Offprint Botanica Marina Vol. 43, 2000, pp. 359–366

Subtidal Understorey Algal Community Structure in Kelp Beds around the Cape Peninsula (Western Cape, South Africa)

F. Leliaert[a] *, R. J. Anderson[b], J. J. Bolton[c] and E. Coppejans[a]

[a] University of Ghent, Department of Biology, Laboratory of Botany, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium
[b] Seaweed Unit, Marine and Coastal Management, Private Bag X2, Roggebaai 8012, Cape Town, South Africa
[c] University of Cape Town, Department of Botany, Rondebosch 7700, South Africa

* Corresponding author

The subtidal understorey seaweed communities were studied along a coastal distance of 104 km around the Cape Peninsula, which is situated in an overlap region between two marine provinces and characterized by a considerable temperature gradient. Sampling was carried out at six sites (4 to 10 quadrats per site) around the Cape Peninsula. For each of the quadrats, biomass of each species, grazing, and environmental variables such as temperature, wave exposure and sand cover were determined. The data were analysed using canonical correspondence analysis (CCA) and two way indicator species analysis (TWINSPAN). A total of 142 seaweed taxa were found at the six sites (21 Chlorophyta, 14 Phaeophyta and 107 Rhodophyta). The two sides of the Peninsula have a very different biomass-composition of Chlorophyta, Phaeophyta and Rhodophyta. The biomass of Rhodophyta in the Atlantic sites is much higher than in the Bay, and the biomass of Chlorophyta is higher in False Bay than on the west coast. A change in floristic composition of subtidal algal communities around the Cape Peninsula can be observed and is principally related to seawater temperature and wave exposure. Next to these physical factors, grazing is demonstrated to be important in determining species composition. A lower degree of wave exposure might result in a higher number of grazers in False Bay. The occurrence of a higher cover of encrusting corallines in the Bay is probably a consequence of the higher grazing pressure. Distinct community types can be recognized from TWINSPAN and CCA.

Introduction

The Cape Peninsula is situated in an overlap region between the Benguela Marine Province and the Agulhas Province (South African west and south coasts respectively). This overlap is a region of rapid temperature change where species from both provinces co-occur, and has been designated the 'Western Overlap' in the literature (Bolton and Anderson 1997). The intertidal seaweed communities in this overlap region tend to show affinities with the Benguela rather than the Agulhas region, with the exception of those in the warmer regions of the partially enclosed False Bay (Fig. 1) which are similar to geographically distant sites with warmer seawater temperature regimes (e.g. Kalk Bay) (Bolton and Anderson 1990).

There have been few studies worldwide of subtidal algal communities in relation to environmental factors. Most of the studies show that wave exposure (sometimes in relation to sedimentation) is the most important factor determining the community structure in space (Shepherd and Womersley 1970, Anderson and Stegenga 1989, Hily *et al.* 1992, Santos 1993, Airoldi *et al.* 1995, Schiel *et al.* 1995, Airoldi and Cinelli 1997, Gorostiaga *et al.* 1998). Other important environmental factors can be light in relation to depth (Shepherd and Womersley 1970, Coppejans 1980), or in relation to turbidity (Hily *et al.* 1992), and substrate slope (Santos 1993). Other studies showed little spatial variation in subtidal communities when compared to intertidal ones (Neto and Tittley 1995). Nam *et al.* (1996) found that seasonal variation of community structure (intertidal and subtidal) is primarily affected by water temperature.

Little is known on the floristics of subtidal algal communities in South Africa. Anderson and Stegenga (1989) studied subtidal algal communities at Bird Island (Eastern Cape). Jackelman (1996) studied the structure and dynamics of the algal understorey in a kelp community at Cape Hangklip (Western Cape). It was found that the two major environmental factors explaining the broad patterns of compositional variation of the subtidal seaweeds were depth and sand cover, while biotic factors such as grazing and competition for light and space, and abiotic factors such as aspect of substrata, were more important at a smaller temporal and spatial scale. Bolton *et al.* (1991) discussed the floristic aspects of the seaweeds of False Bay. A well-documented flora exists for the marine algae of the west coast of South Africa (Stegenga *et al.* 1997); this facilitates identification and gives the opportunity for floristic and ecological studies. The authorities for all the seaweeds mentioned here are in that publication.

The Benguela Province and the Western Overlap are characterized by kelp beds wherever there are

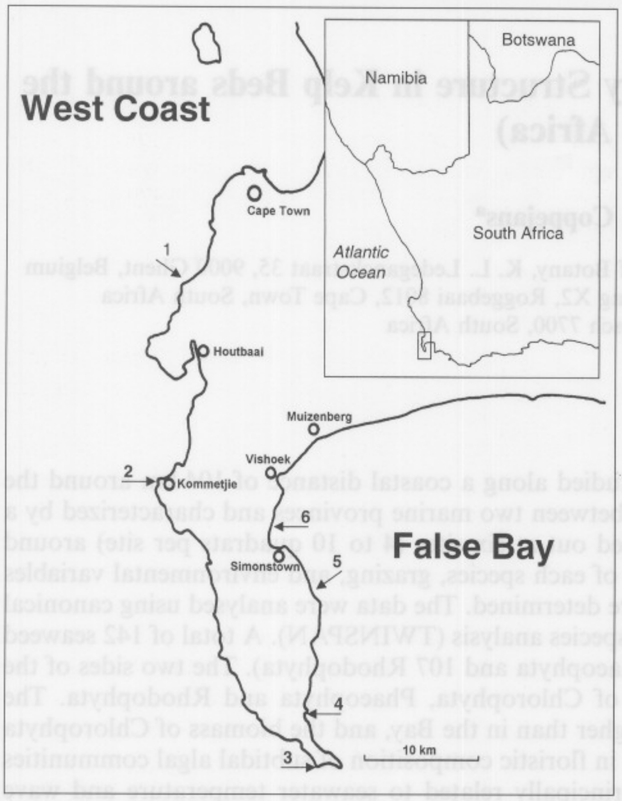

Fig. 1. Study area. Location of the six sites around the Cape Peninsula (South Africa). 1: Oudekraal, 2: Kommetjie, 3: Cape of Good Hope, 4: Bordjiesrif, 5: Spaniard Rock, 6: Glencairn.

rocky substrata in the shallow subtidal. In the southern Benguela Province (and Western Overlap), *Ecklonia maxima* forms extensive beds to depths of around 8 m (Field *et al.* 1980); *Laminaria pallida* is, mainly on the west coast, dominant from 8 to 14 m (occurring to 20 m).

There is a strong seawater temperature gradient around the Cape Peninsula. Annual means differ more than 4 °C over a coastal distance of 104 km [temperature records for Oudekraal (Atlantic Ocean) and Muizenberg (False Bay) of 1995–1996] (Table I). Besides the strong temperature gradient, the Cape Peninsula is biogeographically interesting on account of its high species diversity. Approximately two-thirds of the species of the west coast (from Cape Agulhas to the Orange River) occur in False Bay (Bolton *et al.* 1991). The most likely reasons for this are the high habitat variability in False Bay, in particular the varied temperature regime and the fact that the Cape Peninsula and False Bay lie in the overlap between two different marine biogeographic regions, with very different seaweed floras.

It has been shown that individual seaweed species distributions over a biogeographic scale are overwhelmingly limited by seawater temperature regimes (Breeman 1988). Bolton and Anderson (1990) demonstrated a gradient of intertidal seaweed communities which follows closely the gradient of temperature change around the coastline from Lamberts Bay (west coast) to Potberg (south coast). McQuaid and Branch (1984) found that the major environmental factor controlling the structure of intertidal communities (faunal and floral) around the Cape Peninsula is wave exposure, while seawater temperature selects the framework of the species present. We investigated the hypothesis that there is a change in floristic composition (community gradient) of subtidal algal communities around the short distance of the Peninsula, which is related to seawater temperature.

Materials and Methods

Study site and sampling

Sampling was carried out between December 1996 and March 1997 at six sites around the Cape Peninsula: Oudekraal (8 quadrats), Kommetjie (4 quadrats) and the Cape of Good Hope (8 quadrats) on the Atlantic Ocean side, Bordjiesrif (10 quadrats), Spaniard Rock (10 quadrats) and Glencairn (9 quadrats) on the False Bay side of the Peninsula (Fig. 1). At each site kelp beds are visible from the surface and each one has a reasonable depth range (from 0 to at least 9 m). Sampling was done by divers using SCUBA. The quadrat size was 50 × 50 cm [same size as used by Anderson and Stegenga (1989) in their study of subtidal algal communities in the eastern Cape]. The quadrats were haphazardly placed, with a distance of several metres between each one, and were all located between 2 and 9 metre depth. All quadrats were situated in kelp beds but holdfasts and stipes of mature kelps were avoided (juvenile *Ecklonia maxima* plants were included). Within each quadrat the following information was recorded: depth, % algal cover, % kelp canopy, % cover of sponges, % sand inundation, % cover of encrusting corallines, % cover of the tunicate *Pyura*, number of grazers (urchins, abalones, chitons, turbinid snails) (Table II). These factors were considered as having

Table I. Measured[1]) and extrapolated[2]) temperature records (C °). Method of extrapolating temperatures of some sites explained in text.

	Average temperature of the warmest month	Annual mean temperature	Average temperature of the coldest month
Oudekraal[1])	**13.5**	**12.0**	**10.1**
Kommetjie[2])	15.3	12.9	10.6
Cape of Good Hope[2])	17.2	13.8	11.2
Bordjiesrif[1])	**17.7**	**14.1**	**11.4**
Spaniard Rock[2])	16.8	14.9	13.4
Simonstown[1])	**16.5**	**15.2**	**14.2**
Glencairn[2])	17.5	15.5	14.2
Muizenberg[1])	**19.7**	**16.3**	**14.2**

direct effect on the algal community, or as co-related biological variables possibly being indicators of state of communities (e.g. % algal cover and % coralline crusts as an indicator of grazing). Water temperature was measured continuously at Oudekraal and Bordjiesrif, using submerged electronic recorders, measuring temperature every hour (accurate to 0.5 °C), and twice daily at Simonstown and Muizenberg (Maritime Weather Office) (Table I). Temperature data from January 1995–1996 (overall mean, and means of coldest and warmest month) were plotted against the distance between sites. Temperature at the sites for which data were not available were estimated from their position on the curve. Degree of wave exposure was estimated subjectively from local knowledge of the sites and their exposure to the prevailing south-westerly swells, the values range from 1 to 6. To estimate the swell for each quadrat, the degree of wave exposure was divided by the depth at which the samples were collected (to compensate for the ameliorating effects of depth on swell), then multiplied by 10. This is not a standard procedure, but in the absence of long-term quantitative data, is considered to give a reasonable estimate of swell exposure. All attached algae (except encrusting corallines) in each quadrat were scraped from the rock and collected in fine-meshed bags. Samples were frozen for subsequent sorting in the laboratory. The seaweeds were identified according to Stegenga *et al.* (1997). Dry weight of each species was determined by oven-drying the seaweeds at 70 °C for 72 hours. Voucher specimens (pressed or slide-mounted) are deposited in the Herbarium of the University of Ghent (GENT), Belgium: herbarium numbers FL 393 – FL 549, slide numbers FL 1.1.11 – FL 6.8.17.

Data analysis

Biomass data (dry mass per quadrat) were used for all analyses. The species data set consists of 49 samples and 142 species. For the ordination the FORTRAN program CANOCO (Ter Braak 1988) was used. A canonical correspondence analysis (CCA) was used as a direct ordination method with log-normal transformed species data, and including 12 environmental variables (Table II). A two way indicator species analysis (TWINSPAN) (Hill 1979) was used as a classification method.

Results

In the 49 sample plots, a total of 142 seaweed taxa were recorded (21 Chlorophyta, 14 Phaeophyta, 107 Rhodophyta). The most prominent and typical species on the Atlantic side are the foliose red algae *Botryocarpa prolifera*, *Botryoglossum platycarpum*, *Epymenia capensis*, *E. obtusa*, *Gigartina bracteata*, *Neuroglossum binderianum*, *Pachymenia carnosa*, *Plocamium corallorhiza*, *Thamnophyllis discigera*, *T. pocockiae*, the filamentous red algae *Ceramium obsoletum*, *Polysiphonia virgata*, *Polyopes constrictus* and some turf algae. On the False Bay side the most common and typical species are the encrusting and articulated coralline rhodophytes, *Bifurcariopsis capensis*, *Caulerpa filiformis*, *C. holmesiana*, *Codium stephensiae*, *Champia compressa*, and some turf algae. Other common algae occur on both sides [e. g. *Acrosorium acrospermum*, *Ceramium planum*, *Ecklonia maxima* (juvenile plants), *Griffithsia confervoides*, *Plocamium rigidum*, *Pterosiphonia cloiophylla*, *Rhodymenia natalensis*, *Trematocarpus flabellatus*] (Table III).

At all sites Rhodophyta are more numerous than Chlorophyta and Phaeophyta (Fig. 2). Average biomass of Rhodophyta (mainly foliose) per sample in the Atlantic sites exceeds that of Chlorophyta and Phaeophyta. At Bordjiesrif, Spaniard Rock and Glencairn however, average biomass of Rhodophyta per sample is strikingly low (Fig. 2). The relatively high biomass of Chlorophyta and Phaeophyta at

Table II. Environmental variables used in multivariate analysis with mean (m) and standard deviation (s.d.) for each site. 1: Oudekraal, 2: Kommetjie, 3: Cape of Good Hope, 4: Bordjiesrif, 5: Spaniard Rock, 6: Glencairn.

		1		2		3		4		5		6	
		m	s.d	m	s.d	m	s.d	m	s.d	m	s.d	m	s.d
TMPW	mean temperature of warmest month (°C)	see Table I.											
TMPA	average year temperature (°C)	see Table I.											
TMPC	mean temperature of coldest month (°C)	see Table I.											
ALGC	% algal cover	57	28	73	29	74	15	34	17	73	15	57	19
SPNG	% sponge cover	4	5	0	0	28	32	4	5	2	2	1	3
SAND	% sand inundation	31	26	0	0	2	2	13	17	17	30	23	14
ENCR	% encrusted corallines cover	4	7	28	13	48	30	56	27	58	33	33	25
PYUR	% Pyura cover	0	0	0	0	0	0	0	1	3	2	9	11
KELP	% Kelp canopy	49	22	31	14	35	20	72	17	40	29	22	18
SLPE	slope (0° = horizontal, 90° = vertical)	28	41	0	0	11	32	0	0	12	29	0	0
GRAZ	grazers in number of specimens	0	0	0	0	1	2	2	3	4	7	1	1
EXPS	(estimated exposure/depth) × 10	7	1	18	4	8	1	7	1	4	2	2	0

these sites is due to *Caulerpa* spp., *Codium stephensiae* (Chlorophyta) and *Bifurcariopsis capensis* (Phaeophyta). The occurrence of young *Ecklonia maxima* sporophytes at all sites raised the biomass value for Phaeophyta. The growth of mature *Ecklonia maxima* plants is less dense in False Bay, presumably resulting in a better development of young sporophytes. The relatively high biomass of Chlorophyta at Kommetjie was caused by large plants of *Cladophora mirabilis*, which typically grew on boulders.

The TWINSPAN classification of plots is shown in Figure 3. Indicator species at each division are indicated by an asterisk and preferential species listed below them. At the level of the first division the 'Atlantic' plots (plots from sites 1, 2, 3) are separated from the False Bay plots (plots from sites 4, 5, 6) (except plots 4.6, 5.6, 5.7). The Atlantic group (Atl) is mainly characterized by foliose red algae. The False Bay group (FB) is mainly characterized by some green algae, *Bifurcariopsis capensis* (Phaeophyta) and articulated corallines. Non-preferentials at the level of this first division are *Ceramium planum*, *Cladophora radiosa*, *Ecklonia maxima*, *Plocamium rigidum* and *Pterosiphonia cloiophylla*. The Atlantic plots are then divided into two groups. The first group (Atl-1) contains all the Oudekraal and Kommetjie plots, the second group (Atl-2) contains all the Cape of Good Hope plots and 3 False Bay plots. In the False Bay group (FB), a number of plots are separated from all the others by the presence of *Caulerpa filiformis* and absence of *Codium stephensiae* (FB-2).

These four main groups (ATL-1, ATL-2, FB-1 and FB-2) can be recognized in the canonical correspondence analysis (CCA)-diagram (Fig. 4) (eigenvalues of the first two axes: 0.76 and 0.50; species-environment correlations of first two axes: 0.97 and 0.96; montecarlo permutation test shows the first canonical axis to be significant). In order to select environmental variables for the analysis, a forward selection (option in the program CANOCO which ranks environmental variables in importance and tests the significance of the constribution of each variable) was performed. The following environmental and co-related

Table III. List of the 25 dominant subtidal understorey algae from the Cape Peninsula. Values in columns are the % of plots in which each species was found, and average biomass (g dry weight) of each species per plot (bm), at each locality.

	Oudekraal		Kommetjie		Cape of Good Hope		Bortjiesrif		Spaniard Rock		Glencairn	
	%	bm	%	bm	%	bm	%	bm	%	bm	%	bm
Chlorophyta												
Caulerpa filiformis							20	2.22			22	13.49
Caulerpa holmesiana							20	2.21	30	6.17		
Cladophora mirabilis	38	0.01	100	13.36					10	<0.01		
Codium stephensiae							40	2.19	70	32.82	67	16.97
Phaeophyta												
Anthophycus longifolius					38	9.99	10	0.02	10	2.54		
Bifurcariopsis capensis							20	1.11	60	34.61	33	18.71
Ecklonia maxima	38	0.49	25	1.72	63	14.19	80	5.96	60	5.74	44	5.15
Sargassum heterophyllum											11	4.35
Stypocaulon funiculare					13	<0.01	70	4.57				
Rhodophyta												
Aeodes orbitosa							20	1.17	20	1.49	67	4.70
Amphiroa ephedraea							30	1.72	90	0.61	89	7.95
Botryocarpa prolifera	88	5.21	100	16.27	88	1.46						
Botryoglossum platycarpum	50	0.45	100	44.03	75	8.82						
Epymenia capensis	63	3.51			63	5.03						
Epymenia obtusa	25	11.76										
Gigartina bracteata	25	6.39	75	15.56	13	8.19			10	<0.01		
Hymenena venosa	25	0.03			63	4.36						
Kallymenia agardhii	25	0.78	25	0.05	25	3.60						
Neuroglossum binderianum	13	0.03	50	1.54	100	13.20					11	<0.01
Pachymenia carnosa	25	31.97			13	11.37			10	12.69		
Pachymenia cornea					13	5.01			10	0.60		
Plocamium corallorhiza			50	2.78	100	10.50	10	<0.01	30	6.06	44	0.13
Pterosiphonia cloiophylla	38	0.03	50	0.04	75	0.46	90	2.87	60	1.01	56	0.22
Trematocarpus flabellatus	75	4.05			100	22.82	40	3.85	40	4.39		
Trematocarpus fragilis	25	1.16			38	2.82			30	5.77		

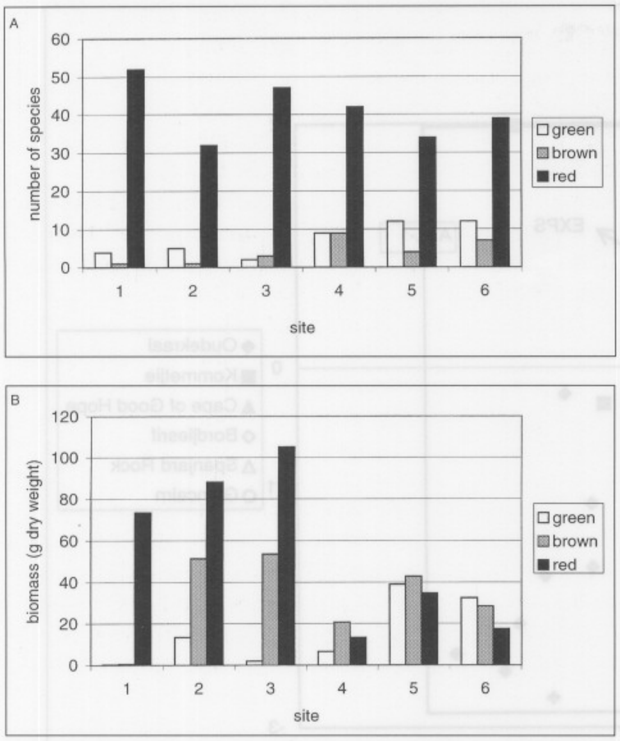

Fig. 2. A. Average number of species of Chlorophyta, Phaeophyta and Rhodophyta in the plots per site. B. Average biomass of Chlorophyta, Phaeophyta and Rhodophyta in the plots per site.

biological variables explained most of the variance: the three temperature variables, exposure, sand cover, encrusting coralline cover and algal cover; kelp canopy explained only little of the variance. Sponge cover, *Pyura* cover, slope and grazers were not significant and are not indicated in Fig. 4. Since the three temperature variables are highly correlated with each other, only one (mean temperature of warmest month) was selected for the analysis. The first axis is mainly negatively correlated with the average annual temperature, and positively correlated with exposure (depth is included in this variable). The second axis is mainly negatively correlated with the level of sand cover. Along the temperature and exposure gradients the False Bay plots (FB-1 and FB-2) cluster towards the warmer and less exposed side, while the Atlantic plots (ATL-1 and ATL-2) group towards the colder and more exposed side.

The TWINSPAN divides the Atl-1 group in two. The first group (Atl-1.1) contains plots from Oudekraal and Kommetjie, the second one (Atl-1.2) mainly contains plots from Oudekraal. These two groups cannot be clearly observed in the CCA-diagram. Here the ATL-1 cluster is separated in two groups along the sand and exposure gradient: Kommetjie plots with low sand cover and high exposure, characterized by high *Cladophora mirabilis* biomass, and Oudekraal plots with high sand cover and low exposure, characterized by *Botryocarpa prolifera*.

In the TWINSPAN the three Atl-2 plots from False Bay (Atl-2.2) are separated from the rest of this group by the absence of most foliose Rhodophyta and presence of some articulated corallines. The rest of the Atl-2 group (Atl-2.1) contains all (and only) plots from the Cape of Good Hope. Two of these plots are from vertical walls and contain typical Atlantic species such as *Trematocarpus flabellatus*, *Plocamium corallorhiza* and *Pachymenia carnosa* together with typical False Bay species such as *Ulva rigida* and articulated corallines.

The TWINSPAN divides the FB-1 group in two: FB-1.1, mainly comprising plots from Spaniard Rock and Glencairn, and FB-1.2, the latter mainly comprising plots from Bordjiesrif characterized by the presence of *Acrosorium venulosum*, *Pterosiphonia cloi-*

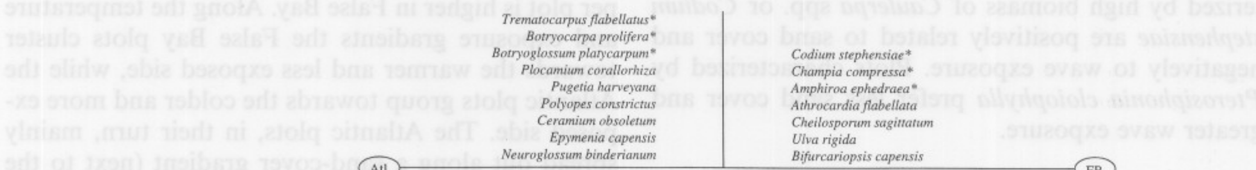

Fig. 3. TWINSPAN classification of plots. Indicator species at each division by an asterisk and preferential species are listed below them. See text for explanation.

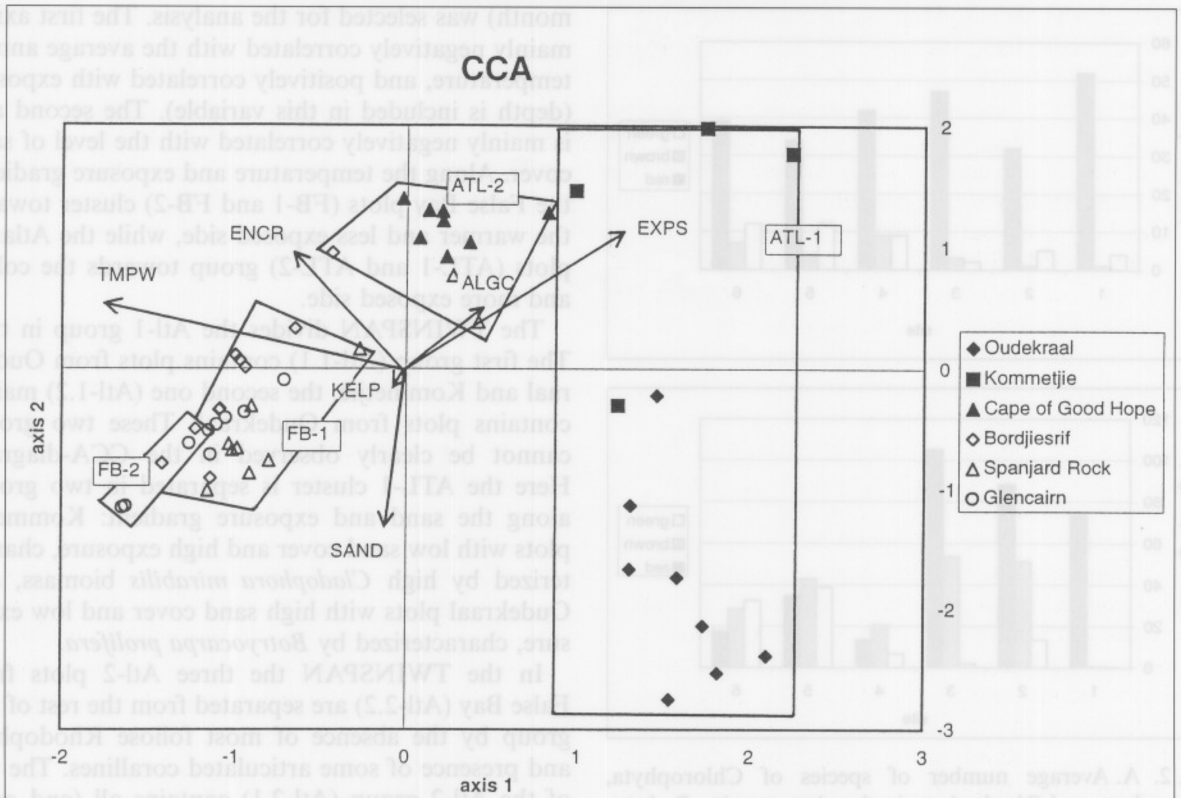

Fig. 4. Canonical correspondence analysis, biplot of quadrats and environmental variables. The four groups (ATL-1, ATL-2, FB-1 and FB-2) have been derived from the TWINSPAN classification. See text for explanation.

ophylla, and by the scarcity of *Codium stephensiae*. At the following division the plots from Spaniard Rock are separated from the rest by their presence of two *Caulerpa*-species (FB-1.1.2). The rest group (FB-1.1.1) is characterized by a high biomass of *Codium stephensiae* and articulated corallines. In the CCA, the False Bay plots tend to spread along the exposure and sand cover gradients. Plots characterized by high biomass of *Caulerpa* spp. or *Codium stephensiae* are positively related to sand cover and negatively to wave exposure. Plots characterized by *Pterosiphonia cloiophylla* prefer less sand cover and greater wave exposure.

Discussion

The number of Rhodophyta, Phaeophyta and Chlorophyta species is relatively constant at all sites, the Rhodophyta exceeding the Chlorophyta and Phaeophyta regarding average species number. However, the two sides of the Peninsula have very different biomass-proportions of Rhodophyta, Phaeophyta and Chlorophyta. On the west coast the biomass of Rhodophyta is much higher than that of Phaeophyta and Chlorophyta. In False Bay the biomass of Rhodophyta, Phaeophyta and Chlorophyta are similar. The biomass of Rhodophyta in the Atlantic sites is much higher than in the Bay, and the biomass of Chlorophyta is higher in False Bay than on the west coast.

A geographical change in floristic composition (community gradient) of subtidal algal communities around the Cape Peninsula can be observed. This change is principally related to seawater temperature and exposure. Temperatures are lower on the west coast than in False Bay. The degree of wave exposure is higher on the Atlantic side than in the Bay. A direct effect of this is that the average degree of sand cover per plot is higher in False Bay. Along the temperature and exposure gradients the False Bay plots cluster towards the warmer and less exposed side, while the Atlantic plots group towards the colder and more exposed side. The Atlantic plots, in their turn, mainly spread out along a sand-cover gradient (next to the temperature and exposure gradient).

A lower degree of wave exposure might result in a higher number of grazers in False Bay. The occurrence of a higher cover of encrusting corallines in the Bay is probably a consequence of the higher grazing pressure. The effect of grazing can be demonstrated by the plots in False Bay (4.6, 5.6 and 5.7) which have a similar species composition to some of the west coast plots. Two of these plots are from vertical walls and the other one contains a dead *Ecklonia maxima*-holdfast. Vertical walls are less accessible to grazers (especially urchins) than horizontal substrates. Here, grazer-sensitive species can establish. Similarly, the kelp holdfast in one outlier plot would have served as a possible grazer refuge, because these holdfasts have been shown to serve as grazing refuges helping the establishment of small kelp sporophytes (Anderson *et al.* 1997). These authors also showed that grazers exert less influence on subtidal seaweed communities on the west coast as compared to False Bay; results of the present study support this statement. Most shallow (2–6 m) subtidal areas of rock in False Bay have a suite of benthic grazers, including sea urchins, turbinid snails, and sometimes chitons (Anderson *et al.* 1997). It is not clear why there are more benthic grazers in the south/west coast transition zone than on the west coast, but reasons may include temperature differences, or even the reduced presence of predators such as rock lobster, which appears to be a keystone species in these kelp beds (Anderson *et al.* 1997).

Some distinct community types can be recognised. The west coast plots are characterized by *Trematocarpus flabellatus*, *Botryocarpa prolifera*, *Botryoglossum platycarpum* and some other foliose Rhodophyta. The False Bay plots are characterized by *Codium stephensiae*, *Champia compressa* and articulated corallines. From the TWINSPAN and CCA two west coast groups can be distinguished: a typical west coast group, containing the plots from Oudekraal and Kommetjie and characterized by *Botryocarpa prolifera*, and an intermediate group, containing plots from the Cape of Good Hope and the atypical False Bay plots. The intermediate floristic composition of the Cape of Good Hope plots is easily explained by the intermediate position of this site. Here, summer south easterlies often drive warm water around from False Bay, so that average water temperature is intermediate between False Bay and typical west coast sites such as Oudekraal. The False Bay plots all have a very similar floristic composition, except for some plots characterized by *Caulerpa filiformis* and the absence of *Codium stephensiae*. Our results therefore show not so much a gradient from the west coast into False Bay, but rather the presence of two relatively distinct subtidal floras with an intermediate flora at Cape of Good Hope. These results confirm the suggestion of Anderson *et al.* (1997) that there are fundamental differences between ecological processes in the south/west overlap zone and the west coast.

The present study did not examine possible seasonal differences in subtidal floristics, but diving observations over more than 10 years (R. J. Anderson, pers. comm.) suggest that these are generally slight, except for seasonal large-scale disturbances such as large swells or exceptional storms. This is also true for the patterns as they develop from year to year, certainly for the sites dealt with in this study.

Future studies could examine the reasons why subtidal communities in False Bay differ from those on the west coast. Temperature tolerance studies on all life-history stages of typical seaweeds would be useful, as well as studies examining the effect of grazers, by, for example, removing them from experimental sites.

Acknowledgements

Participation of R. J. Anderson was supported by the Director, Marine and Coastal Management. We acknowledge the University of Cape Town for the facilities. This study was supported by the international collaboration project 'Marine Biology and Nematology' (nr. ZAFR 9604-P8265).

Accepted 7 March 2000.

References

Airoldi, L. and F. Cinelli. 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a mediterranean rocky shore. *J. Exp. Mar. Biol. Ecol. 215*: 269–288.

Airoldi, L., F. Rindi and F. Cinelli. 1995. Structure, seasonal dynamics and reproductive phenology of a filamentous turf assemblage on a sediment infuenced, rocky subtidal shore. *Bot. Mar. 38*: 227–237.

Anderson, R. J. and H. Stegenga 1989. Subtidal algal communities at Bird Island, Eastern Cape, South Africa. *Bot. Mar. 32*: 299–311.

Anderson, R. J., P. Carrick, G. J. Levitt and A. Share. 1997. Holdfast of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. *Mar. Ecol. Prog. Ser. 159*: 265–273.

Bolton J. J. and R. J. Anderson. 1990. Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. *Bot. Mar. 33*: 447–457.

Bolton J. J. and R. J. Anderson. 1997. Marine vegetation. *In:* (R. M. Cowling, D. M. Richardson and S. M. Pierce, eds) *Vegetation of Southern Africa*. Cambridge University Press. pp. 348–370.

Bolton J. J., H. Stegenga and R. J. Anderson. 1991. The seaweeds of False Bay. *Trans. Roy. Soc. South Africa 47*: 605–610.

Breeman, A. M. 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgoländer Meeresuntersuchungen 42*: 199–241.

Coppejans, E. 1980. Phytosociological studies on mediterranean algal vegetation: rocky surfaces of the photophilic infralittoral zone. *In* (J. Price, D. Irvine and W. Farnham, eds). *The Shore Environment, vol. 2: Ecosystems*. Academic Press, London. pp. 371–393.

Field, J. G., C. L. Griffiths, R. J. Griffiths, N. G. Jarman, P. Zoutendyk, B. Velimirov and A. Bowes. 1980. Variation in structure and biomass of kelp communities along the west coast of South Africa. *Trans. Roy. Soc. South Africa 44*: 145–203.

Gorostiaga, A., A. Santolaria, A. Secilla and I. Diez. 1998. Subtidal benthic vegetation of the Eastern Basque Coast

(N. Spain): structure and evironmental factors. *Bot. Mar. 41*: 455–465.

Hill, M. O. 1979. *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Cornell University, Ithaca, New York. pp. 52.

Hily, C., P. Potin and J. Y. Floc'h. 1992. Structure of subtidal algal assemblages on softbottom sediments: fauna/flora interactions and role of disturbances in the Bay of Brest, France. *Mar. Ecol. Prog. Ser. 85*: 115–130.

Jackelman, J. J. 1996. Structure and dynamics of the algal understorey in a kelp community at Cape Hangklip, Western Cape, South Africa. MSc thesis Botany Department, University of Cape Town. pp. 160.

McQuaid, C. D. and G. M. Branch. 1984. 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.

Nam, K. W., Y. S. Kim, Y. H. Kim and C. H. Sohn. 1996. Benthic marine algae in the east coast of Korea: flora, distribution and community structure. *J. Korean Fish. Soc. 29*: 727–743.

Neto, A. I. and I. Tittley. 1995. Structure and zonation of algal turf communities on the Azores: a numerical approach. *Bol. Mus. Munic. Funchal* (suppl. 4): 487–504.

Santos, R. 1993. A multivariate study of biotic and abiotic relationships in a subtidal algal stand. *Mar. Ecol. Prog. Ser. 94*: 181–190.

Schiel, D. R., N. L. Andrew and M. S. Foster. 1995. The structure of subtidal algal and invertebrate assemblages at the Chatham Islands, New Zealand. *Mar. Biol. 123*: 355–367.

Shepherd, S. A. and H. B. S. Womersley. 1970. The sublittoral ecology of West Island, South Australia: 1. Environmental features and algal ecology. *Trans. Roy. Soc. Austr. 94*: 105–137.

Stegenga, H., J. J. Bolton and R. J. Anderson. 1997. *Seaweeds of the South African West Coast. Contr. Bolus Herb. 18*. 655 pp.

Ter Braak, C. 1988. *CANOCO – a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal component analysis and redundancy analysis (version 2.1)*. Wageningen. pp. 95.