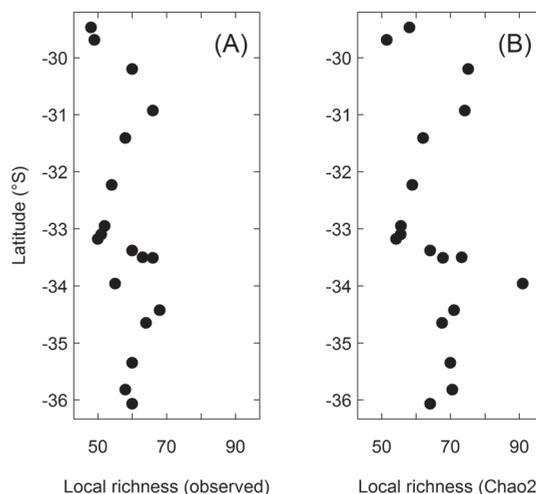


Fig. 4: Spatial patterns of local species richness along central Chile. (A) Total number of species (S_{obs}) observed at each site. (B) Predicted local species richness (Chao2) accounting for the number of rare species observed at each site.

Patrones espaciales de la riqueza de especies local a lo largo de Chile central. (A) Número total de especies (S_{obs}) observada en cada sitio. (B) Riqueza de especies local predicha (Chao2) al considerar el número de especies raras en cada sitio.

lower and higher richness are evident around 33° S (Fig. 5A). In addition, the significant linear fits suggest that the number of red algae ($r^2 = 0.5084$, $F_{1, 16} = 16.55$, $P < 0.001$) and the total number of algal species ($r^2 = 0.3845$, $F_{1, 16} = 9.99$, $P = 0.006$) increased with increasing latitude across the study region. The richness of chlorophycean algae was too low (8 species) to examine spatial trends. Neither herbivores nor carnivores showed linear trends across the region ($P = 0.27$ and $P = 0.69$ for herbivores and carnivores respectively). Herbivore species richness also showed two centers of higher diversity across the region, but the location of those areas did not coincide with those of red and brown macroalgae or the total number of algal species (Fig. 5B, closed and open dots, respectively).

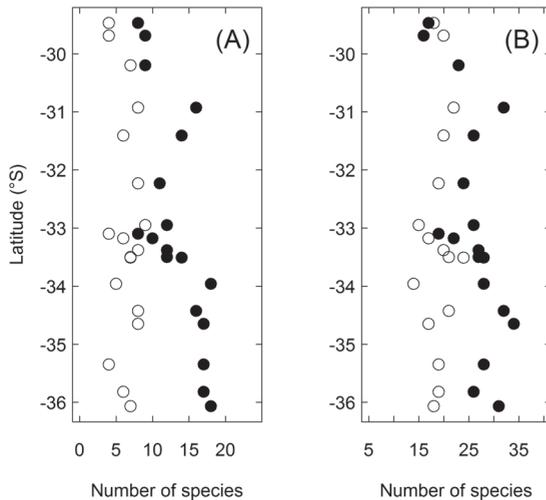


Fig. 5: Spatial patterns of local species richness along central Chile. (A) Total number of rhodophycean (closed dots) and phaeophycean species (open dots). (B) Total number of algal species (closed dots) and total number of herbivore species (open dots). Rhodophycean species richness and algal species richness were significantly related to the latitude (L): Rhodophycean species richness = $-28.6329 + 1.2687 L$; $r^2 = 0.5084$, $F_{1, 13} = 16.55$, $P < 0.001$; algal species richness = $-25.7988 + 1.5668 L$; $r^2 = 0.3845$, $F_{1, 16} = 9.99$, $P = 0.006$.

Patrones espaciales de riqueza de especie local a lo largo de Chile central. (A) Números totales de algas rojas (puntos negros) y cafés (puntos blancos). (B) Números totales de especies algales (puntos negros) y herbívoras (puntos blancos). Tanto el número de algas rojas como el total de especies algales se relacionaron significativamente con la latitud (L): Algas rojas = $-28.6329 + 1.2687 L$; $r^2 = 0.5084$, $F_{1, 13} = 16.55$, $P < 0.001$; número total de especies algales = $-25.7988 + 1.5668 L$; $r^2 = 0.3845$, $F_{1, 16} = 9.99$, $P = 0.006$.

DISCUSSION

Our study provides an exhaustive community-based assessment of the spatial variation in biodiversity of rocky intertidal species richness across central Chile. In broad agreement with previous studies based on latitudinal ranges of mollusks and macroalgae (Santelices & Marquet 1998, Valdovinos et al. 2003), species richness showed no clear latitudinal gradient through our study region. As somehow expected for a between-site study, the smooth patterns suggested by previous large-scale studies concealed a rather complex pattern of variation with coastal sections of high species richness interspersed with areas of low richness of algae and invertebrates.

Our estimates of local species richness provide a conservative estimate of rocky intertidal species richness by excluding numerous cryptic species and microhabitats. However, biodiversity of macroscopic invertebrates and macroalgae found on wave-exposed benches is well represented as confirmed by the tight relationship between S_{obs} and Chao2, which was further improved after removing the site with several single or double species records (Fig. 3). The strength of the sampling scheme is further reinforced by comparisons of the number of species and the spatial patterns observed in the only published field assessment conducted previously in this same region. Rivadeneira et al. (2002) surveyed rocky intertidal macroherbivore grazers (mostly gastropods) inhabiting a range of microhabitats, including wave exposed benches, vertical walls, boulders and tidal pools, between 18° S and 42° S. Even though Rivadeneira et al. (2002) used a different sampling scheme, the number of herbivore species they detected in the region is in broad agreement with our study. Furthermore, the correspondence in spatial patterns of diversity is striking. Rivadeneira et al. (2002) found one of their highest site-scale species richness around 33° S, where they also observed some of the largest between-site variations in richness. In broad agreement with the patterns documented in the study of Rivadeneira et al. (2002), we detected both the lowest and the highest herbivore species richness around 33° S (compare site richness

in Fig. 3 of Rivadeneira et al. (2002) with our Fig. 5B). The correspondence between both spatial patterns supports the occurrence of substantial spatial variation in mollusk species richness across the study region. Hence, our sampling scheme provides a systematic estimate of species diversity at multiple sites spread through a broad geographic region. Complementary sampling schemes, such as those that include species > 5 mm and other techniques involving extensive specimen collections, will increase diversity estimates at the local scale beyond our systematic underestimation. Below we discuss the mechanistic processes that may be involved in the geographic variation in species richness across the region.

Regional trends in macroalgal species richness, as well as those presented for red and brown algae separately were possibly related to an increase in onshore nutrient availability associated with colder waters across these same sites (Nielsen & Navarrete 2004, Navarrete et al. 2005). Although historical effects related to the biogeographic origins of the biota cannot be ruled out (Santelices 1980), the highest local macroalgal diversity was observed at two sites influenced by strong coastal upwelling: Punta Talca (PTAL) and Punta de Lobos (PTL) (Broitman et al. 2001). Coastal upwelling has been shown to drive productivity in at least some intertidal species (Nielsen & Navarrete 2004, Navarrete et al. 2005) and also to mediate biotic interactions in the region (Wieters 2005). Thus, nearshore oceanographic conditions that drive nutrient influx along central Chile may drive the diversity of locally coexisting algal species. But the relationship between upwelling and species diversity might be produced not only by variation in nutrient loadings, but also by the suite of environmental conditions –predominantly sea surface temperature variability– that vary with coastal topography (Tapia et al. 2009, Wieters et al. 2009). Testing such local-scale environmental forcing patterns across will require extensive validation of very nearshore satellite records for the region.

This variability in environmental conditions can produce complex responses in the intertidal biota (Wieters et al. 2009). Indeed, relatively low local macroalgal diversity was

observed at other well-defined upwelling centers in the study region (e.g., Curaumilla, Johnson et al. 1980), suggesting that productivity-diversity relationships interact with unmeasured differences in environmental conditions (e.g., Worm et al. 2002, Rajaniemi 2003). It is unclear which factors generate or maintain the region of low macroalgal diversity around 33° S (Fig. 5B). The low diversity area seems to be located south of Punta Curaumilla, suggesting that the flora with southern and northern affinities described around this biogeographic transition zone do not completely overlap (Camus 2001 and see below). The potential role of local factors in maintaining this region of low diversity should thus be investigated.

Distributional range limits of numerous intertidal species occur at different sites across the region between Punta Lengua de Vaca (~30° S) and Los Molles (~32° S) (Marincovic 1973, Brattström & Johanssen 1983, Hoffmann & Santelices 1997, Camus 2001, Thiel et al. 2007). In this study, we confirmed the northern range limits of the conspicuous intertidal macroalgae *Durvillaea antarctica* (Chamisso) Hariot and *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq, as well as the southern limits of the chiton *Enoplochiton niger* Barnes and the limpet *Scurria viridula* Lamarck (results not shown). Distributional limits of these few species alone, however, do not account for the large variations in species richness we observed in the region (Fig. 4). One potential driver of the biogeographic pattern in the mid intertidal zone may relate to the break in abundance of the dominant space competitor, the mussel *Perumytilus purpuratus*, which is observed at 32° S (Broitman et al. 2001, Navarrete et al. 2005). *Perumytilus* mussel beds host diverse invertebrate assemblages and provide complex habitats for recruits of many intertidal species (Thiel & Ullrich 2002, Prado & Castilla 2006). Thus, a large change in species richness could be expected to occur between regions where mussel beds dominate the shore and where these habitat-forming species are absent.

A number of mechanisms have been shown to regulate the structure and dynamics of local rocky intertidal communities of central Chile, which corresponds to the biogeographic

transition zone described above. For example, intensive and ubiquitous harvesting of shellfish by subsistence fishermen in the mid intertidal zone influences community structure by shifting a landscape dominated by beds of the mussel *Perumytilus purpuratus* into intertidal zones dominated by macroalgae, such as *Mazzaella laminarioides* and fleshy encrusting forms (Moreno et al. 1986, Castilla 1999, Fernandez et al. 2000). A similar situation is observed in the low intertidal zone where harvesting of the kelp *Lessonia nigrescens* Bory de Saint-Vincent and the bull kelp *Durvillaea antarctica* by subsistence harvesters may lead to communities dominated by encrusting algae species (Santelices 1980, Ojeda & Santelices 1984, Bustamante & Castilla 1990). On the other hand, species interactions, notably predation by the large snail *Concholepas concholepas* Brugière and the seastar *Heliaster helianthus* Lamarck, determine the abundance of dominant invertebrate filter-feeders and have implications for the abundance of other invertebrate and algal species (Castilla & Paine 1987, Navarrete et al. 2002, Navarrete & Castilla 2003). Similarly, herbivory strongly influences macroalgal abundance (Ojeda & Santelices 1984, Ojeda & Muñoz 1999, Nielsen & Navarrete 2004), especially of ephemeral algae. In contrast, recruitment limitation might be one of the dominant structuring processes through large regions of the coast (Navarrete et al. 2005). Therefore, to achieve a mechanistic understanding of patterns in biodiversity requires us to consider the role of both natural and anthropogenic factors in structuring intertidal assemblages.

In conclusion, we detected large spatial variation in the diversity of intertidal organisms across a large coastal region previously acknowledged as relatively homogeneous (Santelices & Marquet 1998, Valdovinos et al. 2003). Further studies testing departures from a linear gradient are needed to include the diversity of organisms living in other habitats, such as boulders, crevices, and biogenic habitats generated by mussels and canopy-forming algae. Nevertheless, this study represents a contribution to our knowledge of empirical patterns of intertidal species richness in central Chile and a first step towards a regional baseline of marine biodiversity.

ACKNOWLEDGEMENTS: We would like to thank a large number of people that helped during the long time period spanned by the study including: Franz Smith, Steve Gaines, Miriam Fernández, Álvaro Sotomayor, Hugo Ceballos, Karina Nielsen, Roberto Venegas, Cintia Cornelius, Marcelo Rivadeneira, Allison Haupt, Tamara Contador, Andrea Masuero, Claudio Broitman, Celeste Silva, and Carola Flores. This study was possible thanks to the continuous support of the AW Mellon Foundation to BRB and SAN, and a FONDAP-FONDECYT grant # 15001-001 to the Center for Advanced Studies in Ecology and Biodiversity. BRB gratefully acknowledges financial support from the Coastal Environmental Quality Initiative. Additional funds for field sampling in 2004 were provided by a FONDECYT grant # 1040787 to SAN. FONDECYT grants # 1090488 and # 3100014 for BRB and NV respectively, provided support in the final stages of the manuscript.

LITERATURE CITED

- BALMFORD A & KJ GASTON (1999) Why biodiversity surveys are good value. *Nature* 398: 204-205.
- BRATTSTRÖM H & A JOHANSEN (1983) Ecological and regional zoogeography of the marine benthic fauna of Chile. *Sarsia* 68: 289-339.
- BROITMAN BR, NAVARRETE SA, SMITH F & SD GAINES (2001) Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series* 224: 21-34.
- BUSTAMANTE RH & JC CASTILLA (1990) Impact of human exploitation on populations of the intertidal southern bull-kelp *Durvillaea antarctica* (Phaeophyta, Durvilliales) in central Chile. *Biological Conservation* 52: 205-220.
- CAMUS PA (2001) Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural* 74: 587-617.
- CAMUS PA, DAROCH K & LF OPAZO (2008) Potential for omnivory and apparent intraguild predation in rocky intertidal herbivore assemblages from northern Chile. *Marine Ecology Progress Series* 361:35-45
- CASTILLA JC (1999) Coastal marine communities: Trends and perspectives from human-exclusion experiments. *Trends in Ecology & Evolution* 14: 280-283.
- CASTILLA JC & RT PAINE (1987) Predation and community organization on eastern pacific, temperate zone rocky intertidal shores. *Revista Chilena de Historia Natural* 60: 131-151.
- CHAO A (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783-791.
- CHAPMAN MG (2002) Early colonization of shallow subtidal boulders in two habitats. *Journal of Experimental Marine Biology and Ecology* 275: 95-116.
- ESPOZ C, LINDBERG DR, CASTILLA JC & WB SIMISON (2004) Los patelogastrópodos intermareales de Chile y Perú. *Revista Chilena de Historia Natural* 77: 257-283.
- FERNÁNDEZ M, JARAMILLO E, MARQUET PA, MORENO CA, NAVARRETE SA, OJEDA FP, VALDOVINOS CR & JA VÁSQUEZ (2000) Diversity, dynamics and biogeography of

- Chilean benthic nearshore ecosystems: An overview and guidelines for conservation. *Revista Chilena de Historia Natural* 73: 797-830.
- GOTELLI NJ & RK COLWELL (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391.
- GRAY CA, OTWAY NM & AG MISKIEWICZ (1997) Numerical responses of larval fishes to deepwater sewage disposal: A field assessment. *Marine Pollution Bulletin* 33: 190-200.
- HERNÁNDEZ CE, MORENO RA & N ROZBACZYLO (2005) Biogeographical patterns and Rappaport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. *Ecography* 28: 363-373.
- HILLEBRAND H (2004) On the generality of the latitudinal diversity gradient. *American Naturalist* 163: 192-211.
- HOFFMANN AJ & B SANTELICES (1991) Banks of algal microscopic forms: Hypotheses on their functioning and comparisons with seed banks. *Marine Ecology Progress Series* 79: 185-194.
- HOFFMANN AJ & B SANTELICES (1997) Flora marina de Chile central. Ediciones Universidad Católica de Chile, Santiago, Chile.
- HORMAZÁBAL S, SHAFFER G & O LETH (2004) Coastal transition zone off Chile. *Journal of Geophysical Research* 109: 1-13.
- JOHNSON DR, FONSECA T & H SIEVERS (1980) Upwelling in the Humboldt coastal current near Valparaíso, Chile. *Journal of Marine Research* 38: 1-16.
- LANCELOTI DA & JA VÁSQUEZ (1999) Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *Journal of Biogeography* 26: 1001-1006.
- MARINCOVIC L (1973) Intertidal mollusks of Iquique, Chile. *Scientific Bulletin of the Natural History Museum of Los Angeles* 16: 1-49.
- MENESES I & B SANTELICES (2000) Una re-evaluación de la caracterización fitogeográfica de la costa temperada del Pacífico de Sudamérica. *Revista Chilena de Historia Natural* 73: 615-623.
- MITTELBACH GG, SCHEMSKE DW, CORNELL HV, ALLEN AP, BROWN JM et al. (2007) Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters* 10: 315-331.
- MORENO CA, LUNECKE KM & MI LÉPEZ (1986) The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblage. *Oikos* 46: 359-364.
- NAVARRETE SA, BROITMAN B, WIETERS EA, FINKE GR, VENEGAS RM & A SOTOMAYOR (2002) Recruitment of intertidal invertebrates in the southeast Pacific: Interannual variability and the 1997-1998 El Niño. *Limnology and Oceanography* 47: 791-802.
- NAVARRETE SA & JC CASTILLA (2003) Experimental determination of predation intensity in an intertidal predator guild: Dominant versus subordinate prey. *Oikos* 100: 251-262.
- NAVARRETE SA, WIETERS EA, BROITMAN BR & JC CASTILLA (2005) Scales of benthic-pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control. *Proceedings from National Academy of Sciences USA* 102: 18046-18051.
- NIELSEN KJ & SA NAVARRETE (2004) Mesoscale regulation comes from the bottom-up: Intertidal interactions between consumers and upwelling. *Ecology Letters* 7: 31-41.
- OJEDA FP & B SANTELICES (1984) Ecological Dominance of *Lessonia nigrescens* in central Chile. *Marine Ecology Progress Series* 19: 83-91.
- OLIVA D & JC CASTILLA (1992) Guía para el reconocimiento y morfometría de diez especies del género *Fissurella* Brugiere, 1789 (Mollusca : Gastropoda) comunes en la pesquería y conchales indígenas de Chile central y sur. *Gayana Zoológica* 56: 77-108.
- PIANKA ER (1966) Latitudinal gradients in species diversity. *American Naturalist* 100: 33-46.
- PRADO L & AC CASTILLA (2006) The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: Biodiversity, habitat structural complexity and environmental heterogeneity. *Journal of the Marine Biological Association UK* 86: 417-421.
- R DEVELOPMENT CORE TEAM (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- RAJANIEMI TK (2003) Explaining productivity-diversity relationships in plants. *Oikos* 101: 449-457.
- RIVADENEIRA MM, FERNÁNDEZ M & SA NAVARRETE (2002) Latitudinal trends of species diversity in rocky intertidal assemblages: Spatial scale and the relationship between local and regional species richness. *Marine Ecology Progress Series* 245: 123-131.
- SANTELICES B (1980) Phytogeographic characterization of the temperate coast of Pacific South America. *Phycologia* 19: 1-12.
- SANTELICES B & PA MARQUET (1998) Seaweeds, latitudinal diversity patterns and Rappaport's rule. *Diversity and Distributions* 4: 71-75.
- STENECK RS & MN DETHIER (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476-498.
- THIEL M (2002) The zoogeography of algae-associated peracarids along the Pacific coast of Chile. *Journal of Biogeography* 29: 999-1008.
- THIEL M & N ULLRICH (2002) Hard rock versus soft bottom: The fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. *Helgolander Marine Research* 56: 21-30.
- THIEL M, MACAYA EC, ACUÑA E, ARNTZ WE, BASTIAS H et al. (2007) The Humboldt Current System of northern and central Chile. *Oceanography and Marine Biology: An Annual Review* 45: 195-344.
- UNDERWOOD AJ & MG CHAPMAN (2006) Early development of subtidal macrofaunal assemblages: Relationships to period and timing of colonization. *Journal of Experimental Marine Biology and Ecology* 330: 221-233.
- VALDOVINOS CR, NAVARRETE SA & PA MARQUET (2003) Mollusk species diversity in the Southeastern Pacific: Why are there more species towards the pole? *Ecography* 26: 139-144.
- WALTHER BA & J-L MARTIN (2001) Species richness estimation of bird communities: How to control for sampling effort? *Ibis* 143: 413-419.

- WIETERS EA (2005) Upwelling control of positive interactions over mesoscales: A new link between bottom-up and top-down processes on rocky shores. *Marine Ecology Progress Series* 301: 43-54.
- WIETERS EA, BROITMAN BR & GM BRANCH (2009) Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: Comparisons between South Africa and Chile. *Limnology and Oceanography* 54: 1060-1072.
- WORM B, LOTZE HK, HILLEBRAND H & U SOMMER (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417: 848-851.

Associate Editor: Mario George-Nascimento

Received August 6, 2010; accepted January 21, 2011