Biotic and abiotic influences on rocky intertidal biomass and richness in the southern Benguela region

C.D. McQuaid and G.M. Branch

Zoology Department, University of Cape Town, Rondebosch

A.A. Crowe

FitzPatrick Institute, University of Cape Town, Rondebosch

Species richness and biomass of 12 rocky shores subject to various conditions of substratum type, sea temperature regime, and degree of wave exposure around the Cape of Good Hope were analysed. Zonation and characteristic dominant species are described. Richness values were high (total of 310 species) and were influenced by substratum stability and temperature regime (being highest where the south and west coast biota overlapped) but not rock type or exposure. Richness was greatest where the biomass of either filter-feeders or macroalgae was high otherwise declining upshore. High limpet biomass in the cochlear zone resulted in low algal biomass owing to grazing and an interruption of this vertical gradient. Biomass was influenced by substratum stability and exposure, but not temperature regime. Forty-five species (of which 37 were macroalgae, cirripeds or molluscs) accounted for an average of over 92% of total biomass on each shore. Twenty-one of these favoured exposed conditions resulting in significantly higher total biomass on exposed shores. Biomass also showed an upshore decrease interrupted in the cochlear zone. Herbivore biomass was related to beach slope and was greatest on gently sloping shores. Biotic interactions, particularly grazing and competition for space, are discussed within this framework of abiotic factors.

S. Afr. J. Zool. 1985, 20: 115 – 122

Die spesierykheid en biomassa van 12 rotsstrande, blootgestel aan verskeie toestande van substratumtipe, seetemperatuurregime en golfaksie om die Kaap die Goeie Hoop, is geanaliseer. Sonering en tipiese dominante spesies word beskryf. Spesierykheidswaardes was hoog (totaal van 310 spesies) en is beïnvloed deur bodemstabiliteit en temperatuurregime (die hoogste waardes is aangetref waar die suid- en weskus-biota oorvleuel het), maar nie deur rotstipe of blootstelling nie. Rykheid was eendersyds die hoogste waar die biomassa van òf die filtreerders òf makroalge hoog was; andersyds het dit teen die strand op verminder. Hoë klipmosselbiomassa in die cochleasone het 'n lae biomassa van die alge veroorsaak, as gevolg van weiding en die onderbreking van hierdie vertikale gradiënt. Biomassa is beïnvloed deur bodemstabiliteit en blootstelling, maar nie deur die temperatuurregime nie. Vyf- en-veertig spesies (waarvan 37 makroalge, Cirripedia, of Mollusca was) het gemiddeld meer as 92% van die totale biomassa op elke kus verteenwoordig. Hiervan het 21 blootgestelde toestande verkies, wat 'n beduidend hoër totale biomassa op blootgestelde strande tot gevolg gehad het. Biomassa het ook verder teen die strand op verminder, wat in die cochleasone onderbreek is. Herbivoorbiomassa hou verband met die strandhelling, en was die hoogste op strande met lae hellings. Biotiese wisselwerking, veral weiding en kompetisie vir ruimte, word teen die agtergrond van hierdie abiotiese faktore bespreek.

S.-Afr. Tydskr. Dierk. 1985, 20: 115 – 122

C.D. McQuaid* and G.M. Branch
Zoology Department, University of Cape Town, Rondebosch, 7700
Republic of South Africa

A.A. Crowe
FitzPatrick Institute, University of Cape Town, Rondebosch, 7700
Republic of South Africa

*To whom correspondence should be addressed

The Cape of Good Hope is of particular interest to intertidal biologists as it is an area of overlap between the south and west coast intertidal biota of southern Africa (Stephenson 1944). This is primarily due to differences in sea temperature between the west and south coasts which are bounded by water bodies of very different origins and properties. A gradient of decreasing sea temperatures exists from the south to the west coasts but it is complicated by the fact that at the Cape Peninsula, False Bay forms a body of particularly warm water which interrupts this gradient. Consequently the temperature difference between the cold west coast and the warm east coast of the peninsula is accentuated and there is a rapid shift from one biota to another. Within this framework, local factors, particularly wave exposure, can have a significant influence on community structure both in terms of species presence and biomass (McQuaid & Branch 1984) and trophic structure (McQuaid & Branch 1985). In the present paper we present data on species assemblages and community structure on a series of rocky shores subject to a range of physical conditions on either coast of the Cape Peninsula and examine some of the factors which control community structure.

Methods

Twelve shores subject to various conditions of wave exposure and representing four kinds of rock substrata were selected in the Cape of Good Hope (Table 1). Six of these were on the cold west coast of the Cape Peninsula and six were in False Bay on the warm east coast (Figure 1). Three of the shores selected on each coast were exposed to heavy wave action (i.e. headlands or shores facing the predominant swell) while three were sheltered from strong wave action, being in bays or in the lee of headlands. Three main types of rock form intertidal substrata in this area. Firstly, Cape granite is the only common igneous rock, and forms large coarse-grained rounded boulders with an extremely hard rough surface. Secondly, Table Mountain sandstone, which is very stable chemically and weathers slowly. It has a small grain size and generally occurs in almost horizontal beds forming broad, gently sloping beaches. Finally, Malmesbury shale, which occurs only on the west coast, has a very small grain size and occurs in nearly vertical beds which weather into jagged parallel ridges, sloping gently to the sea. In addition, outcrops of soft unconsolidated beach rock occur along the north coast of False Bay (e.g. Strandfontein). Beach rock has a friable, crumbling nature and erodes as a complex network of small hollows and pools.

The shores examined all exhibited a high degree of both inter and intra-shore heterogeneity, each beach supporting a mosaic of species assemblages or communities (on average 10

Table 1 Physical conditions on the shores examined

Site	Abbre-viation	Temp. regime	Wave action	Sub-stratum	Species richness
Seapoint	SPT	C	E	MS	98
Robben Island	ROB	C	E	MS	90
Oudekraal B	OKB	C	E	CG	81
Oudekraal A	OKA	C	S	CG*	44
Olifantsbos	OFB	C	S	TMS	101
Kommetjie	KOM	C	S	TMS	118
Buffels Bay A	BFA	W	S	TMS	90
Buffels Bay B	BFB	W	S	TMS*	63
Froggy Pond A	FPA	W	S	CG	117
Froggy Pond B	FPB	W	E	CG	98
Dalebrook	DBK	W	E	TMS	137
Strandfontein	STR	W	E	Beach rock	88

C and W refer to cold and warm temperature regimes, E and S to exposed and sheltered conditions, MS = Malmesbury shale; CG = Cape granite; TMS = Table Mountain sandstone; * indicates unstable boulder beaches.

Figure 1 Study sites in the Cape of Good Hope. Rock types are shown as: cross hatching — Cape granite; heavy dots — Table Mountain sandstone; open circles — Malmesbury shale; solid shading — beach rock; light dots — sand. Inset shows the three biotic regions recognized by Stephenson (1944): 1 – east coast; 2 – south coast; 3 – west coast. Note transition from 2 to 3 at the Cape of Good Hope.

per shore) occupying the major zones and sub-zones. As these communities differed both in absolute size and in their contribution to overall intertidal area it was necessary to derive a mean biomass for each species on each shore as a whole. The communities on each shore were therefore mapped using aerial photographs and field observations. Initial trials using 0,01 m² quadrats indicated that cumulative samples of 0,5 m² included 90–100% of the species present in each community. Communities were therefore sampled by clearing randomly placed duplicate 0,25 m² quadrats and identifying all species present. Heavily calcified species (molluscs, barnacles, echinoids and large crustaceans) were acidized in 1 mol dm⁻³ nitric acid and all samples were then dried to constant mass at 60°C. In the case of very common species length/mass curves were derived (see Appendix) and subsequent biomass values taken from length measurements. Some large species were obviously inadequately sampled using quadrats. Data on density and biomass were therefore collected by sampling these species separately using 1 m wide belt transects of 5–10 m running parallel to the shore-line.

Results

Zonation

The generalized pattern of zonation described by Isaac (1937) and Stephenson (1944) for Cape Peninsula shores is applicable to most of the shores analysed in this paper, although sub-zones can be recognized on the basis of the dominant organisms. To supplement Stephenson's data we outline the species composition of these zones, noting the characteristic dominants.

Subtidal fringe

This is characterized by dense beds of macroalgae on sheltered shores and is generally wholly subtidal though it can blend into the lower cochlear zone. Usually a single algal species predominates though dominance can be shared. Common dominants are *Bifurcaria brassicaeformis* (both coasts), *Champia lumbricalis* (west coast), *Plocamium* spp. and *Hypnea spicifera* (False Bay). This zone often yields a very high biomass of algae and contains an extremely rich associated fauna of small crustaceans, errant polychaetes and small molluscs. Particularly important are amphipods (*Hyale* spp., *Lysianassa* spp., *Paridotea* spp., *Paramoera capensis*) and isopods (*Dynamenella* spp., *Exosphaeroma* spp., *Cymodocella* spp.).

On exposed shores dense communities of filter-feeders occur in this zone. These are dominated by the mussel *Aulacomya ater* and the barnacle *Octomeris angulosa* on the west coast and the tunicate *Pyura stolonifera* with the mussel *Perna perna* in False Bay.

Cochlear zone

This zone is completely dominated by the limpet *Patella cochlear*. Macroalgal biomass and total species richness decrease drastically in the cochlear zone although small quantities of algae such as *Aeodes orbitosa*, *Splachnidium rugosum*, *Gelidium pristoides* and *Cladophora capensis* may occur. Small coralline and encrusting algae are abundant (e.g. *Jania* spp., *Lithophyllum* spp., *Arthrocardia* spp.) and symbiotic amphipods associated with *P. cochlear* also occur.

Balanoid zone

This is usually clearly divided into lower, middle and upper components although some species (e.g. the winkle *Oxystele variegata* and *Patella granularis*) can be common over the entire balanoid. Great diversity exists in this zone and different complexes of species may be recognized as separate communities within the sub-zones.

Lower balanoid. A large variety of algae is generally present including *Gelidium pristoides, Gigartina* spp., *Plocamium* spp., *Pterisiphonia cloiophylla* and *Aeodes orbitosa*. Whelks
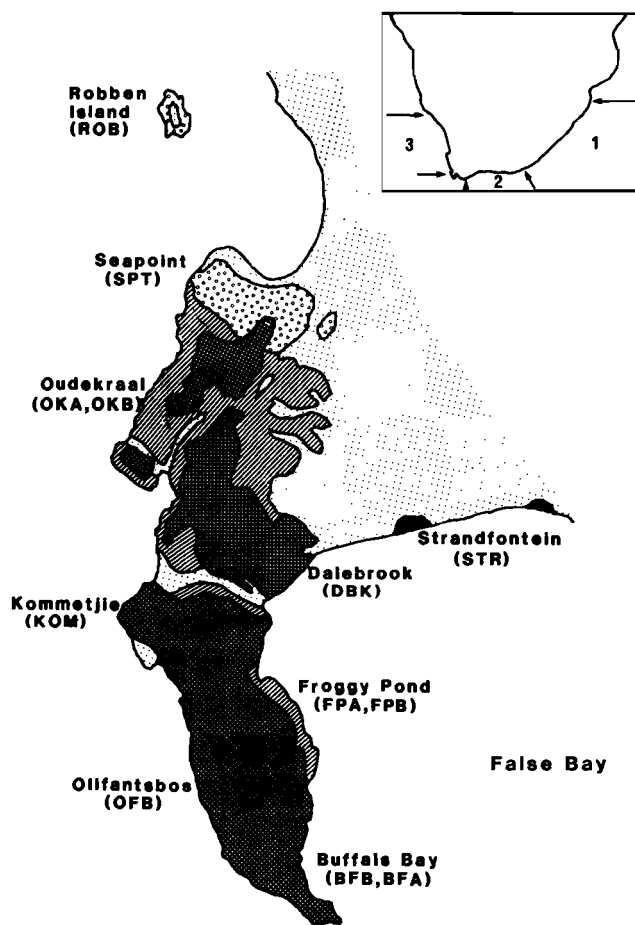
(*Burnupena* spp. and *Nucella* spp.) are abundant and large numbers of limpets characterize this zone (e.g. *Fissurella mutabilis, Patella granatina, P.granularis, P.occulus, P.longicosta*). Large colonies of sedentary polychaetes (*Gunnarea capensis* and *Pomatoleios kraussi*) sometimes occur. Barnacles are generally very sparse but *Balanus algicola* and *Octomeris angulosa* may occur.

Middle balanoid. Fewer algae are present but *Gelidium pristoides* and *Ulva* spp. are often common. Barnacles *(Octomeris angulosa* and *Tetraclita serrata)* are important, especially on exposed shores. *Nucella dubia* is usually abundant among the barnacles and the limpets *Siphonaria* spp. and *Helcion pectunculus* may be present.

Upper balanoid. The few algae present (usually only *Porphyra capensis*) are generally only seasonally abundant. Barnacles, especially *T. serrata* and *Chthalamus dentatus* tend to be abundant as do *Oxystele variegata* and *Helcion pectunculus*. *Siphonaria* spp. may dominate large areas, especially in shallow pools. Dense clumps of *P. capensis* may form separate communities containing many amphipods, usually *Hyale grandicornis* or *H. diastema*. Large numbers of chitons may be found particularly, during the day, in cryptic habitats.

Littorina zone

This represents the upper littoral fringe and is occupied almost exclusively by the winkle *Littorina africana knysnaensis* which often attains very high densities. The tiny bivalve *Kellya rubra* and the whelk *Nucella dubia* may also be present.

Pools

Pools are rare on granite beaches owing to their topography but may be common on other shores. Species richness in pools declines towards the top of the shore but generally remains higher than that of the surrounding exposed rocks. Pools can be very rich in species and are often dominated by algae. The urchin *Parechinus angulosus*, anemones such as *Pseudactinia flagelifera* and *Bunodosoma capensis* and small chitons (*Acanthochiton garnoti, Chiton nigrovirescens*) are frequently abundant. Asteroids (*Henricia ornata* and especially *Patiriella exigua*), ophiuroids, small limpets (*Helcion pruinosus, Crepidula porcellana*) and tiny winkles such as *Tricolia* spp. are also common. Other common balanoid species are frequently numerous in pools.

Species richness

Quadrat samples yielded a total of 310 species from the 12 shores examined with a maximum of 137 species from any one shore (Dalebrook, Table 1). Mean richness for different groups of shores was compared by means of *t* tests. Richness was influenced by both sea temperature regime and substratum but not by wave exposure. Although there were no significant differences when sedimentary and igneous beaches were compared, richness was lower on the two shores with a relatively unstable substratum of small boulders (Oudekraal A and Buffels Bay B) when compared with the remaining 10 shores (*t* test, $P < 0,01$). When temperature regime was considered there was no significant difference between east and west coast shores of the peninsula, but richness was significantly higher ($P < 0,05$) in the region of overlap between the west and south coast biota, defined by Stephenson (1944) as False Bay and the west coast as far as Kommetjie (Figure 1).

Species richness on each shore decreased in an upshore direction (Figure 2) probably owing to higher niche heterogeneity on the lower shore coupled with more extreme and less stable
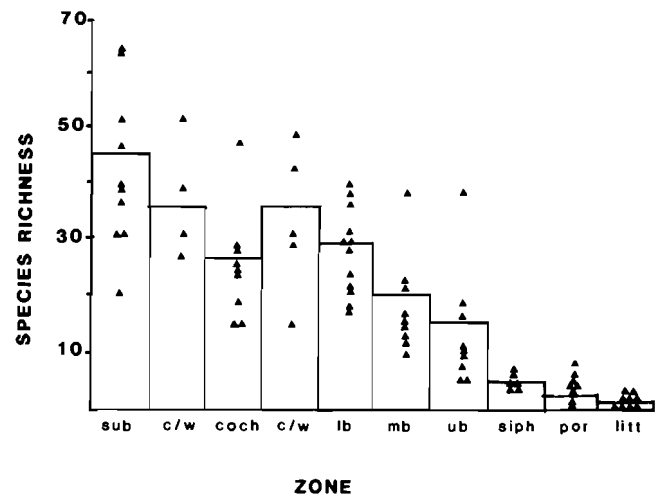

Figure 2 The relationship between species richness and height up the shore. The zones shown are from left to right (i.e. moving upshore): subtidal fringe, cochlear/weed, cochlear, cochlear/weed, lower, middle and upper balanoid, *Siphonaria* and *Porphyra* communities and *Littorina* zone. Not all zones were represented on each shore so that the number of data points given for each zone is variable. Mean values for each zone are indicated by heights of bars.

conditions at the top of the littoral zone (Newell 1979). Dense beds of algae and of filter-feeders offer many microhabitats for smaller species and are associated with high richness. This is illustrated in Figure 3 where richness is plotted against both algal and filter-feeder biomass. Richness is low where both of these are low and increases as either algal or, less clearly, as filter-feeder biomass increases. An important interruption of the vertical gradient of species richness occurs in the cochlear zone where richness is very low (Figure 2). This is associated with a severe decrease in algal biomass in this zone.

Biomass

In order to compare biomass on different shores the mean biomass of each species was calculated for each shore. Species biomass values per m^2 for each community were weighted according to the proportion the community formed of total shore area and summed to give a mean biomass for each species for the entire shore. Summation of these values for all species present provided a total mean biomass for each shore (Table 2).

McQuaid & Branch (1984) have demonstrated that over 90% of intertidal biomass on the shores described here is attributable to the 10 species exhibiting highest biomass on each shore. These species are listed in Table 2 along with the biomass ranks of the 10 most abundant on each shore, the percentage they form of total biomass and their biogeographic affinities. They include 22 species of macroalgae, 10 gastropods, four pelecypods, three cirripeds, two anthozoans and one each from the Polychaeta, Amphineura, Tunicata and Echinoidea. Of these species 10 exhibit biomass trends in response to temperature regime (Mann-Whitney U test, $P < 0,05$) and 25 show biomass trends in response to the degree of wave action (U test, $P < 0,05$; McQuaid & Branch 1984). *t* Tests were carried out to compare biomass on groups of shores with different substratum types, temperature regimes and degrees of wave exposure. Significant differences in biomass occurred in exposed/sheltered comparisons. Biomass was significantly higher under exposed conditions for filter-feeders and omnivores ($P < 0,01$) and for carnivores and total biomass ($P < 0,05$). In addition biomass of benthic carnivores
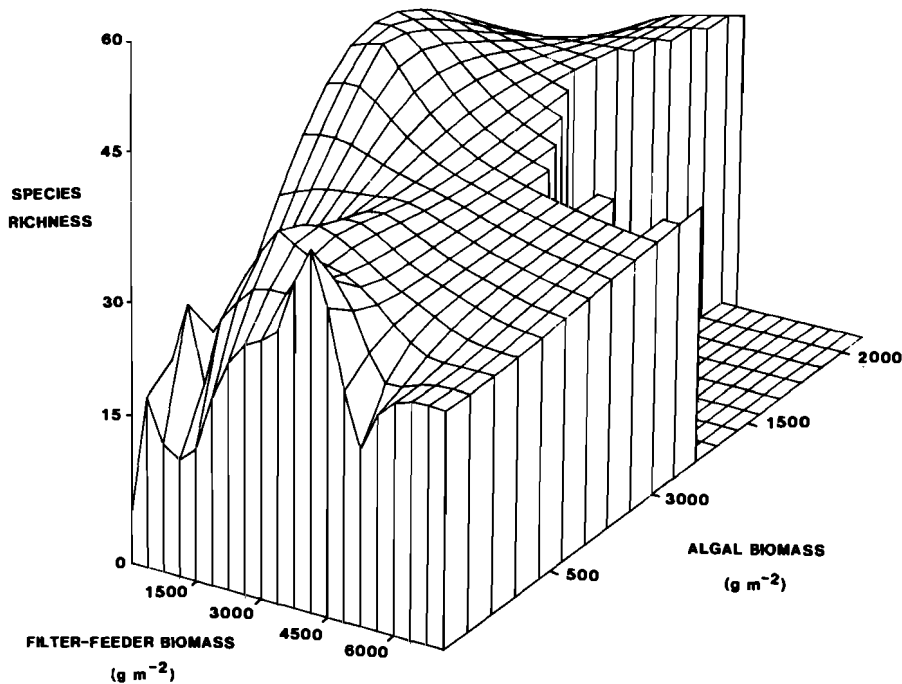
Figure 3 The relationship between species richness, filter-feeder biomass and macroalgal biomass.

was positively correlated with filter-feeder biomass (McQuaid & Branch 1985). There were no significant differences in comparisons of west/east coast shores or between shores in the region of overlap compared with the remaining west coast shores nor was biomass significantly different in igneous/sedimentary comparisons. However, as in the case of species richness, total biomass was significantly lower on the two boulder beaches, Oudekraal A and Buffels Bay B ($P < 0,01$). Substratum also has an indirect effect related to beach slope. Cape granite occurs intertidally as huge boulders and granite shores, besides lacking tidal pools, tend to be very steep. Figure 4 illustrates the relationship between beach slope and herbivore biomass which tends to be greatest on the more gently sloping shores. Buffels Bay A is composed of Table Mountain sandstone which occurs there as very large blocks so that slope is high and herbivore biomass is similar to that on the granite shores (Table 3). This effect is partly due to horizontal compression of zones as the lower zones particularly tend to be very narrow on steep shores. In addition the localized effects of wave action are more severe on near vertical faces making it more likely that mobile benthic herbivores will be displaced from the substratum.
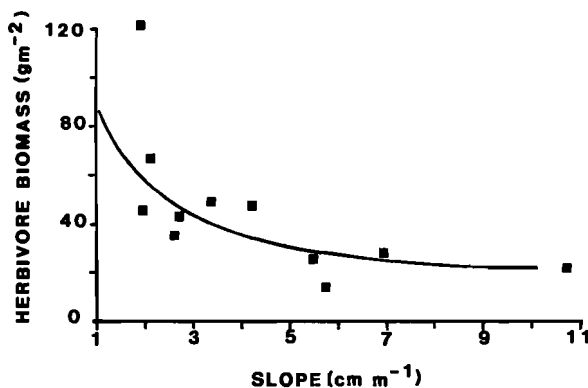
Although 49 of the species recorded were herbivores many were small animals such as amphipods etc. and the bulk of herbivore biomass (78 – 95%) was contributed by *Patella* spp. and, to a lesser extent, by pulmonate limpets (*Siphonaria* spp.) and winkles (*Oxystele* spp.). The percentage of herbivore biomass formed by *Patella* spp. was greatest on the more level shores (Table 3). While *Patella* spp. were largely excluded from Buffels Bay B owing to instability of the substratum, the more mobile *Oxystele variegata* was so abundant that overall herbivore biomass remained high. *Siphonaria* spp. were also most abundant on flatter shores and distinguishable *Siphonaria* sub-zones within the upper balanoid were found only on flat stretches of rock on such beaches.

Total biomass decreased in an upshore direction (McQuaid & Branch 1985) as did algal biomass. The vertical gradient of algal biomass was interrupted in the cochlear zone, where it fell to lower values than in the zones immediately above or below (Figure 5). This was due to grazing by the limpet
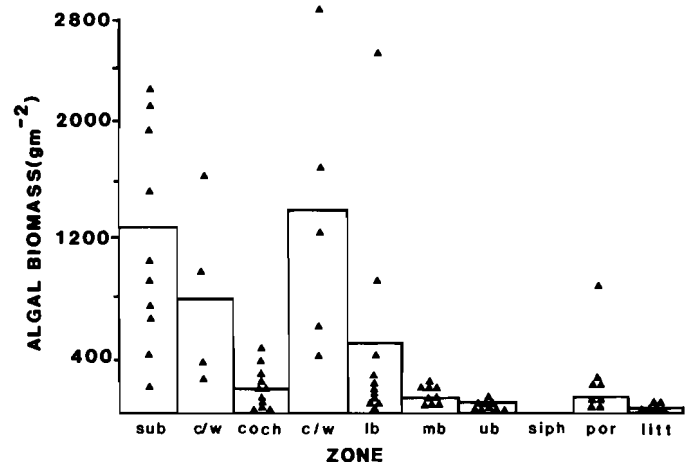

Figure 4 The relationship between mean herbivore biomass for each shore and slope of the shore (calculated as vertical height/horizontal distance). The curve is described by the equation: $y = 92,19x^{-0,65}$; $r = 0,72$.

Figure 5 The relationship between algal biomass and height up the shore. Zones abbreviated as for Figure 2.

Table 2 Biogeographic affinities of the 10 species exhibiting greatest biomass on each of the 12 shores examined. These are pooled to give a total of 45 species. Figures indicate the biomass rank of the 10 most abundant species on each shore

| Species | Cold | | | | | | Warm | | | | | | Biogeographic affinity (based on Stephenson, 1944 and present distributional records) |
| | E | E | E | S | S | S | S | S | S | E | E | E | |
	SPT	ROB	OKB	OKA	OFB	KOM	BFA	BFB	FPA	FPB	DBK	STR	
Caulerpa filiformis												3	East coast dying out in south coast
Laurencia flexuosa												7	Restricted to east and south coasts
Sargassum heterophyllum											9		
Perna perna										10			East-west coast dying out past Cape Point
Plocamium corallorhiza											10	4	
Siphonaria deflexa				6									
Acanthochiton garnoti												10	South coast passing Cape Point
Bunodosoma capensis		9	6						6				
Geldium pristoides			4			5	7		5		5	5	
Patella cochlear		3		1	4		9	10			8		
P. oculus							10	3					
Bifurcaria brassicaeformis	1	1					1	1	1	2			South-west local
Arthrocardia sp.	2			4	6		3	4	4		7		
Centroceras clavulatum				10									Ubiquitous
Jania sp.									5				
Octomeris angulosa	8	2	2				6			1	2		
Parechinus angulosus								8					
Patella barbara							8	7			2		
P. granularis	5	10	10			10						9	
Pseudonereis variegata	10	8								9			
Pyura stolonifera									9	8	1	6	
Tetraclita serrata		7	8			7	4	6	10		4	1	
Ulva sp.	3				9	9			7				
Aulacomya ater	4	4	1							4			West-south coast
Bifurcariopsis capensis							2						(i.e. 'ubiquitous' in Cape Peninsula)
Gigartina radula				8		4			3		3		
Helcion pectunculus								7					
Notomegabalanus algicola										6			
Oxystele variegata				2			5	2					
Plocamium cornutum										3			
Porphyra capensis					2	8							
Pseudactinia flagellifera								9					
Splachnidium rugosum					3								
Venerupis corrugatus											8		
Aeodes orbitosa			7	9	8	1							West coast passing Cape Point
Burnupena catarhacta	9							5					
B. papyracea								8					
Champia lumbricalis		5	3			1							
Choromytilus meridionalis	7												
Cladophora capensis			9										
Dicurella sp.				7									
Gigartina scabiosa						6							
G. stiriata	6	6	5	10	5	3			2		6		
Gymnogongrous dilatatus				3									
Patella granatina				5	7	2							
Mean total biomass (g m^{-2})	562,60	461,36	959,40	58,94	330,88	321,27	387,25	113,08	544,06	2139,87	1432,86	514,63	
% of total biomass formed by 10 most abundant species	90,97	94,91	93,51	89,05	92,72	91,02	95,79	92,78	91,57	95,35	91,99	88,92	

Table 3 Composition of herbivore biomass

Slope (cm m^{-1})		*Patella* spp.		*Siphonaria* spp.		*Oxystele* spp.		Total %	Total herb. biomass (g m^{-2})
OFB	2,00	87,52	(40,13)	5,37	(2,46)	2,68	(1,23)	95,57	45,85
STR	2,00	84,67	(103,49)	3,09	(3,78)	4,86	(5,94)	92,62	122,23
KOM	2,17	82,35	(54,45)	10,08	(6,66)	0,29	(0,19)	92,72	66,12
SPT	2,44	77,28	(28,69)	0,88	(0,33)	14,14	(5,25)	92,31	37,13
ROB	2,75	86,06	(38,54)	4,94	(2,21)	0,36	(0,16)	91,36	44,78
DBK	3,43	58,66	(28,29)	6,45	(3,11)	23,25	(11,21)	88,39	48,23
BFB	4,25	30,65	(14,34)	0	(0)	47,93	(22,42)	78,58	46,78
BFA	5,50	45,56	(13,05)	1,28	(0,37)	31,52	(9,03)	78,36	28,65
FPA	5,71	73,45	(12,63)	0,47	(0,08)	12,36	(2,12)	86,28	17,19
OKA	7,00	80,34	(24,50)	14,89	(4,54)	0	(0)	95,23	30,49
FPB	10,80	69,93	(18,64)	1,22	(0,32)	12,77	(3,40)	83,92	26,65
OKB	11,18	75,86	(24,60)	0,38	(0,12)	5,18	(1,68)	81,42	32,43

Values given below each genus are percentage of total herbivore biomass. Actual biomass values for each genus (g m^{-2}) are in parentheses. Beach slope is calculated as change in height divided by horizontal distance.

Patella cochlear which occurred in extremely high densities often forming a clearly delineated band across the shore. Low algal biomass caused by heavy grazing pressure resulted in decreased microhabitat variety and consequently a considerable reduction in species richness in this zone (Figure 2). The shore at Strandfontein, where the substratum consisted of soft, rapidly eroding beach rock, was the only shore at which not only was a clear cochlear zone absent but at which *P. cochlear* was not recorded at all. It was, however, replaced by the more rapidly growing *P. barbara* which occupied a similar level on the shore in high densities.

Discussion

Stephenson (1939, 1944, 1948) in his early work on rocky intertidal communities in South Africa has provided considerable information on biogeographic trends around the coast and recognizes three major biotic regions. These follow a temperature gradient from the sub-tropical east coast through the warm temperate south coast to the cold temperate Atlantic west coast (Figure 1). The west coast and the endemic south coast biota overlap at the Cape of Good Hope. Although the exact position of the boundary between these two has been disputed, the concept of an overlap region has been accepted by most authors (Brown & Jarman 1978), and Stephenson (1944) considered the transitional area to include False Bay, extending from Cape Agulhas to Kommetjie on the west coast. The Cape of Good Hope supports very diverse rocky intertidal systems and species richness is generally high. For example McLachlan, Lombard & Louwrens (1981) recorded 61 and 67 species from two rocky shores near Port Elizabeth (a total of 88 different species) while 310 species were recorded from 12 shores in the present study. The maximum number of species from any one shore was 137 (Dalebrook) and even the two boulder beaches with notably impoverished biota (Oudekraal A and Buffels Bay B) supported 44 and 63 species respectively (Table 1). However, richness was significantly higher in the region of overlap between the south and west coast biota as defined by Stephenson (1944).

Despite high species richness biomass is dominated by a small number of species, 10 species on each shore accounting for an average of 92,38% (±2,26%) of total biomass. When the 10 species exhibiting highest biomass on each shore are pooled they form a total of 45 different species constituting > 90% of the biomass (Table 2). Most important among these

are the macroalgae, cirripedes and molluscs (gastropods and pelecypods) which between them include 37 of these species. Community structure is influenced by a great variety of factors, both biotic and abiotic and the response of this small number of species to such factors is of key importance. During this study we have been concerned primarily with the influence of three physical factors at the community level: wave action, temperature regime and substratum.

Wave action has long been recognized as being of great significance to intertidal communities and the present study confirms its overriding importance. Wave action influences community structure in two interrelated ways. The first is that many important species exhibit biomass trends in response to the degree of wave action. Of the 45 species which dominate biomass, four exhibit significantly greater biomass under sheltered conditions and 21 under exposed conditions (McQuaid & Branch 1984). Consequently wave action has a strong influence on total biomass which is significantly greater on exposed shores. The second is that wave action also controls the trophic structure of these communities (McQuaid & Branch 1985). Omnivores, carnivores and more particularly filter-feeders all exhibit significantly higher biomass under exposed conditions and the balance in the trophic composition of total biomass shifts in response to differences in wave action. This in turn implies that exposed shores, on which filter-feeders are abundant and may contribute more to total biomass than macroalgae, function as importers of energy from the water column whereas sheltered shores, on which algae form the largest component of biomass, function as net exporters of energy. This effect operates at the trophic level rather than the species level and different species fill the trophic compartments on the two sides of the Cape Peninsula in response to differences in sea temperature. For example, among the species exhibiting greater biomass on exposed shores, there are six important filter-feeders: the bivalves *Aulacomya ater, Choromytilus meridionalis* and *Perna perna*, the barnacles *Octomeris angulosa* and *Tetraclita serrata* and the tunicate *Pyura stolonifera*. The distribution of these species is influenced by temperature effects so that while *A. ater, C. meridionalis, O. angulosa* and *T. serrata* form the bulk of filter-feeder biomass on the west coast, *A. ater, T. serrata, P. perna* and *P. stolonifera* do so in False Bay.

Sea temperature affects community composition by determining which species occur in a given area, influencing

biogeographic trends of distribution. This leads to significantly higher species richness in the region of overlap, as described, and to different species dominating biomass on the two coasts of the Peninsula. Ten of the 45 species described above also exhibit biomass trends in response to temperature regime. Despite this there is no significant difference in biomass on warm and cold water shores, reaffirming that the influence of sea temperature lies primarily in the control of which species make up this biomass.

The effects of substratum type mainly involve an impoverishment of the community where the substratum is unstable or easily eroded. Species richness was lowest at Oudekraal A and Buffels Bay B (Table 1) while Strandfontein (with a substratum of easily eroded beach rock) was the only shore where *P. cochlear* did not occur. Biomass at Oudekraal A and Buffels Bay B was also particularly low (although there was generally no correlation between richness and total biomass), especially among the sessile trophic compartments, i.e. the algae and filter-feeders. Substratum has two further indirect effects. One is the absence of tidal pools on granite shores because granite forms huge rounded boulders in the intertidal zone in the Cape of Good Hope. Tidal pools can be extensive on other shores and support a greater biomass and richness than surrounding zones as they ameliorate desiccation and heat stress, expecially on the upper shore. The second effect of substratum is the relationship between the slope of a shore and herbivore biomass (Figure 4). Although slope depends on the form of the intertidal substratum rather than its composition, the two are usually related and granite shores are generally steep. The four granite shores together with Buffels Bay A (where the sandstone forms huge blocks with vertical or near-vertical surfaces) are the five shores with lowest herbivore biomass (Table 3).

It is essential not to underestimate the influence of biotic factors when considering these systems. For example, from Figure 3 it is evident that if biomass of either macroalgae or filter-feeders is very high then biomass of the other is low, suggesting competiton between these two groups. Interactions of biotic with abiotic factors are clearly demonstrated when vertical gradients of species richness are examined. Firstly, species richness is particularly high in zones where there is a large biomass of macroalgae or filter-feeders which offer many microhabitats for small species (Figure 3) and, apart from this, it declines from the bottom to the top of the shore as physical conditions become more severe.

Secondly, a unique feature of the South African intertidal system is the mosaic of *Patella cochlear* with their algal gardens which characterizes the cochlear zone at the bottom of the shore. This offers a striking example of the influence of intensive grazing pressure on community structure. Heavy grazing in this zone leads to a sharp decrease in the biomass of all macroalgae except the encrusting forms (Figure 5). This in turn means the loss of the rich species assemblages associated with macroalgal beds and an interruption of the normal vertical gradient of richness (Figure 2). A final example of biotic and abiotic interactions is offered by the shore at Strandfontein where the substratum is particularly soft. The slow-growing *P. cochlear* is missing from this shore and is replaced by *P. barbara* which exhibits faster growth rates (Branch 1974). *P. barbara* occurs in exceptionally high densities at the same shore level that *P. cochlear* normally occupies and appears to fulfill the same function since both algal biomass and richness decrease as dramatically where *P. barbara* is abundant as on shores with a well-developed cochlear zone.

Rocky intertidal communities develop in response to a wide range of interacting influences, most obviously the effects of the daily tidal cycle of submersion and emersion which establishes basic vertical gradients of species richness and biomass. We feel that second to this the most significant abiotic influence on these communities is the degree of wave action they experience. In the southern Benguela region this is superimposed on a biogeographic transition from a warm to a cold temperate biota resulting in particularly rich communities in the area of overlap. These are dominated in terms of biomass by a small nucleus of species which respond strongly to wave action. Significant implications arise from this for fundamental patterns of trophic structure and energy flow while details of community structure are further, and often profoundly, influenced by biotic interactions, especially grazing, competition and predation.

Acknowledgements

Appendix Body size/acidized dry mass regression equations for some common intertidal species

Species	Regression equation	Coefficient of determination (r^2)
Pelecypoda		
Aulacomya ater	$y = 0,00049503x^{1,9832}$	0,96
Choromytilus meridionalis	$y = 0,0073217 6x^{0,8241}$	0,86
Perna perna	$y = 0,00260219x^{1,3402}$	0,86
Gastropoda		
Burnupena spp.	$y = 0,00000714x^{3,1940}$	0,90
Fissurella mutabilis	$y = 0,00009937x^{2,2694}$	0,80
*Oxystele sinensis	$y = 0,00114377x^{1,7681}$	0,77
*Oxystele variegata	$y = 0,00001445x^{3,5980}$	0,98
Patella barbara	$y = 0,00000689x^{3,2537}$	0,90
Patella cochlear	$y = 0,00001987x^{2,6699}$	0,88
Patella granatina	$y = 0,00831103x^{1,2483}$	0,67
Patella granularis	$y = 0,00012590x^{2,2035}$	0,92
Patella longicosta	$y = 0,00012851x^{2,0898}$	0,87
Patella oculus	$y = 0,00038411x^{2,0868}$	0,98
Siphonaria aspera	$y = 0,00005673x^{2,6378}$	0,69
Siphonaria capensis	$y = 0,00044894x^{1,7400}$	0,74
Siphonaria deflexa	$y = 0,00010551x^{2,2344}$	0,89
Nucella dubia	$y = 0,0194531x^{1,7181}$	0,92
Echinoidea		
*Parechinus angulosus	$y = 0,00041724x^{2,2479}$	0,95

Mean acidized dry mass for 3 samples of 100 individuals:
Eatoniella nigra   0,0081 g
Kellya rubra   0,01246 g

y = acidized dry mass; x = maximum length or, for species marked with *, maximum diameter.

References

BRANCH, G.M. 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 3. Growth rates. *Trans Roy. Soc. S. Afr.* 41: 161–193.

BROWN, A.C. & JARMAN, N. 1978. Coastal marine habitats. In: Biogeography and ecology of Southern Africa. (Ed.) Werger, M.J.A. Junk, The Hague. pp. 1239–1277.

ISAAC, W.E. 1937. Studies of South African seaweed vegetation

1. West coast from Lamberts Bay to the Cape of Good Hope. *Trans Roy. Soc. S. Afr.* 25: 116 – 151.

McLACHLAN, A., LOMBARD, H.W. & LOUWRENS, S. 1981. Trophic structure and biomass distribution on two East Cape rocky shores. *S. Afr. J. Zool.* 16: 85 – 89.

McQUAID, C.D. & BRANCH, G.M. 1984. The influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Mar. Ecol. Prog. Ser.* 19: 145 – 151.

McQUAID, C.D. & BRANCH, G.M. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Mar. Ecol. Prog. Ser.* 22: 153 – 161.

NEWELL, R.C. 1979. Biology of intertidal animals. 3rd edn. Logos Press, London. 781pp.

STEPHENSON, T.A. 1939. The constitution of the intertidal fauna and flora of South Africa. *J. Linn. Soc. Lond. (Zool).* 50: 487 – 536.

STEPHENESON, T.A. 1944. The constitution of the intertidal fauna and flora of South Africa. Part 2. *Ann. Natal Mus.* 10: 261 – 358.

STEPHENSON, T.A. 1948. The constitution of the intertidal fauna and flora of South Africa. Part 3. *Ann. Natal Mus.* 11: 207 – 325.