Revista Chilena de Historia Natural
72: 377-388, 1999

Effects of substratum topography on species diversity and abundance in Chilean rocky intertidal communities

Efectos de la topografía del substrato sobre la diversidad y abundancia de especies en comunidades intermareales rocosas de Chile

PATRICIO A. CAMUS[1], YANIRE N. ANDRADE[2] and BERNARDO BROITMAN[3]

[1]Facultad de Ciencias, Universidad Católica de la Ssma. Concepción,
Casilla 297, Concepción, Chile
E-mail: pcamus@david.ucsc.cl
[2]Departamento de Fisiología, [3]Departamento de Ecología,
P. Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT

In the study of rocky intertidal community diversity, substratum has been traditionally treated as a potentially limiting resource (space) which is co-used by different species. However, little is known about the converse situation, namely whether the substratum, treated as surface with particular topographic features, can affect the diversity and abundance of species. In this paper we analyse the effect of three topographic variables on both within-community diversity and the abundance of three dominant species, measured in samplings carried out at two mid-intertidal Chilean communities: El Tasbo-El Quisco (central Chile; n = 54) and Mejillones (northern Chile; n = 92). The three selected variables were: (a) slope: defined as inclination of the rocky surface above the horizontal, and categorized into three ranks; (b) roughness: surface relief, estimated as the mean length of the two diagonals of each sampling quadrat (measured only at El Tabo-El Quisco); and (c) orientation: position of the rocky surface with respect to the prevailing direction of water flow. This last variable was interpreted as degree of exposure of subtratum to water flow (with no relation to wave strength), varying from direct exposure to opposite to flow. Overall, substratum topography showed a rather weak effect on both community diversity and the abundance of the three species which dominate intertidal seascapes in the study areas, the barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*, and the chlorophycean alga *Ulva rigida*. However, some variables were clearly important in particular cases, and mainly at El Tabo-El Quisco. On the one hand, species richness exhibited a significant increase with substratum roughness, and on the other hand, the abundance of dominant species tended to increase with decreasing exposure to water flow. Nonetheless, these results have no simple explanation, as topographic variables may interact in complex way and their effect could be strongly dependent on local conditions.

Key words: rocky intertidal, substratum topography, diversity, abundance.

RESUMEN

Tradicionalmente, al estudiar la diversidad en comunidades intermareales rocosas el substrato ha sido tratado como un recurso (espacio) potencialmente limitante que es co-usado por las especies. La situación contraria, sin embargo, es menos conocida, es decir si el substrato, tratado como una superficie con características topográficas particulares, puede o no influir en la abundancia y diversidad de especies. En este trabajo analizamos el efecto de tres variables topográficas sobre la diversidad intra-comunitaria y la abundancia de tres especies sésiles dominantes, medidas en una serie de unidades muestrales en dos comunidades medio-litorales chilenas: El Tabo-El Quisco (Chile central; n = 54) y Mejillones (Chile norte; n = 92). La tres variables analizadas fueron: (a) pendiente: definida como inclinación del substrato sobre la horizontal, y categorizada en tres rangos; (b) rugosidad: relieve de la superficie, estimada como longitud promedio medida en las dos diagonales en cada cuadrante de muestreo (medida sólo en El Tabo-El Quisco); y (c) orientación: posición de la superficie respecto a la dirección predominante del flujo de agua, marcado por el frente de olas llegando a la costa en cada sitio. Esta última variable se interpretó como grado de exposición del substrato al flujo de agua (sin relación a fuerza de oleaje), variando desde expuesto directamente hasta opuesto al flujo. Globalmente, la topografía del substrato mostró un efecto más bien débil tanto en la diversidad comunitaria como en la abundancia de las tres especies que dominan el paisaje intermareal, los cirripedios *Jehlius cirratus* y *Notochthamalus scabrosus*, y la clorófita *Ulva rigida*. No obstante, algunas variables fueron claramente relevantes en casos particulares, aunque principalmente en El Tabo-El Quisco. Por una parte, la riqueza específica aumentó significativamente con la rugosidad del substrato, y por otra, la abundancia de las especies dominantes aumentó progresivamente a medida que disminuía el grado de exposición del substrato al flujo de agua. Sin embargo, estos resultados no tienen una explicación simple, ya que las variables topográficas pueden interactuar de forma compleja y su efecto podría ser altamente dependiente de condicionantes locales.

Palabras clave: intermareal rocoso, topografía del substrato, diversidad, abundancia.

(Received 4 June, 1998, accepted 5 May, 1999; managed by C.A. Moreno)

INTRODUCTION

Population and community attributes in rocky intertidal communities are often assumed to be affected by different features of the rocky substratum. Most published studies treat substratum mainly as a resource dimension, emphasizing how the provision of space constraints the distribution and abundance of interacting populations. In contrast, the role of primary or secondary substratum topography as a potential determinant of the distribution and abundance of species has been much less studied. Moreover, most concerned research focuses on individual populations, and community-level studies seldom evaluate the effects of topography in direct terms.

A number of continuous or categorical variables have been used for obtaining suitable descriptions of substratum characteristics. Nonetheless, three aspects of topography, treated as isolated or interacting factors, have received a greater attention in the literature: (a) slope or inclination; (b) orientation or position on the shore; and more importantly, (c) heterogeneity, a loosely concept used with a variety of meanings, but usually interpreted as microhabitat diversity or either the presence, number or size of distinctive features of the rocky surface. The effects of substratum topography on particular populations in different places are varied. For example: absence of crevices promoted aggregation in *Nucella lapillis* for avoiding mortality due to wave action (Feare 1971); crevice availability and barnacle cover were strongly related with body size and density of *Littorina rudis* (Emson & Faller-Fritsch 1976); size and vertical distribution of crevices determined the size structure of *Littorina rudis* and *L. neritoides* (Raffaelli & Hughes 1978); substratum inclination was related with geotactic behavior in littorinids for maintaining their intertidal position (Petraitis 1982); crevices acted as a refuge against desiccation and constrained foraging displacements of *Nerita funiculata* and *N. scabricosa* (Levings & Garrity 1983); heterogeneity increased survival of *Enteromorpha* when grazed by *Littorina* (Petraitis 1983); crevices and barnacle cover enhanced recruitment of *Concholepas concholepas* (Lépez & Moreno 1988); topographic complexity (measured as an index) affected the spatio-temporal variation in density and population turnover of *Littorina unifasciata* (Underwood & Chapman 1989); experimental rugosity (resin castings of barnacles) favored the settlement of *Mytilus edulis* (Petraitis 1990); rugose substrata such as coarsely-branched coralline algae increased recruitment of *Lessonia nigrescens* (Camus 1994); substratum slope and barnacle cover affected density and body size of *Littorina unifasciata* (Chapman 1994); pits and crevices influenced the distribution and abundance of *Nodilittorina pyramidalis* (Chapman & Underwood 1994); finally, and summarizing other investigations, Raffaelli & Hawkins (1996) noted that substratum texture strongly influences the final site for settlement in a variety of organisms.

From population studies, it is clear that substratum-related variables can be important determinants for many rocky intertidal populations (notably gastropods). However, the effects of substratum on the community as a whole appear rather obscure, and the number of studies dealing with this topic is remarkably smaller, despite the widespread notion that heterogeneity or microhabitat diversity may enhance diversity by providing refuges or more axes to be partitioned among community members (e.g., see the analysis by McGuiness & Underwood 1986 and references therein). As for individual populations, community results are also varied. Among the literature examples, Kohn & Leviten (1976) found that greater complexity (mix of algal turfs, sand and crevices) increased population densities and species richness in coral reef platforms. In contrast, Jernakoff (1985) detected no effect of crevice availability and barnacle cover on algal diversity and cover in a rocky intertidal community. In a more comprehensive study, McGuinness & Underwood (1986) found that, apparently, greater microhabitat diversity (pits and grooves) was related to an overall increase in species diversity and abundance; however, this effect varied markedly for different subsets of species (strong for sessile animals, weak for grazers, and weak or reverse for algae) and also depended on the location of substratum on the shore.

The above results, mainly related with substratum heterogeneity, would suggest that topography have either a weak or a context-dependent effect on rocky intertidal community diversity. However, the disparity of results obtained by different authors in different places does not allow generalizations on the role of substratum characteristics, and very likely the possible outcomes will vary from place to place depending on the particular small-scale configuration of rocky coasts. Additionally, it appears to be no community study so far attempting a systematic assessment for a suite of topograhic variables. Thus, the potential magnitude and direction of the effect of substratum topography on community diversity can hardly be predicted, and therefore they should not be disregarded. Consequently, in this paper we assess the extent to which substratum topography and orientation, described by a series of physical variables, is related with both community diversity and species abundance in two rocky intertidal habitats from the Chilean coast. We show that, overall, topography accounts for a very low fraction of the variance in diversity, although it may have a strong influence on particular cases.

METHODS

During June 1996, we sampled the mid-high rocky intertidal zone at two sites ca. 2 km apart, located between the localities of El Tabo and El Quisco in central Chile (ca. 33°25'S). This coast is formed primarily by large boulders and rocky platforms of

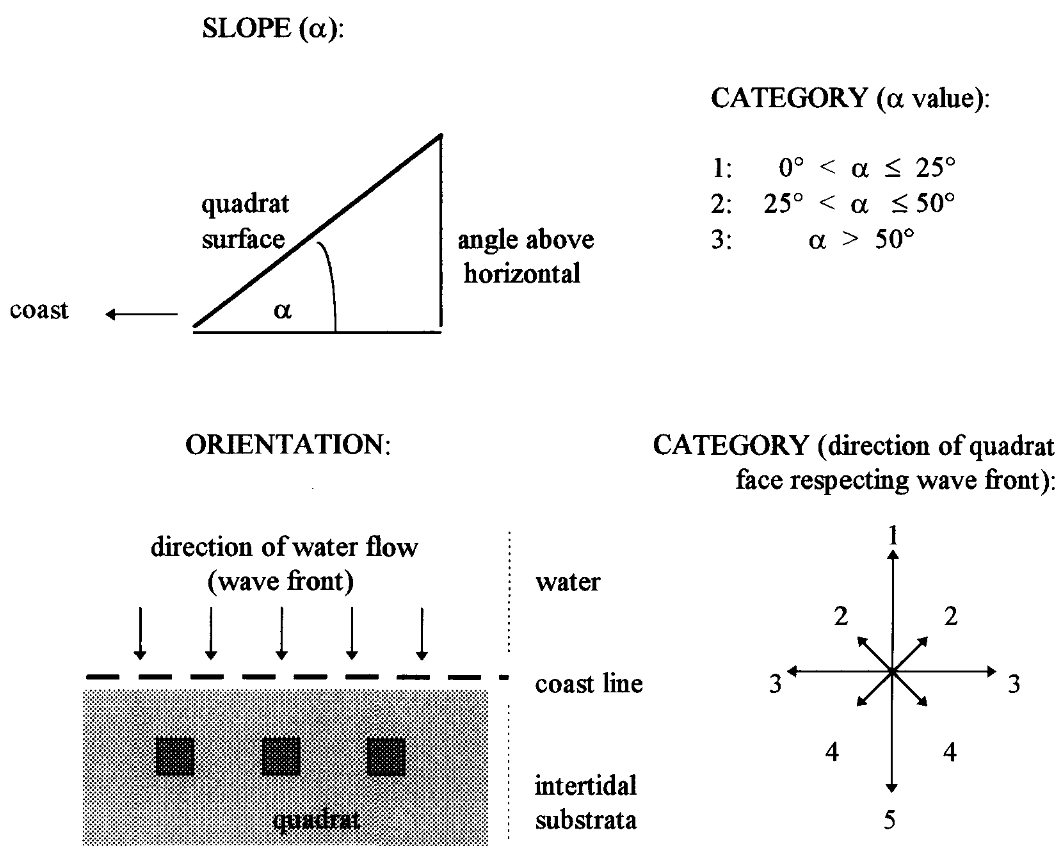

Fig. 1: Categorical variables of rocky intertidal substratum measured in this study, and their corresponding categories as used in the text and statistical analyses.

Variables categóricas del substrato rocoso intermareal medidas en este estudio, y sus correspondientes categorías según son usadas en el texto y en análisis estadísticos.

varying slope, exposed to wave action. The organization, structure and vertical zonation of central Chilean intertidal communities have been extensively described elsewhere (e.g., see Castilla & Durán 1985, Santelices 1990). The two central Chilean sites are very similar in species composition, abundance patterns, and physical configuration, and owing to their proximity we treated them as a single location, referred to as El Tabo-El Quisco hereafter.

Using a total of 54 randomly-placed quadrats (0.25 m^2) in both sites, we measured the number of species per quadrat and the abundance (cover percentage) of three sessile species: the small-sized barnacles *Jehlius cirratus* Darwin and *Notochthamalus scabrosus* Darwin, and the green alga *Ulva rigida* (C. Agardh) J. Agardh, three species of wide vertical distribution and also the most frequent and abundant species in northern and central Chilean intertidal seascapes (Camus 1998). Thus, they represent the dominant secondary substratum and are supposed to be an important component of habitat heterogeneity for other species (which settle or refuge on or within the former), possibly influencing their richness and abundance.

For each quadrat we assessed three characteristics of the substratum: (a) slope, measured as the angle between the rocky surface and the horizontal; (b) orientation, measured as the position of the substratum in reference to the wave front line; and (c) roughness, measured as the length (cm) of a thin chord following the surface relief across the two diagonals of the quadrat, and calculated for each quadrat simply as the average diagonal length. Slope and orientation were expressed as categorical variables; the lowest possible numerical value for roughness was 70, equivalent to a completely flat surface. Figure 1 outlines the measurement of slope and orientation, and their corresponding categories as used in statistical analyses and in Figures. We considered orientation to reflect a gradient of exposition to the prevailing water flow (not to wave strength), defined by the angle between the substratum surface and the direction of the wave front, ranging from direct to reverse exposition (see Fig. 1). When substratum surface was horizontal, orientation was categorized as 0 (zero; perpendicular to the wave front), and thus it become confounded with slope = 0. Therefore, this particular case was not considered in statistical analyses. We remark that our definition of orientation may not apply to semi-exposed or sheltered habitats where water flows can be different under low and high tide conditions.

Additionally, we compare the data for central Chile with data on substratum orientation and slope obtained in an similar sampling for a northern Chilean site (Península de Mejillones, 23°24' S; referred

TABLE 1

Categories of slope and orientation of substratum (see definitions in Fig. 1) analyzed in this paper, and the number and percentage (in parenthesis) of sampling quadrats recorded for each case at the two study localities

Categorías de pendiente y orientación del subtrato (ver definiciones en Fig. 1) analizadas en este trabajo, y número y porcentaje (en paréntesis) de cuadrantes de muestreo registrados para cada caso en las dos localidades de estudio

Variable	Category	Mejillones	El Tabo-El Quisco
Orientation	1	0 (0)	9 (18.0)
	2	36 (51.4)	11 (22.0)
	3	1 (1.4)	11 (22.0)
	4	32 (45.7)	10 (20.0)
	5	1 (1.4)	9 (18.0)
Slope	1	33 (47.8)	20 (40.0)
	2	36 (52.2)	22 (44.0)
	3	0 (0)	8 (16.0)

to as Mejillones, hereafter) during 1990 ($n = 92$); roughness was not measured in this site. Although Mejillones is also formed by large boulders and rocky platforms, it has a slightly different configuration and the occurrence frequency of certain orientation and slope categories did not match that found in El Tabo-El Quisco. Thus, statistical analyses for the northern site provide similar but not equivalent tests of substratum effects.

As the number of observations for a given substratum category depends on its natural occurrence in the field, which in turn depends on the configuration of rocky substratum in a site, it was not always possible to analyze statistical designs including all categories in all factors. Thus, we decided to reduce the number of cells in ANOVA designs instead of estimating sums of squares for empty cells, and perform additional correlation analyses for incorporating observations not included in ANOVAs. The number of sampling quadrats analyzed per category for substratum slope and orientation is shown in Table 1, although the actual sampling size varied among analyses depending on the available units for combining categories, or whether the available sample size for a single category was high enough to be included in a given analysis.

Data from El Tabo-El Quisco were pooled for statistical analyses and assessed by means of two fixed models of ANOVA: (a) two-way ANOVA with slope and orientation as factors; (b) the same analysis but including roughness as a covariable. Slope and orientation were assessed separately by one-way ANOVAs for Mejillones, where orientation included only two levels (categories 1 and 4 in Fig. 1). Correlation analyses, estimating Pearson (r_P) or Spearman (r_S, corrected for ties) coefficients depending on the type of variable, were performed using average values for each category, and including all categories of orientation and slope.

We assessed the possible relationships between substratum variables and: (a) species richness, and (b) coverage of dominant species; for this latter analysis, the two barnacle species were grouped since they usually settle together forming a mixed layer on the substratum (Camus & Lagos 1996). On the other hand, we also took into account that the occupation of primary space by dominant species may be a source of habitat heterogeneity for the remaining species, and the use of secondary biological substrata by sessile species seems to be a usual phenomenon (e.g., Lohse 1983, Camus 1998). Therefore, we evaluated the association between coverage of each dominant species (discarding quadrats with zero values) and species richness (excluding the dominant species), in order to assess their possible effect on diversity.

RESULTS

Effect of substratum on species richness

Average values of species richness per orientation and slope categories are shown in Figure 2, which also includes the scatterplot for species richness as a function of roughness. For El Tabo-El Quisco, two-way ANOVAs showed no significant effects of orientation ($F_{4,32} = 0.99$; $P = 0.327$), slope ($F_{1,32} = 0.70$; $P = 0.600$) or their interaction ($F_{4,32} = 0.55$; $P = 0.698$) on species richness. The same occurred for Mejillones, as shown by one-way ANOVAs for orientation ($F_{1,87} = 0.02$; $P = 0.899$) and slope ($F_{2,87} = 0.01$; $P = 0.989$), irrespective of the wide qualitative differences among factor levels between the two localities. Roughness, on the other hand, revealed a positive and significant association with species richness in El Tabo-El Quisco ($r_P = 0.45$; $P < 0.0006$; $n = 55$; Fig. 2), and thus it could actually be a contributor to the variance of community diversity.

Effect of substratum on dominant species

In El Tabo-El Quisco, the coverage of *Ulva* was not associated with roughness ($r_S = -0.1267$; $P = 0.3659$; $n = 53$), and two-way ANOVAs (including roughness as a covariate) showed no significant effect of orientation ($F_{4,31} = 1.57$; $P = 0.207$), slope ($F_{1,31} = 2.76$; $P = 0.107$), or their interaction

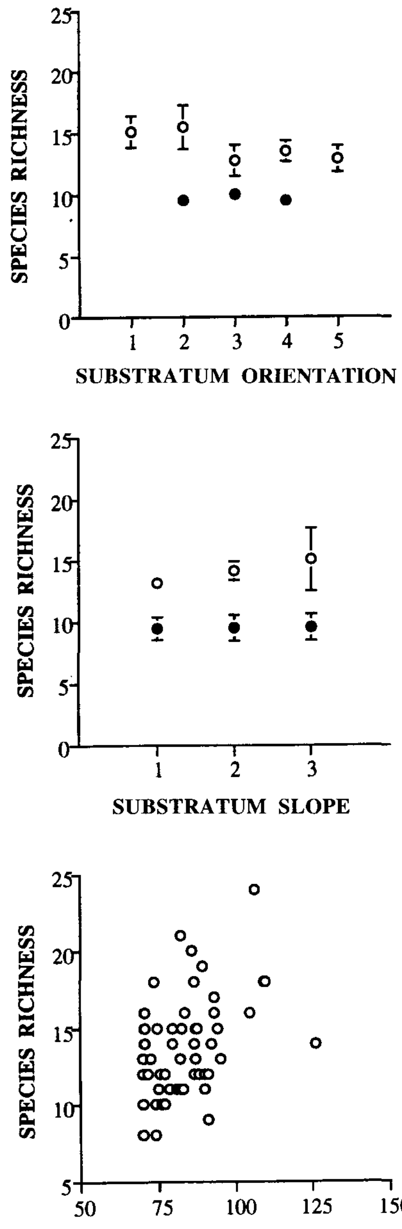

Fig. 2: Species richness (average ± 1 SE) in the mid-high rocky intertidal zone of El Tabo-El Quisco (central Chile; open dots) and Mejillones (northern Chile; filled dots), as a function of the orientation and slope of substratum, and of its roughness only for El Tabo-El Quisco. Categories as in Fig. 1. Standard errors for Mejillones do not appear in the graph owing to their very small values.

Riqueza de especies (media ± 1 EE) en la zona intermareal medio-alta de El Tabo-El Quisco (Chile central; círculos abiertos) y Mejillones (Chile norte; círculos llenos), en función de la orientación y pendiente del substrato, y de su rugosidad sólo para El Tabo-El Quisco. Categorías según la Fig. 1. Los errores estándar para Mejillones no aparecen en el gráfico debido a sus valores muy pequeños.

($F_{4,32}$ = 0.83; P = 0.516). Likewise, orientation ($F_{1,76}$ = 3.36; P = 0.071) and slope ($F_{2,76}$ = 0.20; P = 0.818) revealed no effect on *Ulva* cover in Mejillones. Nonetheless, in El Tabo-El Quisco *Ulva* clearly tended to increase in abundance with decreasing exposition to water flow (Fig. 3), appearing positively, although non significantly correlated with orientation (r_s = 0.700; P = 0.1881; n = 5). We believe that, in this case, the lack of statistical significance does not necessarily mean lack of biological significance, and the potential effect of substratum orientation should not be disregarded. A similar increasing trend of *Ulva* with orientation was apparent in Mejillones, although no correlation was performed because of the small number of categories.

In regard with the abundance of barnacles, ANOVAs showed no significant effect of orientation ($F_{1,79}$ = 0.03, P = 0.869) and slope ($F_{2,79}$ = 2.86; P = 0.063) in Mejillones, but this time contrasting with a clear effect of substratum slope in El Tabo-El Quisco (see Table 2). However, this last effect was detected only when roughness was included as a covariate in the analysis, even though roughness itself was not correlated with abundance of barnacles. Figure 4 suggests that barnacles would be favored by intermediate slopes in El Tabo-El Quisco, a different trend from that observed in Mejillones. Additionally, barnacles also tended to increase in abundance with decreasing exposition to water flow (orientation) in El Tabo-El Quisco (Fig. 4). The means of abundance of barnacles per orientation category did not vary so greatly as to generate a significant within-subject effect in ANOVA, but a positive statistical correlation between both variables was evident (r_s = 0.900; P = 0.0374; n = 5). In contrast, barnacles exhibited no clear trend with orientation in Mejillones.

Dominant species as substratum

Figure 5 shows the relationship between species richness and abundance of barnacles observed in the two study sites. Even though no trend is apparent, the correlation between the two variables was significant both for El Tabo-El Quisco ($r_p = 0.270$; $P = 0.0483$; $n = 53$) and Mejillones ($r_p = -0.278$; $P = 0.0105$; $n = 84$), although of opposite sign. Nonetheless, these low P-values were likely due to the relatively large sample size and the influence of some isolated values than to a real biological effect. However, Fig. 5 also shows that the dispersion of diversity values decreases with increasing coverage of barnacles, sug-

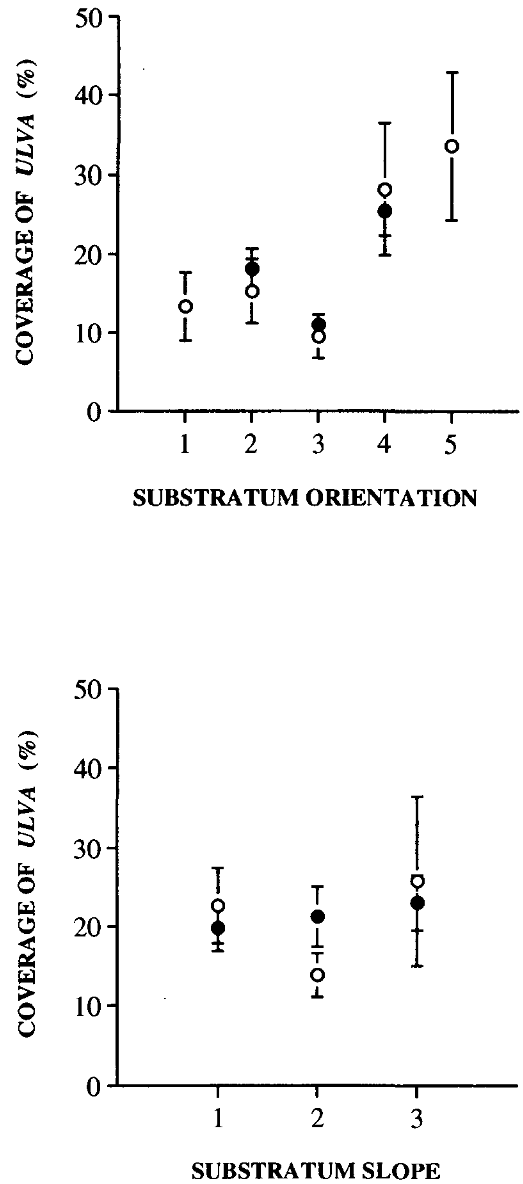

Fig. 3: Coverage (average ± 1 SE) of the Chlorophyta *Ulva rigida* (C. Agardh) J. Agardh in El Tabo-El Quisco (central Chile; open dots) and Mejillones (northern Chile; filled dots) as a function of the orientation and slope of substratum.

Cobertura (media ± 1 EE) de la Clorófita *Ulva rigida* (C. Agardh) J. Agardh en El Tabo-El Quisco (Chile central; círculos abiertos) y Mejillones (Chile norte; círculos llenos) en función de la orientación y pendiente del substrato.

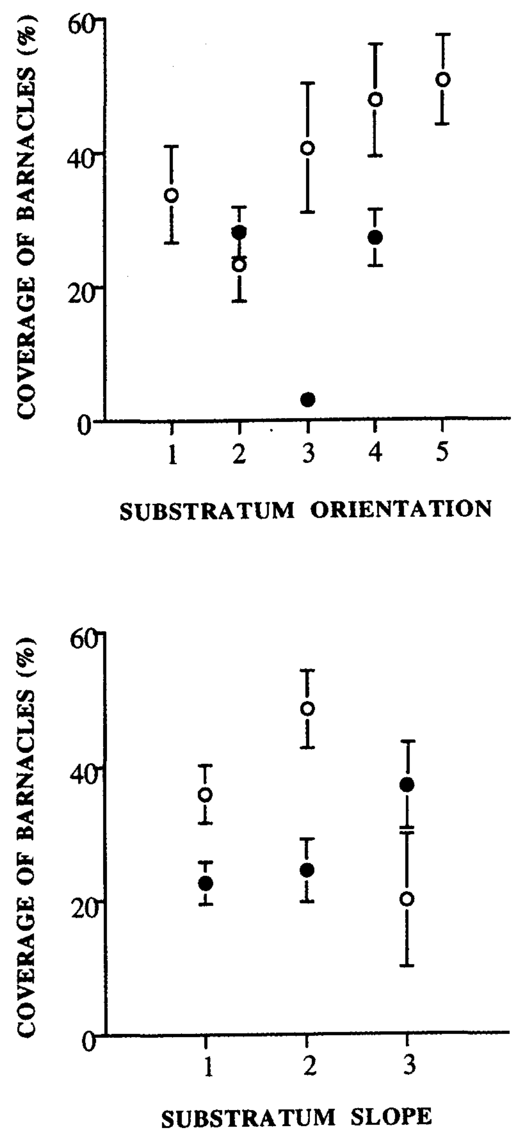

Fig. 4: Coverage (average ± 1 SE) of small-sized barnacles (*Jehlius cirratus* Darwin and *Notochthamalus scabrosus* Darwin) in El Tabo-El Quisco (open dots) and Mejillones (filled dots) as a function of the orientation and slope of substratum.

Cobertura (media ± 1 EE) de cirripedios de pequeño tamaño (*Jehlius cirratus* Darwin y *Notochthamalus scabrosus* Darwin) en El Tabo-El Quisco (círculos abiertos) y Mejillones (círculos llenos) en función de la orientación y pendiente del substrato.

gesting that the latter might rather be limiting than enhancing species richness.

The relationship between the coverage for *Ulva* and species richness (not shown) exhibited no correlation due to a much greater dispersion of values than those for barnacles, both in El Tabo-El Quisco and Mejillones, thus evidencing no decreasing or increasing trend of diversity with the prevailing algal substratum.

DISCUSSION

Diversity and primary substratum

Within-community diversity in the study sites was differentially affected by the selected descriptors of substratum topography, at the spatial scale of our sampling units. Additionally, and when it was possible to analyze, we detected no significant interactions among these variables, although some relationship was evident when the roughness of the rocky surface was considered as a continuous covariable. Even though the overall effect of topography was weak, substratum heterogeneity alone played a significant role enhancing species richness, contrasting with the apparently null influence of slope and orientation. The fact that the observed species diversity in a community is the outcome of many different processes highlights the importance of finding a significant association with a single topographic variable.

On the other hand, we remark that this study was a preliminary step for conducting a larger-scale survey of rocky intertidal diversity, being focused on community diversity as a whole. Therefore, we do not discard that different subsets of species can be differentially affected by topographic features, as found by McGuinness & Underwood (1986). In this perspective, our results suggest that substratum effects probably need not be considered in detail in those community studies where diversity is not the key variable to be assessed. Every time diversity is involved, however, it could be important to include at least some topographic measurement such as roughness, as a covariable or factor likely to affect quantitative estimates.

Substratum and dominant species

Dominant species also responded weakly to substratum topography, although with two exceptions. On the one hand, substratum slope appeared as an important factor for barnacles when interacting with roughness, albeit the relationship between these two variables was unclear, lacking a simple interpretation. On the other hand, substra-

TABLE 2

Two-way, fixed ANOVA model for the coverage of small-sized barnacles (*Jehlius cirratus* Darwin and *Notochthamalus scabrosus* Darwin) in central Chilean rocky intertidal sites as a function of substratum orientation and slope. Substratum roughness was entered as a covariable in the analysis. For substratum slope, only levels 1 and 2 of Fig. 1 were used for avoiding empty cells in the combination of factor levels. d.f.: degrees of freedom; M.S.: mean square

Análisis de varianza de dos vías (modelo fijo) para la cobertura de cirripedios de pequeño tamaño en sitios intermareales rocosos de Chile central en función de la pendiente y orientación del substrato. La rugosidad del substrato fue incorporada como un covariable en el análisis. Para la pendiente del substrato, sólo fueron usados los niveles 1 y 2 de la Fig. 1 con objeto de evitar las celdas vacías al combinar los niveles del factor. d.f.: grados de libertad; M.S.: cuadrado medio

Source	d.f.	M.S.	F-ratio	P
Substratum slope	1	2795.8	6.19	0.0184
Substratum orientation	4	519.5	1.15	0.3524
Slope * Orientation	4	598.5	1.33	0.2823
Error	31	451.5		

tum orientation showed to have an influence on the three dominant species, the two barnacles and *Ulva rigida*, which tended to be more abundant in less exposed substrata in El Tabo-El Quisco, the central Chilean site. This well-defined trend was not found in Mejillones, the northern Chilean site, probably due to its different coastal configuration (dominated mainly by southwest- and northwest-facing surfaces), or to other site-dependent factors. Contrastingly, in El Tabo-El Quisco rocky surfaces face all directions, allowing a better assessment of orientation effects. We suggest that the results obtained in El Tabo-El Quisco could be partly related with the fact that substrata exposed to different directions of the water flow are also differentially impacted by waves, which in turn could affect the intensity of settlement of larvae or spores arriving to them. Substrata indirectly or not impacted by waves (i.e., categories 3 to 5 in Fig. 1) not only experience smaller hydrodynamic disturbances but, secondarily, they could also receive larvae or spores contained in the water running off from higher intertidal levels. To this respect, Camus & Lagos (1996) showed for two northern Chilean localities that, in terms of spatial occurrence, temporal frequency, and cover percent, the three dominant species (particularly barnacles) exhibit the highest recruitment among sessile intertidal species, suggesting that their propagules would be the most abundant in the water. Thus, it is probable that some factor increasing the likelihood of contact between propagules and suitable surfaces may result in an increased recruitment, and probably in a greater adult abundance. Additionally, Hoffmann & Ugarte (1985) demonstrated that, in central Chilean rocky intertidal communities, run-off water carries a greater amount of macroalgal propagules than the arriving surface water, which could help to explain the grater abundance of *Ulva* in substrata facing higher intertidal levels.

The above suggests that the composition or abundance of the species growing in a given rocky intertidal substratum could be determined to some extent by the orientation or slope of its surface. Nevertheless, the study cases reviewed in the Introduction section indicate that a large number of different physical and biotic factors might potentially interact with substratum variables in different places, and general patterns are hardly expectable. Thus, the apparently conflicting evidence on substratum effects in the literature may just be pointing to strong local dependency, and therefore it is not really important whether

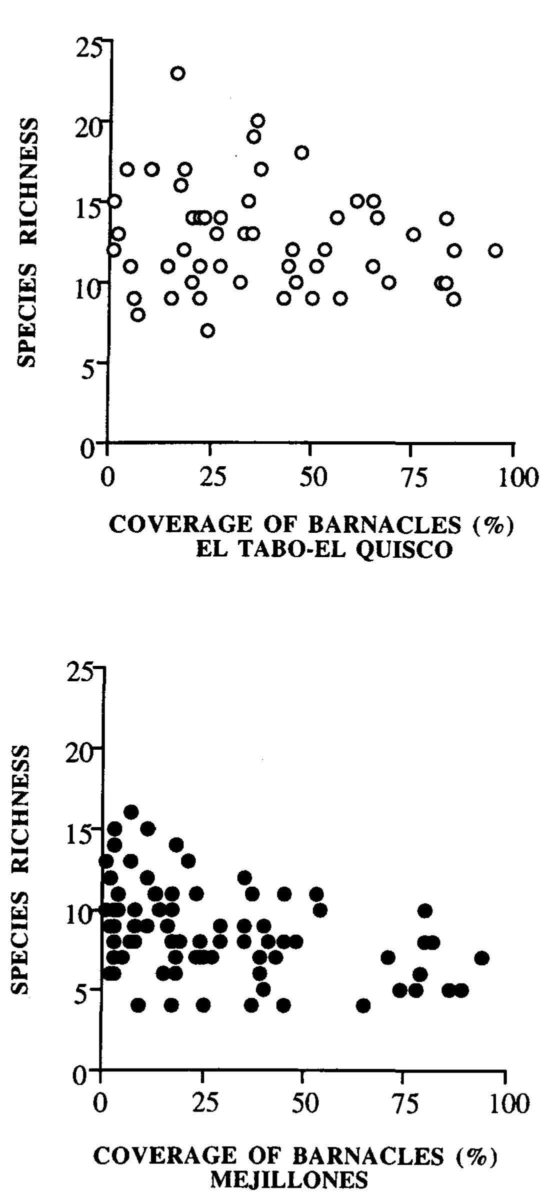

Fig. 5: Relationship between species richness and the coverage of barnacles in central (upper graph) and northern (lower graph) Chilean sites.

Relación entre la riqueza de especies y la cobertura de cirripedios en sitios de Chile central (gráfico superior) y norte (gráfico inferior).

results follow or not some theoretical prediction.

Diversity and secondary substrata

Some earlier studies have pointed already to the absence of correlation between secondary substrata and species diversity (e.g., Kohn & Leviten 1976). This partially reflects in our assessment for *Ulva*, whose abundance showed no appreciable pattern with species richness. Although the fronds of this alga may potentially offer shelter and shadow for certain intertidal inhabitants, its thin and non rigid thallus would be an unsuitable habitat (or settlement surface), and thus a poor contributor to community diversity as a whole. Contrastingly, our results also indicate both positive and negative statistical associations between barnacle abundance and diversity. Nonetheless, the correlations are low and with no clear trend, suggesting a lack of biological significance despite statistical effects. Likely, the variation in barnacle coverage do not relate in direct terms with diversity because of two opposite processes: as barnacles monopolize the available space, the number of some species able to use them as secondary substratum might be possitively affected, while those depending on primary space might be negatively affected. Nonetheless, instead of observing a net change in diversity we found a decreased scattering of diversity values with increased barnacle cover. This is an indirect and more insightful effect suggesting that barnacles would not properly act as a source of habitat heterogeneity, or if they do, that such heterogeneity would not be related with diversity.

Grain and spatio-temporal scales

In terms of scale, the generality or extent of the results in this study (or any study) is linked to the spatial dimension of the sampling unit (its grain), and we used a coarse-grained sampling (0.25 m^2 quadrats) within the usual range used in most community studies. In this sense, large-scale processes, particularly those affecting the distribution and abundance of propagules in seawater, may certainly influence the observed patterns. Furthermore, our study sites were not only located wide appart but also they were sampled in different years. Thus, we are not able to account for the possible spatio-temporal variations in the settlement or recruitment intensity of different species that could have occurred. It is difficult to infer how or to what extent these factors may have altered our assessment of topography effects, but it is also difficult to include such factors in ordinary comunity studies, an emerging trade-off that would require explicit methodological considerations.

On the other hand, the feasibility of detecting topography effects may depend to some extent on factors potentially modifying the prevailing direction of water flows during high and low tide periods (e.g., the shoreline configuration itself, the number and location of islets, or the presence of subtidal kelp beds). Such modifications might influence the results obtained in usual coarsely-grained samplings, but they are less likely to affect processes occurring on smaller spatial scales.

A growing body of evidence reveals that a number of fine-grained substratum characteristics (physical, chemical and biological cues) can affect the settlement of different taxa (e.g., Hadfield 1984, 1986; Burke 1986; Jackson 1986; Pawlik & Hadfield 1990), interacting with determinants posed by life-history strategies and behavior on distribution and abundance patterns (e.g., Levings & Garrity 1983; Petraitis 1983; Atkinson & Newbury 1984). However, it is not easy to incorporate such factors in community-oriented research as they require high levels of effort and technical implementation. Instead, coarsely-grained topographic variables are easy to measure and analyze, and the main problem is to decide which ones and how many are to be considered. Even the geological nature of substratum deserves consideration, although its effect has already been tested and rejected in particular studies (e.g., see Caffey 1982). From this paper and from the literature, substratum variables seem worth to consider a priori, and one is left the choice of defining heterogeneity, which is intimately linked to the selected spatial scale(s), and adopting appropriate descriptor(s) for estimation. Some researchers have considered simultaneous measurements in a wide range of scales at the same time, even some very small ones (ranging from microns to millimeters; e.g., Chabot & Bourget 1988; Le Tourneux & Bourget 1988), rarely used in community studies. Most common measurements involve macroscopic surface accidents such as pits, grooves and crevices, which allow to devise reliable estimates, sometimes in the form of a standardizable index (e.g., Chapman & Underwood 1994; Raffaelli & Hawkins 1996). Moreover, they can be easily manipulated or simulated for experimental field tests (e.g., Jernakoff 1985; McGuinness & Underwood 1986; Petraitis 1990), providing useful and comparable results. The main point we address here is that, whenever a study deals with community diversity estimates, such measurements not only should not be neglected but they could be included as a standard component of sampling protocols in rocky intertidal habitats.

ACKNOWLEDGMENTS

We thank the comments and suggestions by F.P. Ojeda, C.A. Moreno and an anonymous reviewer on this paper, and financial support provided by the Fondo Nacional de Desarrollo Científico y Tecnológico, Chile (project FONDECYT 077090). We are grateful to E.O. Vásquez and E.O. González for their assistance in the field.

LITERATURE CITED

ATKINSON WD & SF NEWBURY (1984) The adaptations of the rough winkle, *Littorina rudis*, to desiccation and to dislodgement by wind and waves. Journal of Animal Ecology 53: 93-105.

BURKE RD (1986) Pheromones and the gregarious settlement of marine invertebrate larvae. Bulletin of Marine Science 39: 323-331.

CAFEY HM (1982) No effect of naturally-occurring rock types on settlement or survival in the intertidal barnacle, *Tesseropora rosea* (Krauss). Journal of Experimental Marine Biology and Ecology 63: 119-132.

CAMUS PA (1994) Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in northern Chile: successional constraints and opportunities. Journal of Experimental Marine Biology and Ecology 184: 171-181.

CAMUS PA (1998) Estructura espacial de la diversidad en ensambles sésiles del intermareal rocoso de Chile centro-norte: la diversidad local como un resultado de determinantes de multiescala. Tesis de Doctorado, Depto. de Ecología, P. Universidad Católica de Chile, Santiago. 262 pp.

CAMUS PA & N LAGOS (1996) Variación espacio-temporal del reclutamiento en ensambles intermareales sésiles del norte de Chile. Revista Chilena de Historia Natural 69: 193-204.

CASTILLA JC & LR DURAN (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropopda). Oikos 45: 391-399.

CHABOT R & E BOURGET (1988) Influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. Marine Biology 97: 45-56.

CHAPMAN MG (1994) Small-scale patterns of distribution and size-structure of the intertidal Littorinid *Littorina unifasciata* in New South Wales. Australian Journal of Marine and Freshwater Research 45: 635-652.

CHAPMAN MG & AJ UNDERWOOD (1994) Dispersal of the intertidal snail, *Littorina pyramidalis*, in response to the topographic complexity of the substratum. Journal of Experimental Marine Biology and Ecology 179: 145-169.

DAYTON PK (1994) Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs 45: 137-159.

EMSON RH & RJ FALLER-FRITSCH (1976) An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. Journal of Experimental Marine Biology and Ecology 23: 285-297.

FEARE CJ (1971) The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillis* (L.). Oecologia 7: 117-126.

HADFIELD MG (1984) Settlement requirements of molluscan larvae: new data on chemical and genetic roles. Aquaculture 39: 283-298.

HADFIELD MG (1986) Settlement and recruitment of marine invertebrates: a perspective and some proposals. Bulletin of Marine Science 39: 418-425.

HOFFMANN AJ & R UGARTE (1985) The arrival of propagules of marine macroalgae in the intertidal zone. Journal of Experimental Marine Biology and Ecology 92: 83-95.

JACKSON GA (1986) Interaction of physical and biological processes in the settlement of planktonic larvae. Bulletin of Marine Science 39: 202-212.

JARA HF & CA MORENO (1984) Herbivory and structure in a midlittoral rocky intertidal community: a case in southern Chile. Ecology 65: 28-38.

JERNAKOFF P (1985) An experimental evaluation on the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. Journal of Experimental Marine Biology and Ecology 88: 287-302.

KOHN AJ & PJ LEVITEN (1976) Effect oh habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia 25: 199-210.

LE TOURNEUX F & E BOURGET (1988) Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides*. Marine Biology 97: 57-66.

LEPEZ I & CA MORENO (1988) Recruitment of *Concholepas concholepas* (Bruguière, 1789) (Gastropoda, Muricidae) in the coast of Valdivia: adults and habitat type influence (in Spanish, with English summary). Biología Pesquera (Chile) 17: 47-56.

LEVINGS SC & SD GARRITY (1983) Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. Journal of Experimental Marine Biology and Ecology 67: 261-278.

LOHSE DP (1993) The importance of secondary substratum in a rocky intertidal community. Journal of Experimental Marine Biology and Ecology 166: 1-17.

McGUINNESS KA & AJ UNDERWOOD (1986) Habitat structure and the nature of communities on intertidal boulders. Journal of Experimental Marine Biology and Ecology 104: 97-123.

PAWLIK JR & MG HADFIELD (1990) A symposium on chemical factors that influence the settlement and metamorphosis of marine invertebrate larvae: introduction and perspective. Bulletin of Marine Science 46: 450-454.

PETRAITIS PS (1983) Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. Ecology 64: 522-533.

PETRAITIS PS (1990) Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. Oecologia 83: 405-413.

RAFFAELLI DG & RN HUGHES (1978) The effects of crevice size and availability on populations of *Littorina rudis* and *Littorina neritoides*. Journal of Animal Ecology 47: 71-83.

RAFAELLI D & S HAWKINS (1996) Intertidal ecology. Chapman & Hall, London. xi + 356 pp.

SANTELICES B (1989) Algas marinas de Chile. Distribuci6n. Ecología. utilizaci6n. Diversidad. Ediciones Universidad Católica de Chile, Santiago. 399 pp.

SANTELICES B (1990) Patterns of organization of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. Hydrobiologia 192: 35-57.

UNDERWOOD AJ & MG CHAPMAN (1989) Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. Journal of Experimental Marine Biology and Ecology 134: 175-196.