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THE INFLUENCES OF PHYSICAL FACTORS ON THE DISTRIBUTION AND ZONATION PATTERNS OF SOUTH AFRICAN ROCKY-SHORE COMMUNITIES

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Vertical zonation and horizontal distribution patterns of both community biomass and species richness of rocky-shore marine invertebrates and algae are described at a broad geographic scale for seven West and seven South-East Coast intertidal rocky-shore communities situated between southern Namibia and KwaZulu-Natal, South Africa. There were consistent patterns for community biomass and species richness, both of which showed similar vertical and horizontal distributions in equivalent habitats, regardless of geographical location. This indicates that the processes which create these patterns operate and vary in a similar way, even between different geographical regions. Multivariate techniques were used to assess, at a local scale, the relative importance of wave energy, rock temperature and shore elevation on the structuring and spatial variability of community biomass. Direct gradient analyses revealed that wave action strongly influences the structure of mid- to low-shore communities, whereas the interaction between rock temperature and shore elevation (both of which influence desiccation potential) produces convergence of high-shore communities. There was a significantly positive relationship between wave action and the per-unit-area community biomass, and a negative relationship between shore elevation and biomass. The potential role that waves may play in determining overall intertidal productivity is discussed.

All species live in a characteristic limited range of habitats and, within their range, they tend to be most abundant at their particular environmental optimum (Whittaker 1975). It has been consistently shown that biological communities exhibit trends along environmental gradients, regardless of the particularities of their habitat (Brown 1984). These "gradients" do not necessarily have physical reality as continua in either space or time, but are a useful abstraction for exploring the distributions of organisms (Austin 1985). Whittaker (1967) developed the first quantitative approaches to ecological *gradient analysis* to assist the interpretation of spatial changes in community composition in terms of species' responses to environmental variations. Such techniques can either be exploratory, i.e. to examine how community composition varies with the environment, or confirmatory, i.e. a means of testing the effects of a particular environmental variable while taking into account the effects of other variables (Ter Braak and Prentice 1988).

Numerical multivariate analyses have been long used in ecology to explore such gradients (see review of James and McCulloch 1990) and applied to a range of different marine communities (e.g. Field *et al.* 1982, McLachlan *et al.* 1984, Austen 1989, Kautsky and Van der Maarel 1990, van der Meer 1991, Castric-Fey and Chassé 1991, van Nes and Smit 1993, Santos 1993), including intertidal rocky communities (e.g. Field and McFarlane 1968, Field and Robb 1970, Kooistra *et al.* 1989, Fuji and Nomura 1990). All these works have explored the importance of the joint relationship between community data and environmental factors. Such analytical methods offer succinct summaries of large datasets, and often play a creative role in suggesting causes; at a later stage these can be formulated into new research hypotheses and causal models (James and McCulloch 1990), and then subjected to experimental manipulation (Underwood 1986).

The body of evidence relating to the ecological structure and regulation of marine communities (especially intertidal ecosystems) has largely concentrated on how particular species respond differentially to ecological processes such as disturbance, predation, competition or recruitment (e.g. Connell 1961, Paine 1966, Underwood and Denley 1984, Lubchenco 1986). Only recently have the effects of the environment on the regulation and structuring of whole marine benthic communities or species assemblages been addressed (Menge and Sutherland 1987, Menge and Farrell 1989, Menge and Olson 1990, McGuiness 1990). However, intertidal ecologists have long recognized that two of the most important local physical forces structuring intertidal rocky shores are gradients of desiccation, which produce a vertical zonation, and the differential effects of wave forces that generate a horizontal zonation (Dayton 1971, Stephenson and Stephenson

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1972, Sousa 1979a, b, Underwood *et al.* 1983, Dayton *et al.* 1984, Menge and Sutherland 1987, Menge and Farrell 1989, Menge and Olson 1990). Those studies suggest that community structure (abundance and diversity of species) depends on a complex interplay between large-scale (e.g. environmental stress and productivity) and small-scale processes (e.g. strong biotic interactions). The studies have highlighted the need for further comparative studies that simultaneously evaluate the contribution of environmental stresses at large and local scales to variations in community structure (Dayton and Tegner 1984, Menge and Sutherland 1987, Foster *et al.* 1988, Menge and Olson 1990). However, comparisons of particular environmental factors, such as temperature and wave action, are of little value when they are made between disjunct localities, because day-to-day changes in local weather can supersede any observed differences. More fruitful are comparisons within different localities (e.g. exposed v. sheltered or high- v. low-shore), because they can be made simultaneously under comparable conditions.

The rocky intertidal biota of southern Africa is among the most varied in the world (Stephenson and Stephenson 1972, Branch and Branch 1981, Branch *et al.* 1994). These rocky shores have been the focus of extensive local ecological research, centred on the identification of forces structuring rocky-shore communities. The majority of these works have dealt with the identification of particular factors, including several biotic interactions (Branch 1985, 1986, Branch *et al.* 1987, Bosman and Hockey 1988, Van Zyl and Robertson 1991), abiotic factors (Field and McFarlane 1968, Field and Robb 1970, McQuaid and Branch 1984, 1985, Huggett and Griffiths 1986, Bosman *et al.* 1987, Branch *et al.* 1987, McQuaid and Dower 1990, Field and Griffiths 1991), or a combination of abiotic and biotic factors (McQuaid *et al.* 1985, Griffiths and Hockey 1987). Griffiths and Branch (1991) concluded that physical factors control the abundance and vertical zonation of dominant species, whereas subordinates are biological controlled. Among the physical factors, those authors recognized that wave action and desiccation are perhaps the most important. Despite the general acceptance of theimportance of these factors, in South Africa and elsewhere (e.g. Lewis 1976, Underwood 1981, Foster *et al.* 1988, Menge and Olson 1990, McGuinness 1990), their variation among sites, and comparisons at local and meso-geographical scales are seldom documented.

The effects of the environment (leading to physiological and/or mechanical stress) have been incorporated into general community models as independent variables (Hairston *et al.* 1960, Connell 1975, Menge and Sutherland 1976, 1987). To evaluate these models, it is necessary to quantify the main environmental gradients independently and the community variation along them. Moreover, this needs to be done at different spatial scales (Menge and Sutherland 1987) before one can synthesize the main environmental factors (and their interactions) that influence variation in community structure.

The purpose of the present study is threefold:

(i) at a broad geographical scale, to describe, evaluate and compare zonational trends in biomass zonation and species richness of rocky intertidal communities at seven localities on the west coast compared with seven localities on the south and east coasts of southern Africa;
(ii) to assess the relative importance of such physical factors as wave force, shore elevation and rock temperature on species richness, biomass and distribution at two specific but geographically disjunct localities, namely Groenrivier on the West Coast and Port Elizabeth on the South Coast;
(iii) to relate zonation patterns of intertidal species to environmental variables at a local scale.

The study is exploratory and descriptive in nature and relies on direct gradient analyses to detect and explore patterns in community structure and their correlations with physical variables. As such, it lays the groundwork for developing specific hypotheses to explain community patterns, which can then be tested experimentally.

MATERIAL AND METHODS

The sites

Data on zonation patterns were collected at 14 different localities around the southern African coast (Lüderitz, Port Nolloth, Tweepad, Rooiklippies, Spoegrivier, Groenrivier, Paternoster, Cape Infanta, Mossel Bay, Tsitsikamma, Port Elizabeth, Dwesa, Ballito Bay and Cape Vidal, see Fig. 1). Data are compared in more detail from the intertidal rocky shores of Groenrivier (30°48′S, 17°30′W) on the West Coast and from Port Elizabeth (34°00′S–26°37′W) on the South-East Coast (Fig. 1). At each of these localities, either two or three sites were selected to represent contrasting grades of wave action – i.e. *sheltered* boulder bays, *semi-exposed* rocky shores (in the lee side of kelp forests and present only on the West Coast) and *exposed* rocky headlands. The sites

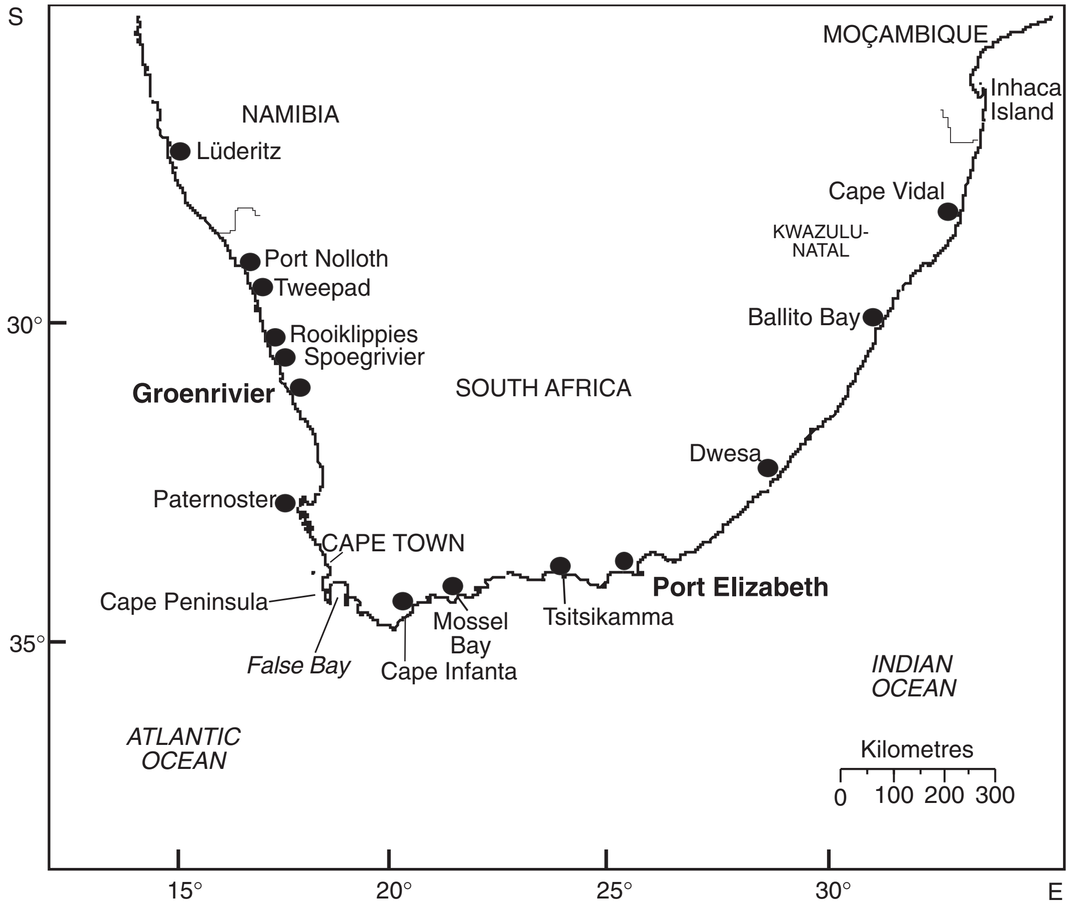


Fig. 1: The coast of southern Africa showing the study sites and other localities mentioned in the text

were chosen to ensure comparability in orientation, slope (between 15 and 45° inclination) and substratum type (sandstone). Both localities experience a similar semi-diurnal tidal regime and tidal amplitude, the latter being respectively 2.21 and 2.40 m at spring tide for Groenrivier and Port Elizabeth (South African Navy 1993).

Data acquisition

The average (± 1 *SE*) values of community biomass per unit area for all sites were used to describe general biomass patterns in relation to rocky intertidal zonation (vertical and horizontal). Standard community surveys were carried out at each locality. In brief, at each site, four replicate transects 15 – 30 m long were laid down perpendicularly to the sea edge. Along each transect, eight quadrats (0.5 m^2 each) were randomly placed, and the biomass contribution per species (converted to $g \cdot m^{-2}$ of ash free dry mass, AFDM), density, species richness (total number of species per quadrat) and trophic structure were recorded. Only the data for the most important species were employed in the biomass analyses (i.e. those contributing >0.01% to the total biomass, including infaunal and epibiont species). To document species richness, all species present in each quadrat were counted; small, cryptic species were also included, down to a body length of 1 mm. By confining the information to the data obtained from quadrats, quantitatively equivalent measures were obtained at all sites. It is recognized, however, that this approach will have failed to detect many of the rarer species, so that total

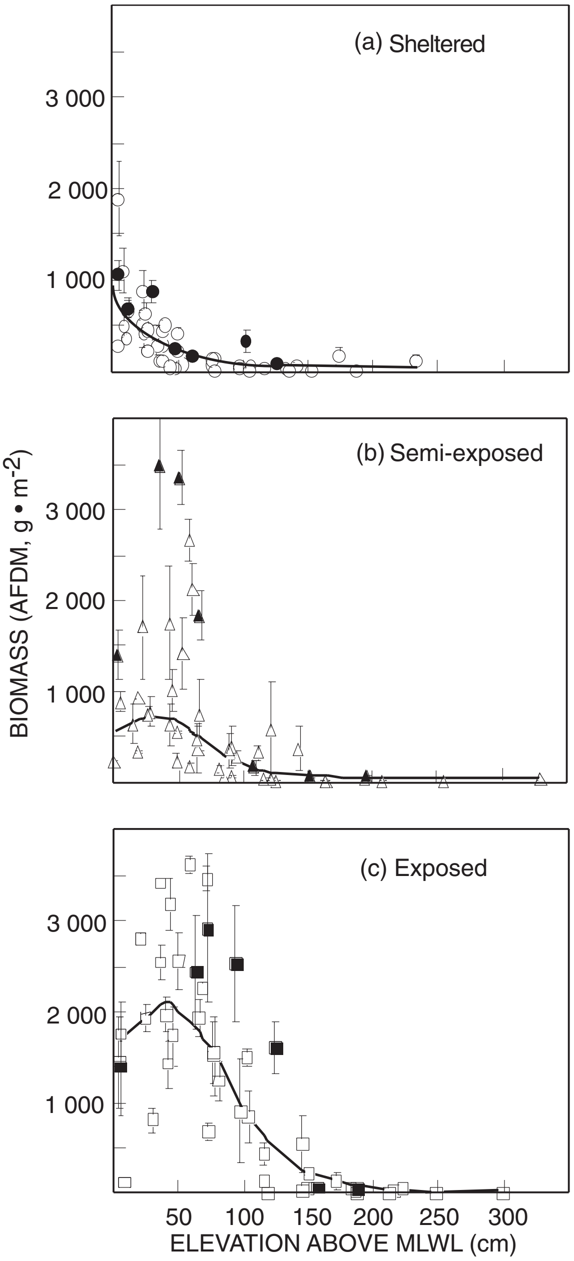


Fig. 2: Vertical zonation of the average (±1 *SE*) biomass at seven localities on the west coast of southern Africa (clear symbols) on (a) sheltered, (b) semi-enclosed and (c) exposed shores. Solid symbols indicate the data from Groenrivier. The trend lines were weight-fitted to the total dataset with a 50% smoothing

biodiversity is underestimated. A more detailed account of the sampling methodology and a full dataset can be found in Bustamante (1994).

At Groenrivier and Port Elizabeth, three environmental variables were recorded. At the positions of all quadrats used to sample the biota, measurements were made of (a) shore elevation (height) above Mean Low Water Spring tide (MLWS), (b) rock temperature, and (c) wave force. Shore elevation was measured using a water-level device which recorded the difference in height between each sampled quadrat and the zero level (MLWS). Wave force (measured in $N \cdot m^{-2}$) was defined as the force exerted by waves over a hollow hemispherical drogue, divided by the cross-sectional area of the drogue, and was measured with dynamometers, using a modified version of the Jones and Demetropoulos (1968) apparatus, described and tested by Palumbi (1984). At the position of each quadrat, a series of three parallel dynamometers was fastened to the rock surface perpendicularly to the direction of waves. The dynamometers were left *in situ* for a period of three days and the maximal wave forces exerted on the dynamometers during each tidal cycle were recorded. For comparisons between sites, absolute or average wave forces are frequently not critical (Denny 1988). However, simultaneous measurements and the use of identical drogues are absolutely essential.

Rock temperatures were measured simultaneously within each quadrat during low tide, every hour for three consecutive days. Using epoxy glue, 30 Ga Type T thermocouples were attached to the rock surface. Temperatures detected with these thermocouples were recorded by a Bat-12 Bailey Instruments digital thermocouple reader.

Data analysis

In total, 140 samples ($70 \cdot m^{-2}$) were taken at Groenrivier and Port Elizabeth – the two particular localities where detailed environmental data were gathered. These yielded 101 algal and invertebrate taxa, all of which were used in the analyses of species richness. For the biomass and multivariate analyses, only taxa that contributed >0.01% to the total biomass were included – i.e. 38 and 34 taxa for Groenrivier and Port Elizabeth respectively. These taxa comprised >71% of the species richness and >95% of the total biomass recorded at each site during the surveys. The contribution of individual species to the community biomass ranged through five orders of magnitude (from 0.2 to c. 1 700 $g \cdot m^{-2}$). Consequently, the biomass data were logarithmically transformed

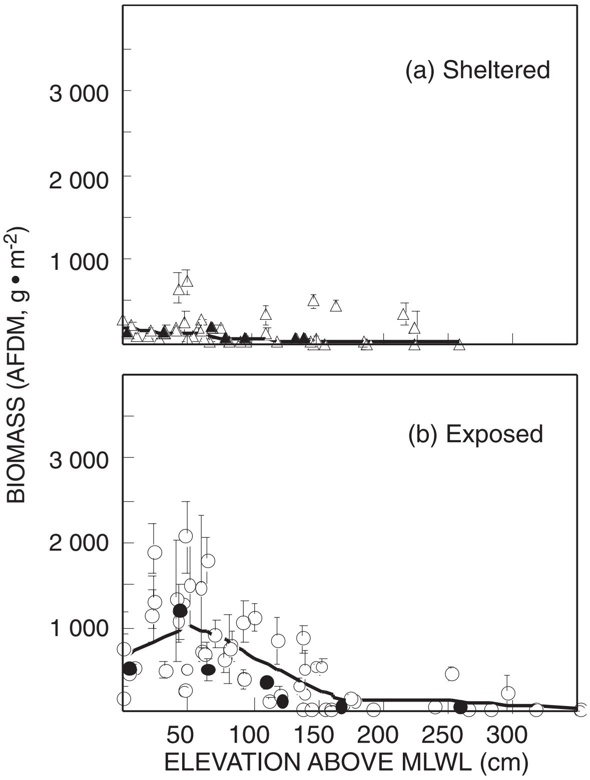


Fig. 3: Vertical zonation of the average (±1 *SE*) biomass at seven localities on the south-east coast of southern Africa (clear symbols) on (a) sheltered and (b) exposed shores. Solid symbols indicate the data from Port Elizabeth. The trend lines were weight-fitted to the total dataset with a 50% smoothing

[$\log_{10}(x+1)$] and standardized (proportions). The ordinal environmental variables (elevation, temperature and wave action) were treated as continuous variables.

To detect trends in the vertical distribution of biomass and of species richness, curves were fitted to the plots by using the locally weighted least-squared error method. This curve fit has no data restrictions and has no parameters associated with it. The result of this curve fit is to plot a best-fit smooth curve through the centre of the data, or 50% smoothing. This is an extremely robust fitting technique and, unlike standard regression methods, is minimally sensitive to outliers (Press *et al.* 1986).

Linear regressions and univariate non-parametric analyses of variance (ANOVA by ranks) with *a-posteriori* mean comparisons of main effects (Bonferroni *t*-test) were performed for the comparison of shore elevation, rock temperature and wave exposure between and within localities. All ANOVAs and regressions were performed using Generalized Linear Models, GLM (SAS 1986).

To explore the joint relationship between the biomass of rocky intertidal species assemblages and the selected environmental variables, a multivariate (ordination) direct gradient analysis was performed. Canonical Correspondence Analysis (CCA) was used to correlate the biomass of the benthic community with the abiotic variables (Ter Braak 1986, Palmer 1993). Direct gradient analysis was carried out using the average biomass per species at each height interval, for Groenrivier and Port Elizabeth independently. The environmental variables used in the analyses were the maximum wave force, maximum rock temperature and shore elevation. The computer package CANOCO v2.1 (Ter Braak 1987) was used to perform CCA (Ter Braak and Prentice 1988).

RESULTS

Biomass

When comparing all the localities around the coast, two different zonation patterns were detected for community biomass, and these could be related to differences in wave exposure. First, on sheltered shores of both the West and the South-East coasts, community biomass was maximal on the low-shore, and decreased exponentially upshore (Fig. 2a), although this pattern was less obvious on the South-East Coast (Fig. 3a). At all shore heights, biomass was lower on the South-East coast than on the West Coast. Maximal values of 2 000 (± 445) g.m^{-2} were recorded on the West Coast, but only 700 (±135) g.m^{-2} on the South-East Coast. At shore height >50 cm, in both West and South-East intertidal communities, the average biomass never exceeded 450 (± 58) g.m^{-2}. The upper limit of intertidal biota was approximately 250 cm above MLWS at both sites (Figs 2a and 3a).

Second, on semi-exposed and exposed shores on both West and South-East coasts, biomass peaked in the mid-shore (50–100 cm). Low on the shore, biomass was intermediate between mid- and high-shore values (Figs 2b, c, 3b). The maximum biomass values on the West Coast were 2 675 (± 168) and 3 726 (± 150) g·m^{-2} for semi-exposed and exposed shores respectively, whereas the biomass on South-East Coast exposed shores never exceeded 2 500 (± 362) g·m^{-2}

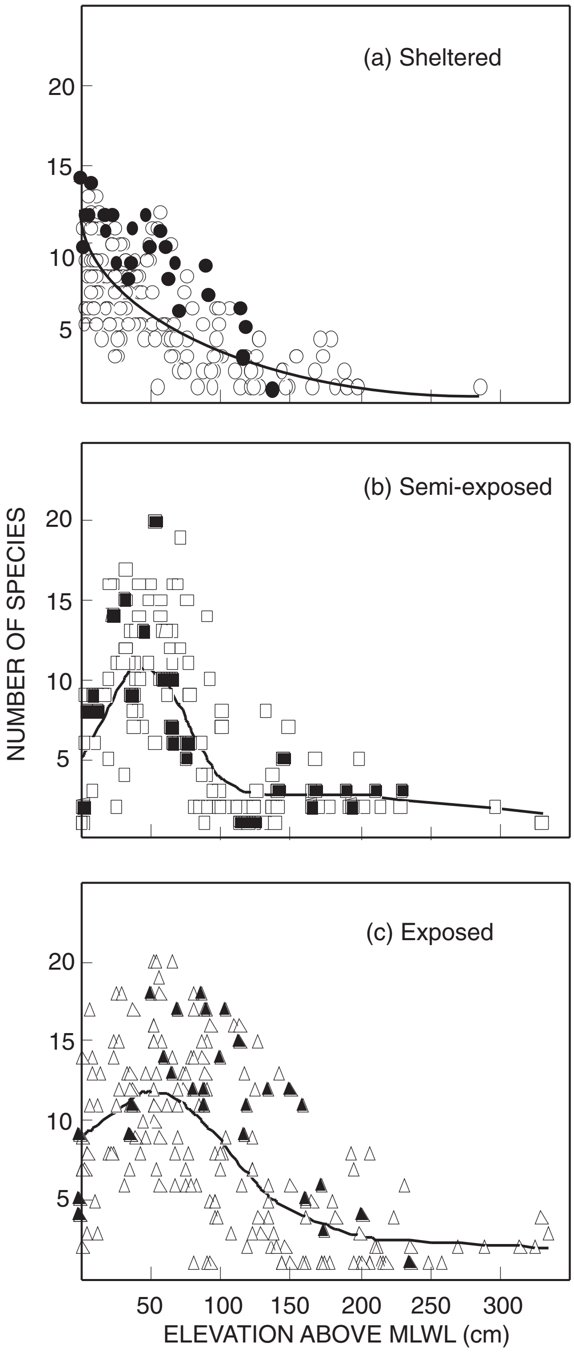


Fig. 4: Vertical zonation of the total number of species per sampling quadrat at seven localities on the west coast of southern Africa (clear symbols), on (a) sheltered, (b) semi-exposed and (c) exposed shores. Solid symbols indicate the data from Groenrivier. The trend lines were weight-fitted to the total dataset with a 50% smoothing

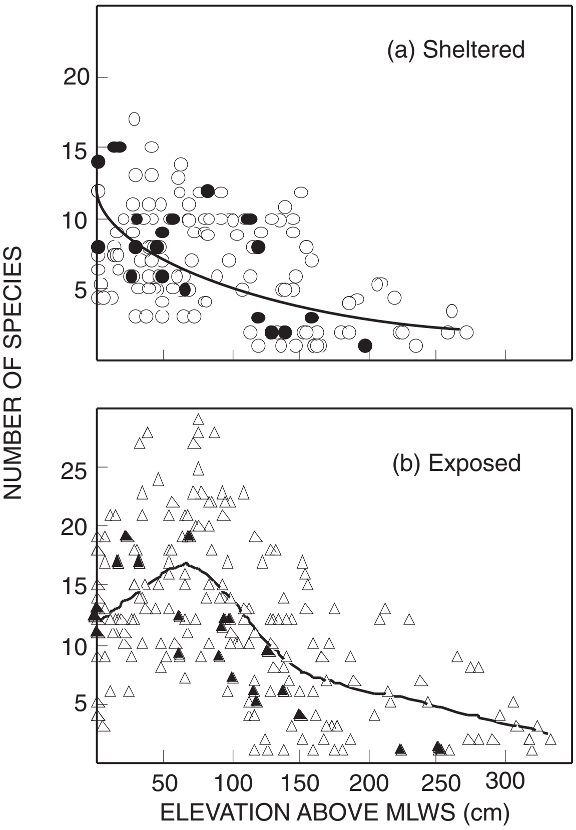


Fig. 5: Vertical zonation of the total number of species per sampling quadrat at seven localities on the south-east coasts of southern Africa (clear symbols), on (a) sheltered and (b) exposed shores. Solid symbols indicate the data from Port Elizabeth. The trend lines were weight-fitted to the total dataset with a 50% smoothing

(Figs 2 and 3). On the West Coast, intertidal communities of the semi-exposed and exposed shores extended significantly higher than on the sheltered shores (ANOVA, $p < 0.001$), the upper limit of the semi-exposed and exposed shores (350 cm) being significantly greater than that of sheltered shores (247 cm, Bonferroni *t*-test, $p < 0.5$, Fig. 2). Similarly, on the South-East Coast, exposed shores had a significantly higher upper limit (350 cm) than sheltered shores (259 cm, Bonferroni *t*-test, $p < 0.05$, Fig. 3). At shore heights >150 cm, average community biomass ranged between 74 and 420 $g \cdot m^{-2}$ and did not differ significantly between sites with different degrees of wave action, or between localities.

In summary, the overall biomass was consistently higher on the West Coast than on the South-East Coast, higher at wave-exposed sites than sheltered

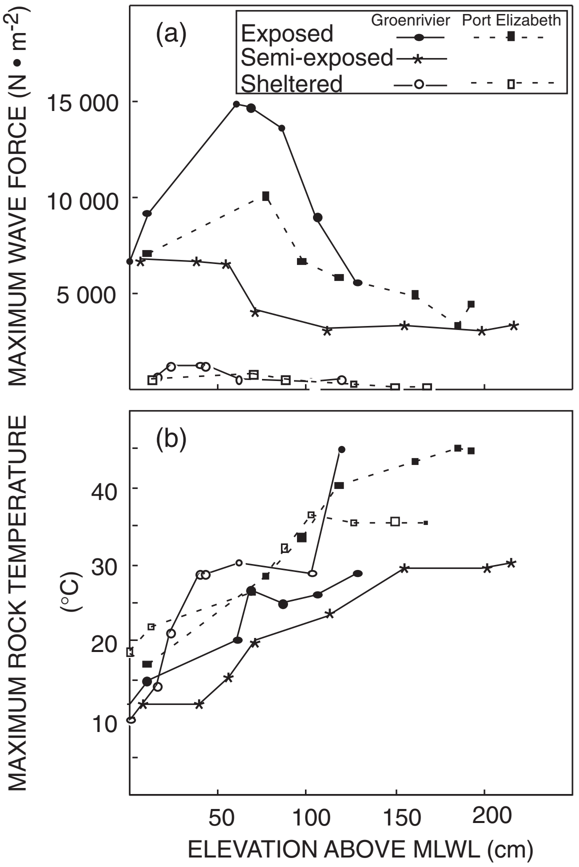


Fig. 6: Maximum values recorded of (a) wave force and (b) rock temperature in relation to tidal elevation on exposed, semi-exposed and sheltered shores at Groenrivier and Port Elizabeth

sites, and peaked low on the shore at sheltered sites but just below mid-shore on more exposed sites.

At both the localities studied in more detail, i.e. Groenrivier and Port Elizabeth, semi-exposed and exposed shores had intermediate levels of biomass on the low-shore (<30 cm), and maximum biomass below the mid-shore (50–100 cm, Figs 2 and 3), and closely followed the patterns described above for the West and South-East coasts as a whole. Similarly, on sheltered shores at these two localities the biomass was concentrated in the low-shore, followed by a sharp up-shore decrease at Groenrivier (Fig. 2a), but a more gradual decrease at Port Elizabeth (Fig. 3b). The average community biomass was significantly greater at Groenrivier than at Port Elizabeth (Fig. 3), at both exposed and sheltered shores (ANOVA, $p < 0.001$; Bonferroni *t*-test, $p < 0.05$).

Species richness

On the West Coast, the maximum number of species per sample was 20, the highest values being reached below the mid-intertidal (50–100 cm above MLWS tide) on semi-exposed and exposed shores (Figs 4b, c). Sheltered shores attained a maximum of only 14 species, being achieved low in the shore (Fig. 4a). Similar patterns were found at exposed and sheltered shores of the South-East Coast (Fig. 5), except that species richness was higher there than on the West Coast. More specific examination of the two sites at which physical measurements were made, i.e. Groenrivier and Port Elizabeth, revealed similar vertical distribution patterns of species richness (Figs 4, 5). The vertical distribution of species richness thus parallels the patterns described for biomass.

Abiotic factors

The abiotic parameters measured at Groenrivier and Port Elizabeth are plotted in relation to shore elevation in Figure 6. The maximum values of wave force recorded on exposed sites at Groenrivier (15 000 N·m^{-2}) were significantly greater (ANOVA, $p < 0.0001$) than those of sheltered shores (1 500 N·m^{-2}). Semi-exposed shores experienced intermediate wave energies, with a maximum wave force of 7 000 N·m^{-2} (Fig. 6a). Similarly, exposed sites at Port Elizabeth (10 000 N·m^{-2}) had significant greater wave forces (ANOVA, $p < 0.0001$) than sheltered shores (1 100 N·m^{-2}). The vertical distribution of wave force at exposed sites followed a similar trend to that of community biomass and species richness (see Figs 2–5), i.e. medium forces on the low-shore (0–20 cm), and a peak on the mid-shore, decreasing towards the high-shore. On sheltered shores, there was no obvious vertical trend in the wave force distribution as elevation increased (Fig. 6a).

There was a positive relation between the maximum rock temperatures and shore elevation at all sites (Fig. 6b). In the low-shore, rocks had a temperature close to that of sea water; higher up the shore, temperatures rose to 45°C. The overall rock temperatures at Groenrivier (23.1 ± 8.5°C) and Port Elizabeth (30.9 ± 9.2°C) were marginally different (ANOVA, $p < 0.049$), but no differences were found between their respective wave forces in habitats with corresponding exposure (ANOVA, $p > 0.810$). No great significance can be attached to these differences, however, because prevailing weather conditions would have strong influences on differences between regions. Within regions, temperature did differ on shores experiencing different grades of wave action, but no consistent pattern emerged (Fig. 6b). At Groenrivier, semi-exposed shores were cooler than sheltered or

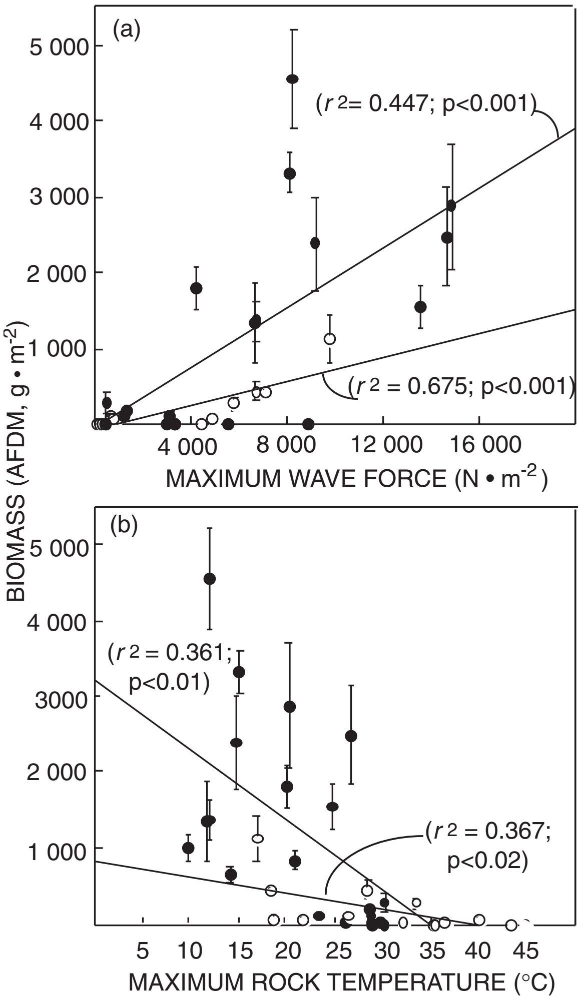


Fig. 7: Relationship between average (±1 *SE*) intertidal community biomass and (a) maximum wave force and (b) maximum rock temperature at Groenrivier (solid symbols) and Port Elizabeth (open symbols)

exposed shores, which did not differ significantly from one another (ANOVA, $p > 0.05$). At Port Elizabeth, no significant differences were found between sheltered and exposed shores (Fig. 6b).

The average community biomass was positively correlated with maximum wave force and negatively correlated with maximum rock temperature at both Groenrivier and Port Elizabeth (Fig. 7). There is an obvious inverse relationship between wave force and rock temperature, one being negatively and the other positively related to tidal elevation. This situation precluded the use of each of these factors in isolation as explanatory variables for local variation in community biomass.

Community structure and species composition

GROENRIVIER

On sheltered sites, 68% of the total community biomass was contributed by five taxa (Table I). These were the kelps *Ecklonia maxima* and *Laminaria pallida* (combined 15.0%), the limpet *Patella granatina* (18.5%), which forms dense monospecific stands in the low- to mid-shore (Bustamante *et al.* 1995), and large colonies of the polychaete *Gunnarea capensis* (17.8%). High on the shore the red alga *Porphyra capensis* (17.2%) formed dense patches. However, the species most frequently found in samples was the limpet *Patella granularis* (12.1%). The next most frequent species were the sea anemone *Bunodactis reynaudii* and two species of the scavenging whelks *Burnupena* spp. (*B. cincta* and *B. catarrhacta*), both present in 9.9% of the samples.

On semi-exposed shores, 90% of the total community biomass accounted for three species, whereas a further 24 different taxa contributed the remaining 10% (Table I). Of the dominant species, the limpet *Patella argenvillei* (29.9%) formed a conspicuous monospecific band of c. 2 m width on the low-shore (Bustamante *et al.* 1995). In the mid-shore, large colonies of the polychaete *Gunnarea capensis* (35.5%) formed a complex mosaic with the alien mussel *Mytilus galloprovincialis* (25.0%). The most frequently encountered species in the samples were *P. granularis* (17.1%) and *M. galloprovincialis* (11.0%).

In exposed sites, *M. galloprovincialis* (77.0%) dominated much of the entire mid- to low-shore, forming dense mussel beds which housed a number of cryptic species. The mussel beds were interspersed with patches of *Gunnarea capensis* (6.7%) and overgrown by epibiont algae (<5%, Table I). The most frequently encountered species were the limpet *P. granularis* (16.1%), the sea anemone *Bunodactis reynaudii* (13.8%) and the indigenous mussel *Aulacomya ater* (11.2%).

PORT ELIZABETH

The community biomass of sheltered shores at Port Elizabeth was dominated by the colonial polychaete *Pomatoleios kraussii* (42.2%), several species of articulate coralline algae (14.7%), the red algae *Gelidium* spp. (7.6%), together with two limpets, *Patella barbara* and *P. oculus,* and the encrusting

Table I: Frequency of occurrence of species per quadrat (%), average biomass, standard error (*SE*), % biomass and minimum and maximum biomass (g·m^{-2} AFDM), for habitats with different wave exposures at Groenvier. Only species contributing >0.01% to the AFDM biomass are listed. *SE*s are omitted for species sampled in one quadrat only

Species	Abbrev.	Sheltered						Semi-exposed						Exposed					
		% Freq.	Mass	*SE*	% Mass	Min.	Max.	% Freq.	Mass	*SE*	% Mass	Min.	Max.	% Freq.	Mass	*SE*	% Mass	Min.	Max.
Algae																			
Articulate corallines	Artcor	5.5	25.1	5.8	2.3	5.6	66.4	1.7	14.1	4.4	0.4	6.9	22.2	4.1	4.9	0.6	0.2	2.6	8.9
Gelidium spp.	Gelspp	–	–	–	–	–	–	0.6	1.5	–	0.0	–	–	–	–	–	–	–	–
Porphyra capensis	Porphy	3.3	190.5	98.9	17.2	21.5	620.0	0.6	4.9	–	0.1	–	–	–	–	–	–	–	–
Ceramium spp.	Cerami	–	–	–	–	–	–	4.4	12.3	3.7	0.3	3.7	36.8	–	–	–	–	–	–
Gymnogongrus spp.	Gymspp	0.6	3.5	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gigartina spp.	Gigaspp	1.1	12.9	0.7	1.2	5.1	20.6	2.2	21.8	14.3	0.6	5.1	64.4	0.4	5.3	–	0.2	–	–
Iridaea capensis	Iridaea	1.7	3.8	0.9	0.3	2.3	5.4	0.6	25.4	–	0.6	–	–	0.4	2.4	–	0.1	–	–
Splachnidium rugosum	Splash	–	–	–	–	–	–	0.6	17.8	–	0.5	–	–	–	–	–	–	–	–
Champia lumbricalis	Chlum	1.7	31.9	21.5	2.9	6.1	74.5	2.2	34.7	16.4	0.9	7.3	72.9	1.5	27.3	15.4	1.2	3.2	69.4
Aeodes orbitosa	Aeodes	6.6	10.1	1.8	0.9	1.8	19.5	3.3	3.7	0.8	0.1	1.4	5.6	1.9	1.5	0.7	0.1	0.3	4.2
Caulacanthus ustulatus	Caulac	0.6	5.7	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ecklonia/Laminaria	EckLam	6.6	166.4	34.4	15.0	3.8	336.9	1.7	37.5	11.1	1.0	23.6	59.5	2.6	107.8	56.9	4.8	4.7	435.9
Chordariopsis capensis	Chorda	2.8	14.8	8.9	1.3	5.1	50.2	0.6	4.1	–	0.1	–	–	–	–	–	–	–	–
Ulva spp.	Ulva	3.9	5.0	1.3	0.5	2.8	12.6	2.2	22.6	19.1	0.6	3.4	80.2	–	–	–	–	–	–
Codium fragile	Codium	1.1	9.6	4.5	0.9	5.1	14.1	–	–	–	–	–	–	–	–	–	–	–	–
Cladophora spp.	Cladoph	1.7	9.4	5.5	0.8	3.4	20.3	–	–	–	–	–	–	0.4	1.0	–	0.0	–	–
Invertebrates																			
Bunodactis reynaudii	Bunod	9.9	52.2	12.4	4.7	2.7	162.7	7.2	10.5	1.5	0.3	2.5	21.0	13.9	42.1	11.8	1.9	0.2	318.5
Patella granatina	Pgranat	8.8	206.0	38.5	18.6	10.6	530.8	–	–	–	–	–	–	0.7	2.5	2.2	0.1	0.3	4.7
Patella argenvillei	Pargv	–	–	–	–	–	–	2.2	1171.4	289.8	29.9	448.5	1864.2	3.0	54.1	21.0	2.4	0.5	153.7
Patella granularis	Pgranul	12.2	36.5	7.6	3.3	1.2	125.7	17.1	18.1	2.6	0.5	2.3	54.0	16.1	12.7	1.5	0.6	0.5	44.8
Patella barbara	Pbarb	1.1	2.8	0.3	0.3	2.5	3.1	–	–	–	–	–	–	0.4	2.6	–	0.1	–	–
Patella miniata	Pmini	–	–	–	–	–	–	–	–	–	–	–	–	0.7	2.1	1.1	0.1	1.0	3.2
Patella cochlear	Pcoch	–	–	–	–	–	–	2.2	68.1	18.1	1.7	23.1	104.1	0.7	1.4	1.1	0.1	0.3	2.5
Crepidula porcellana	Crepid	0.6	1.7	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Siphonaria spp.	Siphspp	–	–	–	–	–	–	1.7	5.0	1.8	0.1	3.0	8.5	0.4	5.1	–	0.2	–	–
Helcion spp.	Helspp	2.2	2.1	0.5	0.2	1.4	3.7	5.0	10.0	2.5	0.3	2.0	22.9	3.7	3.0	0.8	0.1	1.3	10.1
Nucella spp.	Nucell	–	–	–	–	–	–	2.8	2.4	0.5	0.1	1.0	3.8	8.6	7.5	1.3	0.3	0.4	25.0
Burnupena spp.	Burnsp	9.9	12.0	3.2	1.1	0.5	60.9	4.4	7.2	1.6	0.2	1.4	14.3	8.2	5.5	1.0	0.2	0.4	15.6
Oxystele spp.	Oxyspp	2.2	4.4	0.5	0.4	2.9	5.1	6.1	8.8	2.9	0.2	1.7	34.3	0.4	2.5	–	0.1	–	–
Oxystele tigrina	Oxytig	0.6	3.5	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pseudonereis variegata	Pseuspp	–	–	–	–	–	–	4.4	15.0	3.0	0.4	2.6	28.6	7.1	6.2	1.2	0.3	1.0	21.0
Gunnarea capensis	Gunnar	7.2	197.8	47.4	17.9	22.1	575.3	8.8	1389.4	314.2	35.5	17.2	4821.9	3.7	148.4	99.7	6.7	9.8	1030.0
Octomeris angulosa	Octom	–	–	–	–	–	–	–	7.9	–	–	–	–	0.7	6.0	2.0	0.3	4.0	8.0
Tetraclita serrata	Tetraser	–	–	–	–	–	–	0.6	7.9	–	0.2	–	–	0.4	4.1	–	0.2	–	–
Notomegabalanus algicola	Notob	–	–	–	–	–	–	–	–	–	–	–	–	0.7	10.1	2.0	0.5	8.1	12.2
Mytilus galloprovincialis	Mytilus	1.1	54.2	18.1	4.9	36.1	72.2	11.0	981.1	288.6	25.1	24.1	4207.5	7.9	1705.0	245.4	77.0	4.7	4396.2
Aulacomya ater	Aater	7.2	46.5	11.8	4.2	7.4	174.4	6.1	18.5	5.5	0.5	3.9	67.4	11.2	42.6	8.2	1.9	0.8	193.0
Total mass		1 108.3						3 913.9						2 213.0					

Table II: Frequency of occurence of species per quadrat (%), average biomass, standard error (*SE*), % biomass and minimum and maximum values of biomass (g·m^{-2} AFDM), for habitats with different wave exposures at Port Elizabeth. Only species contributing >0.01% to the AFDM biomass are listed. *SE*s are omitted for species sampled in one quadrat only

Species	Abbrev.	Sheltered						Exposed					
		% Freq	Biomass	*SE*	% Mass	Min.	Max.	% Freq.	Biomass	*SE*	% Mass	Min.	Max.
Algae													
Articulate corallines	Artcor	2.9	34.7	19.6	14.7	1.7	80.7	4.8	59.8	34.3	6.1	0.6	277.0
Gelidium spp.	Gelspp	4.4	18.0	5.6	7.6	1.3	39.7	4.2	31.3	10.0	3.1	4.4	83.3
Hildenbrandia sp.	Hiden	5.8	16.5	4.7	7.0	3.9	41.3	0.6	14.1	14.1	1.4	–	–
Laurencia spp.	Lauren	–	–	–	–	–	–	1.2	85.8	80.0	8.8	4.9	166.6
Sargassum spp.	Sargaspp	4.3	3.5	1.2	1.5	0.6	6.9	0.6	4.0	–	0.4	–	–
Invertebrates													
Patella barbara	Pbarb	0.7	10.3	–	4.4	–	–	2.4	1.8	0.7	0.2	0.6	3.2
Patella oculus	Pocul	8.0	10.5	1.5	4.4	5.2	23.6	2.4	0.8	0.2	0.1	0.5	1.4
Patella longicosta	Plong	2.2	5.3	3.2	2.2	1.7	11.7	3.6	5.4	3.0	0.5	0.4	17.1
Patella granularis	Pgranul	2.2	2.3	1.2	1.0	1.1	4.7	8.4	9.5	2.9	1.0	0.1	39.8
Patella argenvillei	Pargv	–	–	–	–	–	–	1.2	21.7	10.9	2.2	10.9	32.6
Patella cochlear	Pcoch	–	–	–	–	–	–	3.1	59.8	31.3	6.1	5.9	168.9
Helcion spp.	Helspp	8.0	1.6	0.4	0.7	0.7	5.1	0.6	0.4	–	0.0	–	–
Siphonaria spp.	Siphspp	8.8	1.1	0.3	0.5	0.1	4.1	6.0	3.9	1.0	0.4	0.6	10.4
Chitons	Chiton	2.2	0.2	0.1	0.1	0.1	0.4	2.4	1.1	0.4	0.1	0.5	1.8
Burnupena spp.	Burnsp	2.9	0.4	0.1	0.2	0.3	0.5	6.6	1.5	0.8	0.2	0.0	9.3
Nucella spp.	Nucell	2.9	0.5	0.1	0.2	0.3	0.8	1.8	0.3	0.0	0.0	0.3	0.3
Turbo spp.	Turbsp	5.1	3.8	1.0	1.6	0.6	7.5	0.6	0.7	0.7	0.1	–	–
Oxystele tigrina	Oxytig	7.3	1.9	0.4	0.8	0.6	4.5	0.6	1.9	1.9	0.2	–	–
Oxystele sinensis	Oxysin	3.6	5.0	1.8	2.1	1.7	11.6	1.8	2.3	0.9	0.2	0.5	3.5
Littorina spp.	Littor	3.6	2.3	0.6	1.0	0.3	4.3	2.4	2.8	0.5	0.3	2.0	4.0
Oxystele spp.	Oxyspp	10.9	4.2	0.7	1.8	0.4	10.5	5.4	2.2	1.0	0.2	0.7	9.8
Parechinus angulosus	Parechy	–	–	–	–	–	–	1.8	4.1	1.9	0.4	2.1	7.9
Patiriella exigua	Patirie	–	–	–	–	–	–	4.2	0.1	0.0	0.0	0.1	0.2
Gunnarea capensis	Gunna	–	–	–	–	–	–	3.6	26.2	10.8	2.7	3.8	76.6
Cucumaria spp.	Cucum	–	–	–	–	–	–	2.4	2.5	1.5	0.3	0.3	6.8
Pomatoleios kraussii	Pomato	2.9	99.7	18.4	42.2	57.0	142.4	2.4	89.0	25.6	9.1	42.7	156.7
Perna perna	Perna	–	–	–	–	–	–	6.0	355.1	156.9	36.3	2.5	1361.3
Pseudonereis variegata	Pseuspp	1.5	4.1	2.5	1.7	1.6	6.6	4.8	1.2	0.7	0.1	0.0	5.9
Octomeris angulosa	Octom	–	–	–	–	–	–	3.0	20.0	12.7	2.0	2.9	70.7
Thecalia concamerata	Thecali	0.7	0.3	–	0.1	–	–	–	–	–	–	–	–
Tetraclita serrata	Tetraser	4.4	5.4	3.0	2.3	0.3	19.5	5.4	99.8	27.3	10.2	1.4	225.4
Chthamalus dentatus	Chtamal	2.2	0.3	0.1	0.1	0.1	0.6	4.8	66.8	22.6	6.8	2.2	153.2
Plagusia chabrus	Plagus	2.2	4.2	1.6	1.8	1.8	7.2	0.6	1.4	–	0.1	–	–
Total mass		236.2						997.2					

Table III: Eigenvalues and percentage of variance accounted for by the four axes of the CCA ordination of samples and species scores for Groenrivier and Port Elizabeth

Axes	Groenrivier		Port Elizabeth	
	Eigenvalue	% Variance	Eigenvalue	% Variance
1	0.805	43.9	0.816	36.4
2	0.559	30.6	0.661	29.5
3	0.306	16.7	0.472	21.0
4	0.162	8.8	0.293	13.1

Hildenbrandia sp. (Table II). All these species were concentrated low on the shore. The mid- and high-shore communities were characterized by numerous mobile grazers and predatory gastropods, but these contributed little to the total biomass. The most frequent species, however, were grazers, specifically two species of winkle, *Oxystele variegata* and *O. impervia* (combined 10.9%), the pulmonate limpets *Siphonaria* spp. (8.7%) and the limpets *Patella oculus* and *Helcion* spp. (8.0% each, Table II).

On the exposed sites at Port Elizabeth, as at Groenrivier, >50% of the community biomass consisted of filter-feeders, in this case the mussel *Perna perna* (36.3%), the barnacle *Tetraclita serrata* (10.2%) and the colonial polychaete *P. kraussii* (9.1%), all concentrated in the low- to mid-shore. However, the most common species in the samples were *P. granularis* (8.4%), *Burnupena* spp. (6.6%) and *Siphonaria* spp. and *P. perna* (6.0% each, Table II).

Direct gradient analysis

The graphical results of the canonical correspondence analyses for the rocky communities associated with the environmental factors are presented in Figure 8. The figure displays the combined 2D-biplot of species (abbreviations), samples (numbers) and the environmental vectors (arrows), where arrows indicate the relative importance (length) and direction of each vector. At Groenrivier (Fig. 8a), the ordination along the *x*-and *y*-axes explained 43.9 and 30.6% of the total community variance respectively (Table III). Similarly, in the ordination for the communities of Port Elizabeth the same axes accounted for 36.4% and 29.5% of the total variance with respect to the environmental variables (Table III). For both localities, the first two canonical axes of the species ordination were significantly linked to the environmental variables (Monte Carlo permutation test, $p < 0.01$), and so indicate significant differences in the species composition between shores of differing wave exposure.

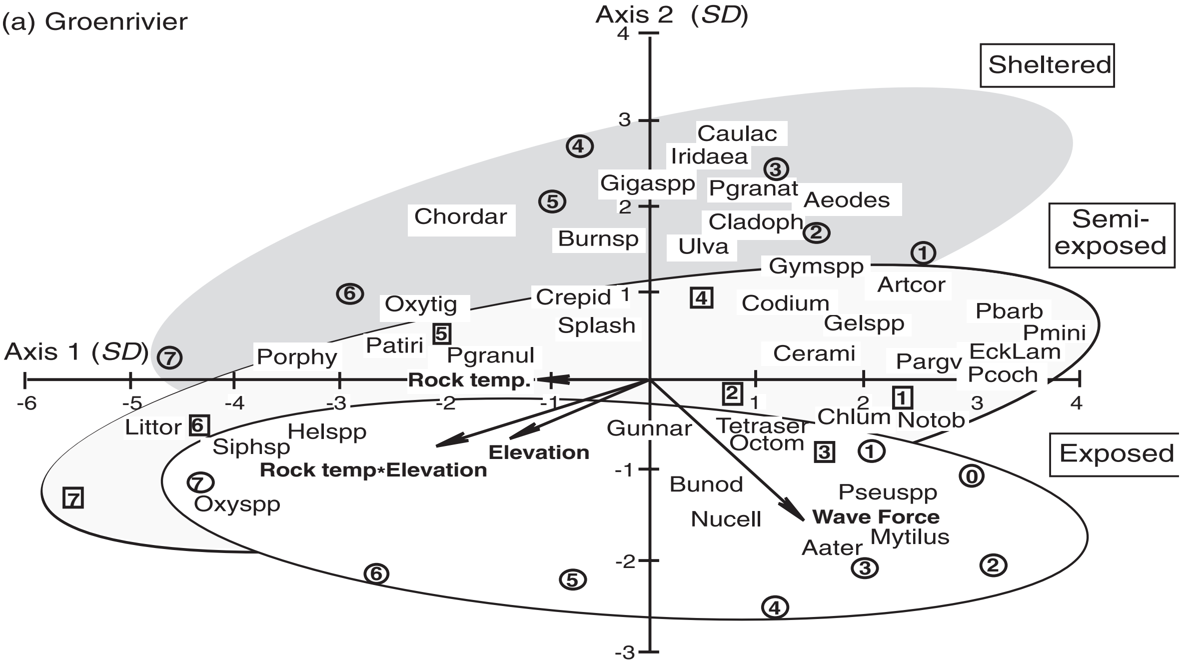
At both sites, the separation of samples along the *x*-axis clearly illustrates the vertical zonation of the community, with the low-shore samples being indicated by smaller numbers (0, 1, 2) and positioned to the right where the *x*-axis is positive, whereas the larger numbers (5, 6, 7), indicating the high-shore samples, are placed to the left where the *x*-axis is negative (Fig. 8). Along the *y*-axes, the samples taken within each of the different wave exposures group together, with the exposed sites at the bottom of the *y*-axis and sheltered sites at the top. The semi-exposed sites at Groenrivier occupied an intermediate position between sheltered and exposed (Fig. 8a). Therefore, the *y*-axis in both ordinations clearly indicates a gradient of wave energy.

At Groenrivier (Fig. 8a), the *x*-axis was significantly correlated with all environmental factors, the highest correlation being obtained with the interaction between elevation and rock temperature ($r = -0.812$, $p < 0.005$, Table IV). Similarly, at Port Elizabeth (Fig. 8b), the

Table IV: Weighted correlation coefficients between the environmental variables and the first 2 axes of the CCA ordination. Degrees of freedom = (Number of samples − Number of factors)−1

Environmental variable	Groenrivier (n=21)				Port Elizabeth (n=14)			
	x-axis	p	y-axis	p	x-axis	p	y-axis	p
Wave force	0.605	<0.005	−0.665	<0.001	0.502	>0.05	−0.842	<0.001
Rock temperature	−0.727	<0.005	−0.095	>0.5	−0.822	<0.001	−0.441	>0.05
Shore elevation	−0.711	<0.005	−0.504	>0.05	−0.834	<0.001	−0.398	>0.1
Rock temp. × Shore elev.	−0.812	<0.005	−0.390	>0.05	−0.888	<0.0005	−0.454	>0.05

(a) Groenrivier



(b) Port Elizabeth

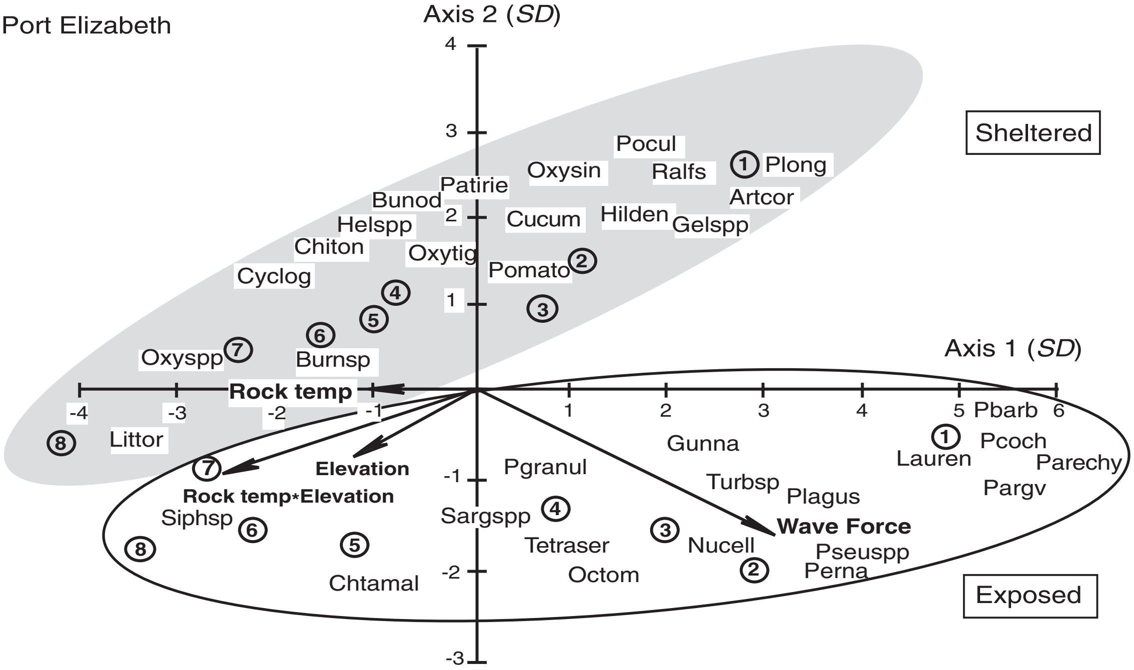


Fig. 8: Ordination diagram based on canonical correspondence analysis of the rocky intertidal communities at (a) Groenrivier and (b) Port Elizabeth with respect to three environmental variables (wave force, rock temperature and elevation). Increasing numbers indicate the sampling stations from low- to high-shore in the different communities. Arrows show the magnitude (length) and direction of the environmental vectors. Full species/taxa names corresponding to abbreviations are listed in Tables I and II

highest and most significant correlation was between the *x*-axis and the interaction of elevation and rock temperature ($r = -0.888$, $p < 0.0005$, Table IV). The *y*-axis was correlated only with maximum wave force at both Groenrivier and Port Elizabeth ($r = -0.665$, $p < 0.001$ and $r = -0.842$, $p < 0.001$ respectively, Table IV). In short, the relative magnitude (length) of the different environmental vectors (arrows in Fig. 8) indicates that maximum wave force principally, and the interaction between elevation and rock temperature (second longest vector), were the most important environmental factors in the ordination of the communities of both Groenrivier and Port Elizabeth.

In all samples taken in the high-shores of both localities, the molluscan genera *Littorina, Oxystele* and *Siphonaria* were always represented, independently of wave exposure or geographic differences (Fig. 8), indicating convergence of the species assemblages in the upper shore. Convergence is also illustrated by the close positioning of the high-shore sites (6, 7, 8) in the ordination (Fig. 8). Conversely, completely different pools of species characterized low-shore samples (0, 1, 2) experiencing different degrees of wave action. Divergence of community structure is therefore a feature of the low-shore samples, and is most obvious on the *y*-axis of the ordination and so linked to differences in wave exposure (Fig. 8). At Groenrivier, several algae are clear indicators of sheltered low-shore sites, together with the limpet *P. granatina.* At Port Elizabeth, this habitat supported a different group of algae and two other limpets, *Patella longicosta* and *P. oculus*.

Semi-exposed low-shore sites featured an assemblage of kelps and *Patella* spp., including *P. argenvillei*, which is tightly associated with growths of the kelps *Laminaria pallida* and *Ecklonia maxima* (Bustamante *et al.* 1995).

The exposed shores were clearly characterized by the presence of filter-feeders, especially the mussels *A. ater* and *M. galloprovincialis* at Groenrivier and the mussel *P. perna* and the barnacles *T. serrata* and *O. angulosa* at Port Elizabeth (Fig. 8). These species tend to be positioned near the end of the wave force vector in the ordinations.

DISCUSSION

Patterns of vertical distribution of intertidal species assemblages have been intensely studied since the early works on zonation (e.g., Stephenson 1942, Lewis 1964, 1976, Stephenson and Stephenson 1972, Moore 1975, Underwood 1978). In contrast, there is little published information on horizontal zonation patterns (Menge and Farrell 1989). In particular, the quantitative responses of intertidal communities to horizontal gradients have not been fully explored (Foster *et al.* 1988).

Southern African rocky intertidal communities show consistent patterns of both vertical and horizontal biomass over spatial scales (Figs 2, 3). Two patterns are consistent over large geographical scales. The first is that exposed shores support a much greater biomass than protected shores, a pattern previously demonstrated on the cold-temperate shores of the Cape Peninsula (McQuaid and Branch 1984). However, the "spread" of the biota from low- to high-shore indicates that the major concentration of biomass on semi-exposed and exposed sites occurs consistently between low- and mid-shore (Figs 2, 3). This contrasts with sheltered sites, where community biomass is concentrated on the low-shore. Although there is no equivalent dataset available in the literature, biomass patterns can be inferred from descriptive works (e.g. Menge and Farrell 1989) and from estimates of relative abundance or percentage coverage. The vertical patterns on exposed shores found in this study are generally comparable with those described for equivalent temperate regions in the South and North-Eastern Pacific (Santelices *et al.* 1977, Foster *et al.* 1988, Menge and Farrell 1989) and the North-Western Atlantic (Menge 1976, Lubchenco and Menge 1978), where the low-shore appears to support intermediate levels of biomass because of the dominance of a few species of encrusting algae and mobile species. There is convincing evidence that, in the low-to-mid zones of rocky shores, biological interactions (either predation or competition) have important influences on community structure, with consumers controlling the abundance of space-occupying species in the low-shore while the mid-shore level is dominated by sessile species, notably mussels and/or barnacles (Paine 1971, 1974, Menge 1976). However, a different vertical distribution pattern has been described for exposed rocky shore in False Bay on the south coast of South Africa (McQuaid and Branch 1985), where large colonies of sessile filter-feeding invertebrates and understory algal turf constitute the majority of the low-shore biomass. This latter situation indicates that consumers are not effective in controlling space-occupying species. Descriptions of part of the British Isles (Lewis 1964, Newell 1979) and South Australia (Stephenson and Stephenson 1972) suggest a similar pattern. Unfortunately, there is no information about the species richness nor the degree of wave exposure of those communities, precluding a direct comparison.

Consistent vertical and horizontal patterns of the species richness were found independent of geographical location (Figs 4, 5). Many of the more recent studies of intertidal ecology have emphasized the role of scale in the maintenance and production of species diversity (e.g. Dayton 1971, Underwood and Fairweather 1985, Petraitis *et al.* 1989, Menge and Olson 1990). However, most of the comparative studies for patterns of species richness have failed to make comparison between shores with comparable abiotic environments (McGuinness 1990). Similarly, most of the studies of intertidal diversity do not include (or do not mention) species occupying secondary substrata (e.g. Foster *et al.* 1988, McGuinness 1990), leading to conclusions that are applicable only to the diversity of species occupying primary rock space. For example, the removal of mussels (space-dominant species) leads to an increase of the diversity of species using rock as a primary substratum (e.g. Harger 1972, Paine 1971, 1974, Suchanek 1978, Paine *et al.* 1985), while decreasing the diversity of the epifaunal and infaunal species associated within the mussel bed (Lohse 1993). In the present study, the consistency of the patterns of species richness is greatly strengthened by the fact that all localities were compared within equivalent physical environments (Figs. 4, 5) and all species living on secondary substrata were included.

The present findings confirm the prediction of Dayton and Tegner (1984) that many of the processes involved in the creation of patterns of species richness and biomass act and vary at a local scale (i.e. at the scale of sites within shores). Wave action impacts strongly on the low- to mid-shore community structure and causes the development of radically different assemblages on a scale of tens of metres. This effect yields comparable responses over very large geographic scales, covering thousands of kilometres and three distinct biogeographic provinces (Emanuel *et al.* 1992).

The relative importance of the determinants of the zonation patterns (vertical and horizontal) for intertidal rocky-shore communities varies with scale (Dayton and Tegner 1984, McGuinness 1990, Menge and Olson 1990). Considered in more detail here are two particular localities where differences in community structure are influenced by coastal geomorphology (headlands, boulder bays, kelp beds, etc.) and, hence, differential wave forces (Fig. 6a). The magnitude of these local differences in wave forces will certainly be greater than any that can be experienced between different geographical regions. Furthermore, the simple local effect of vertical environmental gradients (i.e. rock temperature, elevation and their interaction) on the spatial distribution of the species assemblages were consistently similar within localities and only marginally different between the disjunct geographical localities (Fig. 6b). This implies that the physiological stress imposed by tidal movements on intertidal organisms, although operating at an extremely local scale, has comparable effects over large and meso-geographical scales.

Wave action is often considered as a stressing factor that induces physical disturbance. Hence, it is expected to cause random, localized mortality (Petraitis *et al.* 1989, McGuinness 1990). However, the present findings show that there is a positive relationship between the biomass per unit area and the maximum drag force exerted by waves (Fig. 7a). This relationship agrees with results reported by Leigh *et al.* (1987) for the North-Eastern Pacific, where the sea palm *Polstelsia palmaeformis* produces extraordinary quantities of dry matter per unit area in wave-beaten sites. In summary, Leigh *et al.* (1987) conclude that wave energy enhances the production of intertidal systems. This, together with the results presented here, is an important consideration that needs to be taken into account when deciding which factors (and their respective interactions) need to be incorporated into environmental stress models for community regulation (e.g. Menge and Olson 1990).

The results of the direct gradient analysis support, with quantitative evidence, the traditional assumption that gradients of emersion and magnitude of wave force are major local determinants of rocky intertidal communities (Menge and Farrell 1989). The analyses used only three simple environmental factors and a single interaction, yet explained 65 and 74% of the variance in community biomass recorded at two disjunct geographical localities (Table III).

The first gradient in the ordination diagrams (Fig. 8) was the desiccation gradient, as indicated by the arrows representing the rock temperature, elevation and their interaction. In addition, the overall community biomass (regardless of wave exposure) was negatively correlated with rock temperature (Fig. 7b). Field and Robb (1970), using a quantitative indirect gradient analysis, showed that this vertical gradient has a major effect on the intertidal species assemblages of the rocky shores of False Bay (see Fig. 1). Although the analyses by those authors were done using different statistical techniques and sampling procedures, and on a much more limited geographical scale, their results agree with the present findings. Unfortunately, there are few equivalent multivariate community analyses for intertidal shores, the majority of such studies having been devoted to soft-bottom or subtidal ecosystems (e.g. McLachlan *et al.* 1984, Gray *et al.* 1988, Dawson-Shepherd *et al.* 1992, Van Nes and Smit 1993, Warwick and Clarke 1993). However, in all intertidal rocky shores that have been analysed in this manner, shore elevation plays an important role in explaining the vertical changes in species composition (e.g. Kaandorp 1986, Koistra *et al.* 1989, Takada and Kikuchi 1990).

The second major gradient was one of wave energy, and yielded three (Fig. 8a) or two (Fig. 8b) distinct species assemblages. The fact that sessile filter-feeders are more abundant on exposed shores (McQuaid and Branch 1984, 1985, McQuaid *et al.* 1985) was also clearly shown in this analysis. On wave-exposed shores, filter-feeders contributed >67% of the community biomass at both cold- and warm-temperate sites (Tables I, II). At Groenrivier the mussels *A. ater* and *M. galloprovincialis* and at Port Elizabeth the mussel *P. perna* and the barnacles *T. serrata* and *O. granulosa* were the dominant space-occupying species, and prevailed where wave energy was greatest. This was noticeable in the ordinations (Fig. 8) in which these species were all placed close to the end of the wave force vectors. In part, this association may be related to the fact that wave action enhances the quantity and turnover of food particles for filter-feeders (Bustamante and Branch 1996). Mussel beds provide a suitable (shelter) microhabitat for several co-occurring species that are seldom found living on the bare rock. In the ordinations, cryptic species like the nereid mussel worm *P. variegata*, the predatory whelks *Nucella* spp. and predatory anemones (e.g. *Bunodactis reynaudii*) were all placed close to the mussel species (Fig. 8). All of these species either shelter among, or feed on, mussels.

The convergence of the upper shore and the divergence of low-shore species assemblages was evident in the gradient analyses (Fig. 8). Convergence suggests that the ecological response of the upper shore communities to the constraints of this environment is in many ways similar, as has been suggested by previous studies (Stephenson and Stephenson 1972, Lubchenco *et al.* 1984, McGuinness 1990). Three molluscan genera consistently featured in high-shore samples, irrespective of their geographic situation or the degree of wave action experienced: *Littorina*, *Oxystele* and *Siphonaria*. All are known to be very tolerant of physical stresses such as high temperature, desiccation and low salinity (Broekhuysen 1940, Branch *et al.* 1990). Frequently their densities were very high, although they contributed relatively little to the biomass.

Equally evident was the consistent divergence of intertidal species assemblages in the lower shore, which can be related to differences in wave energy. For some species this has obvious explanations. Flat-bladed algae such as *Ulva*, *Aeode*s, *Gigartina* spp. and *Iridaea*, which are presumably vulnerable to wave action, occurred low on the shore only at sheltered sites. The limpet *P. granatina* (noted for its low powers of attachment) was an indicator of sheltered conditions at Groenrivier, and two other limpets, *P. longicosta* and *P. oculus* (also known to have low tenacity – see Branch and Marsh 1978), occupied sheltered shores at Port Elizabeth. Sessile filter-feeders overwhelmingly dominated exposed low- to mid-shore samples and are both strongly attached and stand to benefit from wave action because it enhances their food supply. However, for many species, these are as yet no rational explanation for the preferences for particular intensities of wave action.

In summary, the implications are that low-shore communities are determined largely by differences in wave action, whereas high-shore communities are influenced by the uniform stress of high temperature and desiccation.

In a similar study using a multivariate approach, Fuji and Nomura (1990) investigated the relationships between community structure and environmental factors (i.e. categories of wave force, height above datum and microtopography) for the rocky-shore macrobenthos of southern Hokkaido, Japan. Their analyses did not include algae. The authors' main conclusion was that community structure of the macrofauna is primarily influenced by microtopographic characteristics, whereas the effects of wave force and shore elevation were not apparent. However, their work only reflects the effects of their sampling procedure. That is, at a particular site, they sampled with different intensity (some microhabitats were under-represented) all possible distinct microhabitats, i.e. nip, bench, ledge, slope and boulders (Fuji and Nomura 1990, Table I). In their analyses, each particular microtopographic category was subjected to a broad range of wave-force categories (which were not determined by direct *in situ* measurements), so that wave force could not be used as a discriminatory environmental variable. Consequently, their conclusion that differences in microhabitat explain most of the variation in intertidal community structure, overriding the effects of other potentially important environmental factors, is a consequence of their methodology more than anything else. This case illustrates the urgent need for standardized methods of sampling and analyses of benthic communities patterns (Menge and Farrell 1989). Unfortunately, in contrast to terrestrial ecology, the use of multivariate analyses in descriptive ecology is not well established in studies of the structure and organization of marine communities.

In relation to the main objectives of this study, distinctive community structures were detected at a local scale, whose differences are strongly related to local environmental conditions. At this level of exploratory analysis, biotic interactions seem of secondary importance. Differences in community structure may result from the small-scale variation of such physical factors as tidal gradient and wave exposure (both explored in this study), and as well as other mechanical disturbances such as ice scour, river runoff, etc. (not covered here), that will "set the stage" for subsequent biological interactions between the survivors of environmental constraints (Menge and Olson 1990).

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