Journal of Biogeography (1996) **23**, 339–351

Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure

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Abstract. In this study we revise the biogeographic delimitation, and large-scale patterns of community structure of the intertidal rocky shores of southern Africa. We use binary (presence/absence) and per-species biomass data collected at fifteen localities and thirty-seven different rocky sites, encompassing the shores of southern Namibia, South Africa and southern Mozambique. Multivariate analyses revealed that the shores of southern Africa (south of 25°) can be divided into three main biogeographic provinces: the west coast or *Namaqua* province, the south coast or *Agulhas* province and the east coast or *Natal* province. The biomass structure of the intertidal rocky shores communities of southern Africa varied at a large scale, corresponding to biogeographic differences, while local-scale variation accorded with the intensity of local wave action. The average biomass of west coast communities was on average significantly greater than that of the south and east provinces. At a local scale, the community biomass on exposed shores was an order of magnitude greater than on sheltered shores, within all biogeographic provinces. Semi-exposed shores exhibited intermediate average biomass. The trophic structure of these communities varied significantly with wave action: autotrophs, filter-feeders and invertebrate predators were more prevalent on wave exposed than sheltered shores, whereas grazers were more abundant on sheltered and semi-exposed shores. Exposed shores were consistently dominated by far fewer species than semi-exposed and sheltered shores, independently of biogeographic differences. Within all biogeographic provinces semi-exposed and sheltered shores were more diverse than exposed shores. West coast intertidal communities therefore had high levels of biomass, but were consistently species-poor. Several working hypotheses that could explain these large and small-scale patterns are presented.

Key words. Rocky-shores, communities, biogeography, wave exposure, trophic structure, biomass, dominance, southern Africa.

Resumen: En este estudio revisamos la delimitación biogeográfica y los patrones a gran escala de la estructura de las comunidades que se encuentran en las costas rocosas intermareales del sur de África. Utilizamos datos binarios (presencia/ausencia) y de biomasa especifica, recolectados en 15 localidades de 37 diferentes sitios rocosos que abarcaron las costas del sur de Namibia, Sudáfrica y el sur de Mozambique. Los análisis multivariados de datos binarios revelaron que las costas del sur de África (al sur de la latitud 25) se pueden dividir en tres provincias biogeográficas principales: la costa oeste o provincia de *Namaqua*, la costa sur o provincia *Agulhas* y la costa este o provincia de *Natal*. La estructura de biomasa de las comunidades intermareales de estos lugares presentó una variación a gran escala que se debió a diferencias biogeográficas; aquellas variaciones de escala local se debieron a la intensidad del oleaje. La biomasa promedio de las comunidades de la costa oeste fue significativamente más alta que aquellas de las provincias del sur y del este. A nivel local, la biomasa de las comunidad en costas expuestas al oleaje fue significativamente mayor que la biomasa promedio encontrada en las costas protegidas dentro de cada una de las provincias biogeográficas. Las costas semi expuestas al oleaje presentaron biomasa de un promedio intermedio. La estructura trófica de estas comunidades varió significantemente con el efecto del oleaje; autótrofos, filtradores e invertebebrados depredadores predominaron más en las costas expuestas que en las protegidas, mientras que los invertebrados pastoreadores fueron más abundantes en costas protegidas y semi expuestas. Independientemente de las diferencias biogeográficas, las costas expuestas exhibieron en forma consistente menos especies que las costas semi expuestas y que las protegidas del oleaje. En todas la provincias biogeográficas las costas semi expuestas y las protegidas mostraron más diversidad que las costas expuestas; por lo tanto, las comunidades intermareales de la costa oeste presentaron altos niveles de biomasa pero fueron consistentemente pobres en especies. En este trabajo se presentan algunas hipótesis de trabajo que podrían explicar estos patrones que se manifiestan a gran y pequeña escala.

Palabras claves. Costas rocosas, comunidades, biogeografía, exposición al oleaje, estructura trófica, biomasa, dominancia.

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INTRODUCTION

Two major water masses meet at the southern tip of Africa—the Atlantic ocean in the west, and the Indian ocean in the east—giving rise to a hydrographically complex area. The west coast is influenced by the upwelled cold Benguela current that slowly drifts northwards, and the east coast by the warm Agulhas current, driving rapidly down the south-east coast under the influence of the tropical Indian Ocean (Shannon, 1985).

The oceanographic characteristics of this region make it ideal for comparative ecological and biogeographic studies of the marine biota. Biogeography can be described simply as the study of the geographical distribution of organisms (Myers & Giller, 1988). The apparent simplicity of this definition is deceptive, for it hides the importance of historical events and processes (including geological and biological evolution) which may profoundly influence modern biogeographic distribution patterns.

The work described here concentrates on ecological biogeography (as defined by Myers & Giller, 1988) and the identification of patterns, rather than the elucidating the processes which influence those patterns. Biogeographic patterns can be recognized at three levels: (a) primary patterns, i.e. all those non-random spatial distributions of species which are responses to large-scale environmental phenomena (underlying controlling processes); (b) secondary patterns which are inferred from a nested set of attributes of a collection of species or taxa, e.g. diversity, richness, endemicity, etc.; and (c) tertiary patterns that describe the relationship between secondary and non-biotic data, e.g. species–area relationships (Myers & Giller, 1988). The main focus of this study is the determination of non-random geographical distribution patterns of the biota of intertidal rocky shores in southern Africa.

During the past 50 years, several studies of intertidal and littoral biota have dealt with the description and composition of the southern African fauna and flora and their geographical distributions (Stephenson, 1936, 1939, 1944, 1947; Stephenson, Stephenson & du Toit, 1940; Brown & Jarman, 1978; Branch & Branch, 1981; Field & Griffiths, 1991; Emanuel *et al.*, 1992).

Biogeographically, three major provinces have been proposed for the southern African region: (a) the cold-temperate west coast, (b) the warm-temperate south coast, and (c) the subtropical east coast (Stephenson & Stephenson, 1972). Until now, studies addressing the biogeographic affinities of littoral taxa have consistently followed Stephenson's biogeographic delimitation. All of them have been descriptive of narrative, mainly based on qualitative data (e.g. Ekman, 1953; Brown & Jarman, 1978; Field & Griffiths, 1991). The existence of, and limits to, these three biogeographic provinces have been questioned by several authors, usually on the basis of analyses of distribution patterns of discrete taxonomic groups. It has been questioned, for example, whether the west coast is a warm rather than cold-temperate province (Ekman, 1953). The boundary between the west and south coast provinces apparently differs depending on the suite of species analysed (see Day (1967) for polychaetes; Griffiths (1974) for amphipods; Gosliner (1987) for opisthobranchs; Thandar (1989) for echinodermata; and Williams (1992) for octocorals). However different taxonomic groups have colonized the region from different centres of dispersion, and have intrinsically different ecological and physiological adaptations. In the above mentioned studies, and in the majority of the biogeographic analyses (e.g. Brown & Jarman, 1978; Gosliner, 1987; Williams, 1992) boundaries between biogeographic regions have been based on each author's *ad hoc* criteria, or 'inferred' from the species distributions. Analysis of multispecies distribution patterns requires objective and repetitive criteria, independent of the ecology of specific groups or taxa. Such independence and objectivity are fulfilled in modern multivariate techniques that provide statistical methods for the study of the joint inter-relationship of variables in data sets (Whittaker, 1973; Pielou, 1979, 1983; McCoy & Heck, 1987; James & McCulloch, 1990). These analytical methods have demonstrated their value in the elucidation of marine biogeographic patterns based on quantitative binary data (Murray & Littler, 1981; Joosten & van den Hoek, 1986; Roberts, Dawson Shepherd & Ormond, 1992; Stegenga & Bolton, 1992; Clarke, 1993).

Most intertidal ecological research in the southern African region has been undertaken on South African shores. Despite detailed localized knowledge of South African rocky intertidal communities, there have been no quantitative comparative studies at a subregional scale. Descriptions of zonation patterns and species composition of the southern African intertidal rocky shores have been documented in a number of qualitative works (e.g. Penrith & Kensley, 1970a, b; Stephenson & Stephenson, 1972; Brown & Jarman, 1978). However, the majority of these (mostly) South African studies were small-scale (spatial and temporal), and quantitative evaluations have been confined to a few sites along the coast (McLachlan, Lombard & Louwrens, 1981; McQuaid & Branch, 1985; Hugget & Griffiths, 1986; Branch & Griffiths, 1988; Field & Griffiths, 1991). From these studies, several structuring factors, both biotic and abiotic, have been postulated. In particular, the role of wave action has been elegantly demonstrated as an important, if not the most important, abiotic factor in structuring South African rocky intertidal communities (McQuaid, 1981; McQuaid & Branch, 1984, 1985; Field & Griffiths, 1991; Emanuel *et al.*, 1992). This is in agreement with research findings elsewhere, which show that wave-induced stress acts as structuring force and mediates biological interactions (Dayton, 1971; Menge & Sutherland, 1976; Denny, 1988; Menge & Olson, 1990). However, its potential effects on the biotic variation at meso and large geographical scales is poorly understood.

Functional descriptions and analyses of natural communities have been a fundamental part of ecological research from the beginning of this century (i.e. Elton, 1927; May, 1973; Terborgh & Robinson, 1986). More recently, functional groups or guilds have increasingly been used as means of understanding the trophic structure of marine communities (e.g. McQuaid & Branch, 1985; Menge & Sutherland, 1987; Menge & Olson, 1990; Hixon & Menge, 1991). The advantage of using functional groups or 'ecological equivalents' (Schoener, 1988) is that they provide

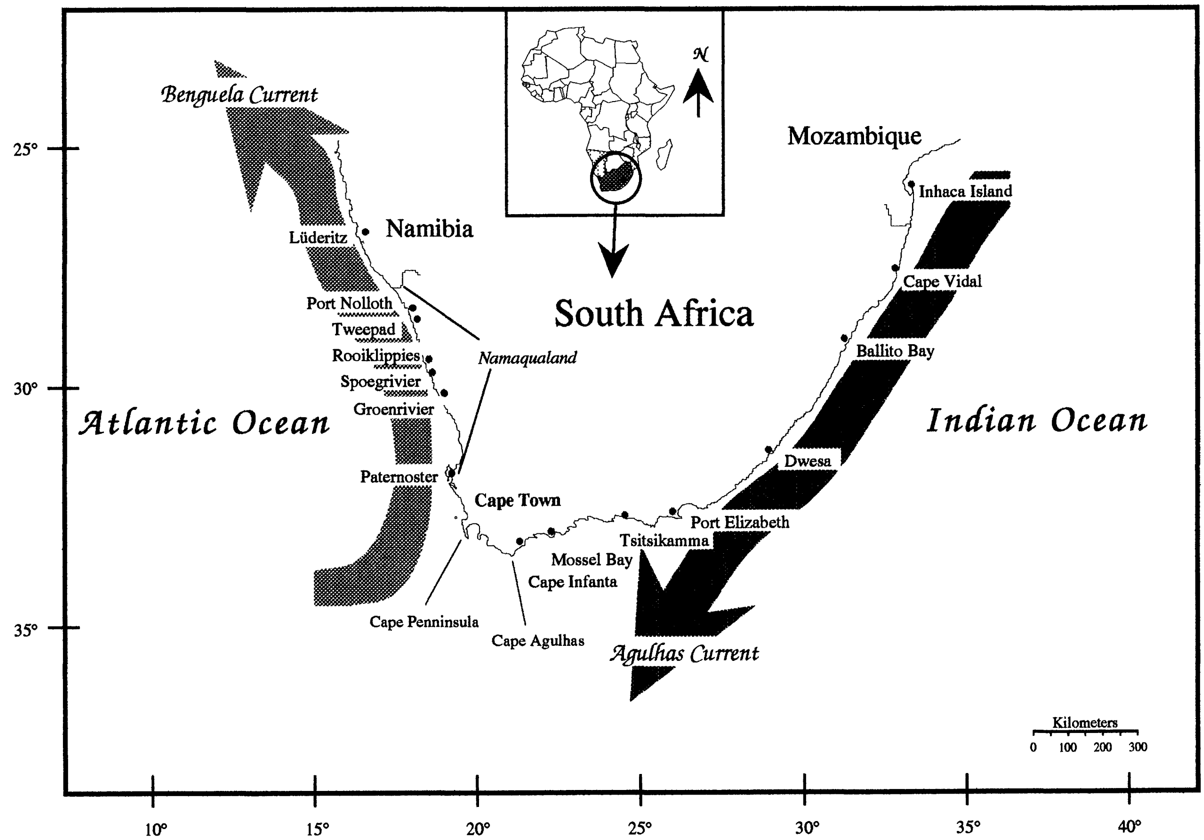

FIG. 1. Outline of the southern African shoreline south of 25°S. Names indicate localities where intertidal communities were surveyed and those mentioned in the text. Shaded areas and arrows indicate the main direction of the Benguela (☐) and the Agulhas (■) Currents.

a common ecological base for comparing sets of taxonomically unrelated species (e.g. barnacles and mussels are both filter feeders and are both functionally similar in being sessile).

This study deals with primary and secondary biogeographic patterns and community structure around the coast of southern Africa between Lüderitz in Namibia and Inhaca Island in Mozambique (see Fig. 1). Analyses are based on quantitative binary (presence/absence) data and biomass data for rocky intertidal species (invertebrates and algae) gathered from fifteen different localities around the coast. The study is divided into three parts. The first part attempts to elucidate the biogeographic patterns of intertidal rocky shores, based on the presence or absence of intertidal species. The second part describes the trophic structure of the intertidal communities that characterize the different biogeographic regions, particularly in relation to degree of wave action. The third part compares the biomass dominance patterns of intertidal communities present on sheltered and exposed shores in the main biogeographic regions.

MATERIALS AND METHODS

Sampling procedures

Surveys of intertidal rocky shore communities were undertaken during 1989–92 at fifteen different localities (Fig. 1). Within each locality surveys were made at two or three different sites, which covered the range of coastal geomorphology and wave action. These sites were subjectively separated into three different categories; (a) *exposed rocky headlands*; normally rocky shores on the seaward side of headlands; (b) *semi-exposed rocky shores*, open rocky shores in the lee of kelp forests; and (c) *sheltered boulder bays*, protected from the wave action and devoid of kelp forests. All three site-types were present along the Atlantic west coast, but on the south and east coasts only types (a) and (c) were present (kelp forest being absent). At each site, surveys were conducted along transects that were set perpendicularly to the shoreline from mean low water spring tide (MLWS) to mean high water spring tide (MHWS). Four replicate transects were randomly chosen, taking care to avoid tidal pools and gullies. Along each transect, eight to twelve quadrats of 0.5 m^2 were randomly stratified according to the intertidal zones described by Branch & Branch (1981). The quadrats consisted of a grid with 171 intersection points over a surface of 0.5 m^2. Within each quadrat, coverage of the major sessile fauna and flora was measured by point intersection counts, and the density of all mobile invertebrate fauna, including epifauna (e.g. limpets on mussels) was recorded. At the same time, species richness of all macro-fauna and flora visible within the quadrats was also recorded. This method underestimates the total species richness, because small species (e.g.

<1.0 mm) are normally missed, but provides information that is comparable between sites.

Along two of the four transects per site, two or three destructive samples of 0.075 m^2 were taken of all space-dominant species in each of the intertidal 'zones' (e.g. limpets, barnacles, foliose algae, mussels, etc.) in order to evaluate the whole wet biomass per species present in each quadrat. Subsamples of each species were taken to obtain conversions between wet, dry and ash free dry weight (AFDW). The data are expressed in terms of their AFDW biomass per m^2. Complete data sets for species richness, including the cryptic infauna in beds of sessile species (e.g. mussels, colonial polychaetes, barnacles, oysters, etc.) were obtained for all fifteen localities surveyed. Biomass data were obtained for all sites except Inhaca Island (Mozambique) (Fig. 1).

Data analysis

Analyses were based on either binary data (presence/absence) or AFDW per taxa. However, due to taxonomic uncertainty, some groups have been treated as a single unit (crustose and articulated corallines, pycnogonids, sipunculids and hydrozoans).

Multivariate techniques were applied to either binary or AFDW data arranged in rectangular matrices where cases = species and samples = localities or sites. Classification of the different samples was performed using a hierarchical clustering method based on the Bray–Curtis similarity index applied to these species-samples matrices (Bray & Curtis, 1957), and using a group average linkage (Field, Clarke & Warwick, 1982; Clarke & Warwick, 1994; Carr, 1994). In addition to classification techniques, the data were also subjected to a non-metric multidimensional scaling (MDS, Kruskal & Wish, 1978) based on the Bray–Curtis similarity of the species-samples matrix. The ordination yielded a graphic representation in two or three dimensions of the similarity between the different samples, in this case geographical localities, based upon the binary presence/absence data for species.

The statistical significance of differences between biogeographic units identified, and the main effects of wave action on intertidal biomass, were tested using a nested design of a Generalized Linear Model (GLM) with *a posteriori* contrast between the biogeographical units (SAS, 1986). The contribution of the different species to the community biomass varied by five orders of magnitude (from 0.2 $g\,m^{-2}$ to *c.* 7400 $g\,m^{-2}$). Consequently, in the analyses, biomass data were standardized and logarithmically transformed [$\log 10(x+1)$].

The trophic structure of the different intertidal communities was described by dividing the species into functional groups using the AFDW data. Species were pooled in the following trophic groups: (a) *autotrophs*, (b) *filter-feeders*, (c) *grazing herbivores*, and (d) *predators.* The main effects of wave action at each locality were tested using one-way ANOVA with *a posteriori* comparison of the average biomasses (Bonferroni inequality test, SAS, 1986).

Univariate methods were also applied to the species biomass in different samples or group of samples. Ranked species abundance or k-dominance curves (Lambshead, Platt & Shaw, 1983) were constructed using the biomass (AFDW) per species on a logarithmic scale (Clarke & Warwick, 1994). We compared the biomass contributions of different species in two large geographic regions: (a) the west coast, which included seven localities from Lüderitz to Paternoster, and (b) seven localities on the south and east coasts between Cape Infanta and Cape Vidal (see Fig. 1). The data for both large-scale geographic regions were sub-divided according to the wave action categories (i.e. exposed, semi-exposed and sheltered).

To detect which species were responsible for the different dominance patterns within community types experiencing different degrees of wave action, an analysis of the contribution by individual species to the overall similarity measure (Bray–Curtis), SIMPER (Similarity Percentages, Clarke, 1993) was performed. For this purpose the data for the west coast were separated into sheltered, semi-exposed and exposed shores, and those for the south and east coasts into sheltered and exposed shores. In each group, an average Bray–Curtis similarity $\bar{S}$ and the standard deviation SD for the group, and the per-species average. $\overline{Si}$, standard deviation $SD(Si)$ and the percentile $\%Si$ contribution to $\bar{S}$ were calculated by SIMPER. Similarly, the per-species average biomass $\bar{Y}$ ($\pm$SD) and the respective percentile $\%\bar{Y}$ contribution to the total biomass were also calculated. Using the ratio $\overline{Si}/SD(Si)$ it was possible to check how consistently each species contributed in an intra-group comparison. Finally, a ranking of importance for the 'top 10' most important species for each group was constructed based on the $\overline{Si}$ value. We have excluded from this analysis those species with a biomass smaller than 0.75% of the total community biomass.

All multivariate and univariate community analyses were done using the Plymouth Routines In Multivariate Ecological Research, PRIMER v3.1a (Carr, 1994).

RESULTS

Biogeographic patterns

A total of 231 intertidal taxa of algae and invertebrates was recorded around the southern African coast: details of species/genus presence/absence or AFDW biomass at each of the fifteen localities sampled are available in Bustamante (1994).

At the subregional level, the similarity on species composition of east coast communities differed by more than the 70% from those of the south and west coasts (Fig. 2). As similarities between localities increased (*c.* 50.0%), three distinct groups of localities were clearly defined. The seven localities of the cool-temperate Atlantic west coast clustered together forming the *Namaqua* province, with an average similarity of 66.7% (SD = 4.1%). A second cluster was formed by all five localities on the warm-temperate Indian south coast. This cluster conforms to the *Agulhas* biogeographic province, and had an average similarity of 62.4% (SD = 3.9%). Also, a distinctive and smaller cluster included all three localities on the subtropical east coasts,

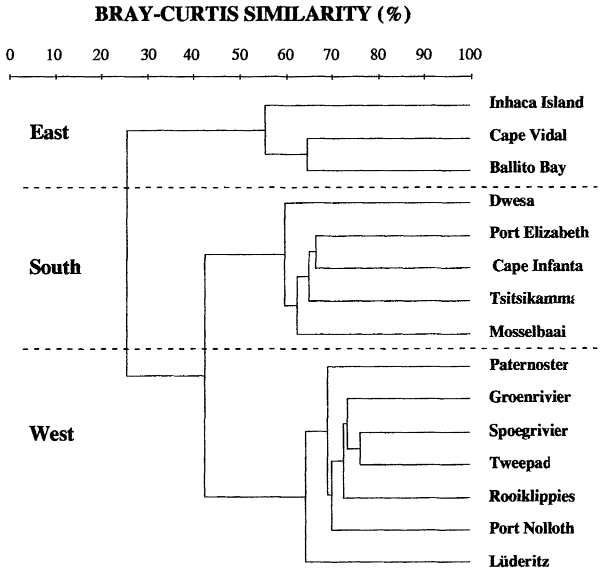

FIG. 2. Dendrogram of classification of fifteen localities around the southern African coasts (Bray–Curtis similarity index) based on presence/absence from 231 intertidal species.

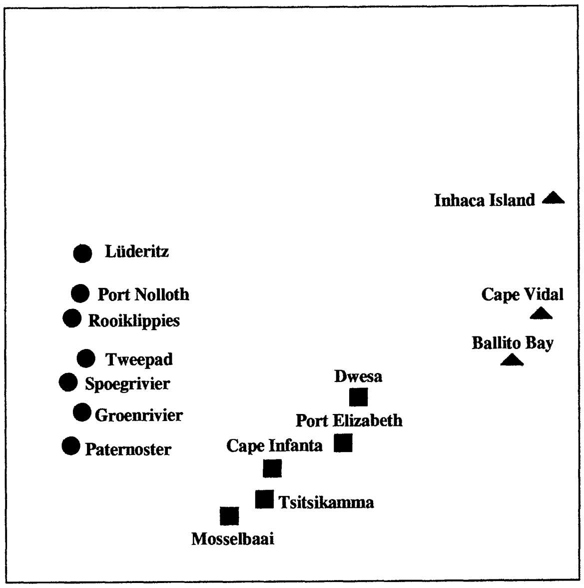

FIG. 3. 2-Dimensional MDS ordination plot (stress = 0.034) based on the presence/absence of 231 rocky intertidal species at fifteen localities around southern Africa. ●, West coast communities; ■, south coast communities and ▲, east coast communities.

conforming to the *Natal* biogeographic province, with an average similarity of 49.8% (SD = 10.6%). However, within this cluster Inhaca Island split at about 55%, reflecting more affinity with a tropical component (Fig. 2).

A two-dimensional plot produced by non-metric multidimensional scaling (MDS), using the same Bray–Curtis similarity matrix (Fig. 3) gives essentially the same picture as the dendrogram, but illustrates how close or separate (by Euclidean distance, Field *et al.*, 1982) the localities are in a 2-D space. The localities on the west coast were ordered geographically in a correct sequence from north to south (see Fig. 1). Sites on the south coast were not ordered sequentially, but formed a distinct and independent group, with a transition zone between the south (Dwesa) and the east province (Ballito Bay). The east coast province appears more diffuse due to the smaller number of localities sampled (Fig. 3).

Thus, there were three clearly distinctive groups of localities identifiable on the basis of their rocky intertidal species composition (Figs 2 and 3). These groups can be equated to different biogeographical regions (or provinces) i.e. the *Namaqua, Agulhas* and *Natal* provinces.

Intertidal biomass patterns

There were major differences in the faunal and floral biomasses supported per-unit-area on exposed as compared with sheltered shores in all three regions (Fig. 4). The average and maximum biomass on exposed shores was more than twice that of sheltered shores. The biomass supported on semi-exposed shores on the west coast was intermediate between that of sheltered and exposed shores (Fig. 4). Also, the intertidal communities on the west coast had average biomasses significantly greater than of those of the south- and east-coast groups, on both exposed and sheltered shores (Bonferroni *t*-test, $P<0.05$). The regional variation in biomass per-unit-area was significantly explained by the differences between the biogeographic provinces (ANOVA, $P<0.0001$), and the local variation was explained largely by wave action (ANOVA, $P<0.0001$). The *a posteriori* contrast of the overall average biomass of the different provinces shows that the west province is significantly different from both the south ($P<0.0001$), and the east ($P<0.0002$) provinces. However, there was no difference between the south and the east provinces ($P<0.1881$) (Table 1).

Trophic structure

The functional classification based on the trophic status of all 231 intertidal taxa (autotrophs, filter feeders, herbivores

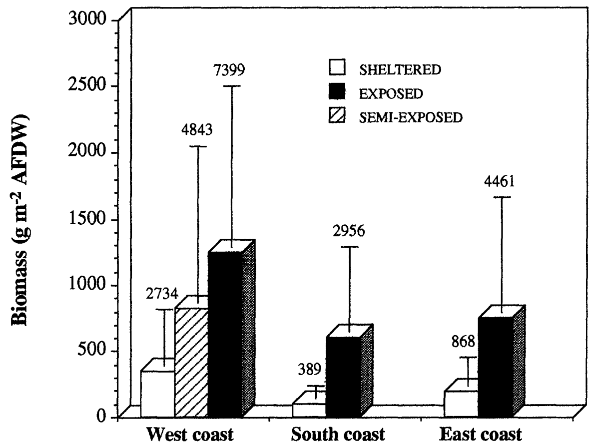

FIG. 4. Average AFDW biomass (1 SD) of intertidal communities as a function of wave action. Numbers above bars indicate the maximum values.

TABLE 1. Results of the nested ANOVA for intertidal biomass in relation to biogeographic provinces (Prov) and wave action (Exp). Data were log transformed prior to the analysis. A contrast of the main effects of the different provinces was tested. Multivariate probability estimates were calculated using General Linear Models procedures (GLM) from SAS (SAS, 1986).

Dependent Variable: AFD Biomass

Source	df	SS	MS	*F*	*P*
Source					
Prov	2	1535084.812	767542.406	33.78	0.0001
Exp(Prov)	4	1458127.455	364531.864	16.04	0.0001
Contrast					
West *v* South	1	1451154.316	1451154.316	63.80	0.0001
West *v* East	1	320213.293	320213.293	14.09	0.0002
South *v* East	1	39381.278	39381.278	1.73	0.1881
West *v* All	1	1046742.703	1046742.703	46.06	0.0001

A *posteriori* Bonferroni (Dunn) *t*-test for variable: AFDW by Provinces (Prov)
$a=0.05$ df$=6541$, Critical value of $t=3.39$, Minimum significant difference$=112.04$

Bon grouping	Mean	*N*	Province
A	856.341	3566	West
B	331.255	837	East
B	323.347	2145	South

and predators) shows that filter feeders achieved the highest biomass values (up to 3300 g m^{-2}), dominating exposed shores, but were much less abundant on sheltered shores (Fig. 5). On west coast localities, the average biomasses achieved by autotrophs, filter feeders and predatory species on exposed shores were in most cases significantly higher than those of sheltered shores. This pattern tended to agree with that found at the south and east localities (Fig. 5). The only cases in which sheltered and semi-exposed shores exhibited greater average biomasses than exposed shores were the grazers on the west (Fig. 5c) and at two localities, the autotrophs in the south coast (Fig. 5a).

As a function of wave action, trends in biomass within each biogeographic province showed distinct patterns for different functional groups: (a) autotrophs in the west province were significantly (ANOVA, $P<0.05$) more abundant on semi-exposed and exposed shores than in sheltered habitats, but this difference was not apparent (ANOVA, $P>0.05$) in the south and east provinces (Fig. 5a); (b) filter feeder biomass was significantly (ANOVA, $P<0.05$) greater on exposed and semi-exposed shores than on sheltered shores in all biogeographic provinces (Fig. 5b); (c) in the west province, grazers were significantly (ANOVA, $P<0.05$) more abundant on semi-exposed and sheltered shores than on exposed shores, but this pattern was not repeated in the other biogeographic provinces (ANOVA, $P>0.05$) (Fig. 5c); (d) predatory species in the west province were significantly (ANOVA, $P<0.05$) more abundant on exposed shores than on semi-exposed and sheltered shores, but there were no differences in predator biomass related to wave action in either the south or east provinces (Fig. 5d).

Patterns of intertidal dominance

The dominance curves represent the ranked order of importance of different intertidal species (in a log x-axis), plotted against their cumulative biomass (% y-axis) for all localities of the west coast (Fig. 6a) and the combined localities of the south and east coasts (Fig. 6b). A steep dominance curve means that a few species account for a great proportion of the biomass, i.e. the community biomass is dominated by those species. A flat curve indicates less domination, with a larger number of species contributing more uniformly to the biomass (greater diversity). There were clear differences in the slopes and forms of the dominance curves depending on wave exposure (Fig. 6). Exposed shores were dominated by fewer species than semi-exposed or sheltered shores. On the exposed shores of the west coast, three species made up more than 75% of the total community biomass (dashed line in Fig. 6); 75% of the biomass was accounted for by seven species on exposed south and east coasts. On sheltered shores, nine species made up 75% of the biomass on the west coast, against seventeen species the south and east coasts. Semi-exposed shores on the west coast had a dominance pattern intermediate between exposed and sheltered shores (Fig. 6a).

The 'top 10' intertidal taxa that characterized communities in the different west and south-east provinces are listed in Table 2. The ranking importance of these species was determined according the average score of individual species ($\bar{S}$) in the overall group's Bray–Curtis similarity ($\overline{Si}$). Sheltered habitats on the west coast (Namaqualand) had an average similarity of 48.24% (±11.88). The patellid

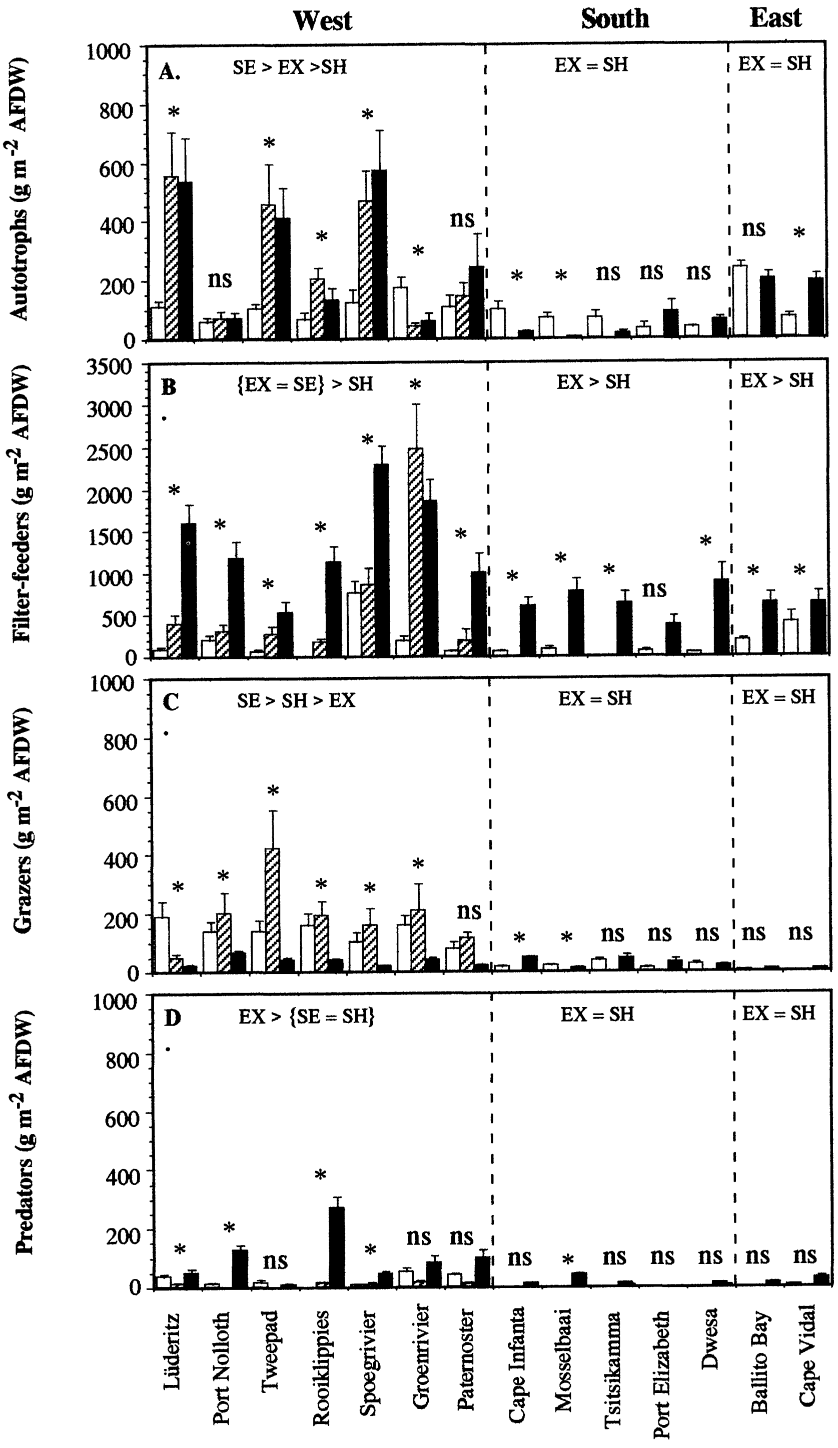

FIG. 5. Average (1 SE) biomass of the four functional groups of the southern African rocky intertidal communities separated by locality and wave action. Sheltered (SH = □), semi-exposed (SE = ▨) and exposed (EX = ■) shores. Localities are ordered from north-west (left) to north-east (right). Asterisks and abbreviation represents the significance of the main effects of wave action in a one-way ANOVA applied to the biomass per locality (* = $P<0.005$; ns = $P>0.05$).

limpet *Patella granatina* Linn. accounted for 41.85% of the group similarity and 25.44% of the total community biomass (Table 2A). Their populations form dense monospecific stands that can achieve average AFDW biomasses of 189.43 g m^{-2} in the low-shore zone they dominate. The other nine 'top' species accounted for 44.86% of the total community similarity. Of these, the most important were the kelps *Ecklonia maxima* (Osbeck) Papenf. and *Laminaria*

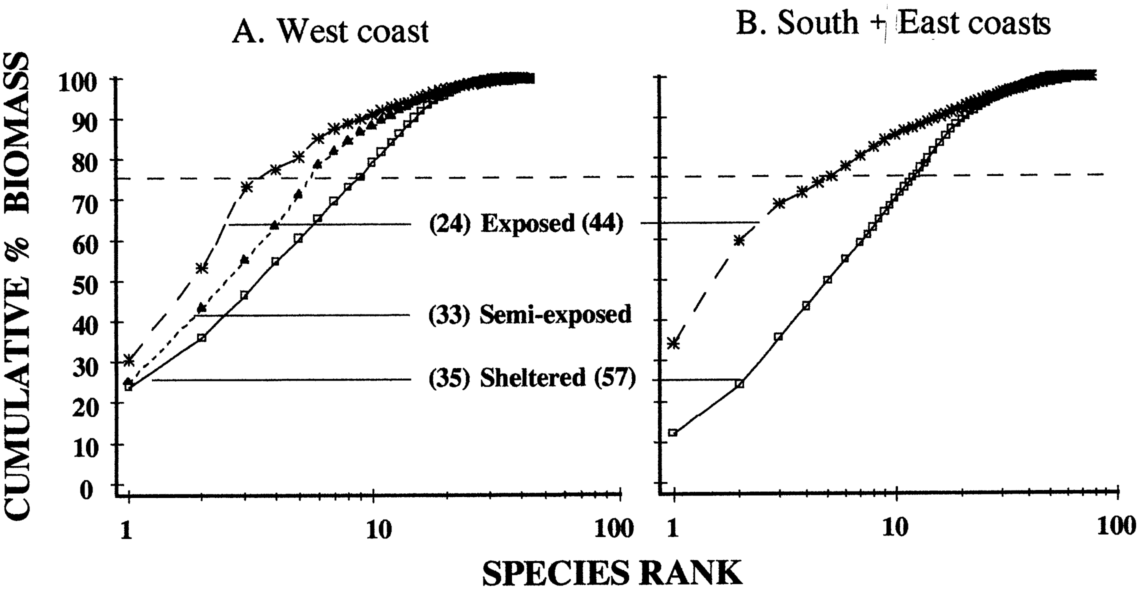

FIG. 6. Dominance curves of three rocky intertidal community-types that characterizes the west, and the two that characterizes the east coasts of southern Africa. Numbers in brackets indicates the total number of species recorded during biomass surveys in each community-types. All species with biomass contribution smaller than 0.75% of the total community biomass were not included ($n = 193$).

pallida Grev., the red alga *Porphyra capensis* Kütz, the colonial polychaete worm *Gunnarea capensis* (Schm.), and the limpet *Patella granularis* Linn. Together these four species accounted for 34.88% of the biomass and 28.26% of the group's similarity (Table 2A).

Semi-exposed habitats on the west coast had an average similarity of 36.79% (±15.15) and were dominated by dense monospecific stands of the limpet *Patella argenvillei* Kr., which form a conspicuous band on the low shore. Their populations had an average AFDW biomass of 346.86 g m^{-2} (±347.71), representing 26.23% of total biomass and 26.15% of the group similarity. Of the remaining nine major species, the red alga *Champia lumbricalis* (Linn.) Desv. was the second most important, averaging 253.14 g m^{-2} (±253.14) and accounting for 18.42% of the group's biomass. None of the remaining eight 'top 10' species accounted for more than 12% of the total biomass (Table 2A).

Exposed shores on the west coast had a group similarity of 39.86% (±16.50), and were dominated by the mussels *Aulacomya ater* Mol., and *Mytilus galloprovincialis* Lam., which accounted respectively for 23.05% and 31.16% of total community biomass. The red alga *Champia lumbricalis* was the third most important species, with an average biomass of 353.43 g m^{-2}, representing 15.36% of total biomass and 19.09% of the group similarity (Table 2A).

Articulate coralline algae dominated the low fringe of sheltered shores on the south and east coasts, where they averaged a biomass of 56.29 g m^{-1}, accounting for 15.14% of the total community biomass; they accounted for 36.04% of the group's similarity. In this habitat, the next most important taxon was the genus of red alga *Gelidium* spp. which made up 14.76% of the total biomass. Although they had levels of average biomass comparable to the corallines, they accounted for only 11.10% of the algae similarity (Table 2B). The other thirty-four species not listed in Table 2B account for 16.32% of the group similarity and 38.05% of total community biomass.

Exposed shores on the south and east coasts, as on the west coast, were dominated by the mussels. The mussel *Perna perna* (Linn.) contributed 66.28% to the community similarity and had an average biomass of 595.14 g m^{-2}, making up 33.87% of total community biomass. In terms of biomass the next most important was the ascidian *Pyura stolonifera* (Hell.). This species made up 24.78% of the biomass, but only contributed 8.12% to group similarity (Table 2B). *Octomeris angulosa* Sow. contributed more to the group similarity, but substantially less to the biomass. None of the remaining seven of the 'top 10' species exceeded the 3% of the group similarity of 3% of the community biomass. The other forty-seven species (not listed in Table 2B) together contributed only 7% of the group similarity.

DISCUSSION

There were substantial geographic differences in the species composition of the rocky shores biota around the southern African coast. These quantitative differences justify the division of the region into three biogeographic provinces: the west, south and east provinces proposed by earlier qualitative analyses (Stephenson, 1936, 1939, 1943, 1944, 1947; Stephenson *et al.*, 1940; Brown & Jarman, 1978; Branch & Branch, 1981; Field & Griffiths, 1991).

Emanuel *et al.* (1992) have produced a definitive zoogeographic analysis, based on analyses of literature records for all well-researched invertebrate taxa and including data for intertidal and subtidal biota (to 15 m depth). They concluded, for a large geographical area (south of 20° latitude), that there are four major zoogeographic provinces in southern Africa. On the east coast there is a subtropical *Natal* province, extending from southern

TABLE 2. The ranked importance of the 'Top 10' intertidal species that characterize the rocky shores of (A.) West and (B.) South and East coast. $\bar{S}$ is the average similarity within each wave exposure; %*Si* is the percentile contribution of each species to $\bar{S}$, while $\overline{Si}/SD(Si)$ is the ratio between them. $\bar{Y}$, sd and %$\bar{Y}$ indicate the average, standard deviation and percentile contribution per-species to the total community biomass (AFDW, ash free dry weight).

Ranking	Names	%$\overline{Si}$	$\overline{Si}$	$SD(Si)$	$\overline{Si}/SD(Si)$	$\bar{Y}$ (gm-2)	sd	%$\bar{Y}$
A. West Coast. Sheltered. $\bar{S}=48.24\%$, $SD=11.88\%$.								
1	*Patella granatina*	41.85	20.20	6.22	3.25	189.43	56.73	25.44
2	*Ecklonia/Laminaria*	9.48	4.60	3.47	1.32	64.57	46.34	8.67
3	*Porphyra capensis*	8.34	4.00	5.65	0.71	94.29	105.66	12.66
4	*Gunnarea capensis*	6.99	3.40	4.33	0.78	82.86	97.91	11.13
5	*Patella granularis*	3.81	1.80	0.58	3.18	18.00	7.21	2.42
6	Anemones	3.73	1.80	1.89	0.95	28.00	23.18	3.76
7	*Aeodes orbitosa*	3.65	1.80	0.54	3.23	21.14	14.28	2.84
8	*Chordariopsis capensis*	3.42	1.70	0.86	1.93	19.71	12.41	2.65
9	Articulate corallines	2.84	1.40	1.10	1.24	26.57	32.37	3.57
10	*Gymnogongrus*	2.60	1.30	3.09	0.41	45.14	62.46	6.06
	Others (14 spp.)	13.29					Total = 744.59	
Semi-Exposed. $\bar{S}=36.79\%$, $SD=15.15\%$.								
1	*Patella argenvillei*	25.15	9.60	9.35	1.03	346.86	347.71	25.23
2	*Champia lumbricalis*	21.26	7.80	8.79	0.89	253.14	265.28	18.42
3	*Ecklonia/Laminaria*	9.49	3.50	5.12	0.68	116.00	138.36	8.44
4	*Aulacomya ater*	9.34	3.40	4.57	0.75	101.71	97.93	7.40
5	*Gunnarea capensis*	6.94	2.60	4.70	0.54	108.00	120.24	7.86
6	*Gigartina spp.*	4.21	1.50	0.85	1.83	32.57	25.32	2/37
7	*Patella granularis*	3.37	1.20	0.44	2.85	17.71	3.15	1.29
8	*Plocamium spp.*	2.50	0.90	1.29	0.71	35.71	42.68	2.60
9	*Mytilus galloprovincialis*	2.47	0.90	0.92	0.99	163.14	365.37	11.87
10	*Porphyra capensis*	2.01	0.70	1.62	0.46	45.43	76.29	3.31
	Others (23 spp.)	12.27					Total = 1374.57	
Exposed. $\bar{S}=39.86\%$, $SD=16.65\%$.								
1	*Aulacomya ater*	32.63	13.00	14.30	0.91	530.29	410.46	23.05
2	*Mytilus galloprovincialis*	22.97	9.20	11.88	0.77	716.86	811.28	31.16
3	*Champia lumbricalis*	19.09	7.60	7.43	1.02	353.43	298.88	15.36
4	Anemones	6.65	2.70	1.98	1.34	108.00	79.29	4.69
5	*Plocamium spp.*	4.37	1.70	4.08	0.43	180.29	255.76	7.84
6	*Ecklonia/Laminaria*	3.30	1.30	2.25	0.58	105.43	129.49	4/58
7	*Patella argenvillei*	1.81	0.70	0.19	3.84	30.86	34.19	1.34
8	Nereid polychaets	1.80	0.70	0.74	0.96	28.57	22.68	1.24
9	*Gunnarea capensis*	1.05	0.40	0.45	0.93	19.43	17.12	0.84
10	*Patella granularis*	1.04	0.40	0.27	1.51	14.29	8.28	0.62
	Others (25 spp.)	5.29					Total = 2300.88	
B. South + East Coast. Sheltered. $\bar{S}=26.95\%$, $SD=14.57\%$.								
1	Articulate corallines	36.04	9.70	5.38	1.80	56.29	26.27	15.14
2	*Gelidium spp.*	11.10	3.00	2.69	1.11	54.86	78.76	14.76
3	*Pomatoleios kraussii*	10.50	2.80	4.96	0.57	30.29	36.76	8.15
4	*Tetraclita serrata*	5.75	1.50	1.77	0.88	18.57	25.79	5.00
5	*Patella oculus*	5.22	1.40	1.49	0.94	8.00	5.54	2.15
6	*Patella longicosta*	4.79	1.30	1.45	0.89	11.71	15.03	3.15
7	*Perna perna*	3.79	1.00	1.79	0.57	19.43	27.29	5.23
8	*Oxystele sinensis*	2.33	0.60	0.84	0.75	4.29	3.90	1.15
9	*Chtamalus dentatus*	2.13	0.60	1.04	0.55	23.71	44.44	6.38
10	*Siphonaria spp.*	2.03	0.50	0.49	1.11	3.14	1.95	0.84
	Others (34 spp.)	16.32					Total = 371.74	
Exposed. $\bar{S}=44.13\%$, $SD=10.08\%$.								
1	*Perna perna*	66.28	29.20	6.71	4.36	595.14	192.01	33.87
2	*Octomeris angulosa*	9.34	4.10	5.23	0.79	159.71	171.94	0.09
3	*Pyura stolonifera*	8.12	3.60	6.34	0.56	435.43	781.44	24.78
4	*Chtamalus dentatus*	2.38	1.00	1.45	0.72	35.71	32.83	2.03
5	Articulate corallines	1.98	0.90	0.80	1.09	30.00	23.94	1.71
6	*Gelidium spp.*	1.74	0.80	1.18	0.65	51.14	73.20	2.91
7	*Tetraclita serrata*	1.65	0.70	0.99	0.73	44.29	56.31	2.52
8	Anemones	0.98	0.40	0.49	0.87	13.14	9.86	0.75
9	*Patella cochlear*	0.85	0.40	1.14	0.33	20.86	30.70	1.19
10	*Crassostrea cucculata*	0.58	0.30	0.92	0.28	55.14	106.32	3.14
	Others (47 spp.)	7.00					Total = 1757.13	

Mozambique to just south of Durban. The warm temperate *Agulhas* province stretches from Dwesa to Cape Point. On the west coast there are two provinces. In the south, the cool temperate south-west province extends from Cape Point to Lüderitz, and is named the *Namaqua* province. The cool temperate *Namib* province extends from Lüderitz to the Cunene River.

The work presented in this study differs from that of Emanuel *et al.* (1992) in that it relies on quantitative data obtained from equal-sized samples at all sites, rather than using records from the literature and from earlier non-quantitative works. The strength of the present study is thus its more rigorously quantitative approach, eliminating bias due to different sampling intensities in different regions. Its weakness is that the sampling methodology is unlikely to detect many of the rare species. Emanuel *et al.* (1992) include data from all species known to occur on the coast of southern Africa. Despite the differences in methodology and data biases, the two approaches yield very similar results.

Based on the rocky intertidal biota, two clear biogeographic contributions can be extracted from the present work. First, the confirmation of the existence of a clear and distinctive west coast biogeographic province. The west coast localities show the most consistent similarity between them (*c.* 67%, see Fig. 2) and they form a compact and homogeneous cluster (Fig. 3). Similar results have been reported for rocky intertidal fish species (Prochazka & Griffiths, 1992) and flora (Stegenga & Bolton, 1992). Much of the controversy related to the boundaries, definitions and existence of west and south provinces has been raised when specific taxonomic groups have been investigated (e.g. Griffiths, 1974; Gosliner, 1987; Thandar, 1989; Williams, 1992). The west coast province defined in this work comes from a multitaxa data set, and fits almost exactly with the definition of the Cool Temperate south west or *Namaqua* province, named by Ekman (1953) and subsequently analytically defined by Emanuel *et al.* (1992).

The second biogeographic contribution of this work comes from the quantitative confirmation of a south or *Agulhas* province, as defined by Stephenson (1944). The extent of this province has been redefined several times in different works. One extreme is the 'mega' Cape province defined by Williams (1992) based on Octocorallia. Williams concluded that it is impossible to separate the south and west provinces. The opposite extreme is the recognition of a 'reduced south coast' (Cape Agulhas to Port Elizabeth) defined by Thandar (1989). However, agreeing with our findings, recent quantitative analyses have consistently defined the south coast as an independent province (e.g. Stegenga & Bolton, 1992; Emanuel *et al.*, 1992).

The above biogeographic patterns remain speculative if no underlying causative processes are inferred or identified (Rosen, 1988). Nevertheless, the consistency and repetition of the patterns provides a solid base for the characterization of geographical areas and their biotic communities (Myers & Giller, 1988).

A comparative scenario can be developed when general attributes or structural secondary patterns can be identified within the biogeographic units defined above. The first general macro pattern is that the observed changes in the rocky intertidal landscape (biomass) around southern Africa are significantly explained by differences at regional (biogeographic) and local (wave action) scales (Table 1). There are striking differences in biomass between the west, south and east provinces. On both sheltered and exposed shores, the west coast supports a significantly greater average biomass than the two other provinces (see Fig. 5). It is also clear that the biomass of intertidal communities increases with wave action. Grazers are the only functional group to depart from this generalization: their biomass is significantly higher on sheltered and semi-exposed shores (Fig. 5c), particularly on the west coast.

Exposed shores support a higher average biomass than sheltered shores, particularly on the west coast (Fig. 4). This pattern is consistent at most localities (Fig. 5). Exposed shores are dominated by filter-feeding species (Fig. 5b, Table 2). This finding is also consistent with those reported for the Cape Peninsula (see Fig. 1), where the filter-feeder biomass on exposed shores was an order of magnitude greater than that of sheltered shores (McQuaid & Branch, 1985). Menge & Sutherland (1987) have proposed a general community structure model in which they incorporate the role of the wave action in moderating the outcome of biological interactions (principally predation and competition). One of the predictions of this, and subsequent works (e.g. Menge & Olson, 1990), is that in stressful (wave-beaten) environments, mobile organisms (mostly consumers) are more likely to be environmentally constrained. The disadvantage of such conceptual frameworks is that they predict the relative importance of particular biological interactions rather than examining the emergent properties of the community as a whole (e.g. Yodzis, 1986; Sebens, 1987; Menge & Sutherland, 1987). None of these models makes predictions about the abundance and distribution of the community components (from single species to trophic levels). Menge & Olson (1990), adopting a broader perspective and working on the effect of scale and environmental factors in regulating community structure, predict that at intermediate to low environmental stress the abundance of mobile consumers should increase while 'basal species' (sessile space occupiers) decrease (see Menge & Olson 1990, Fig. 1). On the other hand, in stressful habitats basal species dominate and the abundance of consumers should decrease. The trophic structure of the southern African communities does not fit the above predictions. For example, although basal species conform to the predictions of Menge & Olson (1990), secondary consumers (predatory species) do not, being consistently more abundant in exposed shores where there is a high physical stress (Fig. 5). On these exposed shores the majority of the predatory species are commonly found living within the matrix provided by the basal species (mussels) and seldom on the open rock. If sheltered shores are considered as a benign habitat, only the communities present in the west province fit Menge & Olson's (1990) predictions for primary consumers, i.e. high abundance of herbivores in sheltered habitats and low abundance in exposed habitats. In the south and east the pattern is reversed or absent (see Fig. 5b).

The use of dominance analysis for comparing different aspects of marine community structure does not seem to have established itself in routine ecological research (Warwick, 1993), although its use in the detection of environmental impact (i.e., pollution, disturbance) on marine systems has increased in the last few years (e.g. Lambshead *et al.*, 1983; Warwick, Pearson & Rushwahyuni, 1987; Clarke, 1990; Warwick, 1993). It is evident from the biomass dominance analyses, that wave action is significantly related to the structure of southern African intertidal communities at a local scale.

On all coasts, the biomass of exposed shores is dominated by a few species, notably of filter feeders, whereas on sheltered shores a larger number of species contribute to the bulk of the biomass, which is dominated by algae and grazing herbivores (Fig. 6, Table 2). Semi-exposed shores of the west coast are intermediate. On the west coast, wave action clearly modifies the biomass structure. For example, 75% of the intertidal biomass (dashed lines in Fig. 6) is explained by three, six and nine species on exposed, semi-exposed and sheltered shores, respectively (Fig. 6a). On the south and east coast these figures are seven and sixteen species for exposed and sheltered shores respectively (Fig. 6b). The patterns of species richness also differ geographically. South and east coast intertidal communities contain on average almost twice as many species as those of the west coast communities (Fig. 6). The net effect is that west coast communities reach higher biomass levels but with fewer species (Figs 4 and 5) than those of the south and east coasts. These patterns can be related to the high productivity of the upwelled west coast (Brown, 1992; Pitcher, Brown & Mitchell-Innes, 1992) which will support a large biomass per-unit-area. Part of the reason that the east and south coasts have a richer fauna may be historical, in that they derive many of their species from the rich Indo-Pacific radiation (Kohn, 1990; Vermeij, 1978, 1992).

Another large-scale biogeographic pattern revealed is the existence of a gradient of species richness around the southern African rocky coast, with low values in the west, increasing towards the south and east coast. In general, the west coast intertidal communities support about half the number of species that occur in equivalent communities on the south and east coasts (Fig. 6).

The use of similarity analysis has proved useful in determining the contribution of individual species to both inter- and intra-community comparisons (Clarke, 1993). Large-scale biogeographic patterns are normally examined using presence/absence data that define the geographic ranges of individual species. However, such data are of limited value in examining community structure and its variation within regions. For example, the community structure of wave-beaten and sheltered shores is radically different when examined in terms of biomass (Fig. 5), even although these two habitats draw on the same regional pool of species.

Furthermore, the use of average biomass values to decide which species most usefully define a community is of little value if standard deviations are large. A species whose biomass is highly variable from site to site is of little use in distinguishing a community. This problem is well illustrated in data from exposed shores of the west coast (Table 2A), where the alien mussel *M. galloprovincialis* had the greatest average biomass, but was less useful in predicting community structure than the indigenous mussel *Aulacomya ater* (Table 2A). In order to look for 'consistence' within a community (and also between communities, a point not treated here), it is more useful to use the ratio between the species average contribution to the overall community similarity ($\overline{Si}$) and the standard deviation ($SD(Si)$) of the species (Clarke, 1993). On the west coast, the most consistent species, across all wave exposures, was the limpet *P. granularis*, which possessed high values of $\overline{Si}/SD(Si)$ in sheltered (3.18), semi-exposed (2.85) and exposed situations (1.51). This means the *P. granularis* was 'evenly' represented from site to site, and always with little variation. Similarly, on the south-east coast the articulate corallines were the most consistent group across wave exposures, with high ratios in both sheltered (1.8) and exposed (1.09) shores.

The aim of this work was to identify geographic patterns and the potential role of local physical disturbance (wave exposure) in the structuring of intertidal rocky shores communities of southern Africa. Underlying these patterns, historical processes are normally invoked in the majority of biogeographical studies (Myers & Giller, 1988). However, several abiotic and biotic features may powerfully influence the extant variation of these patterns. These include nutrient inputs, productivity gradients, export and import to or from adjacent systems (subtidal and/or terrestrial systems), wave action, desiccation and heat stress.

One of the immediate implications of the biogeographic patterns described here impinges on the necessity of establishing priority areas for conservation of the marine coastal biodiversity. World-wide, the lack of a broadly accepted marine biogeographic scheme is a serious gap in marine conservation and management (Ray, 1991; Ray & Gregg, 1991; Orians, 1993). However, even the identification of distribution patterns and the definition of marine biogeographic provinces, although essential, are but one step towards conservation. The results of this work provide a useful starting point towards understanding the role of regional coastal marine biodiversity, emphasizing that the identification of large-scale biotic distribution patterns is necessary. Thus, this work is a reminder of how biogeographic and large-scale community distribution patterns can be directly related to coastal biotic diversity and its future conservation. Arising out of the patterns identified is a need to establish the causes of these patterns, particularly the influence of productivity on biomass and species richness, the reason why some trophic groups are prevalent on wave-beaten shores and others on sheltered habitats, the causes of the unusually high biomass of grazers on the west coast and the significance of trophic subsidy. These issues are addressed more specifically in Bustamante (1994), Bustamante, Getz & Branch (1994) and Bustamante, Branch & Eekhout (1995).

ACKNOWLEDGMENTS

The information synthesized in this work is the result of an immense effort to collect biological and biogeographic data across the borders of three countries and over *c.* 5000 km of shoreline around the southern African coast. In this process, many colleagues and friends assisted in the sampling and data collection. Here we would like to thank Alison and Ricco Sakko for their logistic arrangements, financial support and creation of GRH ('Groenrivier Research Hut', Namaqualand). Long, wet days and nights were devoted to field work, during which a number of people gave us invaluable help. For that we would like to thank our wives Sol and Margo for their support and still 'unpaid' years of field assistance. We especially thank Lisa Kruger, Sean Eekhout, Claudio Velásquez, Alice ('wee tea') Linton, François Odendaal, Tracy Phillips, Ian Davidson, René Navarro, Emily Turner and John Boland, for their hard work and companionship during the extensive, but fun field work. This manuscript was greatly improved by the comments of Phil Hockey, Craig Johnson and Alec Brown. We also thank John G. Field and Carlos Villacastin for the advice, help and use of PRIMER. Financial support for this project was received from the FRD Core Program, and FRD-DEA Joint Venture funding for *Conservation and Exploitation of Rocky Shores* awarded to GMB. RHB was personally funded by an FRD Doctoral Bursary, UCT Foreign Student's Scholarship, UCT Postgraduate Research Grant and an M.B.R.I. Postgraduate Scholarship.

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