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The Change in Macroalgal Assemblages through the Saldanha Bay/ Langebaan Lagoon Ecosystem (South Africa)

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Saldanha Bay and Langebaan Lagoon form together one of the few sheltered habitats within the Benguela Marine Province; a wide gradient in environmental factors is found here. The West Coast National Park was established to protect this unique ecosystem, but at the same time an industrially expanding harbour marks this area. In an effort to understand the biological composition of the Saldanha/Langebaan ecosystem, the intertidal macroalgal assemblages were studied in relation to the relatively well-known South African West Coast flora. Three distinct floral entities were identified using various analytical techniques (similarity coefficients, CCA and TWINSPAN): (i) the species poor, though distinct, salt marshes; (ii) the Lagoon sites; and (iii) the Bay and West Coast sites. The transition between the latter two is located at the mouth of the Lagoon. The species richness of the Bay/West Coast entity is larger than in the Lagoon. The change in algal composition can be explained in terms of the environmental variables of which wave exposure is the most significant. Other important environmental parameters are water surface temperature and salinity, which were found to be negatively correlated with wave exposure. Biogeographical affinities of the different algal entities of the Bay/Lagoon system were also determined in relation to the entire South African shoreline. The Bay/West Coast entity supports a typical West Coast flora, with some noticeable effects of uplift of subtidal species into the infralittoral fringe and morphological variation in less exposed areas. The algal flora of the Lagoon is also dominated by West Coast species, but is typified by species characteristic of sheltered habitats, and with a number of species which otherwise only occur on the geographically distant South Coast (east of Cape Agulhas). The algae from the salt marshes occur widely in tropical mangroves and warm temperate salt marshes.

Introduction

Along the rough South African West Coast Saldanha Bay (Fig. 1), approximately 100 km north of Cape Town, is the only sheltered inlet that can harbour an expanding port; industrial development is still increasing in this area. The Saldanha Bay/Langebaan Lagoon ecosystem (S/L ecosystem) is also an area of great biological importance. The Lagoon is the core of the West Coast National Park, safeguarding a relatively unspoiled terrestrial fynbos flora. Furthermore the park contains 32% (13 km^2) of South Africa's salt marshes (Puttick 1977, Callaghan *s.d.*) and the inner part of the Lagoon is protected by the criteria of the Ramsar Convention. Langebaan Lagoon also functions as breeding ground for many marine organisms and because of its specific environmental gradients it acts as a refuge for species not found elsewhere along the West Coast.

The Lagoon and the Bay form a complex exchange system with the ocean, which is subject to the Benguela Current. Previous sampling in the area indicated that along South Africa's West Coast certain algal species are restricted to the S/L ecosystem (Bolton and Anderson 1990, Chiang 1970, Simons 1977, Stegenga *et al*. 1997).

Simons (1977) synthesises and comments on previous phycological reports (Barton 1893, 1896, Day 1959, Isaac 1937, 1956, and U. C. T. 1955) for the S/L ecosystem. He also presents an inventory of collected algae from Saldanha Bay from his surveys in 1960 and 1976. The algal flora of Saldanha Bay was said to consist almost exclusively of eurythermal species from the cold Atlantic Coast. The only exceptions are the records of *Codium duthieae* Silva and *Sargassum incisifolium* (Turner) C. Agardh from his 1960 survey. In discussing his 1976 inventory, he notes the rich assemblage of infra-littoral and littoral algae at the channel between the Bay and the Lagoon. He typifies the Lagoon by the extensive stands of *Gracilaria gracilis* (Stackhouse) Steentoft, L. Irvine *et* Farnham.

Stegenga *et al.* (1997) describe the unusual zonation pattern of Langebaan Lagoon for the area of the West Coast: low seaweed cover in the mid- to upper-littoral zone; a belt of *Chondracanthus teedii* (Roth) Lamouroux in the lower mid-littoral; and the infralittoral dominated by *Sargassum incisifolium* and exceptionally compressed plants of *Codium duthieae*.

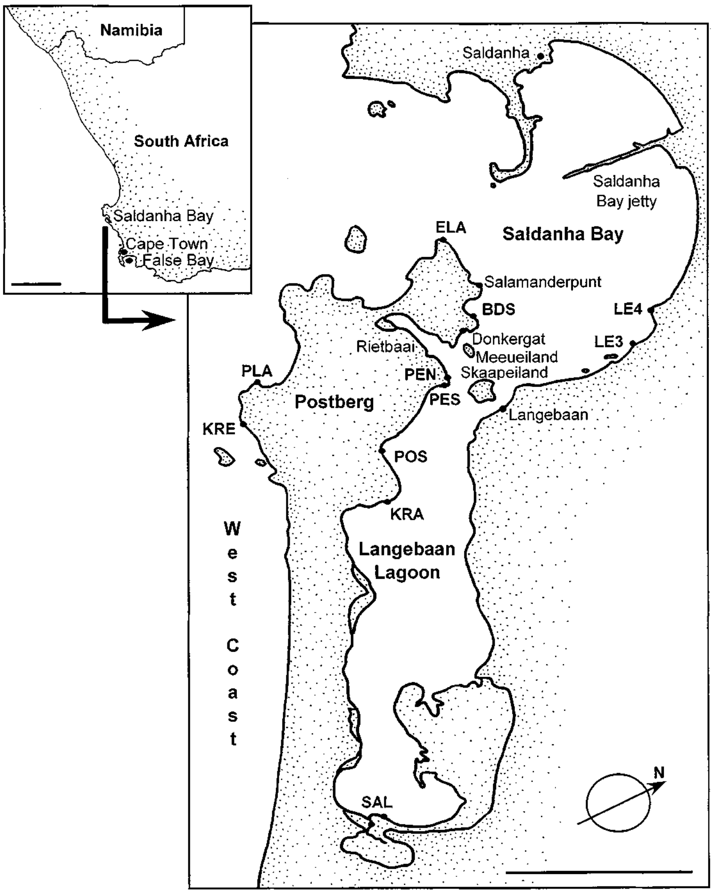

Fig. 1. Map of the Saldanha Bay/Langebaan Lagoon ecosystem with indication of sample sites: SAL, salt marshes; KRA, Kraalbaai; POS, Postberg; PES, Perlemoenpunt South; PEN, Perlemoenpunt North; LE3, Leentjesklip No. 3; LE4, Leentjesklip No. 4; BDS, Between Donkergat & Salamanderpunt; ELA, Elandspunt; PLA, Plankiesbaai; KRE, Kreeftebaai. Scale bars represent 100 km and 5 km (inset).

Furthermore they mention that most of the sheltered-habitat species along the West Coast are only recorded in the S/L ecosystem. This study aims at characterising the different macroalgal assemblages in relation to environmental parameters, and at determining the floristic relationships with adjacent regions.

Material and Methods

Sampling and identification

The sampling was undertaken between June and August 1997. Nine stations in the S/L ecosystem and two additional stations along the wave-exposed West Coast were sampled (Fig. 1): salt marshes (SAL), Kraalbaai (KRA), Postberg (POS), Perlemoenpunt South (PES), Perlemoenpunt North (PEN), Between Donkergat and Salamanderpunt (BDS), Leentjesklip No. 3 (LE3), Leentjesklip No. 4 (LE4), Elandspunt, Plankiesbaai (PLA) and Kreeftebaai (KRE). All sites (excluding the salt marshes) are characterised by a rocky substrate. Sampling took place at low spring tides. In order to approach a complete representation of the algal flora at a certain station, an area of ten meters wide from the upper mid-littoral down to the infra-littoral fringe was sampled. Crustose algae (e. g. Corallinales, Hildenbrandiales, *Ralfsia* spp.) and endophytes were excluded from the study. No sampling was performed in the deeper sub-tidal, since this zone of the Lagoon consists of sandy sediment where only two macroalgae (with their epiphytes) occur: *Sargassum incisifolium* and *Gracilaria gracilis*. The algae were preserved in a solution of 5% formaldehyde in seawater. Permanent slides were prepared by mounting algal specimens in a solution of 50% liquid glucose (corn syrup) containing a few drops of phenol. Some slides were stained with Fast Green or Lugol's solution. Voucher specimens are deposited in GENT and BOL. Authorities for the mentioned seaweeds are given in the appended species list (Table I), based on Silva *et al.* (1996) and Stegenga *et al.* (1997).

Analysis methods

As a preliminary analysis, Jaccard's similarity indices [$S_J = c(a+b+c)^{-1}$] were calculated for the 55 possible site couples. In this equation c stands for the number of shared species between the two sites, a and b represent the number of species that are unique to one of the two sites (Schaminée *et al.* 1995).

Table I. Species list. Names revised since Stegenga *et al.* (1997) are in square brackets. The numbers correspond with the numbered dots in the CCA (Fig. 3), species abbreviations are used in the TWINSPAN (Fig. 4). Species marked with an asterisk were omitted from the CCA.

1. *Aeodes orbitosa* (Suhr) Schmitz
2. *Ahnfeltiopsis complicata* (Kützing) Silva *et* DeCew
3. *Ahnfeltiopsis glomerata* (J. Agardh) Silva *et* DeCew
4. *Ahnfeltiopsis polyclada* (Kützing) Silva *et* DeCew
5. *Ahnfeltiopsis vermicularis* (C. Agardh) Silva *et* DeCew
6. *Amphiroa beauvoisii* Lamouroux
7. *Amphiroa ephedraea* (Lamarck) Decaisne
8. *Anotrichium tenue* (C. Agardh) Nägeli
9. *Aristothamnion collabens* (Rudolphi) Papenfuss
10. *Arthrocardia filicula* (Lamarck) Johansen
11. *Arthrocardia flabellata* (Kützing) Manza
12. *Bifurcaria brassicaeformis* (Kützing) Barton
13. *Bifurcariopsis capensis* (Areschoug) Papenfuss
14. *Blidingia marginata* (J. Agardh) Dangeard
15. *Botryocarpa prolifera* Greville
16. *Bryopsis africana* Areschoug
17. *Bryopsis hypnoides* Lamouroux
18. *Bryopsis plumosa* (Hudson) C. Agardh
19. *Carpoblepharis flaccida* (C. Agardh) Kützing
20. *Caulacanthus ustulatus* (Turner) Kützing
21. *Centroceras clavulatum* (C. Agardh) Montagne
22. *Ceramium arenarium* Simons
23. *Ceramium atrorubescens* Kylin
24. *Ceramium capense* Kützing
25. *Ceramium dawsonii* Joly
26. *Ceramium obsoletum* C. Agardh
27. *Ceramium papenfussianum* Simons
28. *Ceramium planum* Kützing
29. *Ceramium* sp.
30. *Champia compressa* Harvey
31. *Champia lumbricalis* (Linnaeus) Desveaux
32. *Cheilosporum sagittatum* (Lamouroux) Areschoug
33. *Chondria capensis* (Harvey) Falkenberg
34. *Chordariopsis capensis* (C. Agardh) Kylin
35. *Chylocladia capensis* Harvey
36. *Cladophora capensis* (C. Agardh) De Toni
37. *Cladophora contexta* Levring
38. *Cladophora flagelliformis* (Suhr) Kützing
39. *Cladophora isaacii* Simons
40. *Cladophora radiosa* (Suhr) Kützing
41. *Cladophora sericea* (Hudson) Kützing
42. *Codium duthieae* Silva
43. *Codium extricatum* Silva
44. *Codium fragile* (Suringar) Hariot
45. *Codium stephensiae* Dickinson
46. *Colpomenia sinuosa* (Mertens *ex* Roth) Derbès *et* Solier
47. *Corallina officinalis* Linnaeus
48. *Delesseria papenfussii* Wynne
49. *Desmarestia firma* (C. Agardh) Skottsberg
50. *Dictyota liturata* J. Agardh
51. *Ecklonia maxima* (Osbeck) Papenfuss
52. *Ectocarpus siliculosus* (Dillwyn) Lyngbye
53. *Enteromorpha* sp.
54. *Epymenia obtusa* (Greville) Kützing
55. *Gelidium pristoides* (Turner) Kützing
56. *Gelidium pteridifolium* Norris, Hommersand *et* Fredericq
57. *Gigartina bracteata* (S. G. Gmelin) Setchell *et* Gardner
58. *Gigartina pistillata* (S. G. Gmelin) Stackhouse
59. *Gigartina radula* (Esper) J. Agardh
 [*Gigartina polycarpa* (Kützing) Setchell *et* Gardner]
60. *Gigartina scutellata* (Hering) Simons
 [*Sarcothalia scutellata* (Hering) Leister]
61. *Gigartina stiriata* (Turner) J. Agardh
 [*Sarcothalia stiriata* (Turner) Leister]
62. *Gigartina teedii* (Roth) Lamouroux
 [*Chondracanthus teedii* (Roth) Kützing]
63. *Gracilaria/Gracilariopsis* sp.
64. *Grateloupia doryphora* (Montagne) Howe
65. *Grateloupia filicina* (Lamouroux) C. Agardh
66. *Griffithsia confervoides* Suhr
67. *Gymnogongrus dilatatus* (Turner) J. Agardh
68. *Heringia mirabilis* (C. Agardh) J. Agardh
69. *Herposiphonia heringii* (Harvey) Falkenberg
70. *Herposiphonia prorepens* (Harvey) Schmitz
71. *Hincksia granulosa* (Smith) Silva
72. *Hymenena venosa* (Linnaeus) Kylin
73. *Hypnea musciformis* (Wulfen) Lamouroux
74. *Hypnea rosea* Papenfuss
75. *Hypnea spicifera* (Suhr) Harvey
76. *Iridaea capensis* J. Agardh
 [*Mazzaella capensis* (J. Agardh) Fredericq]
77. *Jania crassa* Lamouroux
78. *Kallymenia agardhii* R. E. Norris
79. *Kallymenia schizophylla* J. Agardh
80. *Laminaria pallida* Greville
81. *Laurencia glomerata* Kützing
82. *Lomentaria diffusa* Stegenga, Bolton *et* Anderson
83. *Myriogramme livida* (Hooker *et* Harvey) Kylin
84. *Myriogramme* sp.
85. *Neuroglossum binderianum* Kützing
86. *Nothogenia erinacea* (Turner) Parkinson
87. *Nothogenia ovalis* (Suhr) Parkinson
88. *Pachymenia carnosa* (J. Agardh) J. Agardh
89. *Pachymenia cornea* (Kützing) Chiang
90. *Petalonia fascia* (O. F. Müller) Kuntze
91. *Phyllymenia belangeri* (Bory) Setchell *et* Gardner
92. *Pleonosporium harveyanum* (J. Agardh) De Toni
93. *Plocamium cornutum* (Turner) Harvey
94. *Plocamium maxillosum* (Poiret) Lamouroux
95. *Plocamium rigidum* Bory
96. *Polyopes constrictus* (Turner) J. Agardh
97. *Polysiphonia incompta* Harvey
98. *Polysiphonia kowiensis* Stegenga, Bolton *et* Anderson
99. *Polysiphonia namibiensis* Stegenga *et* Engledow
100. *Polysiphonia urbana* Harvey
101. *Polysiphonia virgata* (C. Agardh) Sprengel
102. *Porphyra capensis* Kützing
103. *Porphyra saldanhae* Stegenga, Bolton *et* Anderson
104. *Porphyra* sp.
105. *Pterosiphonia cloiophylla* (C. Agardh) Falkenberg
106. *Pterosiphonia spinifera* (Kützing) R. E. Norris *et* Aken
107. *Pugetia harveyana* (J. Agardh) R. E. Norris
108. *Sargassum heterophyllum* (Turner) C. Agardh
 [*Sargassum incisifolium* (Turner) C. Agardh]
109. *Schizymenia obovata* (J. Agardh) J. Agardh
110. *Splachnidium rugosum* (Linnaeus) Greville
111. *Streblocladia camptoclada* (Montagne) Falkenberg
112. *Suhria vittata* (Linnaeus) J. Agardh
113. *Trematocarpus flabellatus* (J. Agardh) De Toni
114. *Trematocarpus fragilis* (C. Agardh) De Toni
115. *Ulva* sp.

* *Bostrychia moritziana* (Sonder *ex* Kützing) J. Agardh
* *Bostrychia scorpioides* (Hudson) Montagne *ex* Kützing
* *Callithamnion hookeri* (Dillwyn) S. F. Gray
* *Caloglossa leprieurii* (Montagne) G. Martens
* *Enteromorpha compressa* (Linnaeus) Nees
* *Enteromorpha intestinalis* (Linnaeus) Nees
* *Enteromorpha linza* (Linnaeus) J. Agardh
* *Enteromorpha prolifera* (O. F. Müller) J. Agardh
* *Gracilaria gracilis* (Stackhouse) Steentoft, L. Irvine *et* Farnham
* *Gracilariopsis lemaneiformis* (Bory) Dawson, Acleto *et* Foldvik
* *Platyclinia* sp.
* *Ralfsia verrucosa* (Areschoug) Areschoug
* *Rhizoclonium riparium* (Roth) Harvey
* *Ulva fasciata* Delile
* *Ulva lactuca* Linnaeus
* *Ulva rhacodes* (Holmes) Papenfuss
* *Ulva rigida* C. Agardh
* *Ulva capensis* Areschoug
 [*Ulva uncialis* (Kützing) Montagne]

These authors mention that shared species are emphasised in Sørensen's similarity index [$S_S = 2c(a+b+2c)^{-1}$]. In order to exclude the decline in species richness through the system as the determinant factor, another similarity index was constructed [$S = ca^{-1}$], where a is the species number unique to the species-poorest site of the couple. After calculating these similarity indices no difference was noticed in the resulting similarity pattern. In the following treatment the regression line of the Jaccard's indices of each site was drawn.

Temperature, salinity and wave exposure data were obtained from Shannon and Stander (1977) and Flemming (1977). Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were performed with CANOCO (Ter Braak 1988). A two way indicator species analysis (TWINSPAN, Hill 1979) was used as a classification method. The species numbers used in the ordination are listed in Table I, the abbreviations used in the TWINSPAN can be deduced from this list by taking the first three letters of the generic name and the species epithet.

In order to determine the floristic affinities, the species compositions of the different sites were compared with various areas of the South African coastline. A database compiled by Bolton and Stegenga (2001) divides the South African coastline in 58 coastal blocks, each 50 km in length, and is used as a reference for the occurrence and distribution of the algae. The coastal blocks are numbered consecutively, starting from the Namibian border (block 1), following the coastline eastward to the Mozambican border (block 58). Coastal block 13 represents the S/L ecosystem. The biogeographical affinity of a sampling site is examined by calculating the percentage of species of that site being recorded for a specific coastal block.

Results

Floristics

A total of 130 seaweed taxa were collected. The Lagoon, the Bay and the West Coast sites show a rather constant species number. The West Coast sites, Kreeftebaai (KRE) and Plankiesbaai (PLA), are the most diverse areas. Towards the more sheltered sites the species richness declines slightly (Table II). Perlemoenpunt North (PEN) and Perlemoenpunt South

Table II. Species richness of the 11 sites.

Sampling site	KRE	PLA	ELA	LE4	BDS	LE3	PEN	PES	POS	KRA	SAL
No. of species	51	44	49	46	46	39	27	58	37	39	9

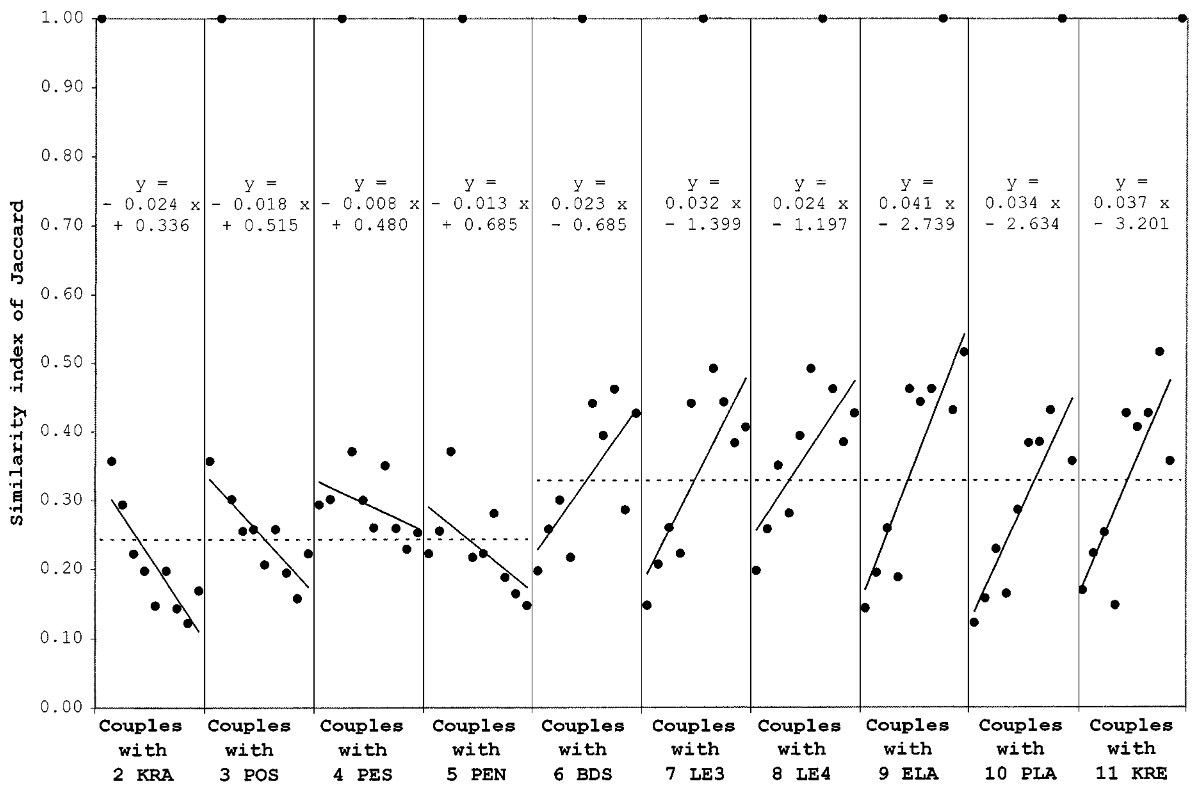

Fig. 2. The similarity of the site couples (Jaccard's similarity index; dots), the regression lines of all the similarity couples of one site (solid lines), and the mean similarity of the 2 entities (dashed lines). The salt marshes are not incorporated.

(PES) do not follow this decrease in the geographical series. There is no direct explanation for the lower species number at Perlemoenpunt North. Perlemoenpunt South on the contrary, is a markedly species rich area. A sudden decline in the species number is observed in the salt marshes (SAL), situated at the innermost end of Langebaan Lagoon.

At Postberg, large *Codium* clumps and dense *Enteromorpha* and *Ulva* stands were typical indicators of the greening effect, i. e. a dominance of early successional or opportunistic algae (e. g. certain Chlorophyta) with high capacities for growth and reproduction (Murray and Littler 1978). Furthermore *Colpomenia sinuosa*, another proliferating alga in eutrophicated areas (Simons 1977), was abundant with unusually large specimens (up to 17 cm in diameter). A small holiday village at Postberg seems to be the source of a seasonal nutrient influx (sewage).

Similarities (S_J) between the different sites are calculated. A first observation is the low mean species similarity of 1.8 % between the salt marshes (entity 1, excluded from further similarity calculations) and the other sites, while the other sites have a mean similarity of 26.7 %. The higher similarity index illustrates the penetration of typical West Coast algae throughout the S/L ecosystem. Figure 2 shows that the remaining sample sites can be divided into a Lagoon entity (KRA, POS, PES, PEN) and a Bay/West Coast entity (LE3, BDS, LE4, ELA, PLA, KRE) due to the turnover from a negative to a positive regression coefficient and a corresponding change in the mean similarity of the two entities (24.3 % and 32.9 %, respectively). The Bay/West Coast entity harbours 99 algal species, the Lagoon entity 86 and the salt marshes 9.

Ordination

Preliminary ordinations showed that the salt marshes were too different in their species composition (species poor and a low species similarity with the other sites of the system) to include them in the ordinations. The overall structure of the DCA is similar to the CCA, which incorporates environmental parameters. This is reflected in the extremely high species-environment correlations (0.99 for both axes). Therefore only the CCA will be discussed (Fig. 3; eigenvalues of the first two axes: 0.39 and 0.22), more details in Schils (1998). The wave exposure is the most important environmental parameter and is negatively correlated with the other three environmental variables (the surface temperature in July and January, and the salinity in January). The species, which are plotted near the centre of the graphs, are the typical West Coast algae that are prominently present throughout the system. A clear distinction is shown between the Bay/West Coast sites versus the Lagoon sites. West Coast sites (ELA, PLA, KRE) are positively correlated to wave exposure and negatively to salinity and temperature. The Lagoon sites (KRA, POS, PES, PEN) are positively correlated with salinity and temperature and negatively with wave exposure.

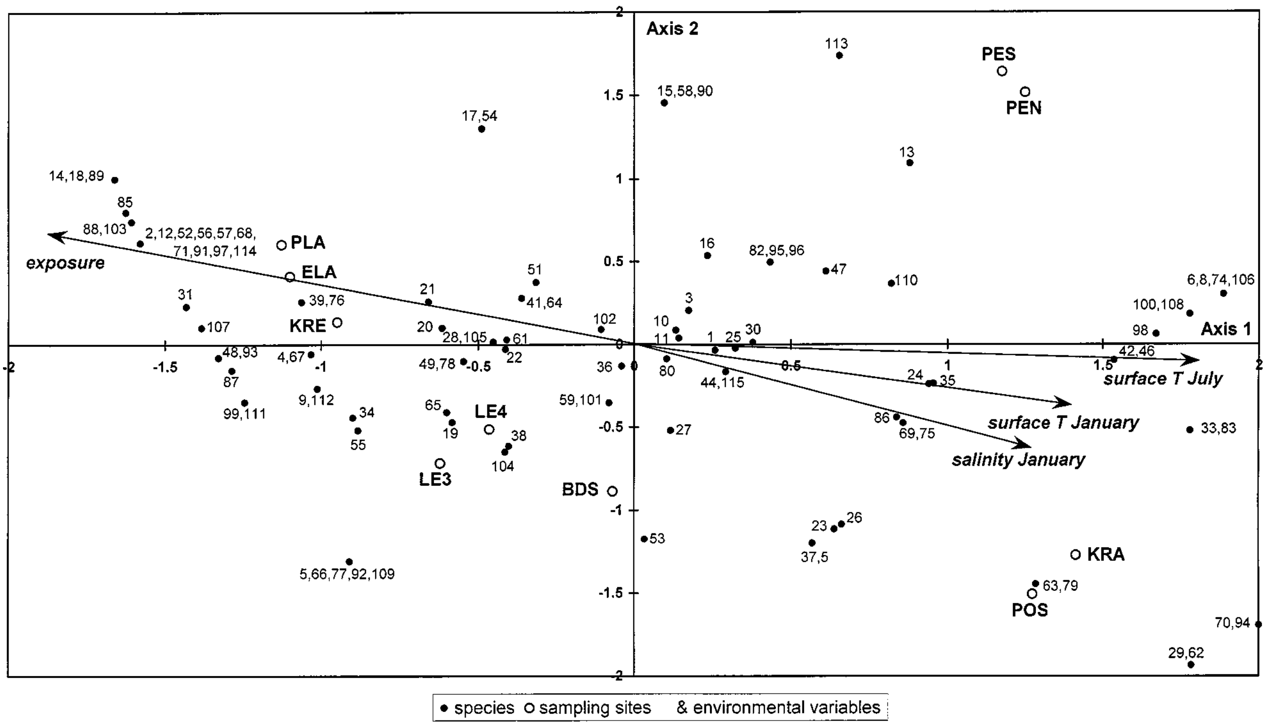

Fig. 3. The CCA of 10 sites (excluding the salt marshes) and 4 environmental variables. The numbered dots correspond with the taxons in Table I.

TWINSPAN

The division in sampling sites resulting from the TWINSPAN (Fig. 4) is consistent with the previously found site groupings. In the first division SAL is split off from the other sites. This division has a high eigenvalue (0.457), which indicates the uniqueness of its algal composition in the S/L ecosystem. The se-

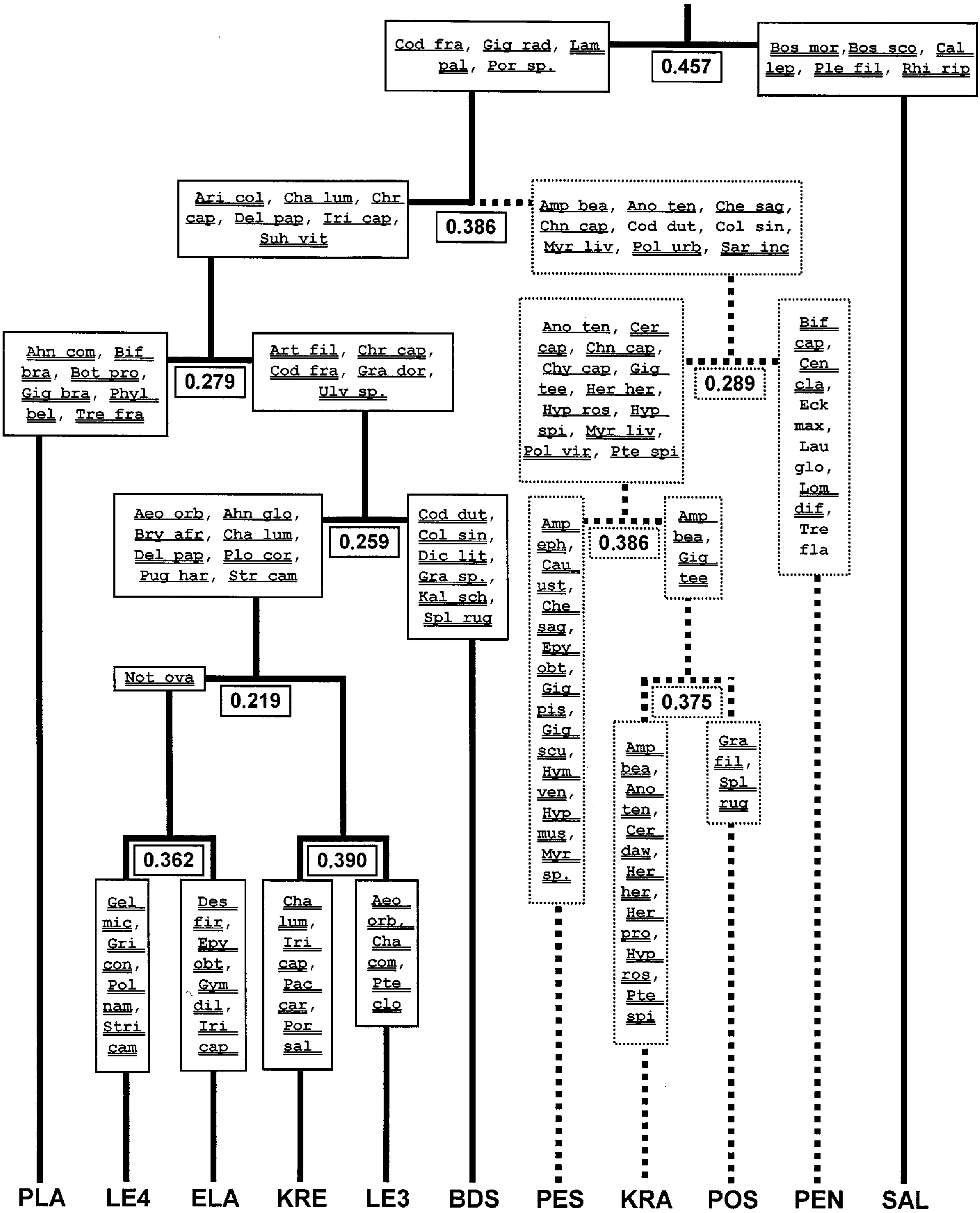

Fig. 4. The TWINSPAN dendrogram with the indication of the preferential species. In this figure the species with a 100% presence in one branch and a 100% absence in the other are double underlined. Preferential species that occur also in some sampling sites of the opposite branch are simply underlined. Species that are limited to one side of the division, but are absent in certain of those sampling sites, are not underlined. Preferential species of branches without further divisions (and consequently 100% present) are not underlined either.

cond division creates two subgroups: the Bay/West Coast and the Lagoon entities. In the Lagoon entity, PEN is the first site to be split off. The eigenvalues of this division are not high (0.289), and 5 out of the 9 most important preferential species of PEN are also preferential for PES. The next site to be separated is PES. This division has a relatively high eigenvalue, which justifies the previous division and indicates that these two sampling sites can be united as one grouping. The last division between POS and KRA can be interpreted as superfluous based on the ordination data. The high eigenvalue of this division results from the absolute species difference in a division between two sites.

In the Bay/West Coast entity all eigenvalues are low. Only the last degree of division is characterised with high eigenvalues, once again due to the absolute species difference between two sites. The splitting is not accepted for this entity, a statement supported by the analysis of the preferential species. For example, in the third division *Nothogenia ovalis* (rarely sampled and low in density in the system) is the only preferential species which is restricted to one branch (LE4 and ELA) of the division. The most important preferential species are indicated in Figure 4 and are mentioned in the 'Discussion'.

Biogeographical affinities

The species distribution of the algal flora of the 11 sites (Schils 1998) confirms the 3 entities. An extra subdivision between Saldanha Bay (BDS, LE3, LE4) and the West Coast (ELA, PLA, KRE) is recognised. Postberg (POS) does not fit into the Lagoon cluster and shows an intermediate affinity pattern between the Bay and the West Coast cluster, most likely the result of a decline in species specificity (a decrease in species richness and a high proportion of generalist species) due to eutrophication. The biogeographical affinity patterns of the three clusters (excluding the salt marshes and Postberg) are represented in Figure 5.

The Bay/West Coast sites share a high number of species with the coastal blocks of the West Coast. The algal communities of the Lagoon sites show a high similarity with the area of the South Coast, in particular with the flora between the Cape Peninsula and Cape Agulhas. In this interval (coastal blocks 17−22) a dominance shift in the percentage of species co-occurrence (between a specific site and one coastal block) takes place among the site groupings of the Bay/West Coast entity and the Lagoon entity. The area between the Cape Peninsula and Cape Agulhas

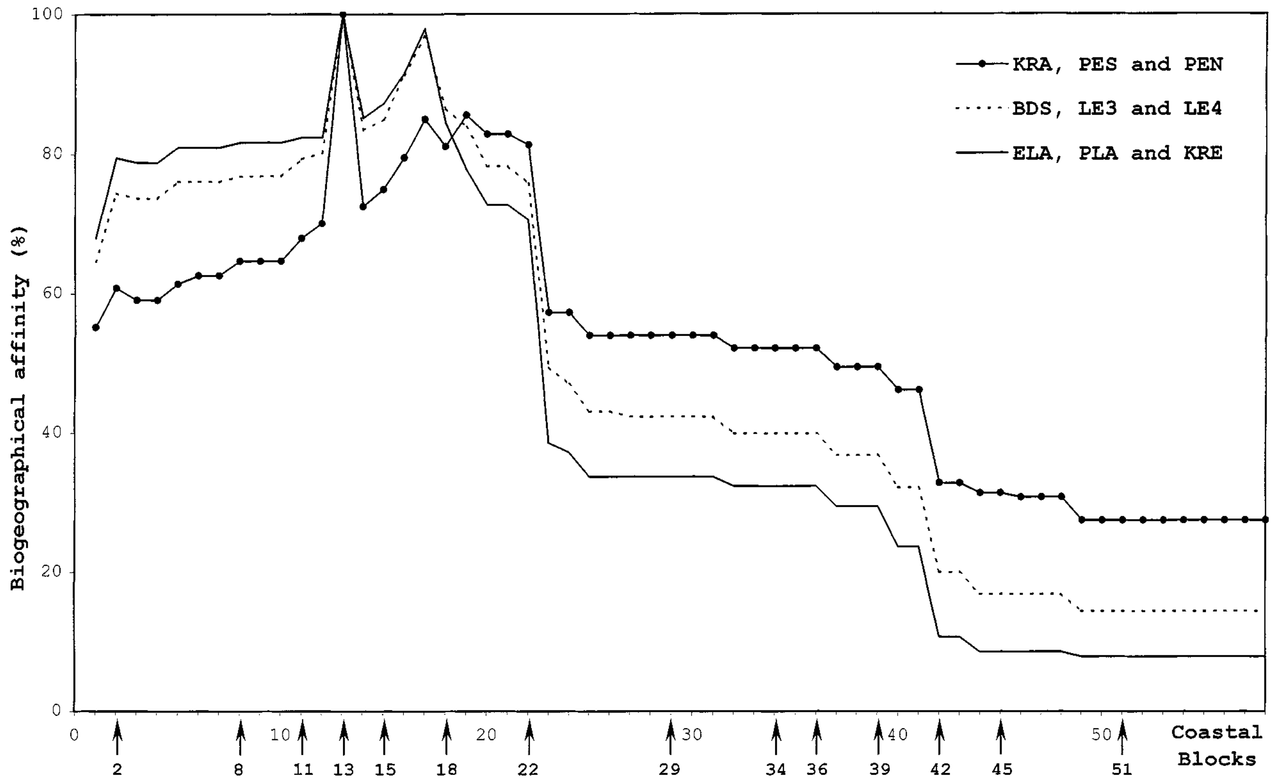

Fig. 5. Biogeographical affinity of 3 site groupings (excluding salt marshes and Postberg) with the coastal blocks of South Africa's shoreline (Bolton and Stegenga 2001). The indicated coastal blocks (arrows) represent the subsequent geographical landmarks: 2. Port Nolloth, 8. Olifants River, 10. Elands Bay, 11. St Helena Bay, 13. Langebaan Lagoon, 15. Table Bay, 18. Muizenberg, 20. Hermanus, 22. Cape Agulhas, 29. Wilderness, 34. Jeffreys Bay, 39. Port Alfred, 42. Gonubie Mouth, 45. Coffee Bay, 51. Durban.

is an overlap region between the South African West and South Coast floras (Bolton and Anderson 1997, Jackelman *et al.* 1991). False Bay (coastal blocks 18 and 19) for example, is a well-studied area with a species rich algal flora, a mixture of West and South Coast affinities (Bolton *et al.* 1991). The algal floras of the three site groupings (excluding salt marshes) of the S/L ecosystem are well represented in the False Bay area. Similarity decreases eastward of False Bay.

Discussion

The linear representation of the sample sites in Figure 2 is justifiable as the change in the macroalgal community composition (slope of the regression lines) is correlated with the geographical position in the system. All analysis techniques distinguish 3 distinct entities in the system: the Bay/West Coast entity, the Lagoon entity and the salt marshes. The landmass between Perlemoenpunt and BDS is separated by Rietbaai, a small bay of fine sediment and low macroalgal richness, which can be regarded as the geographical boundary between the algal floras of the Lagoon and the Bay/West Coast entity.

The West Coast algae are the major constituents of the S/L ecosystem. Figure 5 shows that there is about 20% difference in the proportion of algae with a South Coast distribution between the Lagoon and the West Coast site groupings. The algal flora of the Bay fits between the biogeographical affinity patterns of the latter two clusters. False Bay is the geographical boundary throughout the algal affinity analyses. Field and Griffiths (1991) mention that warm water masses from the Agulhas Bank periodically flow northwards up to Saldanha Bay. Such ocean current patterns can explain the dispersal of South Coast seaweeds into the S/L ecosystem. The algal species composition of the system as a whole shows a great resemblance with that of False Bay. Although the latter is markedly more species rich owing to its larger size and the greater habitat heterogeneity.

Bay/West Coast

The Bay/West Coast entity is positively correlated with wave exposure, and negatively with the other environmental variables. The TWINSPAN analysis (eigenvalues and preferential species) shows that a further division in the Bay/West Coast entity cannot be supported.

Gelidium pristoides and *Streblocladia camptoclada* were previously only recorded southwards from the S/L ecosystem in South Africa. Stegenga *et al.* (1997) already supposed that the distribution range of the latter extends northwards, as the species is recorded for Namibia by Wynne (1986). *Ahnfeltiopsis polyclada* was known from False Bay to Brandfontein (near Cape Agulhas). Specimens were found in Saldanha Bay but were assigned to this species with some doubt (Stegenga *et al.* 1997). We sampled *A. polyclada* in 5 out of 6 sites from the Bay/West Coast entity. *Aristothamnion collabens* and *Suhria vittata* are preferential species that are found in great quantities at these sites, the latter commonly epiphytic on *Ecklonia maxima*.

Lagoon

The sampling sites of the Lagoon are negatively correlated with wave exposure. This is confirmed by the presence of indicator species that are known to be characteristic for sheltered habitats, e. g. *Colpomenia sinuosa* and *Polysiphonia kowiensis* (Stegenga *et al.* 1997). Other representative species from the Lagoon are a reflection of the positive correlation with the water surface temperature and the salinity. In the Lagoon entity two subdivisions (*cf.* CCA) can be distinguished, representing a gradual change in the species composition.

Polysiphonia urbana and *Sargassum incisifolium* were sampled at all sites of the Lagoon entity. *Polysiphonia urbana* has a distribution that covers the West Coast, but since it grows on sand covered substrata it is a common species in the Lagoon. *Sargassum incisifolium* is found eastwards from False Bay (Stegenga *et al.* 1997); the Lagoon is a north-western outpost in its distribution pattern. *Codium duthieae* has a similar distribution. *Myriogramme livida* was only found in the infra-littoral fringe of the Lagoon during this study. Although this species occurs from Swakopmund (Namibia) to Kommetjie (Stegenga *et al.* 1997), it normally grows deeper in the infra-littoral.

In the Lagoon entity two site groupings can be distinguished: PEN & PES and POS & KRA. This separation along the vertical axis in the CCA could be related to the degree of sand cover. This parameter is unfortunately not incorporated in the ordinations, but field observations indicate that this variable is likely to be correlated with the second axis and would be differential between the inner Lagoon sites (higher sand cover) and Perlemoenpunt.

Threshold similarity values (dashed lines in Fig. 2) between sites of a certain entity (Bay/West Coast and Lagoon) can be drawn at the mean similarity of that entity. The Perlemoenpunt sites behave slightly exceptionally, most probably due to their transitional species composition. *Amphiroa beauvoisii*, *Cheilosporum sagittatum* and *Laurencia glomerata*, seaweeds with a South Coast distribution, are preferential species for PEN. The main difference from the other sites in the Lagoon is based on common West Coast species: *Bifurcariopsis capensis*, *Centroceras clavulatum*, *Sarcothalia scutellata* and *Trematocarpus flabellatus*. Five out of the nine most preferential species for PEN also differentiate for PES (TWINSPAN). This observation and the low eigenvalue of the division between PEN and PES, supports the grouping of the latter two in the Lagoon entity. Perlemoenpunt is the southern limit in the distribution of sub-tidal kelp vegetations in the S/L ecosystem, the development of these vegetations is not solely due to the wave exposure as an environmental factor (*cf.* West Coast). The combination of a moderate wave exposure and the significant current velocities (130 cm sec^{-1}; Flemming 1977) make this site a suitable habitat for the Laminariales. *Ecklonia maxima* and *Laminaria pallida* are the kelps which dominate the biologically rich kelp beds on the West Coast of South Africa and Namibia (Bolton and Anderson 1997, Stegenga *et al.* 1997). Individuals of the former species occur up to PES, and do not penetrate further into the Lagoon. Populations of the latter species grow up to PEN, further in the Lagoon (up to KRA) only isolated specimens are found. Perlemoenpunt as a whole can be regarded as a species rich area, with a variety of habitats defined by a diverse range of environmental parameters (exposed/sheltered). It is the transition area between the Bay and the Lagoon, but with a marked Lagoon affinity (high similarity values with the Lagoon sites) in its overall algal composition.

There is an increase in species with a more south-eastern distribution among the preferential species of PES. Such species are: *Amphiroa ephedraea*, *Bryopsis hypnoides*, *Cheilosporum sagittatum*, *Codium stephensiae*, *Gigartina pistillata*, *Hypnea musciformis* and *Laurencia glomerata*. Sites PES, POS and KRA, contain 5 preferential species that typify the Agulhas Marine Province: *Ceramium dawsonii*, *Chondracanthus teedii*, *Hypnea rosea*, *Polysiphonia kowiensis* and *Pterosiphonia spinifera*. The other preferential species have a West Coast distribution but were not found at PEN. It might be that the chance (frequency) of encountering the latter species is higher in the Lagoon, due to beneficial environmental conditions and/or a reduced competition with other algae.

A distinct preferential species of POS and KRA is *Chondracanthus teedii*. Stegenga *et al.* (1997) mention that this species forms a distinct zone in the lower inter-tidal. The similarity of these two sampling sites is primarily based on the high similarity in their qualitative species composition ($S_J = 0.357$), instead of the occurrence of species restricted to both locations. In the last TWINSPAN division of the Lagoon entity, 9 preferential species have a South Coast distribution. The affinity with the Agulhas Marine Province is greater at KRA than at POS. A seasonal eutrophication is probably the cause of the decrease in species specificity (see 'Biogeographical affinities') at POS.

Salt marshes

The algae growing in the salt marshes belong to the Bostrychietum. This association occurs commonly in tropical mangroves and warm temperate salt marshes (King 1990, Post 1966), but for the area of the West Coast they are almost restricted to Langebaan Lagoon. Species that typify the SAL are *Bostrychia moritziana*, *B. scorpioides*, *Callithamnion hookeri*, *Caloglossa leprieurii* and *Rhizoclonium riparium*.

Conclusion

Previous research of the abiotic parameters divided the S/L ecosystem into different entities. Based on the water temperature data Shannon and Stander (1977) identify the Benguela Current (= West Coast), the Bay and the Lagoon, the latter extending up to Salamanderpunt. From a phycological perspective the Lagoon does not reach that far. The boundary between the Bay and the Lagoon occurs at Rietbaai.

Wave exposure is the dominant environmental parameter in regard to the algal composition of the different areas in the system. It causes the distinction of two entities: the Bay/West Coast and the Lagoon entity, which coincide with a marked difference between the algal communities. The salt marshes constitute a third entity, based on their low mean similarity with the other areas of the system, and their low species richness.

The difference in environmental variables between the exposed West Coast sites and the Bay sites is not reflected by algal species composition dissimilarity. A further distinction of specific site groupings in this entity is not justifiable, as these would be based on minor differences in species composition. Raising of the zonation pattern of a *Platyclinia* sp. was noticed; the species was sampled in the infra-littoral fringe as an epiphyte on *Trematocarpus flabellatus*. Previously, this species was observed as epilithic from 6 m downward around the Cape Peninsula (Leliaert *et al.* 2000). Some algae exhibit different morphological growth forms (e. g. broad *Gigartina polycarpa* specimens) in the Bay, similar to those found in other sheltered habitats (Jackelman and Bolton 1990). The biogeographical analysis also shows a pronounced South Coast affinity of the Bay sites, but on the whole the algal flora of this area is composed of typical West Coast species.

Langebaan Lagoon forms a second entity in the S/L ecosystem. All analysis techniques show a coherent entity that is composed of PEN, PES, POS and KRA. Lagoon aspects increase from Perlemoenpunt (PEN & PES) to Kraalbaai. As an entity the Lagoon is typified by a decline in species richness, the occurrence of algae indicative of sheltered habitats and a higher percentage of species with a South Coast affinity. Perlemoenpunt is the turning point in the Bay/Lagoon transition, but it is characterised by a species composition generally indicative of the Lagoon entity. Corresponding to the kelp vegetation noted here, this is also the innermost limit of large filter feeder communities (Christie and Moldan 1977) in the Lagoon. The establishment of these two typical West Coast aspects at Perlemoenpunt results from the combined effect of a moderate wave exposure and high current velocities at the mouth of the Lagoon. This makes Perlemoenpunt a specific species rich area characterised by a mix of various environmental gradients.

As the industrial activity in the harbour is increasing, pollution becomes an acute danger. The Lagoon is particularly vulnerable to pollution due to the limited water exchange with the Bay during each tidal cycle (Flemming 1977). Hey (1977) concludes that it is doubtful that the Bay and the Lagoon will remain unpolluted. In order to safeguard the Lagoon, he suggests that it might become necessary to uncouple the Bay and the Lagoon. The construction of a dike and the excavation of a new mouth would disturb the natural water flux and the environmental gradients. Consequently this would be disastrous for the biotic diversity, the species richness and the specificity of the system. The area at Perlemoenpunt, in particular, would become biotically impoverished since this is the area were the different environmental parameters overlap. Forthcoming preservation actions should envisage maintenance of the natural water flux in the system. Besides chemical pollution and eutrophication, the invasion of exotic biota (e. g. *Carcinus maenas*, Branch *et al.* 1994) carried by the vessels that frequent the harbour threatens this relatively pristine system.

The salt marshes are the third entity distinguished in the system. The algal species that are found here have a large geographical distribution. The salt marshes of Langebaan Lagoon are the biggest along South Africa's shoreline and they are in a relatively pristine condition. It is a biologically valuable area, not only from a phycological point of view but also for its specific terrestrial vegetation, its ornithological and general faunistic importance.

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