CHARACTERISATION AND BIOTIC CLASSIFICATION OF EASTERN CAPE MIXED SUBSTRATE SHORES

Cornelia J. Garner

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Promoter: Prof. E. E. Campbell
Co-promoter: Dr. D.R. du Preez
Abstract

A significant proportion of the South African coastline is composed of both soft (mostly sand) and hard (mostly bedrock) substrata, i.e. “mixed”. This study described and classified macrobenthic assemblages of 20 Eastern Cape mixed substrate shores that differed in shore topography and the extent and position of intertidal rock and sand. A stratified random approach was used. Species richness, composition, abundance and environmental variables were determined. Commonly used beach indices were calculated. A total of 78 macrofaunal and 172 macroalgal species from rock substrate assemblages and 205 macrofauna species from sediment were recorded. Total species richness and richness per substratum exceeded that of sandy beaches devoid of rock and rocky shores with no sand. Rhodophyta were the most diverse and abundant algae, dominating all low-elevation rock surfaces as midlittoral and infralittoral turfs. Chlorophyta diversity was higher than at rocky shores, contributing more to cover-abundance at study sites and in microhabitats with an increased sand load. Sessile macrofauna species richness and abundance was lower than that of rocky shores. Polychaetes and crustaceans were the most diverse and abundant beach infauna. Species richness of both substrates declined from the low shore towards the high shore, but abundance trends varied substantially. The presence and extent of an intertidal biotope/subzone at either substrate depended on substrate availability. The supralittoral fringe in both substrate types was most often affected. Zonal overlap was evident on rock substrate: assemblages of raised midlittoral rock surfaces were enriched by species from lower surfaces sometimes leading to elimination of character taxa. Classification and ordination identified three potential mixed substrate shore biotic types: Biotic type A (Jania-Corallina-Polysiphonia turf) was characterised by robustly-textured algal turfs, a lowered predominance and diversity of polychaetes and an increase in crustacean abundance and diversity in sediment. Biotic type B (Polysiphonia-Tayloriella-Caulacanthus turf) had intermediately and biotic type C (Arthrocardia-Laurencia turf) the most sheltered eulittoral zones and beaches. DCCA identified the major environmental parameters affecting the macrobiota as: the level of wave energy, geological control of waves by hard substrate, sediment grain size and sediment inundation. A strong cross-shore wave attenuation results in sheltered sediments and midshore rock surfaces. Beach macrofauna were highly variable and diverse, which directly opposes previous perceptions about the sediment-bound biota of mixed substrate shores. The hierarchical cluster analysis produced a biotic classification of mixed substrate shores that was indicative of a biotic response to the total effects of leading environmental parameters. Macrobenthos of rock surfaces and sediment therefore showed potential to be used as an alternative or complementary to physical characteristics in classifying mixed substrate shores.
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Exposure rating is according to McLachlan (1980). Values in brackets are scores obtained using shore slope instead of beach slope. The data used for calculating the exposure rating are presented in Addendum 2.

Observed beach type is according to Short (1999). Abbreviations used: R = reflective, I = intermediate, D = dissipative. E = exposed, ME = moderately exposed, VE = very exposed, S = sheltered, VS = very sheltered. Ω = Dean’s parameter, RTR = Relative Tidal Range, BSI = Beach State Index. Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3. 1h/s = high ridge, 1 m/s = low ridge, 2 h/s = high platform, 2 m/s= low platform.

11 Legend for the environmental parameters used in the DCCA of all species.

12 The biotic and environmental attributes of the proposed mixed substrate shore biotic types of this study.

13 Results (2*1-sided p values) of Mann-Whitney U tests for significant difference in species richness of pairs of configurations. Tests are significant at p < 0.05. Significant differences are indicated in bold italized print.

14 R values of correlations between the species richness of macrobenthos of different substrates and selected environmental variables and indices. The t-test statistics given below refer to the significant r-values indicated in bold italics.

15 Results of statistical comparison (1-way ANOVA, Tukey HSD test) of macroalgal and macrofaunal species richness in mixed substrate shore biotic types A, B and C. Tests are significant at p < 0.05. Significant p-values are shown in bold italics.

16 Results of the statistical comparison of the numbers of polychaete, crustacean, mollusc, insect and other species per site. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p = 0.05. Significant differences are indicated by bold italicized p-values.

17 Comparison of the mean numbers of polychaete, crustacean, mollusc, insect and other species at sites of different mixed substrate shore configuration types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

18 Comparison of the mean numbers of polychaete, crustacean, mollusc, insect and other species in the different mixed substrate shore biotic types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

19 Comparison of the mean numbers of different rock surface macrofauna species at sites of different mixed substrate shore configuration types (high ridge sites, low ridge sites, high platform sites, low platform sites). Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

20 Comparison of the mean numbers of different rock surface macrofauna species at sites of different mixed substrate shore biotic types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-
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Composition of macroalgal assemblages given per site and for the overall number of species recorded. Mean and total values given are for all sites combined. P = Phaeophyta, C = Chlorophyta, R = Rhodophyta. Mean values are given for all sites combined ± 1SE. P = Phaeophyta, C = Chlorophyta, R = Rhodophyta. Sites are grouped according to configuration: high ridge sites (WLW – CRW), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB). Site codes are explained in Table 4 of Chapter 4.

The total abundance and mean density of macrofauna in sediment and average beach width (n = 3 transects) per study site. Site codes are explained in Table 3, Chapter 4.

Results of post hoc test for significant differences in abundance of beach macrofauna at sites grouped according to different mixed substrate shore configuration types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

Results of tests for correlations between total abundance, density and environmental parameters used in the DCCA. Parameter codes are explained in Table 11. Valid N = 20 for all correlations and t-tests. Significant correlations are given in bold italicized print and have a t-statistic.

Mean (± 1SE) abundance (ind m$^{-1}$) of major macrofaunal taxa in sediment.

Abundance (ind m$^{-1}$) of major macrofaunal taxa in sediment at each study site. Site codes are explained in Table 3, Chapter 4.

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Results of post hoc statistical tests for significant differences between abundance of major sediment macrofaunal taxa with sites grouped according to mixed substrate shore biotic types (A, B and C). Multiple Comparisons of mean ranks: p values (2-tailed). For significance at p = 0.05, bold italicized p-values. For significance at p = 0.10, italicized p-values. Pol = polychaetes, Iso = isopods, Amp= amphipods, Oli= oligochaetes, Ins = hexapods, Gas = gastropods, Biv = bivalves, Chi = chitons, Nem = nemertines, Mys= mysids. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

The ten most abundant gastropod species per site. Species are arranged according to decreasing abundance (ind m$^{-1}$ of integrated transect). Taxon codes are explained in Addendum 4.
The most abundant species of macroalgae and sessile macrofauna at each site. Species are arranged according to decreasing abundance (percentage cover referenced to a single integrated transect per site). Those given in bold print give a cumulative 75% of estimated cover-abundance of rock substrate per site. The remaining species listed contribute approximately an additional 20%. The mixed substrate shore biotic type code (A, B or C) as well as the mixed substrate shore configuration code is provided with the site code. Configuration legend: 1 h/s = high ridge sites, 1 m/s = low ridge sites, 2 h/s = high platform sites, 2 m/s = low platform sites. Biotic type legend: Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs. Taxon codes are explained in Addenda 3 and 4. Site codes are given in Table 3, Chapter 4.

Results of post hoc test for significant differences in abundance of Phaeophyta at sites grouped according to different shore configuration types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

Results of post hoc test for significant differences in abundance of bivalves at sites grouped according to different biotic mixed shore types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

Results of post hoc test for significant differences in abundance of sessile macrofauna at sites grouped according to different biotic mixed substrate shore types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

Results of post hoc test for significant differences in the mean numbers of species in soft substrate sampling strata S0 to S5. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

Results of post hoc test for significant differences in the mean numbers of species in hard substrate sampling strata R0 to R8. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

Results of statistical comparison of mean macroalgal and macrofaunal species richness in each rock substrate sampling stratum (R0 to R8) (n = 20). Mann-Whitney U-test. Results are significant at p < 0.05 for 2*1-sided p. Significant differences are indicated in bold italics.

The overall length and proportion of shoreline taken up by each mixed substrate shore configuration, as well as purely rocky and purely sandy shores. HWS = spring high tide level, LWS = spring low tide level, MSL = mean sea level.

Species richness compared to relevant previous studies. An asterisk (*) indicates a mixed substrate shore that was sampled as a sandy shore. Possible shore configurations derived from site information are given in brackets. The numbers given in brackets include insects. N = number of study sites. Regions: EC = 1, WC = 2.
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11 The mean (± SE) percentage carbonate in sediment samples (n = 36) given for each site (white bars) and the overall mean for all sites (grey bar) (n = 720). Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.

12 The mean percentage carbonate in sediment samples at each stratum (n = 6) given for each site.

13 The mean (± SE) percentage organic matter in sediment samples (n = 36) given for each site (white bars) and the overall mean for all samples (n = 720) (grey bar). Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.

14 The mean percentage organic matter in sediment samples at each stratum (n = 6) given for each site S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line. Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.

15 The mean percentage rock along shore-normal (cross-shore) profiles (n = 3) and a midtidal shore-parallel (longshore) profile (n = 1) and rock height rating of sites, all in relation to surf zone width. A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: RocL_100 = mean % long-shore rock along profile, Roc_C = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating.

16 The mean percentage rock along shore-normal (cross-shore) profiles (n = 3) and a midtidal shore-parallel (longshore) profile (n = 1) and rock height rating of sites, all in relation to the mean beach slope (1/slope). A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: RocL_100 = mean % long-shore rock along profile, Roc_C = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating.

17 Extent of each sampling stratum in sediment (S0 to S5) and on rock substrate (R0 to R8) given as a segment of the total length (m) of an integrated transect representing one study site. Stratum codes are explained in Table 4 (Chapter 4). Study sites are arranged according to configuration: AVA to WLW are high ridge sites, BCN to PDB are low ridge sites, HPE to TST are high platform sites, and CNR to MPB are low platform sites.

18 The percentage of the total length of an integrated cross-shore transect taken up by each sampling stratum (S0 to S5 in soft substrate and R0 to R8 on hard substrate) in relation to the rock height rating of study sites. Stratum codes are explained in Table 4 (Chapter 4).

19 The percentage of the total length of an integrated cross-shore transect taken up by each sampling stratum (S0 to S5 in soft substrate and R0 to R8 on hard substrate) in relation to the % cross shore rock of study sites. Stratum codes are explained in Table 4 (Chapter 4).
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21 Ward’s classification of sites using importance values of sediment macrofauna species.

22 Ward’s classification of sites using importance values of sessile macrofauna species.

23 Ward’s classification of sites using importance values of macroalgae.

24 Ward’s classification of sites using importance values of macroalgae and sessile macrofauna species.

25 Ward’s classification of sites using importance values of gastropod species (motile macrofauna).

26 Ward’s classification of sites using importance values of all rock surface macrobenthos species.

27 Ward’s classification of sites using importance values of all species.

28 Ward’s classification of sites using importance values of all species and showing mixed substrate shore biotic types A, B and C of this study.

29 Ordination (DCA) of sites (= samples) using importance values of macrofauna species from sediment. Sum of all eigenvalues = 4.661; Axis 1 eigenvalue = 0.700; Axis 2 eigenvalue = 0.373; Cumulative variance of species data = 23.0%. Circle colours correspond to those of groups in complementary classification (Figure 21).

30 Ordination (DCA) of sites using importance values of sessile macrofauna species. Sum of all eigenvalues = 0.934; Axis 1 eigenvalue = 0.240; Axis 2 eigenvalue = 0.081; Cumulative variance of species data = 34.0%. Circle colours correspond to those of groups in complementary classification (Figure 22).

31 Ordination (DCA) of sites using importance values of macroalgae only. Sum of all eigenvalues = 2.0347; Axis 1 eigenvalue = 0.323; Axis 2 eigenvalue = 0.172; Cumulative variance of species data = 24.3%. Circle colours correspond to those of groups in complementary classification (Figure 23).

32 Ordination (DCA) of sites using importance values of attached macrobenthic species (sessile macrofauna and macroalgae) from rock substrate. Sum of all eigenvalues = 1.427; Axis 1 eigenvalue = 0.256; Axis 2 eigenvalue = 0.138; Cumulative variance of species data = 27.2%. Circle colours correspond to those of groups in complementary classification (Figure 24).

33 Ordination (DCA) of sites using importance values of gastropod species. Sum of all eigenvalues = 0.379; Axis 1 eigenvalue = 0.118; Axis 2 eigenvalue = 0.034; Cumulative variance of species data = 40.1%. Circle colours correspond to those of groups in complementary classification (Figure 25).

34 Ordination (DCA) of sites using importance values of all species. Shore configuration types are indicated by colours (green, yellow, blue and red) according to the legend. Sum of all eigenvalues = 1.957; Axis 1 eigenvalue = 0.282; Axis 2 eigenvalue = 0.169; Cumulative variance of species data = 23.1%. Circle colours correspond to those of groups in complementary classification (Figure 26).
Ordination (DCA) of sites using importance values of all species. Mixed substrate shore biotic types A, B and C are indicated by colours (green, red and blue). Sum of all eigenvalues = 1.957; Axis 1 eigenvalue = 0.282; Axis 2 eigenvalue = 0.169; Cumulative variance of species data = 23.1%.

DCCA of all species constrained by selected environmental parameters. A. Environmental parameters. B. Diagram of constrained ordination of sites using all species. The environmental parameters are explained in Table 11. Sum of all eigenvalues = 1.957; Axis 1 eigenvalue = 0.282; Axis 2 eigenvalue = 0.169; Lengths of gradient: Axis 1 = 1.962; Axis 2 = 1.758. Cumulative percentage variance of species data: Axis 1 = 14.4%; Axis 2 = 23.1%. Cumulative percentage variance of species-environment relationship: Axis 1 = 13.8%; Axis 2 = 22.3%. Colours of symbols representing sites correspond to the mixed substrate shore biotic types A, B and C found by classification.

Total species richness per site. Sites are arranged according to site configuration. The sediment load and distribution is indicated by a + symbol, following the scheme set out in Table 2, Chapter 3. 1 h/s+ to 1 h/s ++++: WLW to CRW; 1 m/s+ to 1 m/s++++: BCN to PBE; 2 h/s+ to 2 h/s ++++: TST to HPE; 2 m/s+ to 2 m/s ++++: CRE to MPB. 1 h/s = high ridge sites, 1 m/s = low ridge sites, 2 h/s = high platform sites, 2 m/s = low platform sites. Site codes are explained in Table 3, Chapter 4. The mixed substrate shore biotic types (A, B and C) defined by cluster analysis and ordination are indicated on the x-axis labels.

Mean species richness (+ 1 SE) in the four shore configuration types. Configuration legend: 1 h/s - high elevation ridges, 1 m/s – low elevation ridges, 2 h/s - high elevation platform, 2 m/s – low elevation platform. The shore configuration types that differed significantly in mean species richness are indicated by the letter a.

Mean species richness (+ 1 SE) in the three biotic types obtained by cluster analysis. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

Total numbers of macroalgal and macrofaunal species per site. Rockfauna = motile and sessile macrofauna of rock surfaces, sandfauna = macrofauna of sediment. Sites are arranged according to site configuration. High ridge sites: WLW to MAB; Low ridge sites: BCN to PBE; High platform sites: TST to HPE; Low platform sites: CRE to MPB. The biotic groups resulting from cluster analysis are indicated on the x-axis labels.

The relationship between the species richness of total rock biota, macroalgae and macrofauna.

Sediment macrofauna species richness in relation to mixed substrate shore environmental parameters.

Sediment macrofauna species richness in relation to beach indices.

Rock surface macrobenthos species numbers in relation to environmental parameters and indices.

Mean species numbers (+ 1 SE) of macrobenthos in sediment and on rock surfaces in relation to physical mixed substrate shore types (configuration types). Rock macrofauna includes both motile and sessile forms. Total rock biota = macroalgae, sessile and motile macrofauna of hard substrate. Configuration legend: 1 h/s - high ridges, 1 m/s – low ridges, 2 h/s - high platform, 2 m/s – low platform. A significant difference between numbers of species in sediment and on rock substrate is indicated by the letters a, b, c.
and $d$ for the different shore configuration types. A significant difference between numbers of macroalgal species is indicated by the letter e. A significant difference between numbers of macroalgal and rock macrofaunal species is indicated by the letters $f$, $g$ and $h$.

Mean species richness ($\pm 1$ SE) of macrobenthos in sediment and on rock surfaces in relation to physical mixed substrate shore types (configuration types). Rock macrofauna includes both motile and sessile forms. Total rock biota = macroalgae, sessile and motile macrofauna of hard substrate. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs. A significant difference between numbers of macroalgal species and macrofauna species in sediment indicated by the letters $a$, $b$ and $c$, for biotic types A, B and C respectively. A significant difference between numbers of macroalgal species and rock macrofaunal species is indicated by the letter $f$.

Overall composition of sediment macrofauna assemblages. The number of species is given first, followed by percentage of total number of species. Other Crustacea include species of Mysidacea, Caridea, Brachyura, Cumacea, Copepoda, Ostracoda and Tanaidacea. Other taxa include Nematoda, Platyhelminthes, Porifera, Sipunculida, Echinodermata and Chaetognatha.

Composition of sediment macrofauna assemblages per site. Sites are grouped according to configuration type: high ridge sites (WLW – MAB), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB). Taxa with extremely low numbers of species were lumped together as “Other”.

The composition of beach macrofauna assemblages per mixed substrate shore configuration type. The number of species is given first, followed by proportion (percentage) of total number of species.

The composition of beach macrofauna assemblages per mixed substrate shore biotic type. The number of species is given first, followed by proportion (percentage) of total number of species. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

Overall composition of hard substrate macrofauna assemblages. The number of species is given first, followed by percentage of total number of species.

Composition of hard substrate macrofauna assemblages per site. “Other taxa” is comprised of Porifera, Bryozoa, Echinodermata and Ascidiae. Sites are grouped according to configuration: high ridge sites (WLW – MAB), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB).

The composition of hard substrate macrofauna assemblages per mixed substrate shore configuration type. The number of species is given first, followed by proportion (percentage) of total number of species.

The composition of hard substrate macrofauna assemblages per mixed substrate shore biotic type. The number of species is given first, followed by proportion (percentage) of total number of species. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

Composition of macroalgal assemblages and floristic ratio ($([R + C]/P) \pm 1$SE) per mixed substrate shore configuration type. The number of species is given first, followed by proportion (percentage) of total number of species.
Composition of macroalgal assemblages and floristic ratio \([(R + C)/P\] ± 1SE) per mixed substrate shore biotic type. The number of species is given first, followed by proportion (percentage) of total number of species. Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.

Relative abundance of animal phyla and macroalgal divisions in samples obtained from both substrates based on importance values derived from relative abundance and relative frequency (n = 20 sites).

Mean abundance and density of macrofauna in sediment at sites representing different mixed substrate shore configuration types. Configuration legend: 1 h/s - high ridges, 1 m/s - low ridges, 2 h/s - high platform, 2 m/s - low platform.

Mean abundance and density (± 1 SE) of macrofauna in sediment at sites representing different mixed substrate shore biotic types. Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.

Sediment macrofauna abundance (ind m⁻¹) and mean density (ind m⁻²) in relation to environmental parameters and indices.

Abundance of major taxa usually reported in beach studies as a percentage of total abundance (ind m⁻¹).

The 10 most abundant macrofaunal taxa at sites grouped according to mixed substrate shore configurations. Data labels provide mean abundance (ind m⁻¹) and mean % of total abundance.

The 10 most abundant macrofaunal taxa in the mixed substrate shore biotic types. Data labels provide mean abundance (ind m⁻¹) and mean % of total abundance. Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.

Gastropod abundance (ind m⁻¹ of integrated transect) and density (ind m⁻² of integrated transect). Littorinid numbers are plotted on the second y-axis. Sites are arranged according to site configuration: high ridges (WLW – MAB), low ridges (BCN – PBE), high platform (TST – HPE), low platform (CRE – MPB). Site codes are explained in Table 3 of Chapter 4.

Cover-abundance of macroalgae and macrofauna as well as bare area on the rock substrate as a percentage of an integrated site transect. Macroalgal cover-abundance over 100% is due to inclusion of epiphytic algae in total cover-abundance. Sites are arranged according to site configuration: high ridge sites: WLW – MAB; low ridge sites: BCN – PBE; high platform sites: TST – HPE; low platform sites: CRE – MPB. Site codes are explained in Table 3 of Chapter 4. The mean percentage cover (first data label) and percentage contribution to total sessile macrofauna cover (second data label) of dominant sessile macrofauna (Cirripedes, Bivalves and Porifera) at sites grouped according to mixed substrate shore configurations.

Cover-abundance (% cover) of sessile macrofauna on rock substrate at each study site. Sites are arranged according to site configuration: high ridge sites (WLW – MAB), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB). Site codes are explained in Table 3 of Chapter 4.

The mean percentage cover of macroalgae, sessile fauna and bare rock at sites grouped according to mixed substrate shore configurations.
The mean percentage cover (first data label) and percentage contribution to total sessile macrofauna cover (second data label) of dominant sessile macrofauna (Cirripedes, Bivalves and Porifera) at sites grouped according to mixed substrate shore configurations.

The mean percentage cover of macroalgae, sessile fauna and bare rock in mixed substrate shore biotic types. Biotic type A = *Jania-Corallina- Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.

The mean percentage cover (first data label) and percentage contribution to total sessile macrofauna cover (second data label) of dominant sessile macrofauna (Cirripedes, Bivalves and Porifera) in mixed substrate shore biotic types. Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.

Total and mean (± 1 SE) number of species in sampling strata on rock and in sediment. S0 to S5 are sampling strata of the sediment. R0 to R8 are sampling strata of the rock surfaces. The stratum codes are explained in Table 4 (Chapter 4).

The mean number (± 1 SE) of macrofaunal and macroalgal species in each hard substrate sampling stratum.

KME, Kleinemonde East. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

HPE, Hougham Park east. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

CNR, Cannon Rocks. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

MPB, Pollock South. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

PBE, Pollock North. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

AVA, Avalanche. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

MAA, Maitlands Inner. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

79 MAB, Maitlands Outer. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

80 BCN, Beacon Rock. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

81 HWD, Humewood. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

82 WLW, Willows Beach. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

83 KNB, Kini Bay. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

84 CRW, Cape Recife West. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

85 BRK, Bird Rock. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

86 ASB, Aston Bay. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

87 PDB, Paradise Beach. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

88 HPW, Hougham Park West. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis
Abundance of other species (bars) is shown on the primary y-axis. TST, Three Sisters. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

90 CRE, Cape Recife East. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

91 MLS, Miller’s Beach. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.

92 The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 24° 00' 00" and E 24° 45' 00".

93 The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 24° 45' 00" and E 25° 35' 00".

94 The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 25° 35' 00" and E 26° 25' 00".

95 The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 26° 25' 00" and E 27° 15' 00".
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The earth is the Lord’s and all its fullness,
The world and those who dwell therein.
For He has founded it upon the seas,
And established it upon the waters.”
Ps 24:1
CHAPTER 1  Introduction

On most of the world’s coasts, stretches of consolidated (rocky) shore alternate or intergrade with unconsolidated (sandy, muddy) sections (Knox 2000) and are seldom completely devoid of material such as sand, mud, shingle, pebbles, boulders or rock fragments, (Eltringham 1971; Bally et al. 1984; Knox 2000) except on extremely sediment deficient shores (Sunamura 1992). While rocky shores are estimated to occupy approximately 80% of the world’s coastlines (Emery and Kuhn 1980) and sandy beaches about 10% (Inman and Nordstrom 1971; Bird 1985) to 34% (Hardisty 1994), global estimates of the amount of coast composed of a combination of rock and sediment are lacking.

In both their physical environment and attendant biota, rocky shores and sandy beaches are, and have been studied as, distinct and separate systems. With regard to rocky shores, the insights provided by Paine (1966), Dayton (1971), Menge and Sutherland (1976), Connell and Slatyer (1977), Connell (1978, 1985), Sousa (1979a, 1979b, 1984, 1985), Norton et al. (1981), Connell and Keough (1985), Lubchenko and Menge (1987), Westoby et al. (1989), Russell (1991) and Menge et al. (1994), amongst others, serve as a sound basis for fairly advanced experimental and theoretical investigations in these systems. Distribution patterns in rocky shore communities have been explained in terms of their response to a number of variables ranging from physical conditions (e.g. Norton et al. (1981), Norton (1985), Lubchenko and Menge (1987), Russell (1991)) to biotic interactions (e.g. Paine (1966), Dayton (1971), Menge and Sutherland (1976), Menge et al. (1994)), disturbance (e.g. Connell and Slatyer (1977), Connell (1978, 1985), Sousa (1979a, 1979b, 1984, 1985), Connell and Keough (1985)), and stress (e.g. Grime (1977), Taylor and Littler (1982)). For sandy beaches, the work of McLachlan (1980a, 1980b, 1983a, 1983b, 1990), McLachlan and Jaramillo (1995), Defeo and McLachlan (2005), also McLachlan and Dorvlo (2005, 2007), and overviews in Brown and McLachlan (1990), McLachlan (2001) as well as McLachlan and Brown (2006), serve a similar purpose. Hypotheses centre mainly on the influence of physical conditions on community structure, but the role of biotic interactions is beginning to gain interest (overviews in McLachlan and Erasmus (1983), Brown and McLachlan (1990), Defeo and McLachlan (2005), McLachlan and Brown (2006)). It is therefore fair to say that the community structure, population interactions, trophic structure and food web processes of rocky shores and sandy beaches are now quite well understood.
Based on structural attributes, mixed substrate shores are usually seen as rocky or sandy shores, e.g. Littler et al. (1991), Mathieson et al. (1991), Santelices (1991), Foster et al. (1991), John and Lawson (1991), Knox (2000) and Schiel et al. (2006), perhaps because of local predominance of one of these habitat-forming substrates. They have furthermore been described as systems in a chronic state of stress due to increasing sedimentation (see Airoldi 2003) or disturbed due to radical erosion events (e.g. Hubbard and Dugan 2003). Bally et al. (1984) were the first to stress the physical and biological uniqueness of shores combining sand and rock and called these ‘mixed shores’. The term was adopted by other South African authors, e.g. McQuaid and Dower (1990), Brown et al. (1991), Field and Griffiths (1991), Campbell and Bate (1997), Lombard et al. (2004) and Anderson et al. (2008), and received mention in the reviews by Knox (2000) and Airoldi (2003).

The biota of sand-inundated rock substrates and some processes operating in such systems have received increasing attention in recent years (see Airoldi 2003). While the effects of natural sedimentation continue to be studied (e.g. Irving and Connell 2002; Kelaher and Castilla 2005; Schiel et al. 2006; Carballo 2006; Balata et al. 2007), it is largely the need to understand the effects of anthropogenically induced sedimentation on natural rocky shore communities that drives this development (e.g. Littler and Murray 1975; Airoldi et al. 1996; Airoldi 2001; Shepherd et al. 2009). However, it is also possible that these sections of shoreline have been subjected to sand accretion-erosion cycles for a long enough time to allow the development of an assemblage of organisms well-adapted to prevailing environmental conditions (Bally et al. 1984; Brown 1996). Mixed substrate shores provide suitable habitats and food sources for tertiary consumers frequenting both sandy beaches and rocky shores (Griffiths et al. 1983), which implies trophic linkages between those environments as well as adjacent terrestrial systems (Hockey et al. 1983). If biota primarily associated with rocky or sandy sections are able to utilize food and other resources from both habitat types, the trophic structure of shores where rock and sand intermingle may, in fact, be intermediate between purely rocky and purely sandy shores.

The mixed substrate shore and its communities could be viewed as an ecotonal transition zone between adjacent sandy or rocky shores (Odum 1971; Johnston et al. 1992; Ray and Hayden 1992) combining selected attributes of both systems. This shore type could well provide a combination of conditions supporting communities that comprise both tolerant rocky or sandy shore species and those that are specialized for prevailing conditions (Bally et al. 1984; McQuaid and Dower 1990; Brown et al. 1991). Ecotones often have highly diverse communities due to an ‘edge effect’ (Odum 1971; Holland and Risser 1991), particularly where a high degree of abiotic heterogeneity is accompanied by much fine scale
biotic variability (Gosz 1991). The intertidal zone is an integral part of the coastal ecotone (Ray and Hayden 1992), supporting a unique biotic assemblage. It is subject to sharp environmental gradients and characterised by intense interaction between biotic and abiotic components within the system, as well as across boundaries with adjacent marine and terrestrial systems (Holland and Risser 1991; Colombini and Chelazzi 2003). Connectivity between the different parts of the coastal ecotone depends on coastal configuration which comprises the static (headlands, capes, man-made structures) and dynamic features (e.g. currents, wave patterns, salinity gradients) forming along-shore boundaries (Ray and Hayden 1992). As transition zones, mixed substrate shores, may therefore serve as refugia for migrant species as well as those permanently requiring environmental conditions not offered by climax communities (Littler et al. 1983; Brown 1996) and may even have been the backdrop against which species developed the necessary attributes to make the transition from a sedimentary to a hard substrate habitat and vice versa (Littler et al. 1983; Brown 1996).

South African mixed substrate shores are poorly known. Where rock and sand occur together, the physical nonconformity of the shore led to the assumption that the communities were impoverished and atypical, particularly during a phase in South African marine research when basic community structure was still being investigated and patterns established (Bally et al. 1984; Brown et al. 1991; Brown et al. 2000). While some of the earliest studies of sandy beaches involved sites with some associated rock (e.g. Brown 1971; Wooldridge et al. 1981), little is known of the sediment macrofauna of sandy shores with a more prominent rock component or, indeed, of the communities on rock surfaces surrounded by a sea of sand (Bally et al. 1984). After Bally et al. (1984) pointed out that a major portion of the South African coastline is mixed in nature and a virtually unknown system, a small raft of studies followed, e.g. Dower (1989), McQuaid and Dower (1990), Brown et al. (1991), Marshall and McQuaid (1989), Engledow and Bolton (1994), Engledow (1998). In recent years, interest in the biotic and functional aspects of these systems has been rekindled, e.g. Anderson et al. (2008), Zardi et al. (2006, 2008, 2011). Despite the paucity of South African research on the topic, there are indications that these highly variable environments known for their bewildering array of spatial and temporal configurations, potentially support unique communities that could contribute significantly to the overall biodiversity, connectivity and functionality of the South African coastline (Bally et al. 1984; McQuaid and Dower 1990; Brown et al. 1991; Brown 1996).

Until more is known about the resident biota of mixed substrate systems, no meaningful conclusions may be drawn about their functional relationships with sandy beaches and rocky shores. Questions that arise include: How do abiotic attributes of mixed substrate shores
differ from sandy beaches and sand-deficient rocky shores? What relative contributions do the resident biota of the sediment component, surf zone (if present) and hard substrate, make to the ecological processes and services associated with the system? Do abiotic variations between mixed substrate shores necessarily impose variations in the biotic assemblages and functionality of such systems?

Mixed substrate shores are often located in areas where human access is easy and many are exploited, which makes them particularly vulnerable to degradation by human impact (Bally et al. 1984; Dobkins1992; Griffiths et al. 2000). A representative proportion should enjoy protection against exploitation and other anthropogenic threats to ensure optimal system functionality. If variation among mixed substrate shores is sufficient to justify separation into different biotic/functional types, the present conservation targets for South African mixed substrate shores will need to be revisited and brought in line with those of rocky shores and sandy beaches as proposed by Lombard et al. (2004).

Observed variations in South African mixed substrate shores have led to shore classifications based on spatial and temporal attributes (Bally et al. 1984; Brown et al. 1991) as well as wave exposure rating (Lombard et al. 2004), but community descriptors are also widely used to classify rocky shores, e.g. Ballantine (1961), Lewis (1964), Blamey and Branch (2009), and beach types, e.g. Campbell and Bate (1997), Brown (2001), since they serve as indicators of dynamic variables. A recently proposed biotic classification of beaches based on benthic and surf zone biota, proposed four functional sandy beach types (Todkill et al. 2004). Mixed substrate shores were included as a unique fifth with potential subtypes.

This study is based in the Eastern Cape where the highest proportion of mixed substrate shore is found (Bally et al. 1984). The null hypothesis of this study is that biotic assemblages have the same composition as those of purely sandy or rocky shores, showing no level of modification that may be linked to the presence of the alternative substrate.

The aims of this study were as follows:

1. To characterise macroalgal and macrofaunal assemblages of mixed substrate shores differing in the proportion and distribution of sand and rock.

2. To investigate relationships between the biotic assemblages and selected physical and dynamic environmental variables.
3. To classify mixed substrate shores based on macrobiotic (macroalgal and macrofaunal) assemblages.

4. To show the extent and distribution of mixed substrate shore types along the section of coast between Cape St Francis and Great Fish River Point based on the biotic classification.

CHAPTER 2 Literature review

2.1 Introduction

Coasts are the interface between the marine and terrestrial environments. They range in type from steep, high-energy, sediment deficient bedrock outcrops in the form prominent cliffs and headlands, to low-gradient, low-energy, muddy shores edged by salt marshes and mangroves (Roy et al. 1994). The physical composition and dynamics of wave-exposed shores, specifically those composed of rock and/or sand, are of particular interest to this study. These factors have not been studied on shores composed of a mixture of consolidated and unconsolidated substrata. Interactions between the physical and dynamic components of mixed substrate systems may shed light on processes and developmental trends in their morphology. Furthermore, they constitute the major influences on resident biota which, in turn, exhibit morphological and physiological adaptations to the environmental conditions characteristic of their habitat.

2.2 The physical component: shore morphology

2.2.1 Consolidated shores

The suite of conditions prevailing at the coast is highly conducive to the erosion of rock. Repeated pounding by waves periodically generates stress within rocks, while wave action, coupled with the tidal cycle, brings about alternate periods of wetting and drying, as well as cooling and heating, all of which cause fatigue, cracks and rock weathering (Sunamura 1992). Epilithic biota further influence the rate of substrate wear and tear: boring and grazing animals weaken and remove rock, whereas other encrusting organisms slow down the process of weathering (Sunamura op. cit.). The rate at which coastal rock formations erode depends on their mechanical strength and age: younger sedimentary rocks (e.g. Tertiary rock formations) and softer types of rock (e.g. mudstone, shale, glacial sediments) tend to erode away sooner than older formations (e.g. Mesozoic-Paleozoic formations) and more resistant rock types such as granite and basalt (Sunamura 1992; Trenhaile 2002).
Contemporary marine processes have sculpted three major morphological configurations in coastal rock formations all over the globe, namely, near-horizontal platforms that extend below sea level with a sudden drop at their seaward edge, sloping platforms that do not have such an abrupt change in topography, and, plunging cliffs that descend steeply far below sea level without any platform (Bird 1976; Sunamura 1992). Several different terms have been employed to denote the two types of platform. Terms like ‘wave-cut platform’, ‘abrasion platform’ or ‘storm wave platform’ imply a formative process rather than being purely descriptive in the morphological sense and have been deemed unsuitable (Sunamura 1992, p. 141). In this text the term ‘shore platform’ (Bird 1976), regarded as more appropriate (Sunamura 1992), has been used.

For either of the two platform types to develop, cliff erosion must take place (Sunamura 1992). Loose material deposited may then either assist in further abrasion of the platform or protect it against erosion (Sunamura 1992). The magnitude of the force exerted by wave action is linked to tidal level: consequently, sloping platforms are more common on macrotidal coasts and horizontal platforms in microtidal environments (Trenhaile 2002). Horizontal platforms also often occur at headlands, usually composed of more resistant material, whereas sloping platforms may be found in adjacent embayments, composed of less resistant material (Edwards 1951; Hills 1972; Storlazzi and Field 2000). Cliffs without a seaward platform occur on coasts dominated by hard, erosion-resistant rock able to withstand strong wave action (Pitty 1971; Sunamura 1992) and are characteristic of convergent coasts, occurring near the younger, less stable margin of a tectonic plate, while fine-grained beaches occur on the lee side (Inman and Nordstrom 1971; Short 1999). Horizontal shore platforms with both a seaward scarp and landward cliff, usually evident above or near the spring high water level, in the lower intertidal or shallow subtidal reaches, are often undercut, forming shelves that fracture and collapse (Gill 1972; Sunamura 1992). The elevation of the platform correlates with the hardness of the rock: platforms cut in soft rock (e.g. aeolianite) tend to occur near the low water mark, whereas supratidal platforms are composed of more resistant rock (Gill 1972; Trenhaile 1987).

Since the end of the Holocene transgression, sea levels have remained more or less stable (Sunamura 1992; Trenhaile 2002). Considering the time scales involved, the change observed in shore platforms are extremely slow and the shore configurations we see today are mostly inherited features (Trenhaile 2002). The seaward edges of such platforms are populated by a rich marine fauna and flora that maintain a presence even after attack by storm waves: clearly these platforms persist long enough to allow stable, long-term marine communities to develop (Sunamura 1991, 1992). Whether they are inherited from previous
interglacials, during which sea levels were similar to present-day levels, or contemporary (postglacial) features, modern coastal rock platforms were all shaped by the combined action of waves and tides since the sea reached its present level a few thousand years ago (Carter and Woodroffe 1994; Trenhaile 2002).

2.2.2 Sedimentary shores

Rivers are the main sources of terrigenous sediment to the coast (Brown and McLachlan 1990; Woodroffe 2002). The type and quantity of sediment brought down are determined by the climate, geology and topography of the landscape through which the river flows (Short 1999; Woodroffe 2002). Coastal (intertidal and subtidal) sediments vary in composition according to origin: a terrestrial origin is indicated by quartzitic particles, while marine sediments are characterized by high carbonate content (Short 1999; Little 2000).

In the subtidal seascape sediment predominates (Short 1999; Connell and Keough 1985). Where waves deposit sediment above mean sea level on a shore platform, a beach is formed (Short 1999; Woodroffe 2002). On coasts dominated by wave-action, sedimentary shore type is largely determined by the interactions of wave energy, tidal range, sediment supply, substrate gradient, accommodation volume and sea level (Roy et al. 1994). Most shore platforms are gently sloping (0.5° to 2°) and retain sediment (Roy et al. 1994; Trenhaile 2002). Substantial sand volumes tend to accumulate on rocky shelves with a slope of 1° or less (Roy et al. 1994; Short 1999) provided the supply is sufficient (King 1972; Short 1999). Well-developed ‘permanent’ sandy beaches would thus remain where the sediment budget is sufficient to keep an underlying rock platform deeply buried (Short 1999).

Beach sediments of wave-dominated coasts have a low proportion of very fine sediment (clay, silt) as these particles are quickly winnowed out in the turbulent environment of breaking waves (Short 1999; Little 2000). Consequently, beach material on such coasts commonly consists of sand, gravel/shingle (pebbles and cobbles), boulders or a mixture of these (Eltringham 1971; Short 1999; Little 2000; Mason and Coates 2001; Woodroffe 2002). The sands clothing present-day sedimentary coasts have to a large degree been derived from the reworking of ancient coastal plains during the most recent marine incursion (Walker 1990; Short 1999).

Sandy shores consist of two component systems: a marine wave-driven system, the beach and surf-zone, and a terrestrial wind-driven system, the adjacent dune field (Tinley 1985;
Mucina et al. 2006). The two systems function independently, but are inextricably linked into a single geomorphic unit, the *littoral active zone* of Tinley (1985), by exchange of sand between frontal dunes, beach and surf zone. Sediment is stored in each of these compartments and a change in sand load of any one affects the others. There is a dynamic state of equilibrium where sand continually shifts between terrestrial and marine systems (Tinley 1985; Cowell et al. 1999) due to sorting and redistribution by wind, waves, tides and currents (King 1972; Knox 2000; Roy et al. 1994; Woodroffe 2002).

Sand is highly mobile, yet its movement is regionalized: longshore and across-shore transport occurs within and between adjacent coastal process units, the boundaries of which are to some degree dictated by the configuration of the coastline (Bray et al. 1995; Carter and Woodroffe 1994; Cowell et al. 1999; Woodroffe 2002). The mobility of sand explains short-term variation in volume and shore profile of beaches (King 1972; Knox 2000; Roy et al. 1994; Woodroffe 2002), as well as their effective continuity, even on coasts where rocky headlands disrupt transport processes and cause embayment of sand deposits (Cowell et al. 1999; Little 2000; Storlazzi and Field 2000; Pontee et al. 2004).

### 2.2.3 Mixed substrate shores

In a structural sense, the mixed substrate shore appears to occupy a position intermediate to that of a sand-free rocky shore and a sandy beach with a substantial sand prism (Bally et al. 1984) and is most likely to occur along sediment deficient-coasts where the shore platform slope is slightly less gentle (Roy et al. 1994; Short 1999). On sediment-deficient coasts, the beach veneer is diminished, partly exposing underlying bedrock or a lag of coarse material, so that wave processes are influenced directly by hard substrate, a phenomenon termed ‘structural control’ (Short 1999) or ‘geological control’ (Jackson et al. 2005).

The periodic inundation of rocky shores by sand followed by its sudden and complete removal during a storm is a well-known phenomenon (Airoldi 2003). In such a season- or tide-driven accretion-erosion cycle, the beach is a transitory feature of the coast, i.e. an ephemeral beach *sensu* McLachlan and Brown (2006). From the literature, the hallmark of an ephemeral beach appears to be that high wave action periodically causes a radical change in the appearance of the beach prism. Rapid removal of massive amounts of mobile sediment exposes the underlying coarse lag or even the rock bed itself: an event followed by a slow rebuilding of the beach (Short 1999; Storlazzi and Field 2000; Hubbard and Dugan 2003, McLachlan and Brown 2006).
There are plentiful examples of rocky coasts with small, shallow permanent sand deposits (Littler et al. 1983; Sunamura 1992; Knox 2000). These include the high shore beach deposits of rocky shores, up-shore platform beaches (Short 1999), pocket beaches and shores where the sediment supply is sufficient to maintain deposits, with various degrees of temporal fluctuation, around and over bedrock outcrops (see Daly and Mathieson 1977; Littler et al. 1983; D'Antonio 1986; Short 1999; Knox 2000; Anderson et al. 2008). Transport of sediment between such embayed or structurally isolated beaches is under geological control by bedrock and headland configurations: under calm conditions geological barriers prevent alongshore beach to beach transport, needing storm episodes to effect the mobilization of sediment (Storlazzi and Field 2000). Very sheltered enclosed pocket beaches may, indeed, have no net alongshore sediment movement (Woodroffe 2002).

2.3 The dynamic component: wave environment

Wave activity and water movement play a central role in determining the living conditions of intertidal biota whether they inhabit beach sediment or rock surfaces (Lobban et al. 1985; Norton 1985; Brown and McLachlan 1990; Short and Hesp 1999; Knox 2000). Shore slope and the height of approaching waves ultimately determine the wave type on making landfall: given a constant wave height, a gentle slope would produce dissipating waves and the steepest slopes waves of the surging kind (Sunamura 1992).

2.3.1 Consolidated shores

Resistant coastal landforms influence wave direction and activity: waves tend to be refracted towards rocky headlands jutting out to sea, resulting in more concentrated wave action at headlands than at adjacent embayed beaches (Short 1999). As at sandy beaches, waves arriving at a rocky shoreline with an off-shore platform, lose energy to turbulence and bottom friction on approaching the shore (Sunamura 1992). There is a reduction in wave height and, depending on water depth over the shore-zone slope, waves reaching the rocky shore could be broken, breaking or standing (Lobban et al. 1985; Sunamura 1992). Breaking waves (~ plunging) exert the greatest force, their action characterized by intense pressure changes, while broken waves (~ spilling or collapsing) exert slightly lower pressure and do so more evenly (Sunamura 1992; Gaylord 2000).

Waves mainly interact with the rock topography at the seaward edge of the shore, impinging on seaward-facing surfaces and elevated points, and in this way the degree of attenuation and shelter within a site is determined (Lewis 1964; Hopley 1982; Sunamura 1992; Gaylord 2000). Within the intertidal zone, wave energy is reflected (Sunamura 1992), but also
dissipated during horizontal movement over hard bottom, when bottom roughness increases turbulence (Lobban et al. 1985) and slows down flow rate (Koehl et al. 1993). Shore topography further controls the flow of water (Jeffery and Underwood 2000) and dictates drainage patterns on an outgoing tide (Lewis 1964).

2.3.2 Sedimentary shores

Short’s (1999) definition of a beach includes all the wave-deposited material between modal wave base (the depth at which waves ‘feel the bottom’ and entrain sediment) and the swash limit (the landward extreme of wave action and sediment transport on the shore face). This definition provides for wave transformations and other associated processes as waves make landfall. Natural beaches are dynamic, changing systems that respond to a range of variables related to its regional and/or latitudinal situation, sediment and wave characteristics, giving expression in its morphodynamic state (Short 1999). Wave activity in the surf zone changing with tidal phase is the primary factor in moulding the sand prism of sandy beaches (Short 1999).

The resultant beach profile is the physical expression of the forces acting on a beach (Short 1999; Muñoz-Pérez et al. 1999), provided, of course that there is no impeding or obstructing hard substrate present (Larson and Kraus 2000; Wang and Kraus 2005). Beach profiles are constantly adjusted, in so far as the beach material allows, in response to wave action, but, in turn, also influence the breaking behaviour of waves (i.e. spilling, plunging, collapsing or surging) on the shore (Short 1999). Waves expend slightly more energy at their initial breaking point in the surf zone, and then again in the swash zone, than over the intervening distance (Wang and Kraus 2005). The fate of wave energy at the shoreface can be deduced from predominant breaker type: spilling and plunging breakers result as wave energy is dissipated on entering the surf zone, while surging breakers are typical of a reflective environment where wave energy is finally only expended on and reflected off the beach (Aagaard and Masselink 1999).

The classification of beaches into three morphodynamic types, i.e. dissipative, intermediate and reflective, and the parameters that influence type, is given a clear exposition in Short (1999). Depending on wave height, wave period and sediment grain size, beaches can transform from one state to another over time (Short 1999, Woodroffe 2002). Dissipative sandy beaches lie at the high energy side of the scale: they form on wave-exposed coasts composed of fine sand and are characterized by a high wave regime (spilling breakers) and a broad, flat surf zone and beach (Short 1999; Little 2000; Woodroffe 2002). Steep (high energy) waves transport more sediment offshore than onshore, which tends to lower beach
slope especially in fine-grained beaches (King 1972; Brown and McLachlan 1990; Cowell et al. 1999; Hughes and Turner 1999). Intermediate beaches occur in a variety of settings, depending on coastal structure, consist of fine to medium sand and experience lower energy wave conditions than fully dissipative beaches (Short 1999). They are characterised by steeper near-shore and intertidal beach gradients and more variable surf zone topography than dissipative beaches (Short 1999). Waves reaching these beaches transition first into spilling or plunging breakers (in the surf zone) and may reform into surging or collapsing breakers (in the swash zone) as they traverse the shore (Aagaard and Masselink 1999; Masselink and Turner 1999; Short 1999; Woodroffe 2002). At the lower end of the energy scale are narrow, steep, reflective beaches with greatly reduced surf zones (Short 1999). Waves shoal up over a steep near shore topography and surge or collapse directly onto a beach composed of fine to very coarse grained sediment (Short 1999; Woodroffe 2002). The proportion of sand in the sediment mixture strongly influences beach response: at 25% or more the beach gradient is lowered and beach type shifts towards the dissipative end of the scale (Mason and Coates 2001; Pontee et al. 2004). Fine sediment reflective beaches will only form in a low wave climate (wave-sheltered), while coarse beaches (medium sand to boulders) are reflective regardless of wave exposure (Short 1999).

2.3.3 Mixed substrate shores

The nature and size of any beach deposit depends on the characteristics of the geological substrate, particularly, its gradient (Roy et al. 1994), its morphology relative to sea level and prevailing wave climate (Short 1999), and the coastal topography, also termed ‘geological inheritance’, (Roy et al. 1994), as this last factor directly affects dynamic processes such as wave shoaling and transformations (Short 1999). Non-erodible hard surfaces, whether natural or man-made, within the surf zone of a beach has been shown to modify wave behaviour and disrupt surf circulation patterns (Short 1999; Short and Masselink 1999; Larson and Kraus 2000).

The orientation of the hard substrate relative to wave direction is a major determinant of its effect on the behaviour of the beach. Shore-linear structures that cause wave breaking and dissipate wave energy include off-shore coral reefs (Hopley 1982; Jokiel and Morrissey 1993; Woodroffe 2002), fringing reef systems (Roberts et al. 1975; Short 1999; Woodroffe 2002), near-shore beach rock reefs (Short and Masselink 1999; Hesp and Short 1999), breakwaters (Short and Masselink 1999) and exposed rock substrates at the seaward edge (Hopley 1982; Short 1999) or in the middle reaches (Jackson et al. 2005) of sandy shores, as well as sea grass beds (Peterson et al. 2004), algal reefs (Short 1999) and kelp beds...
(Schiel et al. 2006). All of these increase bottom roughness (Hopley 1982; Short 1999) which, in turn, brings about lower wave height, a truncated surf zone and a steep, low energy reflective beach where wave activity is restricted to the swash zone (Short 1999; Muñoz-Pérez et al. 1999). Shore-perpendicular rock outcrops on a beach have similar effects to headlands and groynes. They disrupt normal surf zone circulation, change wave shoaling and refraction patterns, cause up-drift accumulation and down-drift erosion of sand, realignment of the beach, and, induce rip currents with the added effect of erosion due to scour (Short and Masselink 1999; Larson and Kraus 2000; Nordstrom 2000). All of these effects lead to changed beach shape, type and length (Short 1999; Short and Masselink 1999). In addition, wave refraction and greater variation in wave direction produce a crenulated shoreline, which directly affects the living conditions of beach biota (Short 1999). At mixed substrate shores where the rock component predominantly occurs within the surf zone, mainly as shore normal reefs, it results in the formation of a dissected beach with an irregular shoreline (Short and Masselink 1999; Hesp and Short 1999; Larson and Kraus 2000).

Many mixed substrate shores consist of horizontal shore platforms of beach rock (beach calcarenite) or dune rock (aeolian calcarenite) with a thin sandy veneer. Platform topography exerts control over moisture and sediment retention by shore surfaces (Lewis 1964; Koehl et al. 1993) and if close to the surface, possibly even exposed in places, would greatly reduce beach permeability and percolation rates (Short 1999). Increased beach saturation makes the beach less stable and promotes sediment removal (Short 1999). A sediment-deficient beach has a limited ability to respond to the dynamics of its wave environment (Jackson et al. 2005). Periodic fluctuations in the depth of the sand veneer will result where removed sand is not replaced soon enough.

Where high relief rocky shores permit the accumulation of up-shore sand deposits, platform beaches are formed (Short 1999). As a result of wave energy dissipation over the rocky traverse and strong reduction in wave height, wave activity on platform beaches tends to be limited and they resemble stable, accreting wave-sheltered sandy shores. Like pocket beaches, however, the sediment supply of platform beaches is restricted (Woodroffe 2002) and their potential for profile adjustment limited, as they are active only during mid to high tide levels (Short 1999). Both pocket beaches and platform beaches with their associated rock substrates could potentially be regarded as mixed substrate shores.

2.4 The macrobiota of intertidal rock surfaces

2.4.1 The influence of the wave environment
At rocky shores under heavy wave attack, sessile filter-feeders dominate the upper exposed rock surfaces, while seaweeds are mostly confined to lower elevations (Velimerov et al. 1977; Lubchenko and Menge 1978; Lobban et al. 1985; McQuaid and Branch 1984, 1985; Schiel 2004). As one moves from highly exposed to sheltered shores, there is a change in algal species composition and physiognomy: delicate species become more common and individuals of other taxa become less robust (Norton et al. 1981; Lobban et al. 1985; Schiel et al. 2006). At moderately wave-exposed and sheltered rocky shores seaweeds reach their highest levels of abundance and diversity (Norton 1985). The dominance shift from filter-feeders to algae under milder wave conditions may be facilitated by more effective predation on sessile filter-feeding competitors (Lubchenko and Menge 1978; Lubchenko 1980), but Schiel (2004) highlighted the complexity of interactions among deciding factors and proposed that more processes should be considered, e.g. propagule supply, pre- and post-settlement processes involving substrate, wave action and sedimentation, as well as oceanographic features such as upwelling and circulation.

2.4.2 The influence of sediment on rock surface communities

The significance of sedimentation as an ecological factor capable of influencing community composition of hard shores has long been recognized (Airoldi 2003). Early studies of rocky shore assemblages reported local exclusion of species (e.g. Kitching et al. 1934; Chapman 1941; Stephenson 1943), changes in species composition (Sloane et al. 1961; Stephenson and Stephenson 1972; Moore 1972) and increased abundance of ephemerals (Chapman 1941).

The mechanisms by which sediment controls community biodiversity and functioning are as yet poorly understood (D’Antonio 1986; Airoldi 2003). Responses of biota, reported in the literature, do not always follow simple, predictable patterns and appear to be largely due to the interplay between the imposed sedimentation regime with associated effects, such as smothering and scour, water movement regimes and the ability of the species to tolerate a certain degree of inundation. While in some instances the mere presence of sediment could eliminate some species, others might be indifferent to it or tolerant of its presence provided the water movement regime suits them (Sears and Wilce 1975; Suchanek 1981; Stewart 1982, 1983; D’Antonio 1986; Pineda and Escofet 1989; Airoldi et al. 1996; Airoldi 2003).

Airoldi (2003) provides a comprehensive review of progress made in unravelling the complex relationships between sedimentation regimes (natural or anthropogenic) and the biota of littoral and sublittoral rocky habitats. The interpretation of sediment effects is often confounded by the reality that trends in sediment deposition co-vary with wave action and
water movement (Stephenson and Stephenson 1972; Daly and Mathieson 1977; Devlinny and Volse 1978; Gibbons 1988b). Add heterogeneous shore topography, and a variable temporal component, and it becomes very difficult to disentangle one effect from the other (Stephenson and Stephenson 1972; Dobkins 1992; Airoldi 2003). Effects of sediment on established biota as well as new settlers have been linked to the extent of sedimentation (volume, depth, area covered), particle characteristics (e.g. size, shape, mineralogy) as well as timing, frequency and locality (Airoldi 2003).

2.4.2.1 Sediment-inundation as a stress or disturbance

Whether sediment-inundation is viewed as an agent of stress or disturbance depends to a large degree on the response of the community. Where inundation by sand reduces productivity it acts as an environmental stress (sensu Grime 1977). Macroalgal assemblages of sand-affected rocky shores have been characterised as stressed or stress-tolerant in a number of studies, e.g. Littler and Littler (1980), Stewart (1983), Littler et al. (1983), Taylor and Hay (1984). Sand inundation can simultaneously induce stress (e.g. through smothering) and cause disturbance (e.g. through scour) eliciting a range of responses in a community linked to different abilities to tolerate these effects (Littler et al. 1983).

Massive sedimentation of rocky shores constitutes a disturbance (sensu Grime 1977) with destructive effects (e.g. loss of biomass) not unlike those of wave-borne logs (Dayton 1971; Connell and Keough 1985), overturned boulders (Sousa 1979, 1984, 1985; Littler and Littler 1981), ice scour (Petraitis and Dudgeon 2005), intense desiccation (Littler and Littler 1981), pollution (Littler and Murray 1975), intense predation (Schiel 2004) or destructive and indiscriminate harvesting (Airoldi 2003). Destructive effects have been attributed to burial per se (Daly and Mathieson 1977; Seapy and Littler 1982; Airoldi 2003), anoxic smothering during burial (Daly and Mathieson 1977; Littler et al. 1983; D'Antonio 1986; Anderson et al. 2008) and abrasion or scouring by coarse clastic material (Robles 1982; Kendrick 1991; Airoldi 2003; Schiel 2004).

In his intermediate disturbance hypothesis, Connell (1978) proposed that intermediate levels of disturbance could allow a much higher species richness than a very high or very low disturbance regime. Results of a number of studies, some based on sand-inundated rocky shores, lend support to this hypothesis. Littler and Littler (1981) reported increased diversity in a stable Corallina officinalis Linnaeus dominated turf on low shore boulders as a consequence of small-scale disturbances (overturned boulders). In a similar way, sediment removal could uncover an area of unoccupied substrate (a patch), soon colonized by new propagules from elsewhere or immigrants from adjacent established communities (Sousa
Many simultaneous patches of different sizes and ages increase spatial heterogeneity and biodiversity (Connell and Keough 1985). McQuaid and Dower (1990) invoked Connell’s (1978) intermediate disturbance hypothesis in linking increased overall faunal species richness of mixed substrate shores, as compared to sandy beaches and rocky shores, to increased habitat heterogeneity because of patchy sand deposits. Along similar lines, Airoldi and Cinelli (1997) reported an increase in overall diversity and evenness with uneven sedimentation. Seasonal inundation-removal cycles of coarse sediment and scouring by sediment under a high wave action regime has been linked to seasonally enhanced community variability at disturbed sites, whereas undisturbed sediment-free areas did not exhibit seasonal variation (Robles 1982).

Pickett and White (1985), however, pointed out some inherent difficulties in testing the intermediate disturbance hypothesis, maintaining that any form of disturbance occurs in a multivariate setting and operates within a particular scale, hence, unless scale is defined, and influences and responses quantified, testing the concept is always going to be difficult.

2.4.2.2 Sediment grain size and type

Modal particle size determines settling velocity and ease of re-suspension of the sediment bulk, which, in turn, affects the mobility of sediment deposits (Short 1999). Where wave action and flow speeds are greater, sediment deposits are predominantly coarse-grained as fine sediment is easily resuspended and swept away (Dommasnes 1968, 1969; D’Antonio 1986; Gibbons and Griffiths 1986; Gibbons 1988b; Schiel et al. 2006).

Sand is most often the sedimentary material affecting benthic assemblages of hard substrate in intertidal and shallow subtidal habitats (Airoldi 2003; Schiel et al. 2006), but silt (Kitching et al. 1934; Moore 1972, 1985; Little and Smith 1980; Jensen 1984), clay (Hicks 1980), organic particulate matter (Moore 1972; Airoldi et al. 1996) and shell fragments/ grit (Moore 1972) have also been reported. Sand suspended under wave-exposed situations scour hard substrate and biotic surfaces with increasing severity as wave activity intensifies (Daly and Mathieson 1977; Craik 1980; Robles 1982; Kendrick 1991; Sunamura 1992).

Fine particulate matter suspended in turbulent water increases turbidity, thereby reducing light availability (Airoldi 2003; Schiel et al. 2006) and, consequently, primary production (Goldberg and Foster 2002) and food availability (Hicks 1980). Studies of the macrobiota of both primary (Sloane et al. 1962; Velimerov et al. 1977; Norton et al. 1981; Airoldi et al. 1996; Schiel et al. 2006) and secondary (i.e. biotic) substrates (Dommasnes 1968, 1969; Seed 1985; Gibbons 1988b; Moore 1972; Warwick 1977; Trotter and Webster 1983; Boaden
1996), showed changed species composition and lower diversity in the presence of fine deposits. Anthropogenically generated sediment may involve types and sizes of particles not natural to the specific environment (e.g. organic and other pollutants) and have been linked to loss of fucoid and laminarian canopy species or reduction in their depth range, reduced overall species diversity, increased abundance of ephemerals and a conversion to low biomass turf and/or encrusting forms, e.g. Littler and Murray (1975), Benedetti-Cecchi et al. (2001), Shepherd et al. (2009).

2.4.2.3 Sediment quantity

Even very low quantities of sediment may reduce settlement success of algal or animal propagules, though the degree varies from species to species and within populations (Devinny and Volse 1978; Robles 1982; Schiel et al. 2006). This differential response could explain the progressive decrease in $\alpha$-diversity (Balata et al. 2007), conversion to algal assemblages dominated by only a few filamentous turf-forming species (Airoldi and Cinelli 1997) as well as shifts in algal and invertebrate dominance patterns (Irving and Connell 2002) in subtidal studies where incremental amounts of sediment were experimentally added. However, macroalgal dominance (measured in biomass) of intertidal surfaces may still be more strongly influenced by the cross shore gradient of desiccation, irradiance, competition for primary space, and different water movement regimes, than sediment (Gibbons and Griffiths 1986).

In the few studies where sediment was quantified, measures used were not uniform. In situ determinations of quantity ranged from estimated percentage sand cover (Stewart 1982; Littler et al. 1983; Schiel et al. 2006), depth (Daly and Mathieson 1977), mass (Stewart 1983; Branch et al. 1990; Engledow and Bolton 1994) or volume per unit area (Gibbons and Griffiths 1986) to relative measures of sediment depth over rock surfaces with irregular topographies, e.g. degree of burial (Trowbridge 1996) or the height of sediment against a static object (Daly and Mathieson 1977; Hubbard and Dugan 2003). Rates of deposition were obtained from traps (e.g. Little and Smith 1980; Airoldi et al. 1996; Schiel et al. 2006).

It is conceivable that there should be a threshold above which the biotic assemblage shows the effects of sediment accumulation. Engledow and Bolton (1994) demonstrated a reduction in $\alpha$-diversity of macroalgae, as well as mussel and limpet biomass where the mass of sediment exceeded 5.6 kg m$^{-2}$, but negative effects of sediment were offset by increased wave action. Similarly, Schiel et al. (2006) found a negative correlation between degree of wave exposure and quantity of sediment trapped and deposited, as well as a change in mollusc and macroalgal species composition with wave action and sediment. High sediment
deposition rates, 1.6 to 52.4 g m$^{-2}$ d$^{-1}$, did not appear to affect shallow subtidal filamentous algal turf in a wave exposed site (Airoldi et al. 1996). The threshold value concept and its relationship with wave action clearly require more investigation.

2.4.2.4 Temporal patterns in sedimentation

Natural sedimentation is often of a cyclical nature and communities that appear to be under long-term inundation are cleared of sediment for brief intervals (Airoldi 2003). Consequently, for at least part of the time, biotic assemblages are relatively sediment-free and able to perform life-functions (e.g. sexual reproduction) that would be impaired or impossible during burial (Taylor and Littler 1982; Stewart 1983; Trowbridge 1996; Airoldi and Cinelli 1997; Eriksson and Johansson 2005; Anderson et al. 2008). This may explain why communities in areas with regular sand-inundation are often composed of species with vastly different degrees of sand-tolerance (Anderson et al. 2008). Natural sediment inundation cycles are mainly seasonal or tide-related: seasonal inundation of rock surfaces tends to be deeper and for longer periods (months) than accretion due to the change from spring to neap tide (Daly and Mathieson 1977; Taylor and Littler 1982; Stewart 1983; D’Antonio 1986; Hubbard and Dugan 2003; Anderson et al. 2008).

Long-term deposition of sand or silt has been implicated in a range of changes in rock substrate communities: suppressed species diversity (Daly and Mathieson 1977; Seapy and Littler 1982; Brown et al. 1991; Airoldi and Cinelli 1997; Carballo 2006; Balata et al. 2007; Shepherd et al. 2009) and lower biomass (D’Antonio 1986); local extinctions (Daly and Mathieson 1977; Branch et al. 1990; Engledow and Bolton 1994; De Clerck et al. 2005; Carballo 2006); truncated intertidal subzones (Stephenson and Stephenson 1972; Brown et al. 1991); shifts in dominance patterns of major habitat-forming macroalgae (Sears and Wilce 1975; Little and Smith 1980; Hiscock 1985; Schiel et al. 2006; Shepherd et al. 2009) and, permanent change in the composition of communities due to increased cover by ephemerals (Littler and Murray 1975; De Clerck et al. 2005), sand-tolerant species (Stephenson and Stephenson 1972, Littler et al. 1983, Stewart 1983; Carballo 2006; Schiel et al. 2006) and turf-forming species (Daly and Mathieson 1977; Taylor and Littler 1982; Airoldi et al. 1996), usually at the expense of less tolerant taxa (Littler and Murray 1975; Carballo 2006; Shepherd et al. 2009).

2.4.2.5 Sediment-tolerance as a factor in the composition of epilithic assemblages

The presence of variable quantities of sediment on and around hard substrate shores and their biota, with the added factor of long-term near static sea level (Trenhaile 2002), would
have led to the development of benthic assemblages suited to prevailing conditions (Littler et al. 1983; Stewart 1983; D’Antonio 1986; Brown 1996; Schiel et al. 2006; Balata et al. 2007). The persistence of particular species of macroalgae and macrofauna on sand-inundated rock substrate appears to depend on their ability to cope with prevailing conditions (e.g. Stewart 1982; D’Antonio 1986; Pineda and Escofet 1989; Williams et al. 1995; Airoldi et al. 1996; Trowbridge 1996; Airoldi 2003; De Clerck et al. 2005; Carballo 2006; Balata et al. 2007; Sloan and Irlandi 2008; Anderson et al. 2008). Sediment deposition-removal cycles facilitate the regeneration of sediment-tolerant algae that have persistent holdfasts, as well as an increase in opportunistic macroalgae and highly productive sessile macrofauna capable of rapid recruitment to bare surfaces, both of which would bolster biodiversity (Littler et al. 1983; McQuaid and Dower 1990; Bolton and Anderson 1997; Anderson et al. 2008), albeit a temporary effect (Sousa 1979).

The continued presence of mobile sand certainly seems to be a requirement of sand-tolerant algal assemblages on subtidal mixed substrata of pebble-cobble-sand (Hiscock 1985) and shell-sand (Sears and Wilce 1975) that include a high proportion of annuals, many fast-growing, opportunistic species of, for example, Enteromorpha, Chaetomorpha, Ulva and Cladophora, as well as turf-forming filamentous algae (Sears and Wilce 1975; Stewart 1982; Littler et al. 1983). Sand-inundated rocky habitats could serve as refugia for species requiring the presence of sand to thrive (e.g. Airoldi (2003) and references within). Macroalgal species commonly found on sand-influenced rocky shores often occur at steep wave-exposed shores where sand is not an environmental factor, but never attain the same levels of dominance (D’Antonio 1986). The seagrass Phyllospadix, for example, needs sand for anchorage and abundant growth (Stewart 1982; Littler et al. 1983). A low sediment load could then constitute a stress for Phyllospadix. D’Antonio (1986) reported a similar trend for Neorhodomela larix (Turner) Masuda (as Rhodomela larix (Turner) C. Agardh).

Higher sediment loads do seem to universally lead to the development of turfs dominated by filamentous rhodophyceans (e.g. Gibbons and Griffiths 1986; Airoldi and Cinelli 1997; De Clerck et al. 2005; Balata et al. 2007; Shepherd et al. 2009; Fraschetti et al. 2011). A ‘turf’ as defined by Neushul and Dahl (1967) is ‘a taxonomically complex component of subtidal vegetation comprising an aggregate of species of small algae and developmental forms of larger algae’ (in Stewart 1982). Intertidal turfs from various parts of the world share taxonomic elements and, despite variations in species composition linked to locality and sometimes season, generally exhibit high species richness (Stewart 1982). Red algal turfs of the Northern Hemisphere usually comprise species of a few common genera with a robust structure, e.g. Corallina, Gigartina, Laurencia, Lomentaria, Palmaria, intermingled with more

Fine textured, thin and delicate forms of algae also occur in wave sheltered conditions, potentially a response to lower wave action as well as less consistent nutrient supply in slower moving water (Norton et al. 1981). The combination of functional forms occurring within algal turfs does not, however, follow any particular trend with a change in wave exposure or shore gradient (Airoldi 2001). It appears that the turf-forming growth habit is advantageous in both wave-exposed and wave sheltered situations. Often both the turf-form and a larger growth habit is found in the same species, but under different environmental conditions, e.g. the South African midtidal dominant, *Gelidium pristoides* (Turner) Kützing grows as a continuous short turf instead of taller separate tufts where it becomes established on wave-washed rock platforms that experience transient sediment inundation (Carter 1986). Fish foraging for phytal prey items inadvertently help to maintain the turf growth form by cropping the algal fronds of both filamentous and foliose forms (Miller et al. 2009).

Turf-forming rhodophyceans of lower intertidal and subtidal hard substrates have an adaptive advantage in the event of sand-inundation and exhibit long-term stability despite regular disturbance or extended periods of stress (e.g. Stewart 1982; Anderson et al. 2008). Many of these species appear in seral stages that precede the climax community for the region, while others are able to survive extended periods of burial or rapidly colonize vacant substrate once sand is moved off (Littler et al. 1983; Airoldi and Cinelli 1997; De Clerck et al. 2005; Anderson et al. 2008). These characteristics are not mutually exclusive. The presence of sediment generally does not negatively affect their propagules (Airoldi 2003) and may possibly create more favourable conditions for settlement (Robles 1982). Coralline algae, a regular element of turfs, are abrasion resistant and tolerant of sand over a range of inundation levels (Stewart 1982; Schiel et al. 2006).

Particular structural modifications, reproductive strategies and physiological adaptations help sand-tolerant algae to survive anoxia, poor light conditions and nutrient deprivation, amongst others, associated with long-term complete or partial burial. They become locally dominant, while species without those attributes are excluded (Sears and Wilce 1975; Daly and
Mathieson 1977; Hay 1981; Taylor and Hay 1984; Lobban et al. 1985; Williams et al. 1995; Gribben et al. 2008). These algae have an extensive ability to regenerate after removal of the apical meristem (e.g. by abrasion, predation, die-back of fronds due to burial), in that they produce lateral fronds that give rise to an irregular morphology (Norton et al. 1981). Some are obligate in this regard, requiring burial for this to occur. This has been demonstrated in several filamentous algae (Hay 1981; Taylor and Hay 1984) as well as Caulerpa spp (Williams et al. 1995) and Codium setchellii N.L. Gardner (Trowbridge 1996). Others possess persistent (long-lived) crustose, rhizomatous or stolon-like holdfasts that are abrasion resistant and able to survive anoxic conditions due to prolonged sand inundation. These produce uprights from the holdfast or spores from a tetrasporic crust once sediment load is reduced or absent (Bolton and Anderson 1997; Stegenga et al. 1997; Anderson et al. 2008; Gribben et al. 2008), in this way pre-empting space and ensuring long-term persistence (Hay 1981; Taylor and Hay 1984; Lobban et al. 1985; Williams et al. 1995; Anderson et al. 2008; Gribben et al. 2008).

Algal turf and other species carpeting low rock surfaces and colonizing cracks and hollows in rock, usually have a complex physiognomy and accumulate sediment. Coralline turfs, consisting of a few abundant coralline species mixed with filamentous and other algae, usually have many different epiphytic algae and together form a mesh that traps sediment, shell fragments, organic algal debris and provides a habitat for associated invertebrates (Stewart 1982). The highest quantities of sediment have been recorded from filamentous turfs in sheltered positions (Gibbons and Griffiths 1986) and those with greater structural complexity (Gibbons 1988a).

Moisture loss is an important constraint in the upward extension of macrobiota on the shore. Desiccation, and the degree to which it can be tolerated, has often been cited as the cause for the upper limit of species occupying particular intertidal levels (Norton 1985). The vertical extension of biota usually confined to lower elevations has been observed at wave exposed sites (Norton 1985), as well as gently sloping rock platforms (Lewis 1964) and moist or shaded rock surfaces (McLachlan and Jaramillo 1995). On intertidal surfaces, sediment deposits reduce desiccation stress by retaining moisture within small spaces among fronds or small individuals (Taylor and Hay 1984; Gibbons 1988a; Schiel et al. 2006). Turf algae convert to the non-turf morphology and cnidarians occur as single individuals rather than aggregates when desiccation stress is reduced (Taylor and Hay 1984).

Corallina officinalis, a wide-spread anchor species (sensu Stewart 1982) of algal turf exhibits traits typical of climax species, such as low photosynthetic rates (Littler 1980), low productivity, tolerance of stress and wave action, low palatability and low energy content,
and consequently, low losses to predation and slow colonization (Littler and Littler 1980).
Productivity in subtidal filamentous turfs is much lower than in adjacent taller foliose stands
(Miller et al. 2009). Photosynthetic activity in turf-species occurs mainly in the upper parts of
the fronds, while the lower parts, including the perennating holdfast, are resting, lowering
energy costs to the plant (Hay 1981). Frond tips of sand-inundated coralline turf algae
usually protrude above the sand (Stewart 1983). The turf growth form therefore confers a
number of advantages that offset the main disadvantage of slow photosynthesis, i.e. low
productivity and slow growth due to crowding of fronds that increases self-shading (Hay
1981; Taylor and Hay 1984). The tightly packed uprights typical of the turf-habit reduce the
effects of herbivores, bleaching and desiccation, while enhancing substrate retention and
persistence, as well as tolerance to burial (Taylor and Hay 1984).

2.4.2.6 Effects on biotic interactions and trophic relations

Sandy areas could serve as refuges from competition and predation for sand-tolerant algae
(Sears and Wilce 1975; Littler and Littler 1981; Robles 1982; Stewart 1982; Littler et al. 1983;
Taylor and Hay 1984; D'Antonio 1986). Quantities of trapped sediment or a covering of
sediment release slow-growing stress-tolerant species from competition with faster-growing,
less sand-tolerant dominants (Sears and Wilce 1975; Suchanek 1981; Norton et al. 1981;
Stewart 1982; Hiscock 1985). The red alga Neorhodomela larix, for example, dominates
(competes more successfully) on sand-inundated shores because of its greater ability to
survive sand-burial than its competitors (D'Antonio 1986). Suchanek (1981) demonstrated
that periodic inundation by sediment (i.e. disturbance) mediates competition between mussel
species, where the less competitive, but more opportunistic species persist by colonizing
space left vacant when the dominant sand-intolerant competitor is killed. Differences in the
ability to tolerate conditions associated with sand-inundation may explain habitat partitioning
in limpet species with similar grazing preferences (Marshall and McQuaid 1989).

Predator-prey relations can be mediated by sediment inundation-removal cycles and
effectively increase community variability (Robles 1982). Low densities or absence of
important herbivore species have been noted in a number of studies, e.g. Stephenson and
Stephenson (1972), D'Antonio (1986), Branch et al. (1990), Engledow and Bolton (1994),
Schiel et al. (2006), Anderson et al. (2008), although it was not always clear whether this
was a response to increased sand load or a wave action gradient. The absence of grazers
was inferred from reduced biomass loss by macroalgae (see Schiel et al. 2006) and
unchanged species diversity and richness (see Engledow and Bolton 1994). Grazing
herbivores are known to feed on a micro-algal biofilm and macroalgal sporelings on rocks
and biotic surfaces, rather than the seaweed tissues themselves, so would affect community
composition by removal of newly settled propagules (Robles 1982; Branch 1985). Removal of algal biomass rather occurs through cropping by foraging fish (Stewart 1982; Miller et al. 2009). Although all the molluscan grazer groups (*sensu* Steneck and Watling 1982) are represented at mixed substrate shores, coralline and filamentous turfs are extensive, a probable indication of a size refuge from predation and/or persistence because of grazer resistant holdfasts (Steneck and Watling 1982).

2.4.2.7 *Effects of sediment on epibiotic assemblages*

By controlling sediment accumulation and water flow patterns, the structural complexity of macroalgae and sessile macrofauna determines the micro-environment (Seed 1985). Together with food availability, the micro-environment is a leading factor in controlling the distribution and composition of macro- and meiofauna associated with sessile macrobiota of rock substrate (e.g. Mukai 1971; Norton 1971; Trotter and Webster 1983; Boaden 1996). Even in the absence of sediment, macroalgae and some sessile macrofauna harbour a suite of macro- and meiofaunal taxa unique to their associated micro-environment (Hagerman 1966, 1968; Hicks 1980, 1985). Greater structural complexity has been linked to higher macrofaunal and meiofaunal diversity and numbers, as well as a shift in species composition of the animal assemblage (e.g. Wieser 1952; Sloane et al. 1962, Warwick 1977; Beckley and McLachlan 1980; Coull et al. 1983; Hall and Bell 1993; Hicks 1982; Heip et al. 1985; Hicks 1985; Gibbons and Griffiths 1986; Gibbons 1988b).

The micro-environment associated with macroalgae is referred to as the phytal environment (Hicks 1985). Deposited matter modifies the phytal micro-environment and, consequently, the composition of epiphytic assemblages (Wieser 1952; Coull et al. 1983; Hicks 1985; Seed 1985), which has implications for the trophic composition and energy flow patterns of the system. Epiphytic communities (e.g. microalgae – diatoms and cyanobacteria) could be regulated by basiophytes (e.g. seagrasses) through modification of its microenvironment and so determine the nature of the assemblage that may ultimately contribute a meaningful proportion of primary production and serve as food source to herbivores (Pinckney and Micheli 1998). Basiophyte selection is probably linked to surface relief, chemical stimuli, micro-environmental gradients along the algal thallus, or the presence or absence of an anti-fouling agent (Seed 1985). Sediment covering or trapped among fronds of turf algae also prevents fouling by epiphytes (Sears and Wulce 1975; Suchanek 1981; Norton et al. 1981; Stewart 1982; Hiscock 1985).
Substratum complexity of macroalgae is a powerful driver in the provision of refuges to prey of small size, contributing to faunal diversity and density, and algal turfs play an important role in this regard (Hicks 1985). Given optimal conditions, phytal meiofauna densities can rival those of sedimentary habitats, while phytal macrofauna also reach high levels of abundance and diversity (Hagerman 1966; Hicks 1985). Algae with a dense growth form that are covered with detritus and epiphytic growth (food sources) support the highest numbers of phytal macrofauna (Hagerman 1966). Whereas medium to coarse sediment accumulations are positively correlated with high habitat heterogeneity and diversity of phytal assemblages, fine sediment clogs spaces and reduces algal surface relief and availability, which leads to a reduction in habitat complexity (Hicks 1980, 1985). This shifts the microscopic food supply from microalgae to bacteria and limits population expansion of particular phytal species and overall herbivore diversity with a knock-on effect further up the food chain (Hicks 1980, 1985).

2.4.3 Mixed systems: trophic linkage of adjacent habitats

Adjacent dissimilar marine systems could function as single systems by having interlinked food webs (Eltringham 1971). Several studies of intertidal and subtidal marine biota supply evidence of habitat expansion (Round and Hickman 1984; Connell and Keough 1985; Hicks 1985; Chapman 2002), alternating use (Jensen 1981, 1984; Bell and Coen 1982; Bell and Hicks 1991), and trophic coupling involving dissimilar adjacent marine habitats (Bustamante and Branch 1996; Rilov and Schiel 2006; Schaal et al. 2008). Trophic linkage of dissimilar adjacent habitats has been shown to occur via resuspended organic particulate matter produced within one habitat and then utilized by biota of the other (e.g. Bustamante et al. 1995, Bustamante and Branch 1996), but not so much direct consumption of live material (Schaal et al. 2008).

Where sediment beds (sand) and macrophytes or sessile macrofauna of hard substrate occur in close proximity, the sandy habitat serves as a source of vagile immigrant meiofauna and macrofauna (Hicks 1985). These may rapidly colonize new phytal or faunal substrate and subsequently oscillate between habitats (Bell and Coen 1982; Bell and Hicks 1991). Alternate use of sandy and other habitats (e.g. rock areas) in foraging for food has been described for several gastropod species (Vermeij 1978; Brown et al. 1991; Brown 1996). The use of prey from adjacent dissimilar environments forges a trophic linkage between two habitats that would otherwise appear to be entirely separate in their functioning, e.g. seagrass meadow and hard substrate (Schaal et al. 2008), or, intertidal rock platforms close to subtidal reefs (Rilov and Schiel 2008).
2.5 The macrobiota of sediments

The sedimentary shores of wave-exposed coasts consist mainly of sand (Short 1999), while mud and silt are primarily associated with completely wave-sheltered conditions (Knox 2000). The predominant sediment type on South African shores is sand (Lombard et al. 2004). First believed to be biological deserts, sandy beaches harbour a suite of biota well-adapted for the dynamic environment of the shore face (McLachlan et al. 1993; Brown 2001). The literature review is therefore limited to the macrofaunal assemblages of sandy shores.

2.5.1 Factors shaping the environment

The habitats offered by sandy beaches range from the supratidal dunes and dry beach to the periodically submerged intertidal (littoral) where swash reigns and the subtidal surf zone and near shore zone (Brown and McLachlan 1990; Short and Hesp 1999; Brown 2001). As three-dimensional habitats, the sediment and water column are also vertically differentiated (Short and Hesp 1999). In contrast to the static substrates utilised by rocky shore biota, beach sediment is unstable, capable of being lifted off and transported away by wave action and water movement, or at least shifted about in situ (Little 2000). The ability to move quickly, whether on the surface of the substrate or within it, is an important survival tool in such a dynamically changing situation, consequently, the macrofauna that inhabit beaches are for most part highly motile and well capable of burrowing (Brown and McLachlan 1990). The wave (swash) climate, sediment characteristics and tidal range are the major physical parameters affecting the fauna and flora of sandy beaches via their influence on beach morphodynamics (Brown and McLachlan 1990; Defeo and McLachlan 2005).

2.5.2 Beach morphodynamics and community parameters

Dissipative beaches support a more diverse assemblage of macrofauna than reflective beaches, demonstrating the role of the wave climate and beach morphodynamics in determining community structure (Hacking 1998, McLachlan and Dorvlo 2005). A reflective beach is seen as a potentially harsher environment than a dissipative beach because of the swash climate, where waves break directly on the beach and swash is rapid (Brown and McLachlan 1990, Brown 2001). Greater percolation rates at coarse, reflective beaches bring about rapid drainage and promote faster drying of the top layers of sediment where the bulk of the infauna reside (Little 2000, Brown 2001). The unstable, coarse sediment of a reflective beach is a difficult medium to burrow into and for maintaining burrows (Brown 2001).
Simultaneous change in swash conditions and grain size effectively excludes some species from coarse-grained beaches (Nel et al. 2001), a trend that led to the formulation of the *swash-exclusion hypothesis* (SEH) (McLachlan et al. 1993; Defeo and McLachlan 2005), according to which the swash climate is the most important environmental factor determining whether a species will be persist at a beach or not: the harsh swash regime of a reflective beach eliminates all but the most robust and highly motile taxa (McLachlan et al. 1993; McLachlan and Brown 2006).

At meso- to macrotidal beaches, the greater tidal reach increases the range of interaction between waves and beach, pushing the beach state towards the dissipative end of the scale. Tidal influence thus overrides that of waves at these beaches, ameliorating conditions prevailing in the sedimentary habitat, to the extent that more individuals and species can be accommodated, leading to greater diversification of the ecosystem (Short 1999; Defeo and McLachlan 2005; McLachlan and Dorvlo 2005).

Beach length also plays a role in species richness: short beaches or pocket beaches have fewer species than long ones (Brazeiro 1999). As beaches are dynamic systems undergoing change at different spatial and temporal scales it seems reasonable to expect the biota to respond dynamically to these variations. Degraer et al. (2003) found a reduction in species number and abundance with an alongshore steepening beach slope, grain size increase, decreasing beach width and tidal range.

Some species are able to maintain themselves across a range of beach types and environmental conditions. Others, less tolerant of sediments and swash climates not associated with dissipative beaches, are eliminated from intermediate and reflective beaches where wave energy transformations are more variable and sediments not as fine-grained (Nel 1995; Nel et al.1999). Post-settlement processes may furthermore preclude successful establishment of some species (Defeo and McLachlan 2005). Quite possibly, the key to survival and long-term sustainable populations of species typical of highly dynamic beaches could be their innate behavioural, physiological and morphological plasticity that imparts the ability to rapidly adapt to variation in their immediate environment (Brown and McLachlan 1990; Defeo and McLachlan 2005).

The fauna and flora of sandy beaches comprise many major taxonomic groups. The beach sediment and surf zone each have a characteristic assemblage. Except for areas where seagrasses inhabit intertidal and subtidal sands, the major primary producers of the sediment and surf zone are microscopic algae, mostly dominated by diatoms and dinoflagellates (Brown 2001; Defeo and McLachlan 2005). The main taxonomic groups of
beach macrofauna are molluscs, polychaetes and crustaceans (Brown and McLachlan 1990; Brown 2001). Some are filter-feeding and deposit-feeding sessile forms, remaining in burrows in the sand, while others are highly motile scavengers and predators that emerge from the sand to follow the tide or surf wave swash to locate food (Brown 2001). Several insect species frequent the supralittoral zone, many of them depending on a regular input of wrack to maintain a constant presence (Brown 2001; Colombini and Chelazzi 2003).

As at rocky shores, beach biota exhibit cross-shore zonation, but unlike the zonation patterns observed at rocky shores, these zones are dynamic, shifting up or down with the rising or falling tide (Brown 2001). In addition, local variations in water movement, wave action, drainage, shore profile and tidal range, cause the zones to overlap and the boundaries to become blurred (Brown op.cit.). The number of zones possible at a sandy beach is linked to beach morphodynamic state: at a high energy dissipative beach more zones are possible than at an intermediate or reflective beach with the same wave climate (Nel 2000; Brazeiro 2001; Defeo and McLachlan 2005).

Beach macrofauna make up two ecological groups, i.e. intertidal and supratidal forms (Brown and McLachlan 1990; Brown 2001). Intertidal biota respond more strongly to a shift in swash conditions from dissipative towards reflective than the supratidal forms (McLachlan and Jaramillo 1995). Molluscs, polychaetes and crustaceans occupy different positions along the intertidal gradient: crustaceans tend to be more common towards upper intertidal levels and molluscs lower down (Brown and McLachlan 1990; Little 2000; Brown 2001). Isopods and amphipods (whether supra-or intertidal) are less strongly influenced by the swash climate than polychaetes and molluscs and their populations do not exhibit distinct responses to beach type, probably because of their capability of independent and active movement on the beach face (Defeo et al. 1997, 2003; Defeo and Martínez 2003; Giménez and Yannicelli 1997). Semi-terrestrial crustaceans may actually prefer the conditions prevailing at microtidal, reflective beaches, as they are less likely to be immersed there than at a low gradient dissipative beach with slow percolation rates (Defeo and McLachlan 2005). With few exceptions, polychaetes appear to prefer sheltered shores as their numbers and diversity decline with increased wave action (Brown and McLachlan 1990; Brown 2001).

Community abundance and biomass responds to environmental parameters in a less well defined manner than species richness (Defeo and McLachlan 2005). From reflective microtidal to dissipative macrotidal beaches both community parameters increase in an exponential fashion, a trend that has been interpreted as a response to beach gradient (McArdle and McLachlan 1991, 1992; Nel 2000; McLachlan and Dorvlo 2005). The greater
biomass and numbers attained on dissipative beaches in temperate latitudes have been attributed to greater food availability, mainly as a consequence of highly productive surf zone phytoplankton and benthic infauna (McLachlan 1990; McLachlan et al. 1993; Nel 2000; Soares 2003). Higher biomass at maturity, as well as greater fecundity of females at dissipative beaches, has also been linked to increased food supply (Dugan et al. 1994, Defeo and McLachlan 2005). Defeo and McLachlan (op.cit.) summarise the influence of tides and waves as follows: microtidal reflective beaches have the lowest species richness, abundance and biomass and macrotidal dissipative beaches the highest.

2.5.3 Connectivity of communities

Variations in coastal geomorphology superimposed on the biogeographical parameters (e.g. temperature), which basically regulate ranges of species, can give rise to local aberrations in species distribution in the form of a skewed distribution pattern, e.g. unusual reduction in population numbers or disappearance of a species in one part of its distribution range where its optimal habitat is lacking (Soares 2003). Distribution patterns of species also vary over time with large scale climatic episodes (e.g. El Niño Southern Oscillation) that influence reproductive success and recruitment (Defeo and McLachlan 2005). Defeo and McLachlan (2005) recognize the importance of beach interconnectivity via species with planktonic larval forms, regarding these overarching groups as metapopulations (sensu Henderson et al. (1985) in Merriam and Wegner 1992). Where a long-lived planktonic larval stage is present, metapopulations are formed that ensure connectivity and possible gene flow between populations located at beaches influenced by the same hydrographical system; a pattern of ‘source and sink’ populations arise (Defeo and McLachlan 2005). Source populations composed of a range of size classes and ages (juveniles, pre-reproductive and reproductive adults) are expected to occur at a dissipative or low disturbance beach, while sink populations would occur at an intermediate to reflective beach and consist mostly of adults (Lercari and Defeo 2003).

2.5.4 Biotic interactions and trophic relations

While much research demonstrates the overriding control of the physical environment on beach biota (e.g. Brown 1971; Bally 1981; Dye et al. 1981; Brown 1983; McLachlan et al. 1981, 1984, 1993, 1995; McLachlan 1990; McArdle and McLachlan 1991, 1992; Dugan et al. 1994; Nel 1995, 2000; Giménez and Yannicelli 1997; Nel et al. 1999), a growing body of evidence from laboratory and field experiments, as well as observations in the field, indicate that the biotic assemblages of sandy beaches are influenced by both biological and physical

McLachlan (1980a) proposed that beach systems differ in the way they receive their major carbon-inputs. Accordingly, dissipative beaches with well-developed surf zones, deriving their primary production from resident surf zone diatoms, were termed semi-closed ecosystems capable of exporting organic material. Contrasting with those are reflective and low energy intermediate beaches that receive allochthonous carbon inputs or subsidies via periodic wrack deposits (dislodged macroalgae and sea grasses) as well as nutrient and organic input by upwelling events (McLachlan and McGwynne 1986, Colombini and Chelazzi 2003). Wrack deposition also occurs on intermediate beaches and has been associated with increased species richness, abundance and biomass of beach macrofauna (Dugan et al. 2003). Dissipative beaches have greater primary and secondary production, which makes higher predation rates possible, the main predators of beach macrofauna being marine fishes, birds, arachnids, insects and crabs (Brown and McLachlan 1990; Brown 2001; Colombini and Chelazzi 2003; Defeo and McLachlan 2005).

2.5.5 The influence of hard structures on biota

Some of the earliest studies of sandy beaches were based on sites with associated rock, though usually in those instances the rock component was negligible and often confined to the surf zone, leaving a continuous beach (e.g. Brown 1971; Wooldridge et al. 1981; McGwynne et al. 1988). More recent beach studies involving beaches with associated man-made or natural hard structures, e.g. Bayed (2003), Columbini et al. (2003), Degraer et al. (2003), Gauci et al. (2005), have also not considered the potential influence of the proximity of hard substrate on the beach infauna. Studies of infaunal assemblages in subtidal sediments near natural and artificial hard structures showed variations in composition and abundance of infauna linked to sediment characteristics and distance from the reef (e.g. Davis et al. 1982; Ambrose and Anderson 1990; Posey and Ambrose 1994; Barros et al. 2001).

Beach sediments with substantial amounts of associated natural hard substrate were thought to be poor in both species richness and abundance and have not been attractive as research sites (Bally et al. 1984). In a study of such sediments on the Cape Peninsula, Brown et al. (1991) reported the absence of some typical sandy beach species (e.g. Donax
serra Röding and Bullia spp.), proposing that they were excluded by an unfavourable swash climate. Studies of the biotic assemblages of ephemeral beaches of rock platforms or outcrops are also almost non-existent. One such study of a seasonally ephemeral beach, with hugely fluctuating sediment levels, showed that the beach and exposed rocky areas together supported a diverse collection of shore-birds that utilized food sources from both, and attributed it to the great variety of prey and diversified microhabitats (Hubbard and Dugan 2003).

The ecological study of soft shores with emplaced man-made hard structures is a very recent development. These at first focussed only on biota colonizing the hard substrate, e.g. Davis et al. (2002), Chapman (2002, 2003, 2012), but now also incorporate studies of the effects of hard substrate on the normal development of beach communities with a view to improved future coastal management as sea levels rise and coastal transformation increasingly impacts on beaches, e.g. Dugan et al. (2008), Dugan and Hubbard (2010).

Brown (1996) viewed mixed substrate shores as ideal corridors for evolutionary development in marine biota, made possible by the juxtaposition of soft and hard substrates and high spatial and temporal heterogeneity, attributes that could have assisted adaptive change by providing short-term alternative states of stress and release from it.

2.6 The biota of South African mixed substrate shores

The coast of South Africa supports a diverse array of marine flora and fauna, ranging from cool temperate species on the west coast, to warm temperate and tropical species on the south and east coasts, respectively; a situation brought about largely by the juxtaposition of the African continent and the paths of two ocean currents, the cool Benguela and warm Agulhas (Brown and Jarman 1978; Bolton and Anderson 1997; Mucina et al. 2006). Two temperate marine biogeographic provinces have been delineated along the South African coast, each grading into tropical provinces further north and into each other on the south coast, resulting in regions of overlap towards their individual limits (Brown and Jarman 1978; Bolton 1986; Field and Griffiths 1991; Bolton and Anderson 1997). The marine biota of Southern Africa are rich in species and have a high degree of endemism when compared to other regions of the world, probably as a consequence of the isolated position of the southern tip of the continent relative to other landmasses (Brown and Jarman 1978; Bolton and Anderson 1997).

Biogeographical trends have been well documented for several major taxonomic groups, e.g. polychaetes, amphipods, molluscs, fishes (Brown and Jarman 1978). Stephenson and
Stephenson (1972) gave the first comprehensive description of biogeographical distribution trends of rocky shore flora and fauna and provided major insights into the vertical zonation of rocky intertidal biota. Overviews of distribution trends, zonation patterns and ecology of sandy beach biota are given in Brown and Jarman (1978), Brown and McLachlan (1990), and Field and Griffiths (1991). There have also been plentiful studies from an ecological perspective and some of this work is summarized in Brown and Jarman (1978), Branch and Branch (1981), Field and Griffiths (1991).

The west to east temperature gradient along the South African coast is instrumental in two biogeographical trends in macroalgal assemblages: one, a shift in dominant macroalgal life forms, where the large foliose seaweeds characteristic of the cool waters of the west and south-west coast (corresponding to the Benguela Marine Province and Western Overlap, respectively) are gradually replaced by turf-forming algae and articulated corallines in an eastward direction, i.e. in the Agulhas Marine Province and Eastern Overlap, with a concomitant reduction in overall macroalgal biomass; and, two, greatly increased macroalgal species diversity as Indo-West Pacific influences become possible (Bolton and Anderson 1997). Much taxonomic and ecological work has been done on the seaweeds of the Benguela Province, as well as those of Kwazulu-Natal (coinciding with the northern half of the Eastern Overlap and the southern extreme of the Indo-West Pacific Province). The seaweed flora of the South African west coast is described in Stegenga et al. (1997) and that of KwaZulu-Natal in De Clerck et al. (2005). Lubke et al. (1988) and Lubke and De Moor (1998) each include a chapter on seaweeds and many south coast species feature in Stegenga et al. (1997) and De Clerck et al. (2005), but generally, the macroalgal communities of the south and east coasts are less well covered by the literature (Bolton and Anderson 1997).

In addition to the overall effect of a sea temperature gradient on species and life form distribution, a range of different subtidal and intertidal marine habitat types, resulting from variations in geomorphology, topography, wind, wave action and sand deposition, impose their influence on community composition (Field and Griffiths 1991; Bolton and Anderson 1997; Lombard et al. 2004; Mucina et al. 2006). Up to a third of South African shallow subtidal and intertidal habitats are composed of both rock substrate and sand deposits in varying proportions and distributional patterns (Bally et al. 1984; Field and Griffiths 1991; Campbell and Bate 1997; Lombard et al. 2004). The southern and eastern parts of the South African coast, where the Agulhas Marine Province and Eastern Overlap are centred, have a greater proportion of shores with both hard and soft substrata than elsewhere along the South African coast (Campbell and Bate 1997; Lombard et al. 2004).
Much of the ecological and biogeographical information about the biota of mixed substrate shores can be gleaned from publications on either rocky or sandy shores, e.g. Stephenson and Stephenson (1972), Brown and McLachlan (1990), Field and Griffiths (1991), Brown (1971, 2001), McLachlan and Brown (2006), as some of those species extend their range into sections of shore where substrata co-occur. Field guides are useful, especially where habitat information is supplied, e.g. Day (1974), Kilburn and Rippey (1982), Branch et al. (2005, 2010). Several of the macroalgal species mentioned in Stegenga et al. (1997) and De Clerck et al. (2005) have a wide distribution along this coast and are either associated with a degree of sand-inundation or known constituents of sand-tolerant algal turfs.

There is only a handful of Southern African studies featuring or incorporating mixed substrate shores that considered biotic elements of both sand and rock, i.e. Bally et al. (1984), Dower (1989), Brown et al. (1991) and Todkill et al. (2004). In most studies, biota inhabiting only one of the substrate types were investigated, e.g. Brown (1971), McLachlan et al. (1981), Munnik (1989), Engledow and Bolton (1994), McQuaid et al. (1985), Anderson and Stegenga (1989), Engledow (1998) and Anderson et al. (2008). Trends in sand-influenced hard substrate biota were the same as in similar communities elsewhere. At community level, sand inundation was linked to attenuated biodiversity (e.g. Brown et al. 1991, Engledow and Bolton 1994, Engledow 1998), shifts in dominance between macroalgae and sponges (Berry 1982 in Field and Griffiths 1991; Bolton and Anderson 1997), dominance of substrate by algae with persistent holdfasts (Anderson et al. 2008) and greater abundance of sand-binding coralline and filamentous turfs and chlorophycean species with well-developed creeping holdfasts (e.g. Caulerpa filiformis (Suhr) Hering) on sand-influenced subtidal reefs than sand-free reefs (Anderson and Stegenga 1989). The effects of sediment on algal species diversity appeared to supercede those of other environmental factors such as wave action only once a threshold amount was exceeded (Engledow and Bolton 1994). As for the epilithic macrofauna, a number were shown to prefer habitats with a degree of sand-inundation of the rock, for example, the tube-building polychaete Gunnaria capensis (Schmarda, 1861), the anthozoan Bunodactis reynaudi (Milne-Edwards, 1857), the mussel Choromytilus meridionalis (Krauss, 1848) several oyster species and many different gastropod species (Day 1974; Kilburn and Rippey 1982). Physiological ability to tolerate environmental anoxia was shown to be the reason that siphonariid limpets, and not patellids, extend their range into besanded areas for feeding (Marshall and McQuaid 1989).

South African beach ecologists have made major contributions to the study of beach communities and ecological functioning of beaches, e.g. McLachlan (1980a, 1980b, 1990),

Very little data is available on the species diversity and composition of sediment infauna of mixed shores and that which is available does not agree on how it compares to sandy beaches (see Dower 1989; Todkill unpub.). While crustaceans, e.g. *Eurydice longicornis* (Studer, 1883), *Exosphaeroma* spp., *Urothoe* spp., *Talorchestia capensis* (Dana, 1853), and polychaetes, e.g. *Arabella iricolor* (Montagu, 1804), *Eunice* sp., *Glycera tridactyla* (as *G. convoluta* Keferstein, 1862, normally found on sandy beaches, have been recorded at mixed substrate shores, sandy beach molluscs, with the exception of *Bullia digitalis* (Dillwyn, L.W., 1817), appear to be consistently absent (Brown 1971; Wooldridge et al. 1980; Brown et al. 1991).

South African mixed substrate shores play a significant role in supporting a diverse and abundant coastal avifauna and this is thought to be mainly because of the provision of a greater variety of food sources (Hockey et al. 1983). The actual composition of the macrobenthic food base offered resident and migrant avifauna by these systems is, however, largely unknown.
CHAPTER 3  Shore classification

3.1 Introduction

Shores are generally classified based on general physical appearance, hence the reference to rocky shores, sandy beaches and their subtypes resulting from variations in configuration, sediment type and landforms (Knox 2000). This broad-scale approach could lead to underrepresentation of particular marine habitats and communities in marine protected areas (Blamey and Branch 2008). Alternatively, the characteristics of the biotic assemblages could be used as indicators for habitat type and associated processes, an approach that could accommodate small scale variation and ensure detection of significant, unique assemblages (Hill et al. 1998; Blamey and Branch 2008).

3.2 Physical shore classification of the South African coast

Previous shore classifications of the South African coast were undertaken for the purposes of vulnerability assessment (Jackson and Lipschitz 1984), scientific research (Hockey et al. 1983; Campbell and Bate 1997) and conservation assessments (Lombard et al. 2004). Dedicated aerial and land-based surveys, aerial photographs, topocadastral maps, and satellite imaging, often combined with extensive travelling along the coast to ‘ground-truth’ remote observations, have all been employed in order to interpret and map the South African coastline (e.g. Hockey et al. 1983; Campbell and Bate 1997; Lombard et al. 2004). Bally et al. (1984) broadly grouped coastal habitat types of the open shoreline of the Southern African coast as sandy beaches, rocky shores and mixed shores. The latter includes cliffs with sandy bases, sand overlying shore platforms and mixed boulder shores, following the interpretation of Field and Griffiths (1991), but also beaches shorter than 1 km, following the interpretation of Campbell and Bate (1997). The marine biodiversity assessment of the South African coast, undertaken by Lombard et al. (2004), provides a comprehensive classification and broad-scale mapping of South African marine habitats. Major habitat types were identified using large scale biogeographical distribution patterns of species and abiotic characteristics as proxies where biotic data was lacking.

The proportional allocation to different major shore types varies from survey to survey, depending, perhaps, on the particular approach used. Rocky shores, where there are no sand deposits over the intertidal to subtidal rock substrate, are thought to take up around 25% of the South African coastline (Bally et al. 1984), while more than 50% is occupied by sandy beaches, predominantly located on the west coast (Hockey et al. 1983; Campbell and
Lubke et al. (1997), based on Jackson and Lipschitz (1984), estimate that 50% of the coastline consists of fine-grained sand beaches, 12% coarse-grained sand beaches, 19% exposed rocky headlands, 17% shore platforms and less than 1% pebble/shingle beaches. Various estimates put the proportion of mixed intertidal zone on the South African coast at between a tenth and a third of the coastline (Bally et al. 1984; Campbell and Bate 1997; Lombard et al. 2004), the greatest proportion of which lies along the coast of the Eastern Cape Province (Campbell and Bate 1997; Lombard et al. 2004).

3.3 Physical classification of mixed substrate shores

The structural features of mixed substrate shores set them apart from other rocky shores, on the one hand and sandy beaches, on the other. Their spatial and temporal variability result, at least in part, from the interplay of substrates and water movement. Bally et al. (1984) proposed a mixed substrate shore classification based on spatial arrangement of intertidal sand and rock, and Brown et al. (1991) later tested the idea on shores of the Cape Peninsula. Both groups of authors found the lack of objective descriptive terms a problem.

The Bally et al. (1984) classification covers a continuum of shore configurations. Eight subjectively determined ‘compartments’ ranging from ‘pure sand’ at one end of the scale to ‘pure rock’ at the other, represent general variations in the proportion and distribution of intertidal rock and sand. Close to the sandy beach end (‘pure sand’ compartment), are beaches with scattered (‘isolated’) rock and on the rocky shore end (‘pure rock’ compartment), ‘rock with patches of sand’. Towards the middle of the range are ‘sand with many rocks’ on the sandy side and ‘rock with extensive sand’ on the rocky side of the continuum. Two middle-of-the-range categories are shores where rock predominates (100% cover?) in the upper or lower half of the shore, which suggests a 50:50 ratio of rock to sand. They also make provision for a temporal dimension in their classification, recognizing that a mixed section of shore could change categories after an event of major sedimentation or beach erosion, so that a shore would be viewed as temporarily falling in a particular compartment. For that reason, shore wave exposure should be factored into their scheme as it affects the frequency at which shore change could occur. Pebble beach shores are not included in their scheme.

Brown et al. (1991) base their classification on shores of False Bay and propose four major categories: ‘sand with rocky outcrops’ (sandy beach with rocky ridges a few metres apart in the lower intertidal), ‘sand with rock upshore’ (sandy beach with a continuous shore platform that may be above midtidal level), ‘rock with sand upshore’ (rock in lower intertidal with a
platform beach?), ‘rock inundated with sand’ (granite boulders or TMS outcrops throughout
the intertidal zone, sandy subtidal region, seasonal fluctuations in sand-inundation).

Lombard et al. (2004) consider three forms of intertidal substrate, designated
‘unconsolidated’ (e.g. beaches, dunes), ‘consolidated’ (e.g. rocky reefs and ledges), and
‘mixed’ (rock and sand). In this hierarchical habitat classification, the term ‘mixed’ refers to a
substrate consisting of both consolidated and unconsolidated components. Substrate type
thus cuts across different habitat types of that substrate, e.g. mixed back beach, mixed
shore, scattered reef, mixed slope, mixed abyssal plain. The mixed shore is seen as an
intertidal habitat type, on a par with rocky shores, sandy, pebble and boulder beaches. The
intertidal habitat linked to each substrate category, i.e. sandy beach, rocky shore, and mixed
shore, respectively, was classified further on the basis of wave exposure rating (‘very
exposed’, ‘exposed’, ‘sometimes exposed’, ‘sheltered’), so that 12 different intertidal shore
types (or habitats) resulted. The coast was mapped in 50 km segments. Mixed sections of
shore are often much shorter than 50 km, which implies that the assessment scale used
might have been too broad to detect some of the finer nuances of shore structure. It is likely
that some mixed sections were included with beach or rocky shore segments.

3.4 Definitions and criteria used in this study

3.4.1 Mixed substrate shore

For the purpose of this study, a ‘mixed shore’ is viewed as an intertidal system where both
hard and soft substrata are available for colonization by marine intertidal zoo- and
phytobenthos, hence the term mixed substrate shore is used. A mixed substrate shore is
defined here as a length of shore where sand is deposited over and/or adjacent to rocks
anywhere in the upper, middle or lower reaches of the littoral zone, and rocks occupy space
either throughout or at least over part of it (c.f. Bally et al. 1984; Brown et al. 1991). The
ease with which a mixed substrate shore can be distinguished from other shore types
depends on the particular shore configuration, the extent of sand cover and the degree to
which important features may be obscured by a rising tide.

3.4.1.1 Lengthwise delimitation

Depending on the geological and geomorphological character of the coastline, sections of
mixed substrate shore vary from a few metres to several kilometres (Bally et al. 1984).
McLachlan (pers. com. in Bally et al. 1984) suggested that, particularly in the Eastern Cape,
some mixed substrate shores may be less than 100 m in length. A short mixed section,
sometimes only a few metres in length, could be found where a rocky stretch ends fairly abruptly or is interrupted and gives way to a sandy beach. Longer sections, sometimes several kilometres in length, appear where low gradient bedrock at the coastline allows substantial sand deposition around rock outcrops.

For the purpose of this study, the lateral, long shore limit of a mixed substrate shore is taken as the shore-normal position where intertidal sand deposits become minimal or disappear altogether, or, alternatively, where rocky ridges or platform cease to be covered by sand. In this sense, pocket beaches as well as rocky shores with persistent platform beaches have been interpreted as mixed, although I have not included pocket beaches.

3.4.1.2 Cross shore delimitation

The cross shore delimitation of a mixed substrate shore is less simple than the long shore delimitation, as the lower intertidal boundary of the shoreline is interpreted differently for rocky and sandy shores. The question arises as to what degree the vertical and/or horizontal zones of mixed substrate shores conform to that of rocky shores or of sandy shores. The nature of the zones on rocky versus sandy shores is such that it is difficult to find a way to correlate them (Brown 2001). Bally et al. (1984) suggested that the lower boundary of a mixed shore should lie ‘at the seaward limit of the subtidal sand wedge if there is one’. This should be at a level between the lower limit of a rocky shore and a sandy beach.

The intertidal zonation schemes proposed for rocky shores by Stephenson (1943, 1972) and Lewis (1964) are practical and simple and have found application worldwide and have probably even been used at some mixed substrate shores with a small sand component. Three primary littoral zones are recognized, i.e. supralittoral, eulittoral and sublittoral, each characteristic of a particular range of elevations relative to tide marks and characterised, in turn, by a particular suite of biota (Russell 1991). The boundaries of these zones appear to follow a pattern that is remarkably similar throughout the world (Stephenson and Stephenson 1972). At an elevation just above tidal reach, the supralittoral zone (= littoral fringe sensu Lewis 1964) exhibits a distinctly marine character, because of the influence of sea spray. The eulittoral zone, between the mean high water of spring tide (MHWS) and the mean low water of spring tide (MLWS), experiences periodic total immersion (Russell 1991). The sublittoral zone extending downward from the lower boundary of the eulittoral is permanently immersed. Its uppermost subzone, the sublittoral fringe (i.e. infratidal zone sensu Branch and Branch (1981) or subtidal fringe sensu De Clerck et al. (2005)), positioned at the lowermost boundary of the eulittoral zone (Russell 1991, Stegenga et al. 1997), is
recognized as having a distinctive composition (Stephenson and Stephenson 1972) and experiences emersion only when tidal levels are extremely low.

While intertidal subzones are fairly easily discernable on hard substrate, the intertidal zonation in soft substrate is less straightforward. These zones shift vertically up- and downwards over a tidal cycle (Short 1999). The upper limit of the beach, viewed simply as a body of sediment, coincides with the swash limit (i.e. the landward limit of sub-aerial wave action) and the lower limit lies at modal wave base, i.e subtidally. The wave component of the beach includes the swash zone, the region of wave activity over the subaerial beach between the swash limit and the shoreline, the breaker zone (= surf zone) and the nearshore wave shoaling zone that has its outer limit at modal wave base. At macrotidal beaches wave processes are more differentiated resulting in the upper intertidal (swash/surf), mid-intertidal (swash/surf/shoaling), lower intertidal (surf/shoaling) and subtidal zones, but these merge with a reduction in tidal range so that microtidal beaches only have three, i.e. the swash, surf and sub-tidal zones (Masselink and Turner 1999). Within the swash zone further subzones are recognized based on the degree of saturation (Brown and McLachlan 1990; McLachlan and Jaramillo 1995). These habitat zones support characteristic biotic assemblages when sampled at low tide, but often become blurred, with considerable overlap and change during tidal rise and fall (Brown 2001).

For the purpose of this study, the cross shore intertidal delimitation of a mixed substrate shore encompasses the full vertical and horizontal range of zones observed on rocky and sandy shores as any or all of these could be represented. The beach component was delineated according to Salvat (1964, 1967 in Brown and McLachlan 1990; McLachlan and Jaramillo 1995), as modified by Pollock and Hummon (1971) and the rocky component according to Stephenson and Stephenson (1972). The delimitation of a mixed substrate shore between tide marks was therefore as follows: the upper eulittoral boundary coincides approximately with the lowest elevations of the supratidal zone on rocky sections and the upper swash limit (marked by the wrack line) on sandy sections; the lower eulittoral boundary falls at the sublittoral fringe of rocky sections and the beach toe or lower boundary of the swash zone (marked by the swash line) and encompasses the shallow near shore surf zone (pelagic habitat) around rocks, all with reference to spring low tide. This definition allows the inclusion of rocky sections that lie seaward of the shoreline at LWS, but are still found within the nearshore surf zone and of which the emergent parts lie within the eulittoral zone. The position of some of these rocky sections is such that they soon become inundated as the tide rises.
3.4.2 Physical criteria for configuration types

The main physical parameters used as a basis for proposed configuration types in the mixed substrate shore classification scheme of this study are:

1. **Geology** (sandstone and shale, aeolianite, marine deposits), a constant feature of the shore closely tied up with overall distribution, topography and orientation of intertidal rock.

2. **Shore physiognomy** (configuration of intertidal rock), a constant feature of the shore that locally impacts on wave action, water movement and sediment deposition patterns.

3. **Sediment deposits** (distribution and depth of sediment in upper-, mid-, lower and subtidal reaches), the only feature of the shore that is able to respond to wave forcing. Adjustments in sediment depth and distribution can change the proportion of exposed rock on the shore.

Motivation for using these parameters:

1. It was necessary to employ criteria that could be compared to those of previous workers.

2. It was important to use objective, measurable criteria that could be applied unambiguously, instead of subjective criteria. The position of rock or beach components could be described in terms of tide marks and their elevations and extent recorded.

3. The parameters employed are spatial features that could be observed clearly on aerial photographs of the coast at a suitable resolution.

4. As the intention is to replace or at least combine the initial physical classification with another based on biotic components, it is of great importance to have a clear conception of the physical characteristics of each study site and where it fits into the scheme.

3.4.3 Shore configuration types

Because of the temporal variability of some mixed substrate shores, no attempt is made to quantify any of the main parameters (geology, shore topography, sediment) as part of the definition of a category. Rather a philosophy of “absence/presence” is followed. While this brings with it problems of its own, the one advantage is its simplicity.

Descriptors for different configurations are given in reference to tide marks or zones (Table 1) for two reasons: firstly, to allow objective comparison of trends in topography and distribution of the rock component; secondly, to simplify the descriptor.
Table 1. Abbreviations used to encode shore configurations.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Descriptor</th>
</tr>
</thead>
<tbody>
<tr>
<td>h/s</td>
<td>Rock from spring high tide mark to subtidal.</td>
</tr>
<tr>
<td>m/s</td>
<td>Rock from midtidal to subtidal.</td>
</tr>
<tr>
<td>+</td>
<td>Upper intertidal sand deposits only.</td>
</tr>
<tr>
<td>++</td>
<td>Upper intertidal sand deposits and lower intertidal sand in gulleys/patches.</td>
</tr>
<tr>
<td>+++</td>
<td>Upper intertidal sand deposits and lower intertidal sand not limited to gulleys.</td>
</tr>
</tbody>
</table>

Table 2 summarizes the attributes of the four shore configurations recognized on the basis of whether (1) rock occurred in the form of ridges or platforms, (2) rock extended from the high tide mark or midtidal level to the surf zone, and (3) sediment deposits remained on the low shore or not. Shore configurations are all rather broadly based and small-scale variation within a particular configuration type commonly occurred.

### 3.5 Biotic classification

Biotic assemblages have been used as indicators for different physical conditions in previous studies of a range of marine habitats, e.g. Ballantine (1961), Tittley and Neto (2000). Ballantine (1961) devised a biologically defined scale for wave exposure at Northern Hemisphere rocky shores, where the differential presence or absence of species signifies the transition from one wave exposure grade to the next. Individual species have also been used as indicators of habitat conditions at beaches, e.g. *Anaulus australis* G. Drebes & D. Schulz (Campbell and Bate 1997). Lewis (1964) modified the Ballantine Scale to incorporate intertidal macrofaunal and macroalgal communities or assemblages. In a recent study, algal biotopes (Tittley and Neto 2000) and intertidal macrofauna (Blamey and Branch 2008) were found to reliably indicate the degree of wave exposure at a range of rocky shore habitats. In sandy beach studies, species richness alone has been found to be indicative of beach morphodynamic state and the degree of wave exposure has also been linked to the prevalence of particular taxa (Brown 2001, Defeo and McLachlan 2005).

Biotic classification has to be applied with great caution, as it is prone to circular reasoning and bias introduced by subjectivity (Ballantine 1961). It may also only have regional relevance. In this study, the biotic classification of mixed substrate sites was based on species dominance and composition rather than presence-absence.
Table 2. Mixed substrate shore configuration types based on shore physiognomy and sand deposition patterns.

<table>
<thead>
<tr>
<th>Configuration 1:</th>
<th>Shore consists of sandstone or shale ridges or broken slabs of aeolianite. Arrangement shore-normal or shore linear.</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1 h/s:</td>
<td>Rock between spring high water mark and subtidal. Discontinuous upper intertidal sand deposits.</td>
<td></td>
</tr>
<tr>
<td>1 h/s+</td>
<td>Lower intertidal sands absent from gulleys. (= rocky shore)</td>
<td></td>
</tr>
<tr>
<td>1 h/s++</td>
<td>Lower intertidal sands limited to gulleys.</td>
<td></td>
</tr>
<tr>
<td>1 h/s+++</td>
<td>Lower intertidal sands not limited to gulleys.</td>
<td></td>
</tr>
<tr>
<td>1 m/s:</td>
<td>Rock extends from roughly midtidal to subtidal elevations. Upper intertidal sand deposits form a continuous beach.</td>
<td></td>
</tr>
<tr>
<td>1 ms+</td>
<td>Lower intertidal sands absent from gulleys. (= rocky shore)</td>
<td></td>
</tr>
<tr>
<td>1 m/s++</td>
<td>Lower intertidal sands limited to gulleys.</td>
<td></td>
</tr>
<tr>
<td>1 m/s+++</td>
<td>Lower intertidal sands not limited to gulleys.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Configuration 2:</th>
<th>Shore consists of aeolian or marine calcarenite continuous or broken near-horizontal shore platforms. Arrangement shore linear.</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>2 h/s:</td>
<td>Rock between spring high water mark and subtidal. Discontinuous upper intertidal sand deposits.</td>
<td></td>
</tr>
<tr>
<td>2 h/s+</td>
<td>Lower intertidal sands absent from platform. (= rocky shore)</td>
<td></td>
</tr>
<tr>
<td>2 h/s++</td>
<td>Lower intertidal sands limited to patches/small gulleys.</td>
<td></td>
</tr>
<tr>
<td>2 h/s+++</td>
<td>Lower intertidal sands not limited to gulleys/patches.</td>
<td></td>
</tr>
<tr>
<td>2 m/s:</td>
<td>Rock extends from roughly midtidal to subtidal elevations. Upper intertidal sand deposits form a continuous beach.</td>
<td></td>
</tr>
<tr>
<td>2 m/s+</td>
<td>Lower intertidal sands absent from platform.</td>
<td></td>
</tr>
<tr>
<td>2 m/s++</td>
<td>Lower intertidal sands limited to gulleys/patches.</td>
<td></td>
</tr>
<tr>
<td>2 m/s+++</td>
<td>Lower intertidal sands not limited to gulleys/patches.</td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER 4  Methods

4.1 Site Selection

A general requirement for the selection of suitable sites was that they had to have visible sediment deposits, at least in the upper intertidal reaches. The presence or absence of sediment and general shore configurations were verified prior to selection by two visits to each of forty potential study sites, one visit during neap high tide and one during spring low tide.

Twenty sites (Figure 1, Table 3) that conformed to site configurations delineated in the shore classification set out in Chapter 3 (Table 2) were selected for study. The study sites were all located along a 300 km stretch of the Eastern Cape coast between Cape St Francis and Great Fish Point. While the need to work further afield was recognized as an important requirement for wider validation or testing of hypotheses, it had to be weighed against two other important considerations: one, that the study was essentially comparative and having sites within the same biogeographical region (Agulhas Marine Province) would minimize the chance of biotic variation due to a biogeographical effect, and, two, Algoa Bay has been recognized as a coastal stretch with a high irreplaceability rating (Lombard et al. 2004).

Study sites were photographed under different tidal conditions, descriptive notes recorded for each and, together with Google Earth images and information from previous studies (e.g. McLachlan 1977a, Munnik 1987, Fischer 1989, Dower 1989 and Dobkins 1992), used as a basis for selecting suitable shore criteria to identify shore configurations and select representative sites. At some of the study sites, sediment deposits were interspersed with rock sections, not necessarily forming a recognizable beach and at others the sediment was deposited as a continuous beach usually above the rock section. The beach component either spanned the entire intertidal width between the high and low tide swash-lines, with exposed rock substrate within it, or lacked constant contact with the low tide swash i.e. a platform beach (sensu Short 1999).

The definition for a mixed substrate shore could then include even very rocky shores that have small platform beaches and sandy beaches which, on the other hand, always sit on a rocky shelf, albeit buried under metres of sand. Any section of the coast could therefore potentially be mixed. None of the study sites in the final selection were sandy beaches without rocky outcrops or rocky shores completely devoid of sand deposits.
Figure 1. Location of study sites.
Table 3. Site name, site code, sample date, configuration category and GPS co-ordinates of each study site. Detailed configuration codes are explained in Table 2 (Chapter 3).

<table>
<thead>
<tr>
<th>Site Name(code) and sample date</th>
<th>Configuration Type</th>
<th>GPS co-ordinates of middle transect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aston Bay (ASB) 28 September 2007</td>
<td>1 m/s+++</td>
<td>S 34° 04' 50.27&quot;, E 24° 55' 16.07&quot;</td>
</tr>
<tr>
<td>Avalanche (AVA) 5 May 2006</td>
<td>1 h/s +++</td>
<td>S 33° 59' 0.7&quot;, E 25° 40' 13.98&quot;</td>
</tr>
<tr>
<td>Beacon Rock (BCN) 6 December 2006</td>
<td>1 m/s +</td>
<td>S 33° 59' 0.28&quot;, E 25° 40' 17.49&quot;</td>
</tr>
<tr>
<td>Bird Rock (BRK) 26 November 2006</td>
<td>1 m/s +</td>
<td>S 33° 58' 59.13&quot;, E 25° 40' 6.55&quot;</td>
</tr>
<tr>
<td>Cannon Rocks (CNR) 10 December 2007</td>
<td>2 m/s ++</td>
<td>S 33° 44' 40.51&quot;, E 26° 33' 42.77&quot;</td>
</tr>
<tr>
<td>Cape Recife East (CRE) 18 May 2007</td>
<td>2 m/s +</td>
<td>S 34° 00' 37.02&quot;, E 25° 41' 28.97&quot;</td>
</tr>
<tr>
<td>Cape Recife West (CRW) 15 June 2007</td>
<td>1 h/s +++</td>
<td>S 34° 01' 39.48&quot;, E 25° 39' 16.35&quot;</td>
</tr>
<tr>
<td>Hougham Park East (HPE) 2 August 2007</td>
<td>2 h/s +++</td>
<td>S 33° 45' 32.16&quot;, E 25° 45' 42.4&quot;</td>
</tr>
<tr>
<td>Hougham Park West (HPW) 31 August 2007</td>
<td>2 h/s ++</td>
<td>S 33° 47' 2.01&quot;, E 25° 42' 55.88&quot;</td>
</tr>
<tr>
<td>Humewood (HWD) 26 November 2007</td>
<td>2 m/s +++</td>
<td>S 33° 58' 38.33&quot;, E 25° 39' 5.46&quot;</td>
</tr>
<tr>
<td>Kini Bay (KNB) 17 March 2007</td>
<td>1 h/s +</td>
<td>S 34° 01' 24.7&quot;, E 25° 23' 4.66&quot;</td>
</tr>
<tr>
<td>Kleinemonde East (KME) 11 December 2008</td>
<td>1 m/s++</td>
<td>S 33° 32' 18.62&quot;, E 27° 3' 15.42&quot;</td>
</tr>
<tr>
<td>Maitlands Inner (MAA) 20 February 2007</td>
<td>1 h/s +++</td>
<td>S 33° 59' 27.57&quot;, E 25° 17' 52.19&quot;</td>
</tr>
<tr>
<td>Maitlands Outer (MAB) 21 March 2007</td>
<td>1 h/s +++</td>
<td>S 33° 59' 25.79&quot;, E 25° 17' 50.11&quot;</td>
</tr>
<tr>
<td>Miller's Beach (MLS) 26 October 2006</td>
<td>2 m/s ++</td>
<td>S 33° 58' 55.79&quot;, E 25° 39' 53.82&quot;</td>
</tr>
<tr>
<td>Paradise Beach (PDB) 13 November 2007</td>
<td>1 m/s+++</td>
<td>S 34° 06' 29.58&quot;, E 24° 53' 13.12&quot;</td>
</tr>
<tr>
<td>Pollock North (PBE) 5 December 2006</td>
<td>1 h/s +++</td>
<td>S 33° 59' 0.69&quot;, E 25° 40' 18.42&quot;</td>
</tr>
<tr>
<td>Pollock South (MPB) 4 December 2006</td>
<td>2 m/s +++</td>
<td>S 33° 59' 13.28&quot;, E 25° 40' 23.3&quot;</td>
</tr>
<tr>
<td>Three Sisters (TST) 12 December 2007</td>
<td>2 h/s +</td>
<td>S 33° 33' 31.85&quot;, E 27° 1' 32.8&quot;</td>
</tr>
<tr>
<td>Willows Beach (WLW) 23 September 2006</td>
<td>1 h/s +</td>
<td>S 34° 02' 42.77&quot;, E 25° 36' 23.05&quot;</td>
</tr>
</tbody>
</table>

Six sites conformed to Configuration 1 h/s (ridges extend from the high tide mark to the surf zone), six to Configuration 1 m/s (ridges extend from roughly midtidal levels to the surf zone), three to Configuration 2 h/s (rock platform extended from the high tide mark towards the surf zone), and five to Configuration 2 m/s (rock platform extended from roughly midtidal...
levels into the surf zone). For easier reference to the four site configurations in the Results and Discussion, the configurations were referred to as follows (see Table 2): Configuration 1 h/s (ridges above and below midtidal elevation) was ‘high ridge’, Configuration 1 m/s (ridges below midtidal elevation) was ‘low ridge’, Configuration 2 h/s (platform above and below midtidal elevation) was ‘high platform’, and Configuration 2 m/s (platform below midtidal elevation) was ‘low platform’.

4.2 Sampling Strategy

Sampling was done between September 2006 and December 2007. Each study site was sampled once. The main drawback of one-off sampling is that it provides no information of temporal change, especially seasonal variation. The Eastern Cape climate does, however, not exhibit strong seasonality in temperature regime reducing the risk of losing a great deal of information by this sampling approach and the focus of the study. Mixed substrate shores are however well-known for spatial change due to moving sand. Site observations over a period of time prior to sampling identified the degree of short-term change at each site. Sampling was timed to coincide with a period of maximum sand-inundation and had to take place on an extreme low spring low tide under low to moderate swell and wind conditions for safe access to low shore rock surfaces. This curtailed the number of possible sampling days and was the main reason for having to extend sampling over a longer period.

Sampling was done according to a stratified random design (Table 4), where two main benthic habitats (= primary strata) were identified, i.e. soft substratum (sand) and hard substratum (emergent and submerged rock surfaces). Soft and hard substrata were further subdivided into secondary strata or subzones for sampling abiotic parameters and macrobenthos: 6 in soft substratum and 9 on hard substratum. Hard substratum sampling strata were delimited according to the scheme proposed in Stephenson and Stephenson (1972). R0 and R1 represented the supralittoral fringe, R2 to R6 the eulittoral zone and R7 and R8 the infralittoral fringe. Sampling strata were identified in the field by the presence of character taxa (see section 4.4.2 and Table 4). Intertidal beach sediments, on the other hand, are generally devoid of obvious life forms. Soft substratum sampling strata were delimited according to zones generally recognized in sandy beach studies following the scheme proposed by Salvat (1967, in Brown and McLachlan 1990) and modified by Pollock and Hummon (1971) and recognized on the basis of position relative to major tide marks combined with surface characteristics indicative of moisture conditions. The uppermost, S0, coinciding with the wrack line and the lowermost (S5) at the swash line or beach toe. S0 and S1 were located in the supralittoral-littoral boundary, S2 and S3 were within the littoral zone
above the low tide effluent line, and, S4 and S5 were between the low tide effluent line and the low tide swash.

4.3 Sampling and laboratory procedures

4.3.1 Biotic assemblages

4.3.1.1 Sediment macrofauna

One sampling station was located roughly central to each sampling stratum and four sample replicates taken (n =72 per site). Beach macroinfauna were sampled using a steel corer (17.5 cm inner diameter, area = 240 cm²) driven into the sand to a depth of about 30 cm where the sand was deep enough. Shallow sediment (depth < 30 cm) was sampled by removing an equivalent volume of sand using a large spade. Sample cores were wet sieved through a 1 mm mesh size filter bag to remove fine sediment. Specimens and coarse fraction were retained in 1 litre plastic sample bottles. Macrofauna were anaesthetized by soaking in MgCl₂ solution isotonic to seawater after decantation of all the seawater (Day 1974). Most of the macrofauna could be extracted by decantation over a 750 µm mesh sieve and the balance by examining the remaining sediment under magnification (Eleftheriou and Holme 1984). Specimens were preserved in 10% formalin-seawater.

Macrobenthic infauna were counted and identified using a Zeiss dissection microscope. References used for identification are listed in Addendum 1. Voucher specimens were kept in the wet collection housed at the Botany Department, Nelson Mandela Metropolitan University.

4.3.1.2 Rock surface biota

Macroalgae, sessile macrofauna and detectible mobile fauna on emergent rock surfaces occurred as a clearly identifiable single layer with patchy epiphytes and were recorded by photographing 25 cm x 25 cm framed quadrats, randomly placed within each stratum, in macro mode using an Olympus FE-130 (5.1 megapixel) digital camera. This method is non-destructive, rapid and has been used successfully for long-term monitoring of trends in community structure (see Littler and Littler 1981, Seapy and Littler 1982, McQuaid and Branch 1985, Kendrick 1991, Ashton and Richardson 1995, Dye 1998, Ellis 2003). Ten or more quadrats were photographed per stratum. In addition four 10 cm x 10 cm areas of algal turf or epilithic biota were excised, usually within or adjacent to a photographed quadrat.
Table 4. Primary (rock or sand) and secondary (subzone) sampling strata. Sampling codes and descriptors relate to secondary strata. Abbreviations: EHWS = extreme spring high tide, HWN= neap high tide, LWS = spring low tide.

<table>
<thead>
<tr>
<th>Strata</th>
<th>Descriptors: dominant feature / character taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary</td>
<td>Secondary</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R0</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R1</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R2</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R3</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R4</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R5</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R6</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R7</td>
</tr>
<tr>
<td>Emergent rock</td>
<td>R8</td>
</tr>
<tr>
<td>Sand</td>
<td>S0</td>
</tr>
<tr>
<td>Sand</td>
<td>S1</td>
</tr>
<tr>
<td>Sand</td>
<td>S2</td>
</tr>
<tr>
<td>Sand</td>
<td>S3</td>
</tr>
<tr>
<td>Sand</td>
<td>S4</td>
</tr>
<tr>
<td>Sand</td>
<td>S5</td>
</tr>
</tbody>
</table>

The sample material was used to verify species composition of macroalgal turfs, difficult to analyse from the photographs. Digital photographs of epilithic biota were uploaded to a computer and labelled prior to examination. Where more than 10 replicates were available for a stratum, 10 photos were selected randomly using a random numbers table. Digital copies of the photographs used and a dry collection of voucher specimens are held at the Ria Olivier Herbarium of the Botany Department, Nelson Mandela Metropolitan University. Excised turf samples were preserved in 10% formalin-seawater. The macroalgal material of turf samples was retained for sorting and identification.

Estimates of projected percentage cover of basiophytes, epiphytes and sessile fauna and counts of mobile macrofauna on rock substrate were obtained directly from digital photographs. Identification of macroalgae and macrofauna was done from photos and
voucher specimens. Percentage cover of smaller algae that form part of algal turfs was estimated from proportional representation in the scraped material. References used for identification are listed in Addendum 1.

4.3.2 Abiotic site parameters

4.3.2.1 Shore topography

Shore topography (rock topography and beach profile) and stratum identity were recorded along three shore-normal transect lines, at least 50 m apart, between the spring high tide mark (indicated by wrack line) and spring low tide mark (indicated by swash line or infratidal fringe) at roughly 1 m intervals using a dumpy level or theodolite and graduated staff according to Emery (1961). Each cross-shore beach profile also served as a sampling transect: sampling stations were positioned in the middle portions of S-strata (S0 to S5) along the transect line. Mid-shore topography was recorded along a 50 m long shore-parallel transect. Other data recorded along each transect included substratum type, sediment depth and sampling stratum identity on both rocky and sandy sections encountered.

4.3.2.2 Sediment

Two sediment cores (diameter 4.5 cm) of 10 cm depth were collected at each sampling station for determination of sediment particle size, organic content and carbonate content. Sediment depth measurements were taken at 1 metre intervals along cross-shore profiles by hammering a graduated steel rod into the sediment down to the rock bed or a depth of 30 cm, whichever came first. A depth of 30 cm was chosen because that was the maximum depth to which macrofauna samples were taken and also the depth range of most infauna (Eleftheriou and Holme 1984). Each sediment sample was thoroughly mixed and subsamples taken for determination of grain size, organic matter and carbonate content. Subsamples were oven-dried for 24 hrs at 100°C. Sediment grain size fractions were obtained by passing oven-dried sediment through nested sieves graded according to the Wentworth scale corresponding to 1Φ intervals on a mechanical sieve shaker (Buchanan 1984). Organic matter content and carbonate content were determined by loss on ignition (Heiri et al. 2001).

4.3.2.3 Biogeographical parameters

Temperature and salinity were measured in the water column at each transect using a YSI probe.
4.3.2.4 Site observations

Observations recorded at each site on the day of sampling were: geology, extent and orientation of rock (e.g. parallel ridges, platform), geomorphological and man-made features (e.g., dunes, vegetation, cliffs, revetments, groynes), wave height (estimated), wave type (classified using Aagaard and Masselink (1999)), surf zone width (estimated), beach features (e.g. berm, cusps, fresh water flows), depth of reduced layer at MTL (measured) as well as presence or absence of burrows.

4.3.3 Mapping

Digital aerial photographs (1997) obtained from the South African Surveyor General were used in ArcGIS10 to map the extent of the four mixed shore configurations (1 h/s, 1 m/s, 2 h/s and 2 m/s), as well as sandy beaches and rocky shores along the section of coast between longitude E 24° 00’ 00” and E 27° 15’ 00” (Figure 2).

Figure 2. The section of coastline on which mixed substrate shore configurations were mapped in ArcGIS10. Arrows indicate the limits of the distance assessed.
4.4 Data processing and analysis

4.4.1 Site observations and topographic measurements

Topographic data was corrected for chart datum using data obtained from www.satides.co.za and used in graphical representations of overall shore topography, calculation of beach gradient and shore slope. Data collected along each profile were used to estimate the extent of sand and rock surface along each profile and also to record the position and height range of rock substrate. Commonly used simple techniques to assess ruggedness provide a good indication of topographic complexity, but do not give information about rock height at different tidal elevations. A rock height rating scheme based on the position of the rock and the rock height relative to tide marks was devised to compare the position and height range of rock substrate at sites (Table 5). The total rock height rating was obtained by summation of ratings. The maximum rating (19) would be obtained at a site with rock at all height intervals and positions.

Table 5. Rock height rating system used in this study. Mean sea level (MSL) = 0 m.

<table>
<thead>
<tr>
<th>Rock Height</th>
<th>Position of Rock Base</th>
<th>Below LWS</th>
<th>Between LWS and MSL</th>
<th>Between MSL and HWS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Below LWS (&lt; -1.0m)</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Between LWS and MSL (-1 to 0m)</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Between MSL and HWS (0 to +1m)</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Exceeds HWS (&gt; 1m)</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

Qualitative and quantitative site observations (e.g. estimated surf zone width, wave height, depth of reduced layer at MTL, presence or absence of burrows) and topographic data were used to estimate beach morphodynamic state and beach type according to Short (1999) and to calculate the dimensionless fall velocity (Gourlay 1968) (= Dean’s parameter or Ω), Relative Tidal Range (RTR) and Beach State Index (BSI) (McLachlan 1990), as well as exposure rating (McLachlan 1980b; Brown and McLachlan 1990). The exposure rating was calculated in two ways: using beach slope to incorporate any attenuating effect of the intertidal rock substrate on wave action and full shore slope so that only the attenuating processes of the outer surf zone as seen at low tide was taken into account and the exposure on the seaward side of the shore could be estimated.
Percentage organic matter content, percentage carbonate, sediment particle size distribution and average sediment depth were calculated for each site (overall mean per site and also for each sampling stratum across shore).

The extent of each shore type mapped in ArcGIS 10 was calculated as a percentage of the full shore segment mapped between markers.

4.4.2 Community parameters

The community parameters calculated were species richness, composition, abundance (individuals per running metre of shore) and density (individuals per square metre). All data were tested for normality using Shapiro-Wilks W test (Statistica10). Data with a normal distribution were statistically analysed using Students t-tests, one way ANOVAs and Tukey HSD tests and simple correlations for data from the full data set or two main site configurations. Non-parametric data were analysed using Mann-Whitney U-tests, Kruskal-Wallis ANOVA by ranks, Chi-square and Multiple comparisons of p values (2-tailed).

The complementary multivariate statistical techniques of classification and ordination were used to identify and interpret the responses of communities to environmental factors. An importance value was calculated for each species, following Cox (1996), as the average of its relative abundance and relative frequency per site. Relative abundance per site was the sum of relative abundances in sampling strata weighted according to their extent (as a percentage) in an integrated site transect. Relative frequency per site was the sum of relative frequencies in sampling strata weighted according to their extent (as a percentage) in an integrated site transect. Importance values did not require transformation before use in MVA. A redundancy analysis of all environmental variables determined was performed using principal components analysis (PCA) in CANOCO.

Ordination was done by detrended canonical analysis (DCA) and related to environmental gradients by means of detrended canonical correspondence analysis (DCCA) in CANOCO (Ter Braak1996). Classification was done using an R script for Ward’s clustering with the dendrogram delivered by hcoplot in R i386 version 2.15.0 (R Development Core Team 2010). Cluster analyses and DCAs were performed on the full complement of species from both substrata, but also on subsets of the full species data set (macroalgae only, macrofauna of sediment, sessile macrofauna of rock surfaces and motile macrofauna of rock surfaces). The analysis of all species was the most important as it formed the basis for the mixed substrate shore biotic types proposed in this study. Cluster analysis of subsets of species gave an indication of differences in species response to the environment and which
subsets played the leading role in determining the structure of the dendrogram based on all species. Biotic type descriptors were obtained by doing a constancy-fidelity analysis according to Mueller-Dombois and Ellenberg (1974).

Definitions of terms used in relation to macrobenthic assemblages:

**Character taxon:** A highly visible or easily recognizable taxon (or taxa) that imparts a particular character (e.g. tall or short turf growth-form) to a recognizable assemblage, affects micro-habitat conditions where it occurs and is assumed to be indicative of a particular suite of environmental and micro-habitat conditions (Green 1979; Greenwood 1996). In this sense, the hard substrate strata could also be interpreted as biotopes corresponding to the usual intertidal zonation patterns of rocky shores in the region.

**Dominant taxon:** Taxon that was in the top 10 most abundant taxa at a site or in a sampling stratum and reached an abundance of at least 10%

**Indicator:** Taxon assumed to be indicative of a particular set of environmental conditions that were quantified or observed at a locality or associated with localities because it occurs in high abundance only where the condition or set of conditions prevail.

**Endemic:** Taxon that has a narrow biogeographical distribution range and occurs either only in the Eastern Cape, south coast or South African intertidal habitats.
CHAPTER 5  Study sites

5.1 Introduction

Intertidal living conditions are determined by the physical configuration of the shore, tidal rise and fall, fresh water seeps, degree of wave exposure and water movement (Bally et al. 1984). The nature of the hard and soft substrata that are brought together on mixed substrate shores can be traced back to the geology and geomorphology of the Eastern Cape landscape (Bell 1980; Tinley 1985; Illenberger and Smuts 1986; Stear 1987; Marker 1988). Nothing is known about the landward geomorphology and sediment parameters or the anthropogenic influences on these systems (Bally et al. 1984; Brown et al. 1991).

5.2 General features of the south coast and vicinity of Algoa Bay

5.2.1 Geomorphology and wave climate

The South African coast consists of a variety of geological formations and landforms, producing a heterogeneous backdrop for the diversity of marine life inhabiting these shores (Bolton and Anderson 1997; Mucina et al. 2006). It has many inherited features stemming from the influence exerted by previous marine incursions and recessions (Marker 1988). The general outline of the coast is the result of a period of faulting, uplift and volcanic activity at the break-up of Gondwanaland in the Jurassic period (Bell 1980; Marker 1988).

Resistant Table Mountain quartzite of the Cape fold belt features strongly all around the south-western, southern and south-eastern coast, forming predominantly steep cliffs and narrow shore platforms on the southern and western Cape coast and eastward trending headlands along the Eastern Cape coast, each with an eastward facing headland-attached log-spiral (zeta) bay forming a sweeping embayment with a predominantly sandy shore (Craig 1997). Within embayments, bedrock consists of less resistant rock types, e.g. shale or a shale-conglomerate-sandstone combination (Bell 1980; Marker 1988; Craig 1997). Algoa Bay, where most of the study sites are situated, is one of the larger log-spiral bays of the South African coastline (Bremner 1983; Craig 1997).

Along a large proportion of the coast, recent (Neogene) coastal aeolianite platforms overlie the older quartzitic or shale and sandstone shore platforms (Illenberger and Smuts 1986; Craig 1997). In the vicinity of Algoa Bay, and further eastward, recent shore platforms are nearly horizontal, variable in width and have a shallow seaward scarp and in many instances also a landward cliff (Marker 1988). Shore platforms vary in elevation, some being near the
high tide mark and others near the low tide mark, extending subtidally with a seaward dip of about 1° (Stear 1987). Many are undercut and have collapsed, forming broken sections where wave activity deposits substantial quantities of sand over the platform (Dower 1989; Garner pers. obs. 2006).

The predominant direction of alongshore sediment transport on the south and east coast of South Africa is eastwards, thus beaches and dunes are built on the lee side of south-eastward trending promonitories (Schumann et al. 1988; Mucina et al. 2006). Aeolian sands form extensive sandy beaches backed by dunes (Campbell and Bate 1997). They rest on wide, low shore platforms that are exposed at low tide in some localities, forming mixed substrate shores (Stear 1987; Marker 1988; Craig 1997). While some beaches experience accrual, there is evidence of both beach and dune erosion, possibly as a result of sea level rise (Illemerberger and Smuts 1986; Marker 1988), though changed sediment budgets as a consequence of agricultural, urban and industrial activities cannot be ruled out (Dobkins 1992). A few boulder beaches, mostly consisting of coarse clastic material with a small admixture of finer sediment, occur along the east coast as well (Marker 1988; Craig 1987; Coetzee 1991).

Many Eastern Cape mixed substrate shores exhibit both temporal and spatial variability in the distribution and proportion of their beach and rock components (Stephenson and Stephenson 1972). Under heavy wave attack during storm conditions, usually combined with a spring tide, sufficient sediment may be removed to expose a coarse lag of pebbles or the shore platform itself. As seen in other parts of the globe, the beach is then rebuilt to its former level by lower energy waves, a process that could take weeks, months or even years (Short 1999, Jackson et al. 2005).

Like other southern hemisphere coasts, the South African coast experiences storm waves all year round (Short 1999). The entire coast is wave-exposed, though headland-attached embayed beaches are afforded some shelter from wave action due to wave refraction and attenuation at the headland (Short and Masselink 1999). Along the Eastern Cape coast, wave height is seldom less than 1 to 2 m, regularly exceeds 2 to 3 m, and sometimes also 4 to 5 m (Short 1999; Lombard et al. 2004). The energetic South African wave climate ensures that sediment reworking and onshore-offshore transport is for most part rapid. Many mixed substrate shores experience frequent changes in sediment load and distribution, while others have a more stable beach: whether a mixed shore will fall in one or the other category depends to a large extent on its degree of exposure to wave action and the extent to which rock formations interact with water movement and sediment transport.
5.2.2 Sea temperature

Temperature is a significant environmental parameter in marine habitats, determining the geographical ranges of species. Waters of the South African south coast, which includes most of the Eastern Cape coast, are warm-temperate with mean annual ocean temperatures between 17° and 18° C (Bolton and Anderson 1997). The sea temperatures of Algoa Bay are influenced by the Agulhas Current which brings warm waters from the tropics and subtropics into temperate regions. A wind-induced bottom onshore flow over the continental shelf often leads to local upwelling particularly near Cape Padrone, which spreads into the bay (Schumann et al. 1982; 1988). Upwelling also occurs off other rocky headlands along the south coast, e.g. Cape Recife and Cape St Francis (Schumann et al. 1982, 1988). A rapid drop in temperature of several degrees always follows on an upwelling event (Beckley 1983; Schumann et al. 1988). The combination of warming Agulhas Current eddies and cooling by upwelling results in the south coast (which includes the Algoa Bay area) having the greatest range of monthly temperature means (12° C – 22° C) along the South African coast (Mucina et al. 2006).

5.2.3 Wind

The entire South African coast is influenced by a bidirectional wind pattern, with wind directions semi-parallel to the coast (Mucina et al. 2006). In the vicinity of Algoa Bay a typical south coast wind regime prevails: predominant wind direction is west and south-westerly, alternating with easterly winds (Stone 1988, Mucina et al. 2006). The coast near East London, on the other hand predominantly experiences south-westerlies and north-easterlies, which is characteristic of the east coast of South Africa (Stone 1988; Mucina et al. 2006).

5.2.4 Tides

The Eastern Cape coast is microtidal, having a mean tidal range of about 1.6 m at springs and 0.5 m at neaps and extreme spring highs of about 2.1 m (Stone 1988). Tides in Algoa Bay are semidiurnal, exhibiting an inequality of about 10 cm (Beckley and McLachlan 1979; Munnik 1987). Spring low tides occur at about 10:00 and 23:00.

5.2.5 Coastal hydrography

The hydrography of coastal waters of the Eastern Cape is not well known (Ross 1988). There is evidence of a consistent inshore current moving in a west to east direction, mainly due to wind forcing, while current reversals and slacks are known to occur intermittently.
The eastward current plays a dominant role in the transport and distribution of sand along the coast, leading to scouring in the lee of headlands and sediment deposition towards the eastern boundaries of zeta-bays along the coast. Together with wave forcing and localized beach currents (e.g. rips) it plays a major role in the temporal variability of sediment load on mixed substrate shores.

### 5.3 Distribution of study sites

All the study sites are located towards the eastern end of the Agulhas Marine Province. Seven sites are situated within St. Francis Bay, a half-heart bay stretching from Cape St. Francis in the west to Cape Recife in the east, ten within Algoa Bay, a half-heart bay stretching between Cape Recife in the west to Woody Cape in the east, and three lie east of Woody Cape. Figure 1 (Chapter 4 Methods) shows the distribution of all twenty study sites. GPS co-ordinates and classification categories of study sites are given in Table 3 (Chapter 4 Methods).

Several of the sites located within Algoa Bay lie adjacent to one another along the beach front of Port Elizabeth. This was a deliberate choice in line with the study aim to map all mixed substrate shores along the section of coastline between Cape St Francis and Great Fish Point. The particular section of the coast is mixed and has a highly variable configuration, but very similar wave exposure. The proportion of exposed and sand-inundated rock varies considerably, as does shore topography. Intertidal rock outcrops along this section of shore consist of sandstone of the Table Mountain Group and/or aeolionite (Alexandria Formation) with pebbles embedded in calcareous bedrock.

### 5.4 Study site descriptions

Study site observations are reported in order of location from west to east (Figure 1). Site photographs are provided in Addendum 5.

#### 5.4.1 Paradise Beach (PDB) and Aston Bay (ASB)

Paradise Beach and Aston Bay are similar in structure, roughly 3 km apart and situated in the western portion of a mixed substrate shore, several km long, between two long sandy beaches. The subaerial sandy beach is backed by partially vegetated high dunes. The subaquatic beach is dissected at roughly 50 – 100 m intervals by low shore normal to diagonal narrow shale ridges in the surf zone that are partially exposed at spring low tide and fully inundated on a spring high tide.
Both sites are sheltered from the predominant swell by Cape St Francis. The subtidal bottom is sandy and relatively shallow along that section of the bay. Sand banks commonly form among and off shore from the shale ridges. The surf zone is roughly 200 m wide at these two sites. Wave action is dissipative well off shore, with spilling and plunging waves that reform as they enter the inshore regions where more energy is expended over the seaward ends of ridges. Wave action on the beach is characterised by low energy levels under calm conditions.

5.4.2 Maitlands Beach Inner (MAA) and Maitlands Beach Outer (MAB)

These two adjacent study sites are located at the east end of Maitlands Beach in a rock section roughly 500m to the east of Maitlands River mouth. Both Maitlands Beach and the rocky section are backed by high partly vegetated sand dunes built on recent aeolianite overlain on sandstone and quartzite. Maitland Beach is about 120 m wide, but at the mixed section the width is less than 100 m. At spring low tide, the rocks extend into the surf zone for a short distance. Only the lower half of the rocky section is fully inundated on a spring high tide.

MAA is the inner section of the rocky outcrop, which is about 400 m long. Tall sandstone and quartzite rock slabs with the occasional aeolianite remnant lie mostly above spring low tide mark and extend beyond spring high tide mark. Narrow gulleys (2 – 4m across) between rock reefs are sand-bottomed in the lower tidal reaches and have a pebble and boulder bottom higher up. The second study site, MAB, falls in the outer, more sparse, lower rocky sections grading into the higher, less broken rocky section from Maitlands Beach on the west side and Beachview’s beach from the east. The rocky reefs are more widely spaced than in the middle section. Gulleys are wider (5 - 8 m across) and all are sand-bottomed.

Wave action and wave number in the surf zone on the seaward side of these study sites is the same as prevailing surf conditions of Maitlands Beach, a wave-exposed beach which oscillates between different intermediate beach states. Swash period is lower over the beach at the rock section and wave direction more irregular as the rocks reflect waves and control wave movement. Wave movement is more rapid in surge channels than over rock surfaces where much dissipation of energy occurs. The waves in the channels range from plunging and collapsing to surging, while those over rock sections are broken (spilling) or breaking (plunging / collapsing). There is a more notable reduction in wave height in waves as they cross the rocky traverse as compared to the beach. Suspended sand is constantly evident in the wave bores.
5.4.3 Kini Bay (KNB)

The study site is on a fairly uniform rocky section of rocky coast, several kilometres in length, extending from Beachview to Cape Recife. The rock platform consists of almost continuous, closely set rocky reefs of variable height, with the occasional sand-bottomed gulley, wide enough to allow landward transport of sand, and accompanied in part by a platform beach backed by vegetated landward cliffs or low dunes. Because of the extensive rocky intertidal habitat, it is generally viewed as a rocky shore.

In the vicinity of the study area, the steep, narrow up-shore beach consists of a shingle-sand mix and is backed by vegetated dunes. Rocks are of Cape Super Group quartzite, sandstone or shale, also some pre-Cambrian outcrops, an unusual occurrence on the coast (Bell 1980), and the occasional remnant aeolianite cliff and/or platform section overlying the older bedrock. The rock platform is dissected, forming closely set shore parallel and shore normal or diagonal ridges with narrow gulleys, mostly hard-bottomed (bedrock, boulders). The exposed part of the rock platform extends from about spring high tide mark to well below and beyond spring low tide mark ending in a shallow submerged cliff.

Like Maitlands, this is a wave-exposed shore. At the seaward edge of the rocks there is a zone of wave shoaling and a few lines of breakers that are plunging or collapsing. Waves reaching the lower end of the shore are usually broken or breaking and reform over the rocks in an irregular swash of collapsed waves with much lower height. In sandy gulleys, waves are plunging, collapsing or surging. Suspended sand is constantly evident in the wave bores passing into gulleys.

5.4.4 Willows Beach (WLW)

Situated within the Willows Beach Resort, this study site lies several kilometres to the east of Kini Bay, on the same rocky stretch, and would normally be regarded as a rocky shore. Localized sand deposits form strips of platform beach, backed by vegetated aeolianite cliffs. The sub-aerial intertidal to subtidal rock platform consists entirely of sandstone and quartzite as closely set shore-parallel, shore normal and diagonal ridges and boulders with some wide boulder-bottomed gulleys. There are no sand-bottomed gulleys in the near vicinity of the site.

The wave climate is similar to that of Kini Bay. Most wave action occurs on the seaward edge of the shore, where waves may break on the rocks on a spring high tide. Wave energy is reduced rapidly once they enter the rocky traverse. Collapsed or surging waves move up the gulleys, but over the rest of the shore, water movement is strongly modified and impeded.
by the configuration of the rocks, mostly following small channels or being caught and slowed down in rock pools. The platform beach only sees full wave interaction at spring high tides. No suspended sand was noted in waves arriving at the shore.

5.4.5 Cape Recife West (CRW)

This study site is on the western side of Cape Recife along a short embayment called Shelly Bay (Bremner 1983). A series of sandstone reefs interspersed with eroded broken aeolianite slabs alternate with sandy stretches and a wide subaerial beach. The beach is backed by tall semi-vegetated dunes that have accumulated over a thick aeolianite rock base. The sandstone reefs extend into the near-shore surf where a few aeolianite “stacks” stand out from the waves. The beach steepens and narrows rapidly towards its ends until it becomes a platform beach underscored by a rugged rocky shore. Viewed as a mixed substrate shore in the present study, this section of shore has in past studies been treated as a sandy beach (McGwynne et al. 1988).

CRW is exposed to a similar wave regime as the other sites along the stretch of coast west of Cape Recife. It is an intermediate beach with a surf zone similar in width to that of Maitlands. Surf zone waves spill and plunge, reforming on the beach face as small collapsing wavelets in the swash. Swash period on the beach sections is similar to that of Maitlands, but more irregular and notably shorter on approach or rocky sections. Wave bores all transport sand.

5.4.6 Cape Recife East (CRE)

Cape Recife is the rocky headland that defines Algoa Bay and provides some shelter against the predominant swell approaching from the south west (Schuman et al. 1982, 1988). Whereas Cape Recife itself is built of resistant quartzite and sandstone ridges that dip below sea level to extend out to sea as the treacherous Thunderbolt reef, the shore lying in its lee consists mainly of a low, near-horizontal aeolianite platform about 200 m wide which extends subtidally and forms the bottom of a surf zone. The rock platform is continuous except for the occasional break allowing landward transport of sand in wide gulleys. The study site is located at the middle section of the ca 6 km long rock platform. A narrow platform beach, backed by low semi-vegetated sand dunes, covers the landward side of the platform. There is evidence of historic and present beach erosion, as well as of past attempts to stem this by means of groynes. Dune stabilization has severely reduced the sediment budget of this section of shore (Bremner 1983). The rocky component and the beach have previously been studied as separate entities (e.g. McLachlan et al. 1977; Munnik 1987).
As waves are refracted around Cape Recife they enter the surf zone over the wide rocky platform in its lee. Waves quickly lose energy as they spill or plunge in the outer surf zone and convert into surging and collapsing wavelets over the near-shore section of the platform, especially at low tide. At higher tide levels, plunging or collapsing waves pass over the fully inundated platform and then surge onto the beach.

### 5.4.7 Pollock Beach South (MPB) and Pollock Beach North (PBE)

These study sites are located at either end of a sandy beach (Pollock Beach), where the sandy shore is interrupted by rock. Study site Pollock Beach South (MPB) incorporates the broken up end of the aeolianite platform (extending from Cape Recife) where it gives way to Pollock Beach. The shore configuration is similar to that of Cape Recife east, but the rock platform is lower, broken and much narrower, hardly extending into the surf zone. Well separated aeolianite slabs and low relief sandstone outcrops are interspersed with sand bottomed sections. The platform beach above the rocky section becomes a full sandy beach where the rock plate ends and is partly backed by low semi-vegetated sand dunes. The Pollock Beach North (PBE) site is a very short mixed section, with a few mid-beach sandstone outcrops.

The beach is managed by the Nelson Mandela Metropolitan Municipality. Regular beach grooming as well as intermittent beach nourishment, and recently, placement of gabions and sand bags to prevent beach erosion and damage to a parking area and housing development above spring high tide mark, are part of the management programme. The shore armouring has not been particularly effective, as major beach erosion still occurs after storms. The beach has fluctuating sand levels (Garner pers. obs. 2006, 2007, 2008, 2010). After a major erosion event, where bedrock and a pebble base are exposed, the beach is always rebuilt naturally within a matter of weeks.

Pollock Beach experiences high surf from time to time. The surf zone is not as wide as that of Maitlands Beach and the predominant wave type is plunging. The swash period is lower and swash consists of surging and collapsing wavelets, except at very high tides when wave bores collapse directly onto the beach even at the rock section.

### 5.4.8 Beacon Rock (BCN)

This study site is located at a shore linear sandstone ridge forming a small promontory with tombola. The surf zone is greatly reduced as plunging and spilling waves break directly onto the ridge. Wave action is concentrated on the tall rocky outcrop, which leaves the truncated
beach and some low relief sandstone outcrops behind it partly protected from wave action. Waves refracted around the ends of the ridge and also through a central gap surge or plunge-break directly onto the beach at high tides. Shore protection measures in the form of boulder-filled gabions have also been undertaken at this section of shore.

5.4.9 Avalanche (AVA)

The study site is a section of shore, about 100 m in length. Low sandstone outcrops form roughly parallel, broken reefs that do not extend below the spring low tide level, alternating with variable sand patches and shore normal sandy gulleys. There is a pebble berm above the spring high tide mark and the surface of the sand is pebble-strewn. Avalanche is characterized by very rapid and noticeable variations in sand load that occur continuously, not only after storm conditions. The beach has recently been fortified by placement of gabions, which has had the unfortunate consequence of reducing (rather than increasing) the sediment load, an effect commonly associated with hard shore protection (Nordstrom 2000).

Wave action is controlled by the rocky point (Beacon Rock) around which waves are refracted onto this section of shore. The truncated surf zone has a few scattered rocky outcrops. At low tide, surf zone waves are mostly plunging and do not reach the rock section. As the tide rises, waves break directly on the rocks and are dissipated over the relatively narrow rocky traverse, collapsing and surging up the sandy gulleys and onto the upper reaches of the shore.

5.4.10 Bird Rock (BRK)

The site is dominated by a ca. 200 m long shore-linear sandstone ridge at the low tide mark. On the landward side of the ridge, the exposed rock substrate consists of a low aeolianite platform in the mid to lower reaches. Sand waves regularly pass across the platform, resulting in a changeable sedimentary environment. An upper platform beach is backed by a low vegetated dune. The sandstone ridge acts as a natural breakwater, providing shelter against wave action to the area behind it. Waves are refracted around the edges of the ridge and surge or collapse onto the beach. On the landward side of the ridge, wave energy is greatly reduced.
5.4.11 Miller's Beach (MLS)

The site has a low horizontal aeolianite shore platform with few breaks and a narrow platform beach backed for most part by low semi-vegetated dunes. The shore platform is about 500 m long and extends below the low tide mark as sand-covered broken rock slabs.

A narrow surf zone with predominantly plunging to collapsing wave bores forms over the subtidal mixed sand-rock substrate at low tide. At high tides, the surf zone shifts onto the shore platform and spilling waves may also be seen in the outer surf zone. Waves sometimes reform over the platform. The swash lens reaches the beach only once the tide exceeds midtide level. Very little sand is evident in wave bores.

5.4.12 Humewood (HWD)

This study site encompasses two short mixed shore sections, both composed of a low broken aeolianite platform, taller sandstone outcrop and narrow platform beach. The rock component does not extend subtidally. The two sections of shore are separated by Humewood Beach, a mixed pocket beach formed at the mouth of the diminutive Shark River. Humewood Beach itself was not sampled, though it is viewed as part of the mixed section. The one mixed shore section lies to the south of Humewood Beach and borders on Hobie Beach. The other, which is located between Humewood Beach and King's Beach, is backed by a brick-built beach promenade and modified by three groynes and a low shore breakwater, all of which have been in place since the early 20th century.

The entire section of shore is more sheltered from direct wave action than the adjacent sites due to its position in the bay and relative to prominent rocky features. As at Miller's Beach, waves generally break before they reach the shore at low tides, but traverse the rocky platform as the tide rises and then break closer inshore. Predominant wave types in the truncated surf zone are plunging and collapsing, while the swash consists of surging and collapsing waves with the occasional plunger at spring high tides. Sand is evident in wave bores, but swash is mostly clear.

5.4.13 Hougham Park West (HPW) and Hougham Park East (HPE)

The well-developed sandy beach that extends eastward from the mouth of the Swartkops River ends abruptly at the Nqura River mouth and is replaced, to the east of the mouth, by a mixed section of shore with a partly exposed aeolianite platform as rock substrate, which disappears again a few kilometres before the Sundays River Mouth. The platform underlies
a dune field and protrudes at the coast where its elevation varies. Sections that lie at an elevation just above mean sea level have a shallow seaward scarp near spring low tide mark and a landward aeolianite cliff, and bear shallow, patchy sand deposits. Some of these sections are clearly undercut. Long sections of the intertidal shore platform are low, broken slabs of aeolianite that are partly sand-covered and lie at the base of a long sandy beach backed by partly vegetated dunes. The shore platform is narrow and does not extend much subtidally. The study sites are located roughly 3 km apart along this stretch of coastline. The site named Hougham Park West (HPW) is located about 3 km to the east of the Nqura River mouth and the recently constructed deepwater harbour, whereas Hougham Park East (HPE) lies towards the Sundays River end of the mixed section. At Hougham Park West (HPW) the platform is slightly higher than at Hougham Park East (HPE) and is mostly horizontal whereas it slopes at Hougham Park East (HPE). This section of coast experienced great short-term fluctuations in sedimentation prior to the building of the harbour wall (A. Cloete, pers. com. 2007). The effect of the harbour wall on sand transport is unknown.

Both sites are exposed to wave action, as they lie too far to the east to be protected by Cape Recife. At low tide the surf zone at this section of shore has a sandy substrate with no rocky outcrops. The surf zone is wide and the predominant breaker types spilling and plunging. The morphodynamic state is intermediate. As the tide rises, the surf zone envelops the narrow platform which makes out much of the shoreface. Very little dissipation of wave energy occurs over the smooth platform as waves rush up and often break directly over the platform at high tides, especially at HPE where platform elevation is lower and the platform itself more inclined. At both these sites off shore sediment transport is enhanced by the presence of rock platform under shallow deposits of sand because of reduced beach permeability. At HPW where the platform is horizontal or inclined landward wave energy is dissipated directly on the seaward scarp of the platform. The swash consists of surging and collapsing wavelets.

5.4.14 Cannon Rocks (CNR)

Cannon Rocks lies to the east of Cape Padrone which marks the eastern limit of Algoa Bay. Along much of this stretch of coast, an aeolianite platform lies at the base of a steep reflective beach backed by well-developed coastal dunes that are partly vegetated. Where the aeolianite has been eroded away, a bouldery sandstone platform or shale ridges are seen instead. The study site is located at the aeolianite platform. The aeolianite platform has few breaks and stretches at least 200 m out to sea allowing a surf zone to develop over it.
This site is fully exposed to waves. The waves of the outer surf zone are spilling or plunging and, having dissipated their energy over the platform, reform as much smaller wavelets that plunge, collapse or simply surge up the beach face, depending on the state of the tide.

5.4.15 Three Sisters (TST)

Roughly 14 km to the east of Port Alfred, three well-known rocky promonitories, the Three Sisters, jut out from a sandy shoreline, a pattern that characterizes much of the coast between Cape Padrone and East London. Like several other such promonitories, the Three Sisters are composed of tall aeolianite cliffs, each fronted by a narrow, near-horizontal shore platform with a seaward scarp. In contrast, adjacent to the headlands, cliff remnants are much reduced in size and partly covered by a sandy beach. The study site involves one of these promonitories and the adjacent shore platform and beach.

This section of coast is also well exposed to wave action. At low tide the surf zone is sand-bottomed and disconnected from the intertidal shore platform. Breakers are spilling or plunging, but are always broken by the time they reach the platform, except at the promontory itself, where waves may break directly on the rock even at low tide. As the tide rises, the surf zone shifts onto the platform and much wave energy is dissipated at its seaward edge. Smaller plunging, collapsing or surging waves reform over the platform as the swash rushes up and onto the beach.

5.4.16 Kleinemonde East (KME)

This study site is located near the middle of a mixed shore section adjacent to the East Kleinemonde river mouth. The shore is characterized by a well-developed subaerial sandy beach backed by partly vegetated dunes. The subaquatic beach is dissected by a series of shore-normal or diagonal shale ridges that extend some distance into the surf zone and are variously spaced. The shale outcrops extend over a distance of about 1 km alongshore.

An exposed beach, the sand-bottomed surf zone at KME is wide and the wave type mostly spilling and plunging. Waves are usually broken when they reach the low rocky outcrops, but their energy is reduced rapidly as they traverse the rocks and reform as much smaller collapsing or surging waves of the swash lens. At the rocky section the swash run-up is irregular and reduced as compared to the adjacent beach without rock outcrops.
CHAPTER 6 Physical and dynamic attributes of study sites

6.1 Geology and intertidal topography

The high ridge sites mostly had a greater rock height range relative to tidal elevation and consequently higher rock height ratings than most of the low ridge as well as platform sites (Table 6). Low ridge sites either had a rock substrate of shale, in which case the rock was in the form of low, jagged ridges, with low rock height ratings, or sandstone-quartzite, e.g. Bird Rock (BRK), and Beacon Rock (BCN), that gave a rock height rating in the same range as high ridge study sites.

Aeolianite platforms ranged from a narrow, almost continuous base, e.g. at Three Sisters (TST) and Hougham Park West (HPW), through broken, narrow rock slabs, e.g. at Hougham Park East (HPE), Pollock South (MPB) and Humewood (HWD), to very wide platforms, e.g. at Miller’s Beach (MLS), Cannon Rocks (CNR) and Cape Recife East (CRE), with a concomitant decrease in platform elevation. At high platform sites the hard substrate was positioned at an elevation between the spring low and neap high tide marks with landward cliffs extending well above spring high tide level, whereas at low platform sites, the entire platform was situated below mean sea level and extended subtidally into the surf zone. An associated landward cliff, e.g. at HPW, HPE and TST, or tall sandstone outcrops, e.g. HWD, increased the rock height rating (Table 6). Low platform sites had the lowest ratings for rock height as at these localities the aeolianite platform was nearly horizontal with very few taller outcrops.

Intertidal topography (Figure 3) of study sites ranged from steep and complex, e.g. Willows Beach (WLW) and Kini Bay (KNB), to gentle and featureless, e.g. Cannon Rocks (CNR) and Pollock South (MPB). It was not possible to differentiate meaningfully between sediment and rock components in the graphical representations of shore profiles as sand and rock segments alternated over too short distances at some sites, e.g. Avalanche (AVA), Hougham Park East (HPE). At least one shore normal profile (T1, T2 or T3) per site represented the full vertical topography from spring high tide level (HWS) to spring low tide level (LWS). The only exception was Cannon Rocks (CNR) where the furthest point at LWS level was not surveyed due to unfavourable wave and tide conditions.

High ridge sites (Figure 3) were the steepest and most complex and had a greater proportion of rock surface above the midtidal elevation than other sites. Of the high ridge sites, the ‘rocky shore’ sites, Willows Beach (WLW) and Kini Bay (KNB), had the most rugged topography.
Table 6. Geology, rock topography, position, height range and rock height rating of study sites. S & Q = sandstone and quartzite, aeolian = aeolianite, M or MTL = midtidal, L or LWS = spring low tide level, H or HWS = spring high tide level, HWN = neap high tide level, sub = subtidal. Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3. 1 h/s = high ridge, 1 m/s = low ridge, 2 h/s = high platform, 2 m/s= low platform.

<table>
<thead>
<tr>
<th>Site Name</th>
<th>(Code)</th>
<th>Configuration</th>
<th>Geology</th>
<th>Topography</th>
<th>Rock Base Position</th>
<th>Range of Rock Heights</th>
<th>Rock Height Rating</th>
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<tbody>
<tr>
<td>Willows Beach</td>
<td>WLW</td>
<td>1 h/s</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>H - L</td>
<td>HWS - sub</td>
<td>15</td>
</tr>
<tr>
<td>Kini Bay (KNB)</td>
<td></td>
<td>1 h/s</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>H - L</td>
<td>HWS - sub</td>
<td>12</td>
</tr>
<tr>
<td>Cape Recife West (CRW)</td>
<td>1 h/s+++</td>
<td>S &amp; Q, Aeolian</td>
<td>Ridges</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Avalanche (AVA)</td>
<td></td>
<td>1 h/s+++</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>5</td>
</tr>
<tr>
<td>Maitlands Inner (MAA)</td>
<td>1 h/s+++</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Maitlands Outer (MAB)</td>
<td>1 h/s+++</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>10</td>
<td></td>
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<tr>
<td>Pollock North (PBE)</td>
<td>1 m/s+++</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>M - MTL</td>
<td>HWS - LWS</td>
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<tr>
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<td>S &amp; Q</td>
<td>Ridges</td>
<td>M - L</td>
<td>HWS - LWS</td>
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<td></td>
</tr>
<tr>
<td>Bird Rock (BRK)</td>
<td>1 m/s+</td>
<td>S &amp; Q</td>
<td>Ridges</td>
<td>M - L</td>
<td>HWS - LWS</td>
<td>9</td>
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</tr>
<tr>
<td>Kleinemonde East (KME)</td>
<td>1 m/s+</td>
<td>Shale</td>
<td>Ridges</td>
<td>M - L</td>
<td>HWS - sub</td>
<td>8</td>
<td></td>
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<tr>
<td>Aston Bay (ASB)</td>
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<td>Shale</td>
<td>Ridges</td>
<td>M - L</td>
<td>HWN - sub</td>
<td>5</td>
<td></td>
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<tr>
<td>Paradise Beach (PDB)</td>
<td>1 m/s+++</td>
<td>Shale</td>
<td>Ridges</td>
<td>M - L</td>
<td>HWN - sub</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Three Sisters (TST)</td>
<td>2 h/s+</td>
<td>Aeolian</td>
<td>Platform, tall cliff</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>7</td>
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<tr>
<td>Hougham Park West (HPW)</td>
<td>2 h/s++</td>
<td>Aeolian</td>
<td>Platform, low cliff</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Hougham Park East (HEPE)</td>
<td>2 h/s+++</td>
<td>Aeolian</td>
<td>Platform</td>
<td>H - L</td>
<td>HWS - LWS</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Cape Recife East (CRE)</td>
<td>2 m/s+</td>
<td>S &amp; Q, Aeolian</td>
<td>Platform</td>
<td>M - L</td>
<td>HWN - sub</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Cannon Rocks (CNR)</td>
<td>2 m/s++</td>
<td>Aeolian</td>
<td>Platform</td>
<td>M - L</td>
<td>HWN - sub</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Miller’s Beach (MLS)</td>
<td>2 m/s+</td>
<td>Aeolian</td>
<td>Platform</td>
<td>M - L</td>
<td>HWN - sub</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Humewood (HWD)</td>
<td>2 m/s++</td>
<td>S &amp; Q, Aeolian</td>
<td>Platform</td>
<td>M - L</td>
<td>HWN - LWS</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Pollock South (MPB)</td>
<td>2 m/s+++</td>
<td>Aeolian</td>
<td>Platform</td>
<td>M - L</td>
<td>HWN - sub</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>
High ridge sites:

Figure 3. Shore topography along three shore normal profiles (T1, T2 and T3) and one mid-tidal shore-parallel profile (T4). Profiles are given relative to mean sea level (MSL). Study sites are arranged according to configuration type as explained in Table 2. High ridge sites: WLW, KNB, AVA, MAA, MAB, CRW; Low ridge sites: BCN, PBE, BRK, ASB, PDB, KME; High platform sites: TST, HPW, HPE; Low platform sites: MLS, CNR, CRE, HWD, MPB.
Low ridge sites:

Figure 3 (cont.). Shore topography along three shore normal profiles (T1, T2 and T3) and one mid-tidal shore-parallel profile (T4). Profiles are given relative to mean sea level (MSL). Study sites are arranged according to configuration type as explained in Table 2. High ridge sites: WLW, KNB, AVA, MAA, MAB, CRW; Low ridge sites: BCN, PBE, BRK, ASB, PDB, KME; High platform sites: TST, HPW, HPE; Low platform sites: MLS, CNR, CRE, HWD, MPB.
High platform sites:

Figure 3 (cont.). Shore topography along three shore normal profiles (T1, T2 and T3) and one mid-tidal shore-parallel profile (T4). Profiles are given relative to mean sea level (MSL). Study sites are arranged according to configuration type as explained in Table 2. High ridge sites: WLW, KNB, AVA, MAA, MAB, CRW; Low ridge sites: BCN, PBE, BRK, ASB, PDB, KME; High platform sites: TST, HPW, HPE; Low platform sites: MLS, CNR, CRE, HWD, MPB.
Low platform sites:

Figure 3 (cont.). Shore topography along three shore normal profiles (T1, T2 and T3) and one mid-tidal shore-parallel profile (T4). Profiles are given relative to mean sea level (MSL). Study sites are arranged according to configuration type as explained in Table 2. High ridge sites: WLW, KNB, AVA, MAA, MAB, CRW; Low ridge sites: BCN, PBE, BRK, ASB, PDB, KME; High platform sites: TST, HPW, HPE; Low platform sites: MLS, CNR, CRE, HWD, MPB.
Low ridge sites had very little rock on the beach face and profiles therefore mainly reflected the response of beach sediment to reworking by waves. The majority of rock outcrops were in the lower intertidal to shallow subtidal in the form of low shore-normal ridges with steeply sloping sides (Figure 3). High platform sites and low platform sites (Figure 3) had the least complex topography, as the greater proportion of rock surface consisted of near-horizontal rock platforms, those of high platform sites being generally of higher elevation than those of low platform sites.

The shore-linear profile (T4) of vertical shore topography at roughly mid-tidal elevation, demonstrated greater long-shore topographic variability in ridge sites than platform sites at approximately midtidal elevation.

### 6.2 Cross-shore and long-shore extent of rock and sand

The proportions of sand and rock varied not only from site to site, but also from profile to profile (Table 7). The two sites with the highest percentage rock along cross-shore profiles (T1, T2 and T3) were Willows Beach (WLW), a high ridge shore, and Cape Recife East (CRE), a low platform shore. The sites with the highest percentage of sand along cross-shore profiles were Pollock North (PBE) and Pollock South (MPB). PBE had a small midtidal rock outcrop and MPB a narrow midtidal to subtidal broken shore platform.

High ridge sites mostly had a greater proportion of intertidal rock (Table 7), and therefore less sand, in both a shore-linear and shore-normal direction. In contrast, low ridge sites tended to have more uninterrupted beach face than other ridge type shores, although this was not clearly demonstrated by the T4 and other profiles. Shales form low, long ridges, usually separated by stretches of sand several metres wide, so that all those sites had a lower proportion of rock on the beach face both along -and across-shore, the rock being mostly confined to the surf zone. Aeolianite platforms that lie more or less at spring low tide level (LWS), as in low platform sites, were more extensive than those of high platform sites. Both types had relatively narrow beaches between the spring high tide level and either LWS or slightly beyond that and variable, patchy sand deposits over the rocky platform.

Except for Willows Beach (WLW) and Kini Bay (KNB), all sites were backed by or close to sand dunes, i.e. less than 1 km, some with no vegetation and others vegetated to different degrees (natural or transformed). WLW and KNB were backed by a fully vegetated aeolianite cliffs and mature, vegetated dunes, respectively.
Table 7. Extent of rock substrate and beach deposits along shore normal (T1, T2 and T3) and shore linear (T4) shore profiles per site, with distance to closest sandy beach or dunes. The shore linear profile was taken approximately at midtidal elevation. The total distance taken up by sand (first line) and rock (second line) along the profile is given in metres (m) and as a percentage (in brackets) of total distance of measured profile. Distance to the nearest up-drift sandy beach is given in kilometre (km). Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3. 1h/s = high ridge, 1 m/s = low ridge, 2 h/s = high platform, 2 m/s= low platform.

<table>
<thead>
<tr>
<th>Configuration</th>
<th>Site Name (Code)</th>
<th>Length of profile (m)</th>
<th>Extent of sand (1st line) and rock (2nd line) per profile in m (% in brackets).</th>
<th>Nearest sandy beach/dune (km)</th>
</tr>
</thead>
</table>
|               |                 | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1       | T2       | T3       | T4       | T1�
Table 7 (cont.). Extent of rock substrate and beach deposits along shore normal (T1, T2 and T3) and shore linear (T4) shore profiles per site, with distance to closest sandy beach or dunes. The shore linear profile was taken approximately at midtidal elevation. The total distance taken up by sand (first line) and rock (second line) along the profile is given in metres (m) and as a percentage (in brackets) of total distance of measured profile. Distance to the nearest up-drift sandy beach is given in kilometre (km). Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3. 1h/s = high ridge, 1 m/s = low ridge, 2 h/s = high platform, 2 m/s = low platform.

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<tr>
<th>Configuration</th>
<th>Site Name (Code)</th>
<th>Length of profile (m)</th>
<th>Extent of sand (1st line) and rock (2nd line) per profile in m (% in brackets)</th>
<th>Nearest sandy beach/dune (km)</th>
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<tr>
<td>2 h/s +</td>
<td>Three Sisters (TST)</td>
<td>143 49 36 40</td>
<td>T1 131 (86) 14 (19) 2 (7) 64 (93) 15 (7) 12 (21) 40 (100) 0 0.1</td>
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<td>Hougham Park West (HPW)</td>
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<td>T1 60 (81) 14 (19) 36 (47) 17 (22) 32 (58) 23 (42) 0 84 (100) 0.1</td>
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<td>Hougham Park East (HPE)</td>
<td>64 76 73 73</td>
<td>T1 22 (34) 42 (66) 59 (78) 17 (22) 61 (84) 12 (16) 47 (64) 26 (36) 0.1</td>
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</tr>
<tr>
<td>2 m/s +</td>
<td>Cape Recife East (CRE)</td>
<td>165 147 127 53</td>
<td>T1 24 (15) 141 (85) 36 (24) 111 (76) 27 (21) 100 (79) 0 53 (100) 0.1</td>
<td></td>
</tr>
<tr>
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<td>Cannon Rocks (CNR)</td>
<td>105 85 90 40</td>
<td>T1 69 (66) 36 (34) 48 (56) 37 (44) 51 (57) 39 (43) 40 (100) 0 0.1</td>
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</tr>
<tr>
<td>2 m/s ++</td>
<td>Miller’s Beach (MLS)</td>
<td>85 127 91 40</td>
<td>T1 60 (71) 25 (29) 39 (31) 88 (69) 26 (29) 65 (71) 16 (33) 33 (67) 0.1</td>
<td></td>
</tr>
<tr>
<td>2 m/s +++</td>
<td>Humewood (HWD)</td>
<td>71 76 65 36</td>
<td>T1 25 (35) 46 (65) 37 (49) 39 (51) 30 (46) 35 (54) 27 (75) 9 (25) 0.5</td>
<td></td>
</tr>
<tr>
<td>2 m/s +++</td>
<td>Pollock South (MPB)</td>
<td>70 71 72 43</td>
<td>T1 63 (90) 7 (10) 69 (97) 2 (3) 72 (100) 0 43 (100) 0 0.1</td>
<td></td>
</tr>
</tbody>
</table>

The mean percentage cross-shore rock increased with the linear extent of rock along profiles (Figure 4). In further comparisons involving the cross-shore rock parameter, the mean percentage cross-shore rock was substituted for the mean distance of rock along the profile. The mean percentage long-shore rock (along the midtidal long-shore profile) was highest at high ridge sites with closely packed rock ridges, e.g. Avalanche (AVA), Willows Beach (WLW), Kini Bay (KNB) and Maitlands inner (MAA), and lowest at low ridge sites with widely spaced ridges, e.g. Aston Bay (ASB) and Paradise Beach (PDB), but was not related to the actual extent or % of cross-shore rock (Figure 4). Similarly, rock height rating was not related to the cross- or longshore extent of rock but did appear to be linked to the position of rock.
relative to tide marks (Figure 4), as sites with rock substrate only below the midtidal level mostly had lower ratings for rock height.

Beaches were very narrow and discontinuous at sites further away from a well-developed beach or dune system or that had a high proportion of cross-shore or mid-longshore rock or a high rock height rating (Figure 5). Two sites, i.e. Willows Beach (WLW) and Kini Bay (KNB), ranked highly in all of these attributes and had the narrowest beaches. Both had ridges throughout the intertidal. The four widest beaches occurred at Maitllands Outer (MAB), Aston Bay (ASB), Three Sisters (TST) and Pollock South (MPB), each of a different configuration type (Figure 5). This implied that beach accretion occurs independently of gross shore configuration, i.e. ridges or platforms, but is more strongly influenced by the rock height and intertidal continuity of the rock substrate.

6.3 Sediment depth

Sediment depth varied, not only from site to site, but also from profile to profile. The mean percentage of depth measurements exceeding 30 cm, ranged between 17% and 100% per site (Figure 6). At three sites, Aston Bay (ASB), Maitllands Outer (MAB) and Kleinemonde East (KME), sediment depth exceeded 30 cm at all measured points. At six of the sites sediment depth measured along profiles was often less than 15 cm (Figure 6). Sediment depth (Figure 7) appeared to be inversely related to distance from the nearest beach or dune system, as well as the percentage of exposed rock cross-shore and long-shore, and rock height rating, although the trends differed for the two main shore configurations (ridges and platforms).

While shallow sediment (depth < 30 cm) was more prevalent at sites further away from dunes or fully sandy beaches, overall, sediment depth measurements were not strongly related to distance from nearest beach or dune system (Figure 7). Some study sites with shallow sediment were adjacent to active beaches and dunes, e.g. Avalanche (AVA), Beacon Rock (BCN), Maitllands Inner (MAA), Hougham Park East (HPE) and West (HPW) in Figure 7. With one or two exceptions, ridge sites with a high percentage of exposed rock across-shore, long-shore or a high rock height rating gave shallower sediment.

Sediment depth measurements at platform shores did not suggest a particular trend with an increased percentage of cross-shore rock, as sites at both ends of the scale predominantly had deep sediment (Figure 7). However, except for Three Sisters (TST), in Figure 7, platform sites with a higher percentage of midtidal rock and greater rock height rating tended to have shallower sediments.
Figure 4. The mean percentage rock along shore-normal (cross-shore) profiles (n = 3) and a midtidal shore-parallel (longshore) profile (n = 1) and rock height rating of sites, all in relation to mean cross-shore rock width (m) (n = 3). A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: RocL_100 = mean % long-shore rock along profile, Roc_C = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating.
Figure 5. The mean percentage rock along shore-normal (cross-shore) profiles (n = 3) and a midtidal shore-parallel (long-shore) profile (n = 1), rock height rating of sites and distance from nearest dune or well-developed beach, all in relation to mean beach width. A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: RocL_100 = mean % long-shore rock along profile, Roc_C = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating.
Figure 6. The proportion of sediment depth measurements exceeding 30 cm and the mean depth of shallow patches less than 30 cm deep. Bars give the % of depth measurements (n = 54 per site) over 30 cm. Squares give the mean (± SE) measured depths of shallower sediments. Sites are arranged according to configuration: WLW to MAB are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.
Figure 7. The mean percentage rock along shore-normal (cross-shore) profiles ($n = 3$) and a midtidal shore-parallel (long-shore) profile ($n = 1$), rock height rating of sites and distance from nearest dune or well-developed beach, all in relation to percentage sediment depth measurements > 30 cm. A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: RocL$_{100}$ = mean % long-shore rock along profile, RocC$_{100}$ = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating, Dun_Dis = Rock Height Rating/dune distance (km).
At most sites sediment depth changed across shore (Table 8). For sites where measured sediment depth was greater than 30 cm at all sampling stations, no depth variation could be demonstrated. Shallow patches of sediment occurred most often in a midtidal to low position, measuring between 11 cm and 28 cm deep. At most sites there was a decrease in depth down-shore (from spring high tide level to spring low tide level), at a few sediment depth increased down shore and a third group had their deepest sand deposits mid-shore.

6.4 Sediment characteristics

6.4.1 Sediment grain size composition

The mean sediment grain size composition indicated that study sites had predominantly fine to medium sand (Figure 8). The percentage “fines”, i.e. very fine sand (0.063 – 125 µm) and mud (< 0.063 µm) was negligible (< 2 %). At sites with a large coarse fraction (> 500 µm), there was an admixture of large shell fragments and small pebbles.

The modal particle size class ranged from fine (125 to 250 µm) to coarse sand (500 to 1000 µm). At Avalanche (AVA), Beacon Rock (BCN), Bird Rock (BRK), Pollock North (PBE), Humewood (HWD), Miller’s Beach (MLS), Pollock South (MPB) and Cape Recife East (CRE), sites that lie adjacent to one another in the south-western corner of Algoa Bay, the modal particle size class was fine sand. All these sites were sheltered from the predominant swell by Cape Recife. Fine sand was also the predominant size class of the embayed beach at CRW (Cape Recife West). The headland bypass dune system at Cape Recife is a potential natural source of sediment for all these beaches. Two other sites with mostly fine sand were Aston Bay (ASB) and Paradise Beach (PDB), both within St Francis Bay, down-drift of the headland bypass dune system at Cape St Francis and also not directly exposed to the predominant swell.

At Kini Bay (KNB), Maitlands Inner (MAA), Maitlands Outer (MAB), Kleinemonde East (KME), Three Sisters (TST), Hougham Park East (HPE), Hougham Park West (HPW) and Cannon Rocks (CNR) the modal size class was 250 to 500 µm (medium sand). All of these sites were in wave-exposed positions and adjacent to or not far from a beach-dune system. At Willows Beach (WLW) and Kini Bay (KNB), the coarse fraction (>500 µm) was the dominant component of the sediment composed of a sand, large shell fragments and small pebbles. They were also directly exposed to the predominant swell. Willows Beach (WLW) and Kini Bay (KNB) were ridge shores with a rugged rock base and narrow platform beach, both several kilometres away from the nearest land-based source of sand.
Table 8. Mean depth of sediment across-shore. Mean (± SE) sediment depth is only given for strata with a sediment depth less than 30 cm. Where depth measurements exceeded 30 cm, it is entered as 30+. S0 and S1 are high shore strata, S2 and S3 are mid-shore strata, and S4 and S5 are low shore strata. Sampling stratum codes are explained in Table 4 (Chapter 4). Sites are arranged according to configuration: WLW to MAB are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites. Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3.

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</tr>
<tr>
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<td>(1 h/s++)</td>
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</tr>
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<td>(1 h/s +++)</td>
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<td>(1 h/s ++++)</td>
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<td>(1 m/s +)</td>
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<td>MPB</td>
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Figure 8. Sediment grain size composition (n = 36 per site). Legend: > 2000 µm is very coarse sand; 1000 – 500 µm is coarse sand; 500 – 250 µm is medium sand; 250 - 125 µm is fine sand; 125 - 63 µm is very fine sand; < 63 µm is silt. Sites are arranged according to configuration: WLW to MAB are high ridge sites, BCN to PBE are low ridge sites, TST to HPW are high platform sites, and HWD to MPB are low platform sites.
Mean grain size increased with a higher proportion of cross-shore rock at ridge shore sites, but did not show any trend at sites with wider platforms (Figure 9).

Particle size composition varied across-shore at most study sites (Figure 10). At some study sites (e.g. WLW, KNB, CRW, MAA, MAB, BCN, HPE, TST and MLS in Figure 10) particle size composition coarsened from spring high tide level (HWS) to spring low tide level (LWS) due to an increase in the proportion of coarse sediment and a loss of fine size classes. A second tendency was for sediment to be coarsest in the midtidal reaches than higher up or lower down (e.g. BRK, ASB, PDB, CRE, HPW, HWD and CNR in Figure 10). Both these trends are associated with reflective beaches as well as beaches under structural control, i.e. influenced by the presence of hard structures such as rock reefs and platforms (Short 1999).

6.4.2 Carbonate content

The carbonate content ranged from 15% to 25% (Figure 11). Hougham Park West (HPW) had the highest mean percentage of carbonate in sediment (25%), followed closely by Kini Bay (KNB) and Willows Beach (WLW). At all three these sites, shell grit fragments were evident in the sediment. At most of the other sites the mean carbonate content of sediment was below 20%. Cape Recife West (CRW) had the lowest (15%). At most of the sites the percentage carbonate in sediment samples increased slightly towards the lower reaches of the shore (Figure 12). At the Hougham Park West (HPW) and East (HPE) sites, however, there was quite a marked difference in the amount of carbonate across the shore.

6.4.3 Organic matter content

The mean percentage organic matter in sediment was low (Figure 13), ranging from about 1.8% to about 3.5%. Humewood (HWD) and Bird Rock (BRK) had the highest overall mean percentage organic matter and MAA and MAB (Maitlands Inner and Outer, respectively) the lowest. At some sites the organic matter content of sediment was almost constant across-shore (Figure 14). Most sites, however, had a variable organic content with only one potential trend, i.e. that it increases towards lower shore elevations. At most of the study sites the organic matter content of sediment was highest in the lower littoral strata (S3, S4 and S5). Sediment from about neap high water level (S1) generally had the lowest organic content. The high overall organic content of sediment at BRK and HWD was mainly due to the contribution made by sediment from lower littoral strata (S3, S4 and S5).
Figure 9. Median and mean grain size in relation to percentage cross-shore rock. A. High ridge and low ridge sites. B. High platform and low platform sites.
Figure 10. Cross-shore variation in grain size composition of sediment at different sites. Legend: Sediment: > 2000 µm is very coarse sand; 1000 – 500 µm is coarse sand; 500 – 250 µm is medium sand; 250 - 125 µm is fine sand; 125 - 63 µm is very fine sand; < 63 µm is silt. Sampling strata: S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line.
Figure 10. (cont.) Cross-shore variation in grain size composition of sediment at different sites. Legend: Sediment: > 2000 µm is very coarse sand; 1000 – 500 µm is coarse sand; 500 – 250 µm is medium sand; 250 - 125 µm is fine sand; 125 - 63 µm is very fine sand; < 63 µm is silt. Sampling strata: S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line.
High platform sites:

Figure 10. (cont.) Cross-shore variation in grain size composition of sediment at different sites. Legend: Sediment: > 2000 µm is very coarse sand; 1000 – 500 µm is coarse sand; 500 – 250 µm is medium sand; 250 - 125 µm is fine sand; 125 - 63 µm is very fine sand; < 63 µm is silt. Sampling strata: S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line.
Figure 10. (cont.) Cross-shore variation in grain size composition of sediment at different sites. Legend: Sediment: > 2000 µm is very coarse sand; 1000 – 500 µm is coarse sand; 500 – 250 µm is medium sand; 250 - 125 µm is fine sand; 125 - 63 µm is very fine sand; < 63 µm is silt. Sampling strata: S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line.

Low platform sites:
Figure 11. The mean (± SE) percentage carbonate in sediment samples (n = 36) given for each site (white bars) and the overall mean for all sites (grey bar) (n = 720). Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.

Figure 12. The mean percentage carbonate in sediment samples at each stratum (n = 6) given for each site. S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line. Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.
Figure 13. The mean (± SE) percentage organic matter in sediment samples (n = 36) at each site (white bars) and the overall mean for all samples (n = 720) (grey bar). Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.

Figure 14. The mean percentage organic matter in sediment samples at each stratum (n = 6) given for each site. S0 = wrack line, S1 = drying sand, S2 and S3 = upper and lower mid-shore, S4 = zone of resurgence, S5 = zone of saturation/low tide swash line. Study sites are arranged according to configuration: WLW to MAA are high ridge sites, BCN to PBE are low ridge sites, TST to HPE are high platform sites, and CRE to MPB are low platform sites.
6.5 Beach parameters and exposure rating

The sediment deposits at study sites were treated as beaches, even though some were rather far removed in appearance and extent from a sandy beach devoid of rock. Beach width, the mean cross-shore extent of sand between tide marks, was variable, ranging from less than 20 m wide to over 80 m (Table 9).

Surf zone widths ranged from an estimated 50 m to 200 m wide (Table 9). Surf zones of ridge shores related differently to shore configuration attributes than those of platform shores (Figure 15). At the ridge shores the surf zones were least well developed at sites with a high percentage cross-shore and long-shore rock as well as high rock height ratings. Surf zone width increased at sites with a reduction in long-shore rock extent, even where cross-shore rock extent or rock height rating remained high. Among the platform shores, surf zones were widest at sites with a high percentage cross-shore rock and very low rock height ratings.

Wave number relates to the number of breaking waves in the surf zone. A weakly developed surf zone is truncated and usually has only few breaking waves. At Willows Beach (WLW) and Kini Bay (KNB) the wave number was relatively high despite the small extent of the surf zone that formed over the sloping shore zone. Wave types observed were mostly spilling and plunging, indicating the dissipation of wave energy on entering the surf zone.

Beach slope ranged from moderate (1/55) at Bird Rock (BRK) to steep (1/8) at Kini Bay (KNB). Beach slope exhibited different trends at ridge shores and platform shores (Figure 16). At ridge sites, beaches were steepest at the sites with the highest percentage cross-shore and long-shore rock and rock height rating, becoming flatter as the rock component decreased in amount and height. Platform sites on the other hand appeared to demonstrate the opposite, although the relationship was less clear.

Dimensionless fall velocity (Ω), Relative Tidal Range (RTR) and the Beach State Index (BSI) calculated for sandy beaches have predictive value with regard to beach type, tidal influence and beach mobility, respectively (Short 1999). For these mixed substrate shore study sites several beach parameters (Table 9), i.e. the wave height (range: 0.8 to 1.5 m), the breaker type (spilling/plunging at all sites) as well as dimensionless fall velocity, RTR and BSI (Table 10) predicted an intermediate to reflective beach state. Microtidal beaches have RTR values below 3 and are said to be wave-dominated, i.e. the processes of the surf zone and swash have overriding control of the beach. All the study sites clearly fall in this category.

The dimensionless fall velocity (Gourlay 1968, Wright and Short 1984, Short 1999) also called Dean’s parameter (see Brown and McLachlan 1990) was developed to separate
Table 9. Mean shore width, beach width and slope as well as wave number, breaker type and tidal range of mixed substrate shore study sites. Beach slope was calculated using mean beach width. Wave number = no of waves in surf zone. Breaker type: s = spilling, p = plunging. Tidal reach = vertical distance between high and low spring tide marks, including observed run-up. Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3. 1h/s = high ridge, 1 m/s = low ridge, 2 h/s = high platform, 2 m/s= low platform.

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<th>Beach Width (m)</th>
<th>Surf Zone Width (m)</th>
<th>Wave Number</th>
<th>Tidal Reach (cm)</th>
<th>Median Particle Size Class (µ)</th>
<th>Mean Particle Size (µ)</th>
<th>Breaker Type</th>
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<td>MLS</td>
<td>2 m/s ++</td>
<td>100</td>
<td>42</td>
<td>100</td>
<td>3</td>
<td>142</td>
<td>29</td>
<td>287</td>
<td>s/p</td>
<td>0.8</td>
<td>8</td>
</tr>
<tr>
<td>HWD</td>
<td>2 m/s +++</td>
<td>70</td>
<td>46</td>
<td>80</td>
<td>3</td>
<td>185</td>
<td>25</td>
<td>353</td>
<td>s/p</td>
<td>1.4</td>
<td>8</td>
</tr>
<tr>
<td>MPB</td>
<td>2 m/s +++</td>
<td>72</td>
<td>68</td>
<td>100</td>
<td>3</td>
<td>143</td>
<td>47</td>
<td>269</td>
<td>s/p</td>
<td>1.3</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure 15. The mean percentage rock along shore-normal (cross-shore) profiles (n =3) and a midtidal shore-parallel (longshore) profile (n = 1) and rock height rating of sites, all in relation to surf zone width.  A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: RocL_100 = mean % long-shore rock along profile, Roc_C = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating.
Figure 16. The mean percentage rock along shore-normal (cross-shore) profiles (n = 3) and a midtidal shore-parallel (longshore) profile (n = 1) and rock height rating of sites, all in relation to the mean beach slope (1/slope). A. High ridge and low ridge sites. B. High platform and low platform sites. Legend: Roc_L_100 = mean % long-shore rock along profile, Roc_C = mean % cross-shore rock along profile, Roc_Rating = Rock Height Rating.
Table 10. Dimensionless fall velocity (Ω), Relative Tidal Range (RTR), Beach State Index (BSI), beach type (predicted and observed) and Exposure Score and Rating. Legend: Predicted beach type \(^1\) is according to RTR (Masselink and Turner 1999) and \(^2\) is according to BSI (McLachlan et al. 1993). Exposure rating is according to McLachlan (1980). Values in brackets are scores obtained using shore slope instead of beach slope. The data used for calculating the exposure rating are presented in Addendum 2. Observed beach type is according to Short (1999). Abbreviations used: R = reflective, I = intermediate, D = dissipative, E = exposed, ME = moderately exposed, VE = very exposed, S = sheltered, VS = very sheltered. Ω = Dean’s parameter, RTR = Relative Tidal Range, BSI = Beach State Index. Detailed configuration codes are explained in Tables 1 and 2 of Chapter 3. 1h/s = high ridge, 1 m/s = low ridge, 2 h/s = high platform, 2 m/s= low platform.

<table>
<thead>
<tr>
<th>Site Code</th>
<th>Site Configuration</th>
<th>Ω</th>
<th>RTR</th>
<th>Predicted beach type</th>
<th>BSI</th>
<th>Predicted beach type (^2)</th>
<th>Observed beach type (^3)</th>
<th>Exposure Score (E.S.)</th>
<th>Exposure Rating (E.R.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WLW</td>
<td>1 h/s +</td>
<td>1.31</td>
<td>0.82</td>
<td>R</td>
<td>0.46</td>
<td>R</td>
<td>R</td>
<td>9.5 (14.5)</td>
<td>S (E)</td>
</tr>
<tr>
<td>KNB</td>
<td>1 h/s ++</td>
<td>1.3</td>
<td>1.5</td>
<td>R</td>
<td>0.64</td>
<td>R/I</td>
<td>R</td>
<td>13 (17)</td>
<td>E (VE)</td>
</tr>
<tr>
<td>AVA</td>
<td>1 h/s +++</td>
<td>4.27</td>
<td>1.5</td>
<td>I</td>
<td>0.95</td>
<td>I/R</td>
<td>I</td>
<td>7.5 (9.5)</td>
<td>S (S)</td>
</tr>
<tr>
<td>MAA</td>
<td>1 h/s +++</td>
<td>2.08</td>
<td>1.73</td>
<td>R/I</td>
<td>0.86</td>
<td>I</td>
<td>R</td>
<td>8.5 (11.5)</td>
<td>S (E)</td>
</tr>
<tr>
<td>MAB</td>
<td>1 h/s +++</td>
<td>4.27</td>
<td>1.47</td>
<td>I</td>
<td>1.08</td>
<td>I</td>
<td>I</td>
<td>12.5 (14.5)</td>
<td>E (E)</td>
</tr>
<tr>
<td>CRW</td>
<td>1 h/s +++</td>
<td>2.53</td>
<td>2.31</td>
<td>I</td>
<td>0.92</td>
<td>I</td>
<td>I</td>
<td>15 (15)</td>
<td>E (E)</td>
</tr>
<tr>
<td>BCN</td>
<td>1 m/s +</td>
<td>2.95</td>
<td>1.44</td>
<td>I</td>
<td>0.9</td>
<td>I</td>
<td>R</td>
<td>8 (13)</td>
<td>S (E)</td>
</tr>
<tr>
<td>BRK</td>
<td>1 m/s +</td>
<td>4.27</td>
<td>1.22</td>
<td>I</td>
<td>0.88</td>
<td>I</td>
<td>I</td>
<td>12 (14.5)</td>
<td>E (E)</td>
</tr>
<tr>
<td>KME</td>
<td>1 m/s ++</td>
<td>1.85</td>
<td>1.72</td>
<td>R</td>
<td>0.84</td>
<td>I</td>
<td>I</td>
<td>12 (15)</td>
<td>E (E)</td>
</tr>
<tr>
<td>PBE</td>
<td>1 m/s +++</td>
<td>2.36</td>
<td>1.44</td>
<td>I</td>
<td>0.81</td>
<td>I</td>
<td>I</td>
<td>13 (13)</td>
<td>E (E)</td>
</tr>
<tr>
<td>ASB</td>
<td>1 m/s +++</td>
<td>1.79</td>
<td>2.87</td>
<td>R</td>
<td>0.87</td>
<td>I</td>
<td>I</td>
<td>8 (10)</td>
<td>S (S)</td>
</tr>
<tr>
<td>PDB</td>
<td>1 m/s +++</td>
<td>2.5</td>
<td>2.37</td>
<td>I</td>
<td>0.92</td>
<td>I</td>
<td>I</td>
<td>9 (11)</td>
<td>S (E)</td>
</tr>
<tr>
<td>TST</td>
<td>2 h/s +</td>
<td>2.68</td>
<td>1.35</td>
<td>I</td>
<td>0.89</td>
<td>I</td>
<td>I</td>
<td>11 (16)</td>
<td>E (VE)</td>
</tr>
<tr>
<td>HPW</td>
<td>2 h/s ++</td>
<td>1.09</td>
<td>1.71</td>
<td>R</td>
<td>0.65</td>
<td>I</td>
<td>I/R</td>
<td>15 (17)</td>
<td>E (VE)</td>
</tr>
<tr>
<td>HPE</td>
<td>2 h/s +++</td>
<td>1.99</td>
<td>2.38</td>
<td>R</td>
<td>0.99</td>
<td>I</td>
<td>I</td>
<td>12.5 (13.5)</td>
<td>E (E)</td>
</tr>
<tr>
<td>CRE</td>
<td>2 m/s +</td>
<td>3.37</td>
<td>1.97</td>
<td>I</td>
<td>0.97</td>
<td>I</td>
<td>I/D?</td>
<td>8 (13)</td>
<td>S (E)</td>
</tr>
<tr>
<td>CNR</td>
<td>2 m/s ++</td>
<td>1.3</td>
<td>2.42</td>
<td>R</td>
<td>0.69</td>
<td>I</td>
<td>I/R</td>
<td>11.5 (15.5)</td>
<td>E (E)</td>
</tr>
<tr>
<td>MLS</td>
<td>2 m/s ++</td>
<td>2.7</td>
<td>1.78</td>
<td>I</td>
<td>0.76</td>
<td>I</td>
<td>I/D?</td>
<td>9.5 (11.5)</td>
<td>ME (E)</td>
</tr>
<tr>
<td>HWD</td>
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<td>2.56</td>
<td>1.85</td>
<td>I</td>
<td>0.84</td>
<td>I</td>
<td>I</td>
<td>5 (8.5)</td>
<td>VS (S)</td>
</tr>
<tr>
<td>MPB</td>
<td>2 m/s +++</td>
<td>3.94</td>
<td>1.1</td>
<td>I</td>
<td>0.91</td>
<td>I</td>
<td>I/R</td>
<td>13 (14)</td>
<td>E (E)</td>
</tr>
</tbody>
</table>
microtidal beach types based on beach response to wave energy. A value below 2 indicates that a beach is reflective, between 2 and 6 is intermediate, and above that dissipative.

With reference to Dean’s parameter, the three sites with the largest coarse fraction overall and both median and mean particle size in a coarse size class, i.e. Willows Beach (WLW), Kini Bay (KNB) and Hougham Park West (HPW) (Table 9), were reflective (R) (Table 10). At all three these sites, the surf zones were limited in extent and less wave energy dissipation occurred before waves made landfall. At other sites where beaches were predicted to be reflective according to Dean’s parameter, i.e. Kleinemonde East (KME), Hougham Park East (HPE), Cannon Rocks (CNR) and Aston Bay (ASB), in Table 9 and 10, median and mean particle size were medium sand (KME, HPE and CNR) and fine sand (ASB). The medium sand sites (KME, HPE and CNR) were highly wave exposed and at ASB the beach was sheltered (Table 10). Sites predicted to have intermediate beaches according to Dean’s parameter (Table 10) had predominantly fine (125 to 250 µm) or medium (250 to 500 µm) sand (Table 9).

The BSI index (McLachlan et al. 1993) relates to beach mobility. When the BSI was applied to study sites, only Willows Beach (WLW) was rated reflective, which also implied beach stability, accretionary conditions and low energy interactions between beach and waves. This prediction fitted WLW well as it had a stable platform beach with limited wave interaction. As for the other sites, an intermediate rating was not completely unrealistic, as the BSI values ranged between 0.5 and 1.0 implying low to medium energy beaches with intermediate stability.

Beach type and predominant breaker type were visually assessed under different tidal and sea conditions and rated according to Short (1999). At eleven study sites, wave action and beach characteristics (beach slope and features such as a berm or step) indicated low to medium energy intermediate sandy beaches. Four study sites were predicted to be reflective beaches according to Short (1999) and the beaches of the remaining five sites between reflective and low energy intermediate. All reflective beaches had a small low tide step of coarse-grained sediment. At some sites, i.e. Avalanche (AVA), Beacon Rock (BCN), Hougham Park East (HPE), Hougham Park West (HPW) and Maitlands Inner (MAA), a berm composed of pebbles, shell grit and other coarse material, was present.

Two of the high ridge sites, Maitlands Inner (MAA) (Ω = 2.08, BSI = 0.86) and Maitlands Outer (MAB) (Ω = 4.27, BSI = 1.08), were situated adjacent to a long sandy beach, Maitlands Beach, that has served as a study site in several previous investigations, e.g. McLachlan (1977a,b), Nel (2000), Schoeman et al. (2003). MAA had a higher proportion of intertidal rock than MAB and an upshore beach deposit relatively sheltered from wave action.
for most part of the tidal cycle, whereas the beach at MAB was exposed to wave action to the same degree as the adjacent sandy beach ($\Omega = 3.72$, $BSI = 0.92$ in Nel (2000)). MAA was predicted to be reflective and MAB dissipative, like Maitlands Beach, suggesting a strong decline in wave energy as waves move over and past rocks and onto the beach face.

McLachlan's (1980) beach exposure rating (Table 10) uses physical, dynamic and biotic criteria to predict the degree of wave exposure of a beach. Exposure ratings indicate that the rock traverse had a sheltering effect on the beach (Table 10): at sites with wider and/or more rugged rock sections the degree to which the beach became sheltered was greater than those with smooth and/or narrow rock traverses.

### 6.6 Sampling strata

The cross-shore extent of individual sampling strata varied from site to site (Figure 17) and appeared to be tied up with the availability of a suitable substrate at the appropriate tidal elevation. Rock height and cross-shore extent played a role here as sampling strata were measured along shore-normal transects. The cross-shore extent of sampling strata thus changed in relation to the rock height rating, % cross-shore and % long-shore rock (Figures 18, 19 and 20). Kini Bay (KNB) and Willows Beach (WLW), both sites with a high percentage cross-shore rock as well as a high rock height rating, had narrow beaches with truncated cross-shore zones (= sampling strata). At WLW, stratum/zone S5 (LT swashline) could not be separated from S4 (LT effluent line).

The supralittoral fringe strata were reduced in cross-shore and vertical extent (Figures 17 and 18) at sites lacking high rock surfaces in the upper midtidal to supratidal fringe area or with isolated supralittoral rock outcrops, i.e. Avalanche (AVA), Aston Bay (ASB), Pollock North (PBE), Paradise Beach (PDB), Cannon Rocks (CNR), Cape Recife East (CRE), Miller's Beach (MLS), Hougham Park East (HPE) and Pollock South (MPB). The same applied to the other strata of elevated intertidal positions (R2, R4 and R6), although to a lesser extent. The midlittoral algal turf strata, R3 (upper midlittoral), R5 (lower midlittoral) and R8 (infralittoral fringe), on the other hand, were very well represented and extensive at all the sites regardless of rock height, extent or distribution (Figures 17 to 20). R7 was present at sites with sufficient rock surface at the intertidal elevation preferred by *Scutellastra cochlear* (Born, 1778) and the associated algal assemblage. The low shore sampling strata on rock (R6 – *Perna perna*, R7 - *Scutellastra cochlear*, R8 – infralittoral fringe macroalgae) were reduced in extent and development at sites with less rock substrate in the low intertidal and completely absent at PBE (Pollock north) as the rock section was confined to midlittoral reaches.
Figure 17. Extent of each sampling stratum in sediment (S0 to S5) and on rock substrate (R0 to R8) given as a segment of the total length (m) of an integrated transect representing one study site. Stratum codes are explained in Table 4 (Chapter 4). Study sites are arranged according to configuration: AVA to WLW are high ridge sites, BCN to PDB are low ridge sites, HPE to TST are high platform sites, and CNR to MPB are low platform sites.
Figure 18. The percentage of the total length of an integrated cross-shore transect taken up by each sampling stratum (S0 to S5 in soft substrate and R0 to R8 on hard substrate) in relation to the rock height rating of study sites. Stratum codes are explained in Table 4 (Chapter 4).
Figure 19. The percentage of the total length of an integrated cross-shore transect taken up by each sampling stratum (S0 to S5 in soft substrate and R0 to R8 on hard substrate) in relation to the % cross shore rock of study sites. Stratum codes are explained in Table 4 (Chapter 4).
Figure 20. The percentage of the total length of an integrated cross-shore transect taken up by each sampling stratum (S0 to S5 in soft substrate and R0 to R8 on hard substrate) in relation to the % long shore rock of study sites. Stratum codes are explained in Table 4 (Chapter 4).
CHAPTER 7  Biotic classification of mixed substrate shores

Cluster analyses (classification) and ordination showed that the response patterns of the various ecological species sets, i.e. sediment macrofauna, as well as sessile macrofauna, motile macrofauna (molluscs) and macroalgae of hard substrate, differed. Another trend in the data was that groupings of species or sites, whether obtained from cluster analysis or from ordination, were not a response to shore configuration per se. There was, however, a tendency for particular sites to ‘travel together’ from one analysis to the next, suggesting some similarity in conditions and/or responses by the communities concerned.

7.1 Classification of sites by cluster analysis of macrobenthic assemblages

7.1.1 Macrobenothos of sediment

The four major biotic groups formed (Figure 21) separated on the basis of a few differentiating taxa of high importance. Several species of high or intermediate abundance exhibited a fairly high level of fidelity to all the major clusters in the analysis. Taxa with relatively higher constancy values were often those that were of very low abundance and therefore not useful to distinguish groups.

Group 2, of intermediate heterogeneity, split off early from its sister clade composed of three major groups. The two smaller clusters that made up Group 2 were characterised by high abundance of diverse polychaete assemblages in which the spionid polychaete *Scololepis squamata* (Müller, 1806) was the numerical dominant. However, three other deposit-feeding polychaetes reached high importance, i.e. the capitellids *Notomastus aberans* Day, 1957, and *Nerinides gilchrist* Day, 1961 and orbiniid *Scoloplos (Leodamas) johnstonei* Day, 1934, the latter two both endemic. Haustoriid amphipods were also of high importance at these sites, *Urothoe pinnata* K.H. Barnard, 1955 being the species reaching greatest abundance. The homogeneous Group 4 (Kini Bay/KNB - Hougham Park West/HPW) also separated early from the remaining Groups 1 and 3, differing from those in the complete absence of *Eurydice longicornis* (Studer, 1883), always among the most abundant taxa in the remaining groups, and a high numerical dominance of polychaetes, particularly *Polygordius* sp., usually associated with coarse sediment. None of the remaining taxa of high importance showed high fidelity to this group. In this analysis, Group 1 was the most heterogeneous in composition, consisting of four isopod-polychaete dominated sites. The three most important distinguishing species included the sphaeromatid isopod, *Exosphaeroma hylecoetes* Barnard, 1940B, orbiniid *Scoloplos (Leodamas) uniramus* Day, 1961 (endemic) and rocky/mixed shore nereid *Pseudonereis variegata* (Grube, 1857).
Figure 21. Ward's classification of sites using importance values of sediment macrofauna species.
Group 3 exhibited a similar level of homogeneity to Group 2 and was composed of sites in which the distinguishing common denominators of highest importance were fairly typical intermediate beach species, i.e. *Gastrosaccus psammodytes* O.Tattersall, 1958, *Bullia rhodostoma* L.A. Reeve, 1847, *Excirolana natalensis* (Vanhoefen, 1914), but with two unusual additions to the top five abundant species: *Donax burnupi* G.B. Sowerby III, 1894 and *Lumbrineris heteropoda difficilis* Day, 1963.

### 7.1.2 Macrobenthos of rock surfaces

#### 7.1.2.1 Sessile macrofauna

This classification split sites into two clades: one composed of four groups, the other consisting of a single major grouping (Figure 22). There were surprisingly few distinguishing species that simultaneously displayed high fidelity and constancy in any group and simultaneously a high to intermediate abundance. The distinction therefore had to be made on the basis of abundance.

Group 2, composed of sites with a high degree of similarity, split off early from its sister clade containing the remaining four groups. High abundance of the bivalve *Perna perna* (Linnaeus, 1758) and secondarily *Tetraclita serrata* Darwin and *Octomeris angulosa* were characteristic of Group 2. The reefworm *Gunnarea capensis* (Schmarda, 1861) showed higher constancy and fidelity for this group than those remaining. Two species of *Ostrea* were also fairly constant in this group, but at very low abundance. The encrusting sponge *Hymeniacidon perlevis* (Montagu, 1818) exhibited high constancy in Group 2, at extremely low abundance, but was the dominant filter-feeder at sites of Group 1 where it invariably occurred on low rock surfaces. At these sites mainly barnacles and very low quantities of *Perna perna* were the filter feeders of upper rock surfaces. Group 5 separated from 4 and 3 on account of high *Gunnarea capensis* (Group 5) compared to other major sessile species (barnacles, mussels and sponge). Members of Group 3 had high abundance of the barnacle *Chthamalus dentatus* Krauss compared to other sessile species, as well as *Choromytilus meridionalis* (Krauss, 1848), of high constancy in this group, but absent from most of the members of Group 4. These abundance differences were the only factors separating Groups 3 and 4 in this analysis and these two groupings may well be part of a single entity.

The site combinations in these groups bore little resemblance to that of beach macrofauna, suggesting that these biota responded differently to impinging environmental factors. The PDB-MLS (Paradise Beach and Miller’s Beach) cluster was retained, undoubtedly because of a very high abundance of *Hymeniacidon perlevis*. 
Figure 22. Ward's classification of sites using importance values of sessile macrofauna species.
7.1.2.2 Macroalgae

This dendrogram also produced five major groups (Figure 23). The macroalgal species that appeared to be most useful as character elements were those of eulittoral and infralittoral fringe algal turfs. A large proportion of species were ubiquitous and exhibited low fidelity to any particular community. Unique species of intermediate or high abundance were very few. While the members of Group 1 appeared to be fairly closely related overall, having much in common in their dominant species, those of the remaining groups had no algal species that exhibited high spatial dominance, which may be indicative of periodic disturbance at these sites.

Group 1, a clade composed of two smaller clusters, separated from a larger sister clade composed of the remaining major groups. At these sites coralline algae were the dominant taxa of extensive turfs carpeting low eulittoral rock surfaces. Turf-forming articulated corallines *Arthrocardia flabellata* (Kützing) Manza and *Arthrocardia filicina* (Lamarck) Johansen, as well as *Laurencia* spp., particularly *Laurencia natalensis* Kylin and *Laurencia pumila* (Grunow) Papenfuss, were highly characteristic of the sites forming Group 1 (Figure 23).

Finding character species for Group 2 was problematic as those of high constancy exhibited low fidelity to the group and the remaining species exhibited both low constancy and fidelity. Group 2 was typified rather by the absence of reliable character species found for other groups. On balance, typical eulittoral rocky shore algae (*Gelidium pristoides* (Turner) Kützing, *Porphyra capensis* Kützing, *Leptophytum* spp., *Bostrychia intricata* (Bory de Saint-Vincent) Montagne) appeared in this group at higher abundance than the remaining groups and were, moreover, largely absent or reduced in Group 3. *Jania verrucosa* J.V.Lamouroux, *Halimeda cuneata* Hering, *Arthrocardia filicina* and *Plocamium rigidum* Bory de Saint-Vincent, on the other hand, were appreciably more common and abundant at sites of Group 3 than those of Group 2. PBE (Pollock North) was exceptional in Group 3 in that it lacked many of the species common to the other two sites, but had midlittoral turf taxa (e.g. *A. filicina, J. verrucosa*) in common.

The early separation of Group 5 (CNR, Cannon Rocks) from Group 4 was most likely due to the presence of *Amphiroa bowerbankii* Harvey and *Portieria homemannii* (Lyngbye) P. Silva, both absent from samples of other communities, as well as *Dictyota dichotoma* (Hudson) Lamouroux and *Corallina officinalis* Linnaeus, both highly abundant here and not in other groups. Group 4 was characterised by the superlative abundance of both *Caulerpa filiformis* (Suhr) Hering and *Hypnea spicifera* (Suhr) Harvey, as well as abundant *Polysiphonia urbana* Harvey, *Rhodomelopsis africana* M.A.Pocock and *Codium duthieae P.C.* Silva.
Figure 23. Ward’s classification of sites using importance values of macroalgae.
7.1.2.3 Combined sessile macrofauna and macroalgae

There was a small degree of agreement between the separate cluster analyses of sessile macrofauna and macroalgae (Figures 22 and 23). The major groups of the two analyses were dissimilar suggesting a difference in the responses of macroalgae and sessile macrofauna to the same environmental parameters. Only two minor clusters (MAA-MAB and CRE-ASB) were identical. The MAA-MAB cluster (Maitlands Inner and Outer) were adjacent study sites with similar environmental influences and had many species in common that would have included character species. Similarities in conditions at CRE-ASB cluster (Cape Recife East and Aston Bay) were not linked to proximity, but both sites experience wave-sheltered conditions because of being in the wave shadow of a major headland.

The classification of sites based on a combined macroalgae-sessile macrofauna species matrix (Figure 24) produced a dendrogram composed of altogether six groups. In the major groups resulting from this analysis of combined data sets, the overriding influence of the macroalgal response was evident. Relationships within Group 1 of the macroalgal cluster analysis were retained almost unchanged. Group 6 of the combined analysis was the former Group 5 of macroalgae. There were minor realignments of sites due to new species combinations.

Group 1 separated from the rest at the highest level of dissimilarity. *Arthrocardia flabellata*, *A. filicula*, *Laurencia natalensis* and *Hymeniacidon perlevis* combined with lower levels of abundance of barnacles and *Perna perna* and the absence of *Gunnarea capensis* (except at CRW/ Cape Recife West) characterized the sites in Group 1. MPB (Pollock South) was slightly dissimilar from other members in the group as *H. perlevis* and barnacles were less abundant in comparison to the rest of the sites. At this site, hard substrate was limited in extent.

The presence of *Amphiroa bowerbankii* and *Octomeris angulosa* as well as high abundance of *Dictyota dichotoma*, *Corallina officinalis* and *Hymeniacidon perlevis* characterised CNR (Cannon Rocks), the only member of Group 6. This contrasted with high abundance of *Octomeris angulosa* and *Hypnea spicifera* and the constant presence of *Dictyopteris cf. macrocarpa* (Areschoug) O.C.Schmidt and *Rhodomelopsis africana* in sites of Group 5. *Arthrocardia filicula* and *Laurencia natalensis* were absent from all sites of Group 5 except HPW (Hougham Park West) where the two species were recorded as rare.

The separation of Group 3 from 2 and 4 was made on the basis of very high dominance by *Chthamalus dentatus* and the presence of *Choromytilus meridionalis* (Krauss, 1848) in Group 3, although these may have be tenuous characters to use in view of their lack of
fidelity to this group. Group 3 (Figure 24) further had high abundance of algal turf species *Polysiphonia incompta* Harvey, *Pterocladiella caespitosa* (Kylin) Santelices, pioneer *Blidingia minima* (Nägeli ex Kützing) Kylin and *Plocamium rigidum* Bory de Saint-Vincent, all apparently sand-tolerant, but completely lacked *Caulerpa filiformis* due to an absence of suitable substrate, i.e. no lower eulittoral sand-covered rock surfaces. In this analysis, the main difference between the macrobenthic communities of Group 2 and 3 stemmed from the fact that Group 2 had a limited range of available habitats and resident taxa compared to Group 3. The species of Group 2 members were also present in Group 3, so Group 2 sites had no distinguishing taxa and were rather separated from Group 3 due to the absence of particular prominent species. These two communities should probably be treated as one.

This left Group 4, a cluster for which it was equally difficult to pinpoint characteristic elements with high fidelity and constancy, although the members of the group (MAB/Maitlands Outer and MAA/Maitlands Inner) were very similar in composition. Being adjacent sampling sites, the rock surface biota were subject to nearly identical environmental gradients, the only difference being the physical extent of available substrata. Based on abundance, *Perna perna* was the only potential sessile animal to distinguish this group from others. *Caulerpa filiformis, Hypnea spicifera* and *Polysiphonia urbana* were all relatively high, but lacked high fidelity, as these species were common to all study sites with substantial lower intertidal sand deposits around and over rock surfaces, regardless of their individual physical configurations.

7.1.2.4 Motile macrofauna (gastropods)

In the classification of sites based on motile macrofauna, two major groups, each composed of members showing a high degree of similarity (Figure 25), resulted, suggested a wide split between Groups 1 and 2 as well as strong cohesiveness within Group 1. This may indicate that intertidal gastropods at sites of Group 1 for most part experienced similar environmental conditions significant to their survival, regardless of small-scale variations in shore configuration and topography. Alternatively, it may imply wide environmental tolerance to the conditions prevalent at these mixed substrate shores. The species composition of the gastropod assemblages of sites did not flag up any unusual or unique species that could be used as indicators, as those present were generally wide-spread along the coast.

Though not of the same configuration class, a common feature of sites in Group 2 was low rock topography and limited upper intertidal rock. None of the taxa found at these four sites showed high constancy or fidelity to the group, so were not useful as character species.
Figure 24. Ward’s classification of sites using importance values of macroalgae and sessile macrofauna species.
Figure 25. Ward’s classification of sites using importance values of gastropod species (motile macrofauna).
The only feature with potential as an indicator was the complete elimination or extremely low abundance of *Afrolittorina knysnaensis* (Krauss in Philippi, 1847), a ubiquitous numerical dominant at sites of Group 1. A second possible reason for the split was a reduction in the abundance of the limpet *Scutellastra cochlear* as compared to the remaining sites. The absence or rarity of other species could not be used, as it applied equally to sites of both groups.

The overall species composition and importance pattern at sites of Group 1 (Figure 25) was highly reminiscent of any South African rocky shore. Within this group there was a split between the KME-MAA-AVA-ASB (Kleinemonde East-Maitlands Inner-Avalance-Aston Bay) cluster and the remaining sites. Here, too, *A. knysnaensis* abundance could have been a differentiating factor, as it was less abundant in the KME-MAA-AVA-ASB group than the rest.

The remaining members of Group 1 formed 3 minor clusters with a low degree of dissimilarity. In each cluster there was one site that separated from the rest based on a slightly more diverse gastropod assemblage, but these variations were not so marked as to be reason to suspect significantly different responses to the environment. A strong common factor was the presence of *A. knysnaensis* often in great densities at all these sites.

7.1.2.5 All rock surface macrobenthos

The dendrogram showing classification of sites based on all the hard substrate macrobenthos (Figure 26) strongly resembled the one for gastropod species alone (Figure 25). Two major groups were formed: the one heterogeneous and consisting of five sites (Group 2), the other fairly homogeneous and composed of the remaining sites (Group 1).

The split between Groups 1 and 2 (Figure 26) was linked to a substantial difference in the abundance of the high shore gastropod *Afrolittorina knysnaensis*. It was hugely abundant in sites of Group 1 and very low in Group 2. *Gunnarea capensis*, again, was more abundant in Group 2 than Group 1. Sites of Group 1 were also dominated by extensive midlittoral coralline turfs in a wave-sheltered midlittoral zone. Taxa abundant at these sites, but low in those of Group 2, included *Hymeniacidon perlevis*, *Tetraclita serrata* and *Ralfsia verrucosa* (Areschoug) Areschoug. The most common taxa of high constancy and low abundance at sites of Group 1, that were absent from Group 2, included macroalgal species *Porphyra capensis*, *Leathesia marina* (Lyngbye) Decaisne, *Splachnidium rugosum* (Linnaeus) Greville and *Amphiroa beauvoisii* J.V.Lamouroux, the limpet *Cymbula miniata* (Born, 1778) as well as the oyster *Striostrea margaritacea* (Lamarck, 1819).
Figure 26. Ward's classification of sites using importance values of all rock surface macrobenthos species.
Within Group 1 the MAB-HPW (Maitlands Outer-Hougham Park West) cluster separated from the BRK-KNB-TST (Bird Rock-Kini Bay-Three Sisters) and CRE- CRW (Cape Recife East and West) clusters on a higher abundance of filter-feeders (*Perna perna* and *Octomeris angulosa*), while a difference in abundance of *P. perna* split the BRK-KNB-TST cluster from CRE-CRW. The structure of this hierarchy had much in common with the dendrogram of gastropod species (Figure 25). One site from Group 1 of that analysis, KME (Kleinemonde East), moved into Group 2 in the all rock biota dendrogram, as the reefworm *Gunnarea capensis* was abundant on its rock surfaces. Much of the structure of this dendrogram was conserved in the analysis of all species (Figure 27), indicating the importance of the hard substrate assemblages in determining the general character of the mixed substrate shore at community level.

### 7.1.3 Classification of sites using all species

Six groups resulted from the classification of sites using all species (Figure 27). Sites were distributed over two clades: the one containing the two largest groups, Group 1 (10 sites) and Group 4 (5 sites), and the other consisting of a heterogeneous collection of four small groups, i.e. Group 2 (1 site), Group 3 (2 sites), Group 5 (1 site) and Group 6 (1 site).

The structure of the sediment macrofauna dendrogram (Figure 21) was poorly reflected in this analysis. Only the BRK-MLS-PDB (Bird Rock-Miller’s Beach-Paradise Beach) cluster was retained and all others rearranged. Three clusters from the analysis of sessile macrofauna (Figure 22) were conserved, i.e. MAA-MAB (Maitlands Inner and Outer), ASB-CRE (Aston Bay-Cape Recife East) and PDB-MLS (Paradise Beach-Miller’s Beach), although their relationships to other sites and clusters had changed. Minor clusters MAA-MAB and CRE-ASB from the macroalgal classification (Figure 23) remained, as well as Group 5 (CNR/Cannon Rocks) as a separate entity, while several Group 1 members of that analysis remained closely related.

Many of the features of the combined sessile macrofauna-macroalgae dendrogram (Figure 24) were conserved in the analysis of all species. Group 1 of that analysis retained its identity for most part, with ASB-CRE intact, as did Group 6 (CNR, Cannon Rocks) and its relationship to KME (Kleinemonde East) and HPE (Hougham Park East). The MAA-MAB cluster remained intact, but other clusters of Groups 2 to 4 (Figure 24) were realigned. The strong cohesiveness within Group 1 of the gastropod dendrogram (Figure 25) was largely retained in the analysis of all species combined. Addition of other species (beach macrofauna, macroalgae and sessile macrofauna) increased the levels of dissimilarity among clusters when compared to the gastropod dendrogram. For instance, the HPE-CNR
cluster (Hougham Park East-Cannon Rocks) in Group 2 of the gastropod dendrogram was conserved as is, but with enhanced dissimilarity compared to most other sites and groups.

In this analysis (Figure 27), HPW (Hougham Park West) separated from the remaining 9 sites in Group 1 at a high level, on first glance enough to justify delineation of a separate group. The macroalgal community of HPW had more species in common with sites of Group 4 than the remaining sites in Group 1, but its sessile macrofauna and sediment macrofauna had more in common with the remaining sites of its group than with other groups. However, examination of species composition and abundance by means of a constancy-fidelity analysis did not provide sufficient reason to create a new entity on an equal footing and intermediate to Group 4 and the remainder of Group 1.

The suite of characteristic species common to all the sites of Group 1 comprised midlittoral coralline turf algae *Arthrocardia flabellata*, *A. filicula*, lower intertidal *Laurencia* spp., particularly *L. natalensis* and *Hymeniacidon perlevis*, as well as mid-to upper eulittoral taxa *Afrolittorina knysnaensis*, *Siphonaria* spp., *Leptophytum* spp. and *Hildenbrandia lecannelli*. The macroalgal communities of these sites were dominated by extensive midlittoral coralline turfs as the infralittoral fringe was limited in extent. The sediment fauna at these sites were dominated by polychaetes, mainly *Polygordius* spp., as well as spionids, capitellids and orbiniids, with somewhat less abundant sphaeromatid (*Exosphaeroma* spp.) and cirolanid (*Eurydice*, *Exciramina*) isopods and haustoriid amphipods (*Urothoe* spp.). *Scololepis squamata*, *Notomastus* spp. and *Scoloplos* spp. were among the dominants and *Pseudonereis variegata* common. *Bullia*, *Gastrosaccus* and *Donax* were rare or absent.

Group 2 had one member, PBE (Pollock North). The assemblage of the rock substrate was indicative of considerable levels of disturbance. Midlittoral turf consisted of sand-binding *Pterocladiella caespitosa* and *Polysiphonia incompta*, as well as pioneer species *Blidingia minima*, *Ulva* spp., *Chaetomorpha* spp. The sessile macrofauna present in appreciable abundance at PBE were rapid colonizer *Chthamalus dentatus* and sand-tolerant *Choromytilus meridionalis*. Sediment macrofauna were composed of polychaetes and cirolanid isopods typical of an intermediate beach community: *Scolelepis squamata* and *Eurydice longicornis* reached high dominance. Both *Gastrosaccus psammodytes* and *Bullia rhodostoma* were present.

The members of Group 3 shared high abundance of *Jania verrucosa* on midlittoral rock and *Caulerpa filiformis* in the infralittoral fringe. *Afrolittorina knysnaensis* was uncommon at both sites. The differences between the communities of these two sites also set them apart from sites in the other groups. KME (Kleinemonde East) presented with a high abundance of *Gunnaria capensis* and *Rhodomelopsis africana*, both present at MPB (Pollock South) in low
quantities, while *Halimeda cuneata*, *Plocamium beckeri* and *P. rigidum* formed important components in the macroalgal assemblage of MPB. At both sites *Eurydice longicornis*, *Gastrosaccus psammodytes* and *Bullia rhodostoma* were present in the beach macrofauna community that was isopod-polychaete dominated, indicating an intermediate wave-exposed beach community. Insecta were among the common taxa of the beaches of these two sites.

Members of Group 4 were characterised by sessile macrofauna *Hymeniacidon perlevis*, *Octomeris angulosa* and *Perna perna*, a filamentous midlittoral turf of sand-tolerant *Polysiphonia urbana* and *Tayloriella tenebrosa* and infralittoral fringe algae *Caulerpa filiformis* and *Hypnea spicifera*. The infralittoral fringe and lower midlittoral reaches of all these sites were more sand-influenced than those of Group 1. The sediment macrofauna was dominated by polychaetes (spionids, capitellids and orbiniids) and cirolanid isopods, indicating intermediate beach conditions. Other common taxa of this group comprised haustoriid amphipods (*Urothoe* spp), *Gastrosaccus psammodytes* and *Bullia rhodostoma*.

Group 5 consisted of one member, HPE (Hougham Park East). The dominant elements of the rock substrate communities at this site were sessiles *Perna perna* and *Octomeris angulosa* and macroalgae *Hypnea spicifera*, *Caulerpa filiformis* and *Rhodomelopsis africana*, with *Dictyopteris cf. ligulata* a common constituent. The midlittoral turf of this community was highly sand-influenced and had a robust physiognomy. The isopod dominated sediment fauna had high abundance of *Exosphaeroma* spp., while *Pseudonereis variegata*, *Acanthochitona garnoti*, *Barbatia obliquata*, syllids, *Bullia* spp. were common.

Group 6 also had only one member, CNR (Cannon Rocks). Of the more common species at this site, *Jania* spp. and *Dictyota dichotoma* had some potential as character species, but did not exhibit sufficient fidelity. This site was rather characterized by the total absence of *Porphyra capensis* and extremely low abundance of *A. knysnaensis* and *Scutellastra cochlear*. The sediment macrofauna assemblages were indicative of an intermediate-reflective beach as it was dominated by few cirolanid isopods (*Eurydice longicornis* in high abundance), while *Gastrosaccus psammodytes* and *Bullia rhodostoma* were present in low numbers and insects common.
Figure 27. Ward's classification of sites using importance values of all species.
7.2 Mixed substrate shore biotic types

The dendrogram resulting from the cluster analysis of all species indicated that Groups 1 and 4 each possessed a sufficient degree of within-group cohesion and separation from each other to be deemed distinct entities and be regarded as valid mixed substrate shore biotic types. These two well-defined groups were renamed mixed substrate shore biotic types C and B, respectively, in Figure 28. The groups (Group 2, 3, 5 and 6) of the more heterogeneous clade were lumped as mixed substrate shore biotic type A (Figure 28). Though less cohesive than Groups 1 and 4, these groups possessed sufficient commonality to either represent a third, more diverse valid type or three related subtypes.

Variation in the community composition of sites in mixed substrate shore biotic type C (Group 1) appeared to reflect a wave-exposure gradient, i.e. three sites had comparatively more wave-exposed intertidal substrata (HPW/Hougham Park West, TST/Three Sisters and KNB/Kini Bay) and the rest. Available data could not, however, justify further splitting of the group while retaining sufficient replication of biotic subtypes. This mixed substrate shore biotic type was characterized by Arthrocardia-Laurencia turfs, the encrusting sponge Hymeniacidon perlevis and variable abundance of cirripedes and mussels on midlittoral rock surfaces, as well as polychaetes (particularly spionids, capitellids and orbiniids), isopods (cirolanids, sphaeromatids) and haustoriid amphipods in sediment.

The community composition of mixed substrate shore biotic type B corresponded exactly to Group 4 (Figure 27) of the cluster analysis of all species. Some biotic elements were shared with mixed substrate shore biotic type C, notably abundant turf-forming coralline species, spatial dominance by Hymeniacidon perlevis and abundant Siphonaria and Afrolittorina. This biotic type was distinguishable from mixed substrate shore biotic types A and C, by high abundance of Octomeris angulosa and Perna perna as well as the filamentous character of midlittoral turf due to the addition of the sand-tolerant macroalgae Polysiphonia urbana, Tayloriella tenebrosa and, in the lower eulittoral, Caulacanthus ustulatus. Caulerpa filiformis and Hypnea spicifera were the dominant and characteristic taxa in the infralittoral fringe. The infralittoral fringe and lower midlittoral reaches of all these sites were more sand-influenced than those of biotic type C and thus sand-tolerant species of that zone were of some importance in characterising this group. The sediment macrofauna assemblages were indicative of an intermediate beach as it was dominated by polychaetes (spionids, capitellids and orbiniids) and cirolanid isopods. Other common taxa of this group comprised haustoriid amphipods (Urothoe spp.), Gastroscus psammodytes and Bullia rhodostoma.
Figure 28. Ward’s classification of sites using importance values of all species and showing mixed substrate shore biotic types A, B and C of this study.
The sites of mixed substrate shore biotic type A had the common feature of lacking a supralittoral fringe zone on the rock substrate. Their midlittoral communities had a strong infralittoral flavour in that macroalgae of the infralittoral fringe formed a common and abundant component of midlittoral turfs. This perhaps explained the high degree of variability among the members of this biotic type. At least three of the macroalgal species Hypnea spicifera, Caulerpa filiformis, Rhodomelopsis africana and Dictyopteris cf. ligulata were present at most of the these sites. Their beach assemblages were isopod-polychaete dominated with many species in common with sandy beaches and indicative of an intermediate-reflective beach community.

7.3 Ordination of sites using macrobenthic assemblages

7.3.1 Macrobenthos of sediment

Ordination of sediment macrofauna species (Figure 29) revealed a response to a gradient in the level and type of control exerted by hard substrate on surf zone and swash processes, though not necessarily linked to a particular configuration. This analysis demonstrated a biotic response to an influential environmental factor or factors, possibly sediment grain size, wave action, wave exposure and/or beach morphodynamics acting along the first axis.

Similarities indicated by this analysis showed fair agreement with the classification (Figure 21) of the same data set. The closely grouped sites in the upper left corner of the ordination diagram corresponded exactly to Group 2 of the classification and exhibited a lower level of $\beta$ – diversity than the remaining sites. Except for PBE (Pollock North) and MPB (Pollock South), both under moderate wave action and lacking extensive or high intertidal and subtidal rock outcrops, these sites had fine- to medium grained beaches sheltered from direct wave action by platforms (MLS – Miller's Beach, CRE – Cape Recife East, HWD - Humewood) or ridges (PDB – Paradise Beach, BRK – Bird Rock, BCN – Beacon Rock, AVA - Avalanche) that influenced surf zone processes below midtidal elevation.

There was also a fair degree of agreement between the remaining groups formed by ordination and the clusters resulting from classification. The arrangement of ASB (Aston Bay), TST (Three Sisters), WLW (Willows Beach), HPE (Hougham Park East) in the ordination diagram confirmed the relatively high degree of variability among these sites suggested in the cluster analysis (Figure 21) and suggests a response to wave exposure and/or sediment grain size. ASB and TST had a greater proportion of fine and medium sand, though TST was the more wave-exposed of the two, and had more stable beaches. The far right position of KNB (Kini Bay), HPW (Hougham Park West) and HPE (Hougham Park East)
Figure 29. Ordination (DCA) of sites (= samples) using importance values of macrofauna species from sediment. Sum of all eigenvalues = 4.661; Axis 1 eigenvalue = 0.700; Axis 2 eigenvalue = 0.373; Cumulative variance of species data = 23.0%. Circle colours correspond to those of groups in complementary classification (Figure 21).
agreed with the much coarser grained beaches of those sites combined with high wave exposure levels and unstable beach conditions.

7.3.2 Macrobenthos of rock surfaces

7.3.2.1 Sessile macrofauna

The arrangement of sites in the ordination of sessile macrofauna species (Figure 30) showed lower $\beta$-diversity than for sediment macrofauna. Considering the grouping of sites and their physical and dynamic attributes, it was most likely a response to a combination of available attachment surface and the gradient in the height and energy of waves reaching the eulittoral substrata of these sites.

The position of KME (Kleinemonde) corresponded to the centroid for *Gunnaria capensis* and was in agreement with the cluster analysis of this data (Figure 22), where this site was the sole member of Group 5. At WLW (Willows Beach), however, the polychaete was absent, with higher importance of *Octomeris angulosa* and *Tetraclita serrata* instead. The group (MAA-MAB-TST-HPW-MPB-HPE-CRW) situated in a mid-left position in the ordination diagram corresponded to Group 2 in the classification of sessile macrofauna (Figure 22). These sand-rich, wave-exposed sites had intermediate abundance of *Gunnaria capensis* along with substantial quantities of midlittoral barnacles and *Perna perna*.

The triplet of sites in the upper right quadrant of the ordination diagram corresponded to Group 3 (PBE – Pollock North, BCN – Beacon Rock, BRK – Bird Rock) in the dendrogram (Figure 22). This is a potential case where site proximity would have played a role in the similarities in biota, as these were adjacent sites exposed to similar wave conditions.

7.3.2.2 Macroalgae

The distribution of sites based on macroalgal species (Figure 31) suggested greater site-site dissimilarity (greater $\beta$-diversity) than in sessile macrofauna (Figure 30) and disagreed with the classification of the same data (Figure 23). Some aspects of the classification were conserved in the ordination, as reflected in the positions of KME-HPW-HPE-MAA-MAB in the upper left quadrant (Group 4, Figure 23) as well as CNR (Cannon Rocks) (top centre) of Group 5 (Figure 23). Relationships of the remaining sites partly reflected those suggested by the classification. The positions of sites can probably be attributed mainly to the response of lower intertidal macroalgal turfs and the infratidal fringe macroalgae to environmental factors such as a wave action gradient linked to attenuation effects in the mid-eulittoral and the degree of sand-inundation associated with mid-littoral and low intertidal rock surfaces, acting along the first axis. The response of macroalgae to an environmental gradient represented
Figure 30. Ordination (DCA) of sites using importance values of sessile macrofauna species. Sum of all eigenvalues = 0.934; Axis 1 eigenvalue = 0.240; Axis 2 eigenvalue = 0.081; Cumulative variance of species data = 34.0%. Circle colours correspond to those of groups in complementary classification (Figure 22).
Figure 31. Ordination (DCA) of sites (= samples) using importance values of macroalgae only. Sum of all eigenvalues = 2.0347; Axis 1 eigenvalue = 0.323; Axis 2 eigenvalue = 0.172; Cumulative variance of species data = 24.3%. Circle colours correspond to those of groups in complementary classification (Figure 23).
by the BRK-KNB and TST-BCN pairs was more pronounced in the ordination than suggested by the classification of this data set and the same goes for PBE, AVA and MPB, all members of Group 3 in the classification (Figure 23).

The sites in the upper left quadrant all had abundant Caulerpa filiformis and Hypnea spicifera on periodically sand-covered, wave-exposed lower intertidal rock surfaces. The medley of sites to the right and far-right in the diagram, on the other hand, had more wave-sheltered low intertidal rock surfaces that experienced a much less variable and lower extent of sand-inundation. They were dominated by variable quantities of Laurencia spp, large and small corallines (Amphiroa, Arthrocardia, Jania) and a higher proportion of small filamentous (Polysiphonia) and gelatinous (Caulacanthus) turf species.

7.3.2.3 Combined sessile macrofauna and macroalgae

The combined dataset of macroalgae and sessile macrofauna species (Figure 32) reflected the differential responses, as well as conditions experienced at the same site, of two ecological guilds, the macroalgae (attached primary producers) and sessile macrofauna (predominantly suspension-feeders), both dependent on, and in competition for, attachment surface and both responding to wave-attenuation gradients. These two groups of organisms differ in their environmental requirements and should too in their response to gradients. For example, with increasing wave exposure, sessile filter-feeders are expected to become numerical and spatial dominants, while macroalgae are more partial to wave-sheltered conditions. Within each group, however, there are species that respond most strongly to intermediate wave and water movement conditions.

A clear central grouping of sites was obtained in this analysis, demonstrating a response to intermediate levels of an environmental gradient or gradients operating along axis 1. Although multiple factors impinged on the communities, the primary parameter was probably wave action, changing from relatively higher levels of eulittoral wave-exposure on the left to reduced wave action (greater wave-shelter) on the right, a gradient most likely related to increased levels of wave attenuation by hard and soft substrata. According to these data, the biota of most sites appeared to experience wave conditions of intermediate magnitude in the eulittoral zone.

This ordination showed much less agreement with its complementary classification (Figure 24) than those of other subsets. Most of the relationships in Group 1 of the dendrogram were conserved in the ordination, but all the clusters of remaining groups were dissolved and showed stronger affinities to members of either Group 1 or Group 2 that had also become interspersed (Figure 32).
Figure 32: Ordination (DCA) of sites (= samples) using importance values of attached macrobenthic species (sessile macrofauna and macroalgae) from rock substrate. Sum of all eigenvalues = 1.427; Axis 1 eigenvalue = 0.256; Axis 2 eigenvalue = 0.138; Cumulative variance of species data = 27.2%. Circle colours correspond to those of groups in complementary classification (Figure 24).
The only grouping to retain its identity was the PBE-BCN (Pollock North – Beacon Rock) pair of points. These were adjacent sites that due their close proximity experienced almost identical conditions and are probably part of the same ecological system.

7.3.2.4 Motile macrofauna (gastropods)

In the ordination of sites using motile macrofauna (gastropods) of hard substrate (Figure 33) the dispersion pattern demonstrated low β-diversity and a less pronounced response to the environmental gradient in the majority of sites (central left portion of the larger group), while a much smaller diverse group (right to far right of diagram) exhibited a strong response. Site-site relations were changed compared to the classification.

The large, cohesive grouping corresponded to one major cluster in Group 1 of the dendrogram and consisted of sites with pronounced midlittoral wave shelter due to the attenuating effects of rock surfaces. The smaller divergent group corresponded to the more heterogeneous sub-cluster of Group 1 in the dendrogram (KME-MAA-AVA-ASB) and consisted of sites exposed to greater wave activity and more active sand movement. The constancy-fidelity analysis revealed this group as having intermediate *A. knysnaensis* abundance, whereas the main group had very high abundance of this species and sites of Group 2 (Figure 25) low. The ordination then seemed to confirm the suggested split of sites on the abundance of *L. knysnaensis*, *Siphonaria* spp. and to a lesser degree *Scutellastra cochlear*.

As the littorinid was strongly associated with the upper eulittoral and supralittoral fringe where direct wave action is less than in the eulittoral zone, the distribution of sites possibly indicated an increasing level of direct wave action and/or a reduction in the amount of suitable habitat in the supralittoral fringe zone. The sites furthest to the right (KME-PBE-MPB-HPE-CNR) had reduced supralittoral fringe zones due to height limited rock substrate (not above midtidal elevation) and lower *Afrolittorina knysnaensis* abundance than all the remaining sites. CRE (Cape Recife East) with its broad flat intertidal rock platform, on the other hand, was characterised by very high littorinid numbers.
Figure 33. Ordination (DCA) of sites using importance values of gastropod species. Sum of all eigenvalues = 0.379; Axis 1 eigenvalue = 0.118; Axis 2 eigenvalue = 0.034; Cumulative variance of species data = 40.1%. Circle colours correspond to those of groups in complementary classification (Figure 25).
7.3.3 Ordination of sites using all species

In this analysis (Figure 34), a few sites of similar structure were closely associated as the biotic assemblages probably responded to the environmental gradient associated with axis 1 in a similar manner. This trend was also evident in the complementary classification (Figure 27). The influence of subsets was evident in the composition and interrelations of groupings resulting from this analysis, though not all the relationships between samples were conserved and the degree to which this occurred differed from subset to subset. Interrelations among samples were also less robust.

Inter-sample relationships of the sediment macrofauna species ordination (Figure 29) generally did not hold in the overall analysis, as only one grouping was retained unchanged, i.e. AVA-HWD (Avalanche-Humewood). The response of the sediment macrofauna therefore clearly differed from that of the rock-bound macrobiota. Slightly more inter-sample relationships of the ordination of sessile macrofauna (Figure 30) were conserved in the ordination of all species, e.g. the position of KME (Kleinemonde East) relative to the remaining sites, as well as the spatial relationships of the pairs MAA-MAB (Maitlands Inner and Outer) and ASB-CRE (Aston Bay and Cape Recife East).

Some of the spatial relationships evident in the ordination of all species were clearly due to the response of macroalgae (Figure 31). Where similar to that of sessile macrofauna, it led to a strengthened relationship (closer grouping) between sites (e.g. ASB-CRE). A similarity in the response of macroalgae also had to be the cause of the close proximity of some site pairs and triplets, e.g. BRK-PDB (Bird Rock and Paradise Beach), TST (Three Sisters) relative to MAA-MAB (Maitlands Inner and Outer) and HWD-MLS (Humewood-Miller’s Beach). However, the combined set of macroalgae and sessile macrofauna (Figure 32) threw even more light on the structure of the all biota ordination, explaining more interrelationships, e.g. the position of MPB (Pollock South) relative to BCN (Beacon Rock), and revealed some strengthened responses, e.g. KME-HPE (Kleinemonde East-Hougham Park East). Also the affinity between CRW (Cape Recife West) and MLS (Miller’s Beach) shown in the macroalgae-sessile macrofauna ordination (Figure 32), reappeared in the all species ordination.

None of the spatial relationships evident in the gastropod ordination (Figure 33) were retained as is. Those responses in which the directional aspect was conserved were either weakened or strengthened in the ordination of all biota.
Figure 34. Ordination (DCA) of sites using importance values of all species. Shore configuration types are indicated by colours (green, yellow, blue and red) according to the legend. Sum of all eigenvalues = 1.957; Axis 1 eigenvalue = 0.282; Axis 2 eigenvalue = 0.169; Cumulative variance of species data = 23.1%. Circle colours correspond to those of groups in complementary classification (Figure 26).
The distribution of samples (sites) in the analysis of all species suggested a response to an overriding environmental driver, modified by or interacting with additional environmental variables. Sites in the bottom left corner of the diagram (HPW, HPE, KME) had higher wave exposure ratings than those situated furthest to the right (CRE, ASB, PDB). The surf zones of most of the sites in the left half of the diagram were sand-bottomed at low tide with no intruding hard substrate (HPW, HPE, KME, MAA, MAB, TST). This may also have been the case for MPB, PBE and CRW, but it was unsure as small rock outcrops are not easily seen when fully submerged. The sites on the left either had no or only a limited amount of rock above midtidal elevation.

The remaining sites (WLW, KNB, AVA, BRK, BCN, MLS, HWD, CNR, CRE, ASB and PDB) all had rock substrate of different physical configurations and extent in their surf zones that impinged on surf zone processes during all tidal phases. There was a change in beach characteristics (beach slope, sediment type) and swash climate moving from left to right in the diagram. The distribution pattern of sites therefore suggested a wave-attenuation gradient due to the interaction of waves with hard structures situated in the vertical range between tidemarks.

The positions of the unconstrained sites in this ordination space resulted from a biotic response to the hypothetical environmental gradient composed of probably several interacting parameters: essentially wave characteristics, sediment parameters and geological (structural) control of waves and beach characteristics by hard substrate.

The ordination of all species showed reasonably good agreement with the complementary classification (Figure 27). Group 1 of the classification appeared in the ordination with almost all relationships intact, except for those of CRW (Cape Recife West). In Figure 27, CRW was grouped with CRE (Cape Recife East), yet in the ordination it showed a stronger relationship with MLS (Miller’s Beach). Interestingly, CRW and MLS were paired in the classification of macroalgae (Figure 23), but weakly associated in the corresponding ordination (Figure 31), as MLS showed a greater affinity to the ASB-CRE grouping than CRW. The relationships between the members in each of the two site pairs (ASB-CRE and CRW-MLS) in the ordination of all species (Figure 34) are clearly due to the combined influence of sessile macrofauna and algae as reflected in the classification (Figure 24) and complementary ordination (Figure 32). The explanation for this lack of fit is not obvious, but may be related to the differential influence of macroalgae, sessile macrofauna and the gastropods, or rather their response to the hypothetical gradient. The response of the gastropods must have influenced the classification the most strongly as in both the classification (Figure 25) and ordination (Figure 33), CRE and CRW were close together.
The response of the attached biota of rock substrate was the most important influence on the relationships among these four sites in the ordination. In the ordination of all species, it must then have been the combined response of sessile macrofauna, macroalgae and secondarily beach macrofauna that placed CRW closer to MLS. For instance, *Bullia rhodostoma* was recorded at CRW and MLS, but not CRE and ASB. Both former sites experience more active swash and surf conditions than the latter two.

Group 4 of the classification of all species (Figure 27) was also retained with minor changes in relationships. The response of the heterogeneous collection of sites consisting of Groups 2 (PBE – Pollock North), 3 (KME Kleinemonde East, MPB – Pollock South), 5 (HPE – Hougham Park East) and 6 (CNR – Cannon Rocks) was at variance with the cluster analysis. This was clearly an outcome of the diverse composition of the cluster in the dendrogram of all species (Figure 27). These sites probably represent four different biotic types on a par with Groups 1 and 4 in the classification, but due to lack of replication this could not be inferred with confidence.

As sites were not arranged in response to physical site category, but rather responded to other more important environmental drivers, their symbol codes were changed to reflect their positions and response modes in the ordination (see Figure 35) and clearly indicated the good agreement achieved with the outcome of both the initial classification into groups (Figure 27) and the biotic types found by classification (Figure 28).

**7.4 DCCA of sites using all species**

The constrained ordination (Figure 36B) of all species produced an arrangement of sites that very closely resembled the unconstrained version of this analysis (Figure 35). The environmental parameters used in the DCCA are summarised in Table 12. The analysis indicated that the strongest biotic responses were to the parameters of wave energy (height), sediment grain size, sediment depth, sand cover as well as the general intertidal dimensions of the rock traverse in a shore-normal, shore-linear and vertical direction. The directional relationships between the dynamic parameters, wave energy (WaveH) and swash climate (B WaCli), and the structural parameters of shore-normal width of the rock traverse (Roc_Wid) as well as its proportional contribution to total shore width (Roc_.CS) suggested that wave energy is reduced and swash becomes gentler with increasing extent of wave-hard substrate interaction. Thus a gradient of increasing wave attenuation or wave-shelter due to structural (geological) control of waves by hard substrate is brought about.
Figure 35. Ordination (DCA) of sites using importance values of all species. Mixed substrate shore biotic types A, B and C are indicated by colours (green, red and blue, respectively). Sum of all eigenvalues = 1.957; Axis 1 eigenvalue = 0.282; Axis 2 eigenvalue = 0.169; Cumulative variance of species data = 23.1%. 
Figure 36. DCCA of all species constrained by selected environmental parameters. A. Environmental parameters. B. Diagram of constrained ordination of sites using all species. The environmental parameters are explained in Table 11. Sum of all eigenvalues = 1.957; Axis 1 eigenvalue = 0.282; Axis 2 eigenvalue = 0.169; Lengths of gradient: Axis 1 = 1.962; Axis 2 = 1.758. Cumulative percentage variance of species data: Axis 1 = 14.4%; Axis 2 = 23.1%. Cumulative percentage variance of species-environment relationship: Axis 1 = 13.8%; Axis 2 = 22.3%. Colours of symbols representing sites correspond to the mixed substrate shore biotic types A, B and C found by classification.
Table 11. Legend for the environmental parameters used in the DCCA of all species.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Explanation of parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>.SandCov</td>
<td>Mean % cover by sand in releves.</td>
</tr>
<tr>
<td>Geology</td>
<td>Rock type (sandstone and quartzite, shale, aeolianite)</td>
</tr>
<tr>
<td>RockConf</td>
<td>Configuration type: platforms or ridges.</td>
</tr>
<tr>
<td>RocHeigh</td>
<td>Rock height rating values based on rock height and intertidal position relative tide marks. Higher rating implies greater effect on waves.</td>
</tr>
<tr>
<td>Roc_Wid</td>
<td>Cross-shore extent of platform or ridges (m).</td>
</tr>
<tr>
<td>Roc_CS</td>
<td>Cross-shore extent of rock as % of transect length.</td>
</tr>
<tr>
<td>Roc_LS</td>
<td>Longshore extent of rock as % of 100m distance at midtidal elevation.</td>
</tr>
<tr>
<td>San_Dep</td>
<td>Mean depth of sand at S5, R5 to R8 (cm).</td>
</tr>
<tr>
<td>Bea_Wid</td>
<td>Cross-shore beach width (m) from HWS to LWS.</td>
</tr>
<tr>
<td>Dun_Dis</td>
<td>Distance to nearest coastal dunes (km).</td>
</tr>
<tr>
<td>Mean gra</td>
<td>Mean grain size (mm).</td>
</tr>
<tr>
<td>Median G</td>
<td>Median Grain Size Class (µm).</td>
</tr>
<tr>
<td>BeachSlo</td>
<td>Beach Slope (H:L): Vertical distance between spring tide marks: Cross-shore beach width.</td>
</tr>
<tr>
<td>ShoreSlo</td>
<td>Shore Slope (H:L): Vertical distance between spring tide marks: Horizontal distance between spring tide marks over rock and sand (full shore).</td>
</tr>
<tr>
<td>Sur_WidM</td>
<td>Estimated width of surf zone (m).</td>
</tr>
<tr>
<td>S WaCli</td>
<td>Surf wave climate: Breaker type in surf zone (spilling, plunging, collapsing).</td>
</tr>
<tr>
<td>WaveH</td>
<td>Estimated wave height in surf zone (m).</td>
</tr>
<tr>
<td>B WaCli</td>
<td>Beach wave climate (swash), wave behaviour on beach (surging, collapsing, plunging).</td>
</tr>
<tr>
<td>Temp</td>
<td>Water temperature (°C)</td>
</tr>
</tbody>
</table>
The sites of mixed shore biotic type C (blue) (*Arthrocardia-Laurencia*) had the lowest degree of sand inundation of rock-bound biota, as indicated by their location in the diagram. Although at several of these sites there were intertidal sand deposits adjacent to the rock substrate, the biota probably did not experience the degree of sand-inundation characteristic of the sites in mixed substrate shore biotic types A (green) and B (red). Filamentous turfs with a high abundance of *Polysiphonia* were characteristic of the intertidal communities of those two biotic shore types.

According to the analysis, the communities of biotic type A were the most wave-exposed, had an active swash climate, coarser beach sand and more (frequent?) sand-inundation of rock surface communities than those of biotic types B and C. The positions of HPW (Hougham Park West), KNB (Kini Bay) and TST (Three Sisters) indicated the controlling influence of sediment grain size on the composition of the sedimentary biotic assemblage in a wave-exposed environment. HPW, KNB and to a lesser extent TST had a high proportion of coarse grained sediment and high abundance of *Polygordius*, a tiny marine polychaete associated with coarse sediment. Small corallines such as *Jania* spp and *Arthrocardia* spp had a more robust appearance compared to those of biotic types B and C that were wave-sheltered to different degrees. Gradients in wave-substrate interaction not only existed between sites, but were also set up over the intertidal substrata within sites. For example, the algal turfs at sites of biotic type A were not all fully wave exposed, but experienced more moderate wave action owing to their low position on the shore, compared to the midlittoral beach sediments of these sites.

The increase in surf zone width (Sur_Wid) in the direction of cross-shore extent of rock (Roc_CS) and (Roc_Wid) confirmed that wave energy dissipation occurred over the rock traverse. The biotic composition of the beach macrofauna at those sites was typified by high polychaete abundance and diversity in sediment, many of them deposit-feeders (capitellids, orbiniids, spionids). Greater wave exposure was implied for the remaining communities and this was borne out by the higher abundance of crustaceans in the macrofaunal assemblages of their beaches.

### 7.5 Definition of the mixed substrate shore biotic types

The three mixed substrate shore biotic types (A, B and C) found by Ward's hierarchical classification and confirmed in CANOCO ordination, could be distinguished on the strength of a number of constant biotic and environmental indicators (Table 12).
Table 12. The biotic and environmental attributes of the mixed substrate shore biotic types of this study.

<table>
<thead>
<tr>
<th>Community A: Jania - Polysiphonia turfs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sites:</strong> Cannon Rocks (CNR), Hougham Park East (HPE), Kleinemonde East (KME), Pollock North (PBE) and Pollock South (MPB).</td>
</tr>
<tr>
<td><strong>Indicator species:</strong> Gunna capensis (Schmarda, 1861). Bullia rhodostoma L.A. Reeve, 1847. Dictyopteris cf. ligulata (Suhr) O.C.Schmidt.</td>
</tr>
<tr>
<td><strong>Dominant sandy-substrate species:</strong> Eurydice longicornis (Studer, 1883). Exosphaeroma sp. Scolelepis (Scolelepis) squamata (Müller, 1806). Gastroscos psammodytes O.Tattersall, 1958.</td>
</tr>
<tr>
<td><strong>Environmental indicators:</strong> Robust midlittoral turf. Wave-exposed midlittoral. Beach community indicates wave-exposed intermediate to high energy.</td>
</tr>
</tbody>
</table>
Table 12 (cont). The biotic and environmental attributes of the mixed substrate shore biotic types of this study.

| Community B: *Polysiphonia-Tayloriella-Caulacanthus* turfs |
|-----------------|---------------------------------|
| Sites:          | Avalanche (AVA), Beacon Rock (BCN), Humewood (HWD), Maitlands Inner (MAA) and Maitlands Outer (MAB). |
| Environmental indicators: | Midlittoral turf contains high filamentous component. Wave-sheltered to semi-exposed mid-littoral. Beach community indicates intermediate energy beach state. |
Table 12 (cont). The biotic and environmental attributes of the mixed substrate shore biotic types of this study.

<table>
<thead>
<tr>
<th>Community C: Arthrocardia-Laurencia turfs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sites: Aston Bay (ASB), Bird Rock (BRK), Cape Recife East (CRE), Cape Recife West (CRW), Hougham Park West (HPW), Kini Bay (KNB), Miller’s Beach (MLS), Paradise Beach (PDB), Three Sisters (TST) and Willows Beach (WLW).</td>
</tr>
</tbody>
</table>
CHAPTER 8  Species richness, composition and abundance

Three community descriptors were investigated, i.e. species richness, taxonomic composition and abundance.

8.1 Species richness

In this study the concept of species richness was applied at its very simplest level, i.e. the number of species in a defined area, in this case, the study site (Lawrence 2004).

8.1.1 Total species counts of mixed substrate shore study sites

The survey of 20 mixed substrate sites yielded a total of 446 macroalgal and macrofaunal taxa. Total species richness per site ranged from 75 species to 146 species (Figure 37) with a mean of 116 ± 4 species. Mean species richness of sites with platforms was significantly higher than those with ridges (t = -2.351, d.f. = 18, p = 0.030). Platforms had an average of 126 ± 5 species while ridges had 109 ± 5 species on average.

8.1.1.1 Total species counts in relation to physical mixed substrate shore types

In a comparison of mean species richness of the four configuration types (Figure 38), a significant difference was found only between low ridge and high platform sites (Mann-Whitney U: high platform shores vs low ridge shores: 2*1 sided p, Table 13).

8.1.1.2 Total species counts in relation to biotic mixed substrate shore types

Mean species richness of the mixed substrate shore biotic types (Figure 39) did not differ significantly (Kruskal-Wallis ANOVA: H = 0.637, p = 0.727, N = 2, 20).

8.1.2 Numbers of species of macrobiota from different substrata

The total number of macrofauna species recorded (combining those from hard and soft substrata) was 274 species. Total macrofaunal species richness per site ranged between 48 at ASB (Aston Bay) and 97 at MLS (Miller’s Beach), with a mean of 66 species per site ± 3 species. Macrofauna species recorded from both the substrata numbered 3 each at MLS (Miller’s Beach) and HPE (Hougham Park East) and 1 species each at AVA (Avalanche), MAA (Maitlands Inner) and HPW (Hougham Park West). Ridge shores and platform shores had roughly equal numbers of macrofauna species in total at 217 and 213 species, respectively. Of these, 147 species occurred at both shore configuration types.
Figure 37. Total species richness per site. Sites are arranged according to site configuration. The sediment load and distribution is indicated by a + symbol, following the scheme set out in Table 2 of Chapter 3. 1 h/s+ to 1 h/s +++: WLW to CRW; 1 m/s+ to 1 m/s+++: BCN to PBE; 2 h/s+ to 2 h/s ++++: TST to HPE; 2 m/s+ to 2 m/s ++++: CRE to MPB. 1 h/s = high ridge sites, 1 m/s = low ridge sites, 2 h/s = high platform sites, 2 m/s = low platform sites. Site codes are explained in Table 3 of Chapter 4. The mixed substrate shore biotic types (A, B and C) defined by cluster analysis and ordination are indicated on the x-axis labels.

Table 13 Results (2*1-sided p values) of Mann-Whitney U tests for significant difference in species richness of pairs of configurations. Tests are significant at p < 0.05. Significant differences are indicated in bold italized print.

<table>
<thead>
<tr>
<th></th>
<th>1 h/s (n = 6)</th>
<th>1 m/s (n = 6)</th>
<th>2 h/s (n = 3)</th>
<th>2 m/s (n = 5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 h/s</td>
<td>-</td>
<td>0.4848</td>
<td>0.1666</td>
<td>0.4285</td>
</tr>
<tr>
<td>1 m/s</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.1255</td>
</tr>
<tr>
<td>2 h/s</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.7857</td>
</tr>
</tbody>
</table>

0.0476
Figure 38. Mean species richness (± 1 SE) in the four shore configuration types. Configuration legend: 1 h/s – high elevation ridges, 1 m/s – low elevation ridges, 2 h/s - high elevation platform, 2 m/s – low elevation platform. The shore configuration types that differed significantly in mean species richness are indicated by the letter $a$.

8.1.2.1 Macrofauna of the sediment

The total species count in sediment samples (“sandfauna”) was 205 spp. Of these, 196 spp. were only recorded from sediment samples and 9 also from rock substrate. Species richness of the macrofauna in sediment ranged from 10 at Aston Bay (ASB) to 55 at Miller’s Beach (MLS) with a mean of 32 species ± 3 species (Figure 40). Altogether 149 of these species occurred at ridge shores, 140 at platform shores and 84 species could be found at both types of shore. The mean species richness of macrofauna in sediment was not significantly higher at platform sites ($t = -1.510$, d.f. = 18, $p = 0.148$).
Figure 39. Mean species richness (± 1 SE) in the three biotic types obtained by cluster analysis. Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.

8.1.2.2 Macrobenthos of rock surfaces

The overall mean number of species in biotic assemblages of the hard substrate (85 ± 3 species) was significantly higher than that of the sediment (*t* = 13.944, d.f. = 38, p < 0.001). The total species count (macrofauna and macroalgae) from hard substrate was 250 spp. Species richness of hard substrate biota per site (Figure 40) ranged between 48 at PBE (Pollock North) and 105 at TST (Three Sisters). Altogether 204 spp. occurred on ridge shores, 208 on platform shores and 163 spp. inhabited both types of shore.

**Macrofauna**

A total of 78 macrofaunal species were recorded from the hard substrate samples ("rockfauna" in Figure 40) ranging from 22 spp. at PBE (Pollock north) to 45 at MLS (Miller’s Beach) with a mean of 35 species ± 1 species. Altogether 68 spp. of hard substrate macrofauna were found on ridge shores, 73 on platform shores and 63 species inhabited both types of shore.
Macroalgae

All macroalgae were attached to rock substrate even though some perpetually experienced a degree of sand cover. Macroalgal species recorded totalled 172 spp. Altogether 136 of these species occurred on ridge shores, 135 on platform shores and 100 inhabited both types of shore. The number of macroalgal species per site ranged from 26 species at PBE (Pollock North) to 67 at TST (Three Sisters), with a mean of 50 species per site ± 2 species (Figure 40). When the mean species richness of macroalgae of platform shores in general was compared to ridge shores in general, it was significantly higher at platform shores than ridge shores (t = 2.665, d.f. = 18, p = 0.016).

Variations in total species richness of the rock substrate macrobenthic communities were more strongly related to changes in the species richness of macroalgae than that of the macrofauna (Figure 41). Both macroalgal and macrofaunal species richness were positively correlated with the overall species richness of hard substrate (macroalgae vs. rock biota: r = 0.903; p for r < 0.001, t = -10.957, d.f. = 38, p < 0.001; macrofauna vs. rock biota: r = 0.693; p for r = 0.001, t = -16.297, d.f. = 38, p < 0.001).

8.1.2.3 The numbers of species in macrobenthic assemblages of different substrata in relation to environmental parameters

Species richness trends in soft and hard substrate assemblages were for most part unrelated to environmental parameters (Figures 42 to 44), as in only two cases weak, but significant correlations were found between species richness and environmental factors, i.e. between sediment macrofauna species numbers and the percentage long-shore rock, and between macroalgal species richness and the exposure rating of sites (Table 14).

8.1.2.4 The numbers of species in macrobenthic assemblages of different substrata in relation to physical mixed substrate shore types

The mean number of macrofauna species in the sediment (Figure 45) was significantly lower than that of the biotic assemblages of the hard substrate in each of the four shore configuration types (high ridge sites: t = 10.937, d.f. = 10, p < 0.001; low ridge sites: t = 6.258, d.f. = 10, p < 0.001; high platform sites: t = 10.183, d.f. = 4, p < 0.001; low platform sites: t = 6.050, d.f. = 8, p < 0.001), but did not vary significantly among configuration types (Kruskal-Wallis ANOVA: H = 2.200, p = 0.532, N = 4, 20), regardless of the extent of intertidal sand.
Figure 40. Total numbers of macroalgal and macrofaunal species per site. Rockfauna = motile and sessile macrofauna of hard substrate, sandfauna = macrofauna of sediment. Sites are arranged according to site configuration. High ridge sites: WLW to MAB; Low ridge sites: BCN to PBE; High platform sites: TST to HPE; Low platform sites: CRE to MPB. The biotic groups resulting from cluster analysis are indicated on the x-axis labels.

Figure 41. The relationship between the species richness of total rock biota, macroalgae and macrofauna.
Figure 42. Sediment macrofauna species richness in relation to the mixed substrate shore environmental parameters.
Figure 42 (cont.). Sediment macrofauna species richness in relation to mixed substrate shore environmental parameters.
Figure 43. Sediment macrofauna species richness in relation to beach indices.
Figure 44. Rock surface macrobenthos species numbers in relation to environmental parameters and indices.
Table 14. R values of correlations between the species richness of macrobenthos of different substrata and selected environmental variables and indices. The t-test statistics given below refer to the significant r-values indicated in bold italics.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sand macrofauna</th>
<th>Algae</th>
<th>Rock macrofauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>RocHght-Position</td>
<td>-0.174</td>
<td>0.109</td>
<td>0.009</td>
</tr>
<tr>
<td>Roc_%CS</td>
<td>0.308</td>
<td>0.135</td>
<td>0.255</td>
</tr>
<tr>
<td>Roc_%LS</td>
<td><strong>0.474</strong></td>
<td>0.148</td>
<td>0.122</td>
</tr>
<tr>
<td>%SandCover</td>
<td>0.166</td>
<td>0.127</td>
<td>0.045</td>
</tr>
<tr>
<td>Mean Grain Size</td>
<td>0.027</td>
<td>0.271</td>
<td>-0.057</td>
</tr>
<tr>
<td>Median Grain Size</td>
<td>0.244</td>
<td>0.363</td>
<td>0.028</td>
</tr>
<tr>
<td>BeachSlope</td>
<td>0.157</td>
<td>0.211</td>
<td>0.213</td>
</tr>
<tr>
<td>BSI</td>
<td>-0.006</td>
<td>-0.268</td>
<td>0.047</td>
</tr>
<tr>
<td>Exp_R</td>
<td>-0.054</td>
<td><strong>0.579</strong></td>
<td>-0.339</td>
</tr>
<tr>
<td>Ω</td>
<td>-0.085</td>
<td>-0.328</td>
<td>-0.013</td>
</tr>
<tr>
<td>RTR</td>
<td>0.181</td>
<td>-0.021</td>
<td>0.232</td>
</tr>
<tr>
<td>Sur_Wid</td>
<td>0.011</td>
<td>0.033</td>
<td>0.166</td>
</tr>
<tr>
<td>Bea_Wid</td>
<td>-0.253</td>
<td>0.111</td>
<td>0.005</td>
</tr>
<tr>
<td>% sand &gt; 30 cm</td>
<td>-0.176</td>
<td>-0.094</td>
<td>0.101</td>
</tr>
</tbody>
</table>

| p (for r)                  | 0.035           | **0.007** |
| t                          | -2.258          | 16.616   |
| d.f                        | 38              | 38       |
| p (for t-test)             | **0.029**       | < 0.001  |

Although mean species richness of hard substrate biota was significantly higher at platform shores (91 ± 10 species) than at ridge shores (81 ± 4 species), overall (Mann-Whitney U: platform shores vs ridge shores: 2*1 sided p = 0.039), the number of macrobiota species in hard substrate communities at sites with the least intertidal rock surface and most sand, i.e. low ridges, was not significantly less than in the other three configuration types (Figure 45) that had more intertidal rock substrate (Kruskal-Wallis ANOVA: H = 6.116, p = 0.106, N = 4, 20). There was also no significant difference between the species richness of hard substrate biota at sites with much higher elevation rock (high ridges and platforms) and those with only low elevation rock (Mann-Whitney U: high ridges and platforms vs low ridges and platforms: 2*1 sided p = 0.331). The mean species richness of rock macrofauna was remarkably similar in all site configuration groups and showed no significant difference (Kruskal-Wallis ANOVA: H = 0.665, p = 0.880, N = 4, 20).
Figure 45. Mean species numbers (± 1 SE) of macrobenthos in sediment and on rock surfaces in relation to physical mixed substrate shore types (configuration types). Rock macrofauna includes both motile and sessile forms. Total rock biota = macroalgae, sessile and motile macrofauna of hard substrate. Configuration legend: 1 h/s – high ridges, 1 m/s – low ridges, 2 h/s – high platform, 2 m/s – low platform. A significant difference between numbers of species in sediment and on rock substrate is indicated by the letters a, b, c and d for the different shore configuration types. A significant difference between numbers of macroalgal species is indicated by the letter e. A significant difference between numbers of macroalgal and rock macrofaunal species is indicated by the letters f, g and h.
The trend in mean macroalgal species richness was similar to that of the means for rock biota as a whole, i.e. highest at high platform sites, followed by low platforms, high ridges and finally low ridge sites. A significant difference in macroalgal species richness was demonstrated between the low ridge sites and the high platform sites (Kruskal-Wallis ANOVA: $H = 8.969$, $p = 0.029$, $N = 4, 20$). Macroalgae comprised significantly more species than macrofauna of hard substrate in all site configuration groups except the low ridge sites (high ridges: $t = 4.519$, d.f. $= 10$, $p = 0.011$; low ridges: $t = 1.278$, d.f. $= 10$, $p = 0.230$; high platforms: $t = 5.605$, d.f. $= 4$, $p = 0.005$; low platforms: $t = 2.475$, d.f. $= 8$, $p = 0.038$).

8.1.2.5 The numbers of species in macrobenthic assemblages of different substrata in relation to biotic mixed substrate shore types

The mean species richness of macroalgae varied more among the three mixed substrate shore biotic types than the macrofaunal assemblages associated with sediment and hard substrate (Figure 46). However, like the macrofauna, the number of species of macroalgae did not vary significantly among mixed substrate shore biotic types (Kruskal-Wallis ANOVA: Sediment macrofauna: $H = 0.341$, $p = 0.843$, $N = 3, 20$; Hard substrate macrofauna: $H = 0.629$, $p = 0.729$, $N = 3, 20$; Macroalgae: $H = 3.576$, $p = 0.167$, $N = 3, 20$).

In the communities of biotic types A and B, the number of macroalgal species was only significantly higher than that of the sediment macrofauna, whereas in biotic type C, the macroalgae comprised of significantly more species than the two macrofaunal assemblages (1-way ANOVA, Tukey HSD test, Table 15).

8.2 Taxonomic composition

8.2.1 Major taxa – an overall summary

When species from both substrata were taken into account, three major taxonomic groups contributed the bulk of macrofaunal species in roughly equal abundance, i.e. Arthropoda (mainly Crustacea) 103 spp., 36% of all macrofaunal species; Annelida (mainly Polychaeta) 81 spp., 28%, and, Mollusca (mainly Gastropoda) 76 spp., 26%, making a cumulative total of 90%. Of the three macroalgal divisions (Rhodophyta, Chlorophyta and Phaeophyta), the rhodophytes were the most diverse, contributing 118 spp. or 69% of macroalgal species. Green algae comprised 28 spp. (16%) and brown algae 26 spp. (15%) in the total number recorded.
Figure 46. Mean species richness (± 1 SE) of macrobenthos in sediment and on rock surfaces in relation to biotic mixed substrate shore types (configuration types). Rock macrofauna includes both motile and sessile forms. Total rock biota = macroalgae, sessile and motile macrofauna of hard substrate. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs. A significant difference between numbers of macroalgal species and macrofauna species in sediment is indicated by the letters a, b and c, for biotic types A, B and C respectively. A significant difference between numbers of macroalgal species and rock macrofaunal species is indicated by the letter f.

Table 15. Results of statistical comparison (1-way ANOVA, Tukey HSD test) of macroalgal and macrofaunal species richness in mixed substrate shore biotic types A, B and C. Tests are significant at p < 0.05. Significant p-values are shown in bold italics.
8.2.2 Major taxa of macrobenthic assemblages of different substrata

8.2.2.1 Macrofauna of the sediment

The sediment harboured a diverse assemblage of major taxonomic groups (Figure 47). The most diverse group was Arthropoda, made up of 93 spp. (46% of species in sediment samples). The majority of these were Crustacea (31%), composed mainly of Isopoda (22 spp.) and Amphipoda (31 spp.). The third most diverse group of arthropods was the Insecta (Hexapoda) which comprised 28 spp. belonging to the Diptera, Coleoptera and Hymenoptera. Annelida consisted of 78 spp. (38%). The majority of these were Polychaetes (37%) composed of 37 spp. of sedentary worms and 38 spp. of errant worms. Mollusca comprised 16 spp. (7%), most of which were gastropods. Other taxa included unidentified Nematoda and Platyhelminthes as well as 1 species each of Porifera, Sipunculida, Echinodermata and Chaetognatha.

Of the four most important taxonomic groups of sandy beaches, i.e. polychaetes, crustaceans, molluscs and insects, the polychaetes and crustaceans contributed most to species richness at sites (Figure 48). Except for MAA (Maitlands Inner) and CNR (Cannon Rocks), where equal numbers of polychaete and crustacean species were recorded, either polychaetes or crustaceans contributed the most species at any one site. Polychaetes contributed mostly close to 40% of species per site, ranging from 25% to 70%, crustaceans contributed 30% of species (range: 20% to 50%), while mollusc species, where present, made out between 3% and 25% (7% overall) of species per site.

The number of polychaete species (Figure 48) ranged from 5 species (Aston Bay/ASB, Willows Beach/WLW) to 26 species at Miller’s Beach (MLS). Crustacean species varied between 4 species (Aston Bay/ASB, Pollock South/MPB) and 17 species (Kini Bay/KNB, Hougham Park East/HPE). Molluscan species ranged from zero to 11 species (HPE), but usually there were no more than 5 species per site. Insecta were absent from samples at six sites, varying between 1 and 7 species where present. The number of polychaete and crustacean species did not differ significantly, but were significantly higher than mollusc, insect and others (Kruskal-Wallis ANOVA: $H = 61.732$, $p < 0.001$, $N = 5$, 100; Table 16) and together contributed 60 – 90% of species richness at sites.

Similar numbers of polychaete species were found at all the configuration types (Figure 49), and the same could be said of the numbers of crustacean, insect and mollusc species. Any variations in species richness were not significant (Kruskal-Wallis ANOVA: Polychaetes: $H =$
1.991, p = 0.574, N = 4, 20; Crustaceans: H = 2.266, p = 0.519, N = 4, 20; Molluscs: H = 4.983, p = 0.173, N = 4, 20; Insects: H = 3.894, p = 0.273, N = 4, 20).

Figure 47. Overall composition of sediment macrofauna assemblages. The number of species is given first, followed by percentage of total number of species. Other Crustacea include species of Mysidacea, Caridea, Brachyura, Cumacea, Copepoda, Ostracoda and Tanaidacea. Other taxa include Nematoda, Platyhelminthes, Porifera, Sipunculida, Echinodermata and Chaetognatha.

Figure 48. Composition of sediment macrofauna assemblages per site. Sites are grouped
according to configuration type: high ridge sites (WLW – MAB), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB). Taxa with extremely low numbers of species were lumped together as “Other”.

Table 16. Results of the statistical comparison of the numbers of polychaete, crustacean, mollusc, insect and other species per site. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

<table>
<thead>
<tr>
<th></th>
<th>Polychaetes</th>
<th>Crustaceans</th>
<th>Molluscs</th>
<th>Insects</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polychaetes</td>
<td>1.000</td>
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<tr>
<td>Insects</td>
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</tbody>
</table>

The general pattern was that polychaete and crustacean species contributed the bulk of the taxonomic richness (Figure 49) almost equally, as there were no significant differences between the mean numbers of polychaete and crustacean species from one site configuration group to the next (Kruskal-Wallis ANOVAs, Table 17).

At low ridge and low platform sites there were significantly more polychaete species than molluscs and insects (Kruskal-Wallis ANOVA: Low ridge sites: H = 17.512, p = 0.002, N = 5, 30; Low platform sites: H = 25.133, p < 0.001, N = 5, 25; Table 17). There were significantly fewer mollusc species than of other major taxa at high ridge shores (Kruskal-Wallis ANOVA: High ridge sites: H = 17.512, p = 0.002, N = 5, 30; Table 17). At high platform shores the beach communities were composed of more or less equal numbers of polychaetes, crustaceans and molluscs as only the number of insect species was very much lower (Kruskal-Wallis ANOVA: High platform sites: H = 12.219, p = 0.016, N = 5, 15; Table 17).

In the three mixed substrate shore biotic types, the mean numbers of species of polychaetes, crustaceans, molluscs, insects and other minor taxa showed slightly changed patterns in each biotic type (Figure 50). There were small adjustments in the means of species, as well as their mean percentage contribution to the total, in the different major sandy beach taxa, from one biotic assemblage to the next. Biotic type A had the lowest proportion of polychaete species, B intermediate and C the highest. In biotic types A and B, the mean numbers of polychaete and crustacean species were near-equal, whereas in type C, the crustacean assemblage contributed proportionally less to total number of species compared to the other two biotic types. The number of insect species was significantly lower than that of polychaetes and crustaceans in the beach communities of all three biotic types and the number of molluscan
species was significantly lower only in assemblages of biotic type C (Kruskal-Wallis ANOVA: Biotic type A: $H = 13.530$, $p = 0.009$, $N = 5, 25$; Biotic type B: $H = 16.146$, $p = 0.002$, $N = 5, 25$; Biotic type C: $H = 31.044$, $p < 0.001$, $N = 5, 50$; Table 18).

High ridge sites

Low ridge sites

High platform sites

Low platform sites

- Polychaetes
- Crustaceans
- Molluscs
- Insects
- Other
Figure 49. The composition of beach macrofauna assemblages per mixed substrate shore configuration type. The number of species is given first, followed by proportion (percentage) of total number of species.

Table 17. Comparison of the mean numbers of polychaete, crustacean, molluscan, insect and other species at sites in different mixed substrate shore configurations. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

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<thead>
<tr>
<th>High ridge</th>
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<th>Crustaceans</th>
<th>Molluscs</th>
<th>Insects</th>
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<td></td>
</tr>
<tr>
<td>Insects</td>
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<th>Molluscs</th>
<th>Insects</th>
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</tr>
<tr>
<td>Insects</td>
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</table>
Figure 50. The composition of beach macrofauna assemblages per mixed substrate shore biotic type. The number of species is given first, followed by proportion (percentage) of total number of species. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.
Table 18. Comparison of the mean numbers of polychaete, crustacean, molluscan, insect and other species in the beach sediment of different mixed substrate shore biotic types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at $p < 0.05$. Significant differences are indicated by bold italicized p-values. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

<table>
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<td>Insects</td>
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8.2.2.2 Macrofauna of the rock surfaces

The majority of species on rock substrate were Mollusca (55 spp in total, 70% of all rock biota), composed of 11 bivalve species, 5 chitons (Polyplacophora) and 39 gastropods of which 18 were various limpet species (Figure 51). Other taxonomic groups (Crustacea, Polychaeta, Porifera, Echinodermata, Ascidiae, Bryozoa, Cnidaria) contributed much smaller numbers of species. The Crustacea were all barnacle species (Cirripedia) and Polychaetes were all colonial tubiculous forms. Porifera were all encrusting forms.

At every study site, gastropods were the most diverse and composed of slightly more limpet than other gastropod species (Figure 52). The number of gastropod species ranged from 15 (Pollock North/PBE) to 28 species (Kleinemonde East/KME). The number of bivalve species ranged between 1 and 7, with most sites having 2 to 4 species, while 1 to 4 chiton
Figure 51. Overall composition of hard substrate macrofauna assemblages. The number of species is given first, followed by percentage of total number of species.

Figure 52. Composition of hard substrate macrofauna assemblages per site. “Other taxa” is comprised of Porifera, Bryozoa, Echinodermata and Ascidiae. Sites are grouped according to configuration: high ridge sites (WLW – MAB), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB).
(Polyplacophora) species were present at every study site. This may be an underestimate of the chitons as individuals are easily overlooked because of their cryptic colouration. No chitons were found in samples taken at Pollock North (PBE) and Hougham Park West (HPW). Of the 4 anthozoan (Cnidaria) species detected, there were never more than 3 present per site. Anthozoans were not recorded at all the study sites. Anthozoa and polyplacophora were absent from Pollock North (PBE) and gastropods, barnacles, mussels and polychaetes represented by very few species compared to other sites.

The number of species per major animal taxon on rock substrate (Figure 53) did not vary significantly from one configuration type to the next (Kruskal-Wallis ANOVA: All gastropods: $H = 0.285, p = 0.962, N = 4, 20$; Limpets: $H = 0.062, p = 0.998, N = 4, 20$; Other gastropods: $H = 0.083, p = 0.993, N = 4, 20$; Chitons: $H = 5.326, p = 0.149, N = 4, 20$; Bivalves: $H = 2.479, p = 0.479, N = 4, 20$; Cirripedes: $H = 1.615, p = 0.656, N = 4, 20$; Anthozoans: $H = 0.718, p = 0.868, N = 4, 20$; Polychaetes: $H = 2.360, p = 0.501, N = 4, 20$). Species counts for limpets and other gastropods were almost unchanged relative to each other, but other taxa were more variable, in some cases significantly so (Kruskal-Wallis ANOVA, Table 19).

At high ridge shores, there were significantly more limpet and other gastropod species than chitons, polychaetes, anthozoans and ‘other taxa’ (Kruskal-Wallis ANOVA: High ridge sites: $H = 36.839, p < 0.001, N = 8, 48$; Table 19). At low ridge shores, this list was shortened to polychaetes, anthozoans and ‘other taxa’ (Kruskal-Wallis ANOVA: Low ridge sites: $H = 36.602, p < 0.001, N = 8, 48$; Table 19).

At low platform shores, limpets and other gastropods consisted of significantly more species than only anthozoans and polychaetes (Kruskal-Wallis ANOVA: Low platform sites: $H = 31.150, p < 0.001, N = 8, 40$; Table 19). The number of limpet and other gastropod species had not changed, but there were marginally more of some of the other taxa. At high platform shores, there were no significant differences between the numbers of species of the hard substrate macrofauna (Kruskal-Wallis ANOVA: High platform sites: $H = 20.323, p = 0.005, N = 8, 24$; Table 19).

The mean numbers of species of different hard substrate macrofaunal taxa per biotic mixed shore type varied very slightly (Figure 54). The mean number of gastropod species (limpet and other) was constant and significantly higher than that of the other taxa in each biotic type (Kruskal-Wallis ANOVA: Biotic Type A: $H = 37.270, p = 0.005, N = 8, 40$; Biotic Type B: $H = 39.712, p < 0.001, N = 8, 40$; Biotic Type C: $H = 73.719, p < 0.001, N = 8, 80$; Table 20). There were minor changes in mean numbers of species of the other taxa. In the communities of mixed substrate biotic type C, the numbers of species of chiton, polychaete, anthozoan and rarer taxa were significantly lower than that of the gastropods and in biotic types A and B,
Figure 53. The composition of hard substrate macrofauna assemblages per mixed substrate shore configuration type. The number of species is given first, followed by proportion (percentage) of total number of species.
Table 19. Comparison of the mean numbers of different rock surface macrofauna species at sites of different mixed substrate shore configuration types (high ridge sites, low ridge sites, high platform sites, low platform sites). Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at $p < 0.05$. Significant differences are indicated by bold italicized p-values.

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<tr>
<th>High ridge</th>
<th>Other taxa</th>
<th>Anthozoans</th>
<th>Cirripedes</th>
<th>Bivalves</th>
<th>Chitons</th>
<th>Polychaetes</th>
<th>Limpets</th>
<th>Gastro-pods other</th>
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</thead>
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<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
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only anthozoans had significantly fewer species (Kruskal-Wallis ANOVA: Biotic Type A: $H = 37.270, p = 0.005, N = 8, 40$; Biotic Type B: $H = 39.712, p < 0.001, N = 8, 40$; Biotic Type C: $H = 73.719, p < 0.001, N = 8, 80$; Table 20).

8.2.2.3 Macroalgae

The majority of macroalgal species (Table 21) were rhodophycean (red seaweeds). These ranged between 18 (Pollock North/PBE) and 52 species (Kleinemonde East/KME) and made out between 67.5% (Cape Recife East/CRE) and 86.7% (KME) of site totals. Brown algae (phaeophytes) were few, ranging between 1 (PBE) and 10 species (Three Sisters/TST) per site and contributed between 3.5% (PBE) and 19.7% (Hougham Park West/HPE). Green algae (chlorophyceans) occupied an intermediate position in species number ranging from 4 (Aston Bay/ASB) to 10 species (PDB/Paradise Beach CRE/Cape Recife East) and contributing between 8.3% (KME) and 26.9% (PBE) of species.

The %P: %C: %R ratio calculated for the total number of species recorded was similar to the mean ratio calculated for sites (Table 21), but the (R + C)/P for the total number of species differed markedly from the mean (R + C)/P ratio for sites. Ratio’s varied from site to site and also among configurations. Variations were mainly due to changes in the numbers of Phaeophyta and Chlorophyta relative to Rhodophyta, as the number of rhodophycean species at sites was fairly constant.

The mean values for both the number and percentage contribution of red algae at sites showed very little variation from one mixed substrate shore configuration type to the next (Figure 55). There was also little variation in mean values for both the number and percentage contribution of green algae between configuration groups. The mean species number and percentage contribution of brown algae were highest at wave exposed sites with a rocky traverse extending throughout the intertidal, i.e. high ridge and high platform sites. A significant difference in the number of species could only be demonstrated for brown algae, and that between high platform sites and low ridge sites (Kruskal-Wallis ANOVA: Chlorophyta: $H = 2.447, p = 0.485, N = 4, 20$; Rhodophyta: $H = 5.177, p = 0.159, N = 4, 20$; Phaeophyta: $H = 8.398, p = 0.039, N = 4, 20$, Multiple Comparisons p values (2-tailed) for low ridges vs high platforms: $p = 0.050$).
Figure 54. The composition of hard substrate macrofauna assemblages per mixed substrate shore biotic type. The number of species is given first, followed by proportion (percentage) of total number of species. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.
Table 20. Comparison of the mean numbers of different rock surface macrofauna species at sites of different mixed substrate shore biotic types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p = 0.05. Significant differences are indicated by bold italicized p-values. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

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<th>Bivalves</th>
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<th>Gastro-pods other</th>
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<td>1.000</td>
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</tr>
<tr>
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</table>

The mean (R + C)/P and %P: %C: %R ratios of low ridge and low platform sites, both characterised by continuous stretches of sand bottom and beach, were similar. For the high ridge sites, both ratios fell between the values obtained for the former two mixed shore configuration types and the mean ratios for high platform sites that were appreciably lower than the rest. High (R + C)/P values obtained for sites with low ridges and platforms was due to a smaller number of brown algal species (Phaeophyta) as compared to sites with higher elevation rock (high ridges and platforms), but could also be a due to a response to wave action as most of the low ridge and low platform sites were wave sheltered.
Table 21. Composition of macroalgal assemblages given per site and for the overall number of species recorded. Mean and total values given are for all sites combined. P = Phaeophyta, C = Chlorophyta, R = Rhodophyta. Mean values are given for all sites combined ± 1SE. P = Phaeophyta, C = Chlorophyta, R = Rhodophyta. Sites are grouped according to configuration: high ridge sites (WLW – CRW), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB). Site codes are explained in Table 4 of Chapter 4.

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Figure 55. Composition of macroalgal assemblages and floristic ratio \( ((R + C)/P \pm 1SE) \) per mixed substrate shore configuration type. The number of species is given first, followed by proportion (percentage) of total number of species.
There were no significant differences in the numbers of species in each algal division from one biotic type (Figure 56) to the next (Kruskal-Wallis ANOVA: Chlorophyta: $H = 5.648$, $p = 0.058$, $N = 3, 20$; Rhodophyta: $H = 3.728$, $p = 0.155$, $N = 3, 20$; Phaeophyta: $H = 3.043$, $p = 0.219$, $N = 3, 20$). There was also less variation among the means of species, percentage composition and floristic ratio’s obtained for mixed substrate shore biotic types than for site groups based on the mixed shore configuration types.

Biotic type A had on average more rhodophyte species than the other two biotic types and consequently a higher $(R + C)/P$ ratio. The $\%P: \%C: \%R$ ratio was also more in favour of red seaweed, indicating appreciable tropical affinities in the flora of this type and/or a more sand-tolerant flora. Biotic type C had a higher phaeophyte component on average, double the number of species than in the communities of biotic type A. Biotic type B occupied an intermediate position with regard to the $(R + C)/P$ ratio, but had the lowest numbers of red algal species of the three biotic types. As these three biotic types hardly differed on the basis of floristics, variations in proportional abundance of macroalgal taxa and differences in the species composition of each major division (not forgetting the macrofauna) were the main criteria for separation into types.

### 8.3 Abundance and community composition

The abundance of organisms is a significant indicator of the condition of populations and communities at the time of sampling. Various approaches are employed to collect data that would provide a meaningful measure of abundance.

In beach studies abundance is commonly expressed as (estimated) number of individuals per running metre of beach (ind m$^{-1}$), although density (ind m$^{-2}$) is still used (e.g. Degraer et al. 1999, 2003; Nel 2000; Bayed 2003; Gauci et al. 2005; Janssen and Mulder 2005). Cover-abundance, on the other hand, is useful as a means to obtain percentage or scaled abundance values for sessile biota (macrofauna and macroalgae) on rock surfaces, particularly those that form thickly settled beds or attain small individual sizes or where individual units are difficult to distinguish for counting. However sometimes both cover-abundance and density is used for sessile fauna (e.g. Underwood et al. 1983) or density alone (e.g. McKindsey and Bourget 2000; Erlandsson and McQuaid 2004). Gastropod abundance on rock substrate is commonly given as a density measure (e.g. Underwood 1981; Boaventura et al. 1999, 2002).
Figure 56. Composition of macroalgal assemblages and floristic ratio \( ([R + C]/P) \pm 1SE \) per mixed substrate shore biotic type. The number of species is given first, followed by proportion (percentage) of total number of species. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.
In this study, both the abundance (ind m$^{-1}$) and density (ind m$^{-2}$) were calculated for the macrofauna of the beach sediment (cf. Rodil and Lastra 2004) and also applied to the motile macrofauna (gastropods) of the hard substrate. Cover-abundance was used to show the abundance of macroalgae and sessile macrofauna, but sessile fauna were not counted. As the % cover-abundance and other measures of abundance were not comparable, importance values (based on relative abundance and relative frequency in samples) were calculated as a proxy to compare the relative abundance of macrofauna and macroalgae from both substrata simultaneously.

### 8.3.1 Overall abundance of macrobenthos

Based on their relative importance values, the macroalgae were the most abundant, contributing 70% to the total abundance of macrobiota from both substrata (Figure 57). The Rhodophyta contributed most to macroalgal abundance, attaining substantially greater cover than Chlorophyta and Phaeophyta. Mollusc abundance was mainly due to the large numbers of gastropods on hard substrata as molluscs were rare in sediment. Annelid abundance was greatest in sediment as numerous small individuals with irregular, patchy distribution, whereas large sized sessile forms of rock substrate gave relatively low cover-abundance. Annelid relative frequency therefore tended to be low. In the Arthropoda, motile crustaceans and insects were associated with sediment and sessile crustaceans (cirripedes) with rock substrate, both as large numbers of individuals. The taxa present in very low quantities or rarely encountered and lumped as “Other” included Nematoda, Nemertea, Anthozoa, Halacaridea, Platyhelminthes, Sipunculida, Echinodermata and Chaetognatha.

### 8.3.2 Abundance of macrobenthos from different substrata

#### 8.3.2.1 Total abundance and density of sediment macrofauna

The total abundance of macrofauna in the beach sediments ranged from 505 ind m$^{-1}$ to 24 071 ind m$^{-1}$ with an average of 8381 ind m$^{-1}$ ± 1660 ind m$^{-1}$ per study site (Table 22). The total density of macrofauna per site ranged from 7 ind m$^{-2}$ to 867 ind m$^{-2}$ with an average of 184 ind m$^{-2}$ ± 45 ind m$^{-2}$ (Table 22). Nematoda were excluded. The high platform sites yielded higher mean abundance and density of beach macrofauna than sites of the remaining mixed substrate shore configuration types (Figure 58). Low ridge and low platform sites had the lowest abundance and density. Abundance of beach macrofauna at the low ridge sites was significantly different from that of the high platform sites (Kruskal-Wallis ANOVA: Abundance: $H = 7.372, p = 0.061, N = 4, 20$; Table 23), but their density did not vary significantly among site configuration types (Kruskal-Wallis ANOVA: Density: $H = 5.243, p = 0.159, N = 4, 20$).
Figure 57. Relative abundance of animal phyla and macroalgal divisions in samples obtained from both substrata based on importance values derived from relative abundance and relative frequency (n = 20 sites).
Table 22. The total abundance and mean density of macrofauna in sediment and average beach width (n = 3 transects) per study site. Site codes are explained in Table 3, Chapter 4.

<table>
<thead>
<tr>
<th>Site Code</th>
<th>Abundance (ind m$^{-1}$)</th>
<th>Density (ind m$^{-2}$)</th>
<th>Beach Width (m)</th>
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</table>

Table 23. Results of post hoc test for significant differences in abundance of beach macrofauna at sites grouped according to different mixed substrate shore configuration types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

<table>
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<tr>
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<th>High ridges</th>
<th>Low ridges</th>
<th>High platform</th>
<th>Low platform</th>
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<td>1.000</td>
<td>0.520</td>
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<td>Low ridges</td>
<td>-</td>
<td>-</td>
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<tr>
<td>High platform</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.426</td>
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Figure 58. Mean abundance and density (± 1 SE) of macrofauna in sediment at sites representing different mixed substrate shore configuration types. Configuration legend: 1 h/s - high ridges, 1 m/s – low ridges, 2 h/s - high platform, 2 m/s – low platform.
Mixed substrate shore biotic type C had the highest abundance and density of sediment macrofauna (Figure 59). Variability among sites was considerable. No significant difference in the total abundance or density of beach macrofauna could be demonstrated between biotic types A, B and C (Kruskal-Wallis ANOVA: Abundance: H = 1.054, p = 0.590, N = 3, 20; Density: H = 2.988, p = 0.224, N = 3, 20).

8.3.2.2 Total abundance and density of sediment macrofauna in relation to environmental parameters

Both abundance and density of the beach macrofauna increased significantly with a higher percentage of long-shore mid-tidal rock substrate (Figure 60, Table 24). Abundance and density was therefore greater at study sites where the rock traverse showed greater continuity in a shore linear direction at a midtidal elevation. These beach deposits were mostly narrower, steeper and more coarse-grained than those where sections of the rock traverse was separated by expanses of sand.

Density was also positively correlated with an increase in sediment grain size and beach slope (Figure 60, Table 24). This correlated more strongly with median grain size than mean grain size.

8.3.2.3 Percentage contribution of major taxa to total abundance of sediment macrofauna

Polychaetes were the most abundant overall, followed by isopods and amphipods (Figure 61, Table 25). Together, these three groups contributed an estimated 80% of total abundance. Molluscs, comprising bivalves, gastropods and chitons, were the next most abundant major taxon. Unexpectedly, oligochaetes were numerically well-represented overall. “Other Taxa” (Figure 61) included Anthozoa, Halacaridea, Platyhelminthes, Sipunculida, Echinodermata, Araneae and Chaetognatha, all rarely encountered, were also poorly represented numerically.

8.3.2.4 Abundance and density of macrofaunal taxa in sediment per site

The first ten major taxa listed (Table 26) make a cumulative total of 97% to100% of all individuals per site. Polychaetes were numerical dominants at the majority of study sites, isopods were the numerical dominants at three sites (Maitlands Outer/MAB, Hougham Park East/HPE and Pollock South/MPB) and amphipods, though never the most numerous, were among the three most abundant taxa at several study sites. Oligochaetes were the numerical dominants at Willows Beach /WLW, the site with the narrowest and least active beach. Insects reached appreciable abundance at several study sites backed by semi-vegetated dunes.
Figure 59. Mean abundance and density (± 1 SE) of macrofauna in sediment at sites representing different mixed substrate shore biotic types. Biotic type A = *Jania*-Polysiphonia turfs, Biotic type B = *Polysiphonia*-Tayloriella-Caulacanthus turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.
Figure 60. Sediment macrofauna abundance (ind m$^{-1}$) and mean density (ind m$^{-2}$) in relation to environmental parameters and indices.
Figure 60 (cont.). Sediment macrofauna abundance (ind m$^{-1}$) and mean density (ind m$^2$) in relation to environmental parameters and indices.
Figure 60 (cont.). Sediment macrofauna abundance (ind m$^{-1}$) and mean density (ind m$^{-2}$) in relation to environmental parameters and indices.
Figure 60 (cont.). Sediment macrofauna abundance (ind m\(^{-1}\)) and mean density (ind m\(^{-2}\)) in relation to environmental parameters and indices.
Table 24. Results of tests for correlations between total abundance, density and environmental parameters used in the DCCA. Parameter codes are explained in Table 11. Valid N = 20 for all correlations and t-tests. Significant correlations are given in bold italicized print and have a t-statistic.

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<th>Environmental Parameters</th>
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<td><em>p for r</em></td>
</tr>
<tr>
<td>RocHeightand Position</td>
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<td>0.868</td>
</tr>
<tr>
<td>Roc_%CS</td>
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<td>0.737</td>
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<td>Roc_%LS</td>
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<tr>
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<tr>
<td>Median Grain Size</td>
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<td>BSI</td>
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<td>0.897</td>
</tr>
<tr>
<td>Exp_R</td>
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<td>0.100</td>
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<td>Ω</td>
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<td>0.985</td>
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<td>RTR</td>
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<td>Sur_WidM</td>
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<tr>
<td>Bea_Wid</td>
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<td>0.710</td>
</tr>
<tr>
<td>% sand&gt; 30 cm</td>
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<td>0.295</td>
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</table>
Figure 61. Abundance of major taxa usually reported in beach studies as a percentage of total abundance (ind m\(^{-1}\)).

Table 25. Mean (± 1SE) abundance (ind m\(^{-1}\)) of major macrofaunal taxa in sediment.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Abundance</th>
<th>SE</th>
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<td>Isopoda</td>
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<td>Amphipoda</td>
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<td>Oligochaeta</td>
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<td>137</td>
</tr>
<tr>
<td>Hexapoda</td>
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<td>47</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>136</td>
<td>59</td>
</tr>
<tr>
<td>Copepoda</td>
<td>133</td>
<td>80</td>
</tr>
<tr>
<td>Bivalvia</td>
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<td>64</td>
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<tr>
<td>Polyplacophora</td>
<td>115</td>
<td>108</td>
</tr>
<tr>
<td>Nemertea</td>
<td>114</td>
<td>36</td>
</tr>
<tr>
<td>Mysidacea</td>
<td>59</td>
<td>26</td>
</tr>
</tbody>
</table>
Gastropods and nemertines, usually present in appreciable numbers at sandy beaches, were found in low numbers at most of the study sites. In a similar trend, mysids and bivalves were poorly represented numerically and found in samples of only about half of study sites. The highest abundance of gastropods was recorded at Hougham Park East/HPE, a narrow platform beach and for mysids and bivalves at Maitlands Outer/MAB, adjacent to a long, intermediate sandy beach. Chitons, usually not recorded at sandy beaches, were found at three platform sites, occurring in greater abundance at Hougham Park East/HPE than other molluscs.

Each major taxon exhibited a pattern of high numerical dominance by few species (Table 27) that accounted for 70% or more of its total abundance. The higher degree of site-site variability in major taxa is attributable to variability in species abundance. Oligochaetes were not identified to species; genera shown in Table 27 were the only ones recorded. All mysids found belonged to one species, *Gastrosaccus psammodytes*.

The low abundance of some genera that often reach high numbers in sandy beaches, e.g. *Donax, Bullia* and *Gastrosaccus*, was noteworthy and was probably due to sub-optimal environmental conditions for these taxa. A number of taxa did not usually appear at sandy beaches, e.g. *Acanthochiton, Zygomaera, Paramoera, Barbatia*, but were known from the rock surfaces, macroalgal turfs or sandy substrata at rocky shores.

8.3.2.5 Abundance of macrofaunal taxa in sediment per physical mixed substrate shore type

Polychaetes were the numerical dominants (> 50% of individuals) in all configuration types and reached highest abundance at low platform sites (Figure 62), although not significantly so (Kruskal-Wallis ANOVA: Polychaetes: \( H = 5.570, p = 0.134, N = 4, 20 \)). Isopods contributed more to total abundance at high platforms than other configurations, but the difference was not significant for \( p < 0.05 \) (Kruskal-Wallis ANOVA: Isopods: \( H = 7.189, p = 0.066, N = 4, 20 \)).

Amphipod abundance was highly variable, reaching lowest abundance at high platform sites and greatest at low ridge sites, though differences were not statistically significant (Kruskal-Wallis ANOVA: Amphipods: \( H = 1.581, p = 0.663, N = 4, 20 \)). Oligochaetes, insects, nemertines, gastropods and mysids were much less abundant than polychaetes, isopods and amphipods, with little variation from one mixed shore configuration type to the next (Kruskal-Wallis ANOVA: Oligochaetes: \( H = 3.442, p = 0.328, N = 4, 20 \); Insects: \( H = 2.812, p = 0.421, N = 4, 20 \); Gastropods: \( H = 2.656, p = 0.447, N = 4, 20 \); Nemertines: \( H = 1.070, p = 0.784, N = 4, 20 \); Mysids: \( H = 3.858, p = 0.277, N = 4, 20 \)).
Table 26. Abundance (ind m⁻¹) of major macrofaunal taxa in sediment at each study site. Site codes are explained in Table 3, Chapter 4.

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<tr>
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<th>KNB</th>
<th>CRW</th>
<th>MAA</th>
<th>MAB</th>
<th>BCN</th>
<th>BRK</th>
<th>ASB</th>
<th>KME</th>
<th>PDB</th>
<th>PBE</th>
<th>TST</th>
<th>HPW</th>
<th>HPE</th>
<th>CRE</th>
<th>CNR</th>
<th>MLS</th>
<th>HWD</th>
<th>MPB</th>
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Table 27. Density (ind m$^{-2}$) of most abundant species of dominant taxa in sediment.

| Taxon                          | WLW | AVA | KNB | CRW | MAA | MAB | BCN | BRK | ASB | KME | PDB | PBE | TST | HPW | HPE | CRE | CNR | MLS | HWD | MPB |
|-------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| **Amphipoda**                |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Paramoera capensis           | 0   | 0   | 14  | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 3   | 5   | 0   |
| Talorchestia spp             | 1   | 0   | 12  | 1   | 2   | 0   | 0   | 0   | 0   | 1   | 2   | 0   | 0   | 0   | 0   | 2   | 0   | 0   | 0   | 0   |
| Urothoe spp                  | 0   | 1   | 0   | 1   | 1   | 12  | 3   | 107 | 0   | 0   | 13  | 1   | 0   | 0   | 1   | 30  | 0   | 41  | 5   | 1   |
| Zygomaera emarginata         | 0   | 0   | 98  | 0   | 0   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| **Isopoda**                  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Eurydice spp                 | 0   | 5   | 0   | 15  | 8   | 12  | 12  | 4   | 0   | 6   | 6   | 10  | 9   | 0   | 4   | 3   | 1   | 5   | 13  | 16  |
| Excirolana latipes           | 0   | 0   | 45  | 5   | 2   | 1   | 1   | 0   | 1   | 1   | 2   | 0   | 1   | 0   | 4   | 0   | 1   | 0   | 3   | 2   |
| Excirolana natalensis        | 0   | 0   | 35  | 1   | 3   | 10  | 0   | 1   | 0   | 2   | 0   | 0   | 6   | 2   | 2   | 0   | 1   | 0   | 1   | 1   |
| Exosphaeroma spp             | 18  | 8   | 0   | 2   | 6   | 6   | 64  | 0   | 4   | 1   | 0   | 36  | 37  | 131 | 8   | 0   | 3   | 7   | 0   |
| **Mollusca**                 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Acanthochitona garnoti       | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 2   | 31  | 0   | 0   | 1   | 0   | 0   |
| Akera soluta                 | 0   | 0   | 7   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 2   | 1   | 0   | 0   | 0   | 0   | 0   |
| Barbatia obliquata           | 0   | 2   | 2   | 0   | 4   | 3   | 0   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 6   | 0   | 0   | 1   | 1   | 0   |
| Bullia rhodostoma            | 0   | 0   | 0   | 2   | 1   | 2   | 0   | 0   | 0   | 2   | 1   | 2   | 0   | 1   | 0   | 1   | 0   | 5   | 1   |
| Donax burnupi                | 0   | 0   | 0   | 4   | 8   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 1   | 0   | 0   |
| **Polychaeta**               |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Notomastus aberans           | 1   | 10  | 0   | 2   | 0   | 0   | 4   | 18  | 0   | 0   | 1   | 2   | 1   | 0   | 0   | 0   | 0   | 4   | 92  | 3   |
| Polygordius spp              | 0   | 6   | 474 | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 2   | 0   | 0   | 339 | 0   | 0   | 0   | 27  | 0   | 0   |
| Scololepis squamata          | 0   | 103 | 0   | 1   | 0   | 0   | 11  | 61  | 0   | 0   | 19  | 9   | 1   | 0   | 107 | 1   | 7   | 25  | 2   |
| Scoloplos spp                | 0   | 26  | 1   | 5   | 13  | 2   | 2   | 46  | 2   | 3   | 23  | 1   | 80  | 4   | 0   | 23  | 9   | 26  | 6   | 0   |
| **Insecta**                  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Bledius spp                  | 0   | 0   | 32  | 0   | 5   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| Formicidae spp               | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 1   | 0   | 5   | 0   | 5   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 2   |
| **Oligochaeta**              |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Enchytraeidae sp             | 0   | 0   | 13  | 0   | 0   | 0   | 0   | 1   | 0   | 0   | 8   | 0   | 0   | 0   | 22  | 0   | 1   | 0   | 0   | 0   |
| Marionina spp                | 82  | 3   | 85  | 0   | 46  | 0   | 0   | 0   | 0   | 1   | 0   | 1   | 1   | 10  | 4   | 0   | 0   | 1   | 84  |

184
Figure 62. The 10 most abundant macrofaunal taxa at sites grouped according to mixed substrate shore configurations. Data labels provide mean abundance (ind m\(^{-1}\)) and mean % of total abundance.
Bivalves and chitons were absent or rare at low ridge and low platform sites, giving significantly lower abundance there compared to high ridge and high platform sites (Kruskal-Wallis ANOVA: Bivalves: \( H = 7.881, p = 0.048, N = 4, 20 \); Kruskal-Wallis ANOVA: Chitons: \( H = 8.738, p = 0.033, N = 4, 20 \); but see post hoc tests in Table 28).

Polychaetes and isopods were significantly more abundant at high ridge sites (Table 29) than only chitons (Kruskal-Wallis ANOVA: High ridges: \( H = 27.681, p = 0.001, N = 10, 60 \)). At the low ridge sites bivalves, chitons and oligochaetes were significantly less abundant than other taxa (Kruskal-Wallis ANOVA: Low ridges: \( H = 36.956, p < 0.001, N = 10, 60 \)) and at low platform sites the bivalves, chitons and mysids were significantly less numerous than other taxa (Kruskal-Wallis ANOVA: Low platform: \( H = 34.882, p = 0.001, N = 10, 50 \)). The same could not be shown for insects and mysids relative to other taxa at high platform sites (Kruskal-Wallis ANOVA: High platform: \( H = 19.068, p = 0.024, N = 10, 30 \)).

8.3.2.6 Abundance of macrofaunal taxa in sediment per biotic mixed substrate shore type

Polychaetes were numerical dominants in the sediment of biotic types B and C (Figure 63) and co-dominant with isopods in biotic type A. In biotic type C, polychaetes reached much higher abundance relative to the other taxa, while the abundance of isopods and polychaetes in biotic type B exhibited an intermediate trend to biotic types A and C. Abundance of different taxa changed little relative to each other and showed little variation between biotic mixed substrate shore types (Kruskal-Wallis ANOVA: Polychaetes: \( H = 1.571, p = 0.456, N = 3, 20 \); Isopods: \( H = 0.094, p = 0.954, N = 3, 20 \); Amphipods: \( H = 1.465, p = 0.480, N = 3, 20 \); Oligochaetes: \( H = 0.813, p = 0.665, N = 3, 20 \); Chitons: \( H = 1.041, p = 0.594, N = 3, 20 \); Insects: \( H = 3.120, p = 0.210, N = 3, 20 \); Gastropods: \( H = 3.141, p = 0.207, N = 3, 20 \); Bivalves: \( H = 1.131, p = 0.568, N = 3, 20 \); Nemertines: \( H = 3.060, p = 0.216, N = 3, 20 \); Mysids: \( H = 3.636, p = 0.162, N = 3, 20 \)).

Table 28. Results of post hoc test for significant differences in abundance of bivalves and chitons at sites grouped according to different shore configuration types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at \( p < 0.05 \).

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Table 29. Results of post hoc statistical tests for significant differences between abundance of major sediment macrofaunal taxa with sites grouped according to configurations. Multiple Comparisons of mean ranks: p values (2-tailed). For significance at \( p < 0.05 \), bold italicized p-values. For significance at \( p < 0.10 \), italicized p-values. Pol = polychaetes, Iso = isopods, Amp= amphipods, Oli= oligochaetes, Ins = hexapods, Gas = gastropods, Biv = bivalves, Chi = chitons, Nem = nemertines, Mys= mysids. 1 h/s = high ridges, 1 m/s = low ridges, 2 h/s = high platform, 2 m/s = low platform.

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Figure 63. The 10 most abundant macrofaunal taxa in the mixed substrate shore biotic types. Data labels provide mean abundance (ind m\(^{-1}\)) and mean % of total abundance. Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs.
In Biotic type A (Table 30), chitons and nemertines were much less abundant than most other taxa (Kruskal-Wallis ANOVA: Biotic type A: $H = 24.114$, $p = 0.004$, $N = 10, 50$). In Biotic type B chitons and insects were significantly fewer in number than most other taxa (Kruskal-Wallis ANOVA: Biotic type B: $H = 28.334$, $p = 0.001$, $N = 10, 50$) and in Biotic type C, most other taxa were significantly less numerous than polychaetes, isopods and amphipods (Kruskal-Wallis ANOVA: Biotic type C: $H = 53.987$, $p < 0.001$, $N = 10, 100$).

Table 30. Results of post hoc statistical tests for significant differences between abundance of major sediment macrofaunal taxa with sites grouped according to mixed substrate shore biotic types (A, B and C). Multiple Comparisons of mean ranks: $p$ values (2-tailed). For significance at $p < 0.05$, bold italicized $p$-values. For significance at $p < 0.10$, italicized $p$-values. Pol = polychaetes, Iso = isopods, Amp= amphipods, Oli= oligochaetes, Ins = hexapods, Gas = gastropods, Biv = bivalves, Chi = chitons, Nem = nemertines, Mys= mysids. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

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189
8.3.2.7 Abundance and density of intertidal gastropods (motile macrofauna) on hard substrate

Littorinids were present at all study sites and consistently the most abundant gastropods (Figure 64), exceeding the numbers of other gastropods by two or three orders of magnitude. The second most abundant gastropod types were the limpets (patellid and siphonariid) and they usually outnumbered the remaining gastropod types. Polyplacophora (chitons), present in very low numbers, were seen in samples at most sites. At the low ridge and low platform sites where the rock surfaces were more often sprinkled by sand or covered by patches of sand, siphonariid abundance was higher than at high ridge and high platform sites where the probability of complete sand-inundation was reduced. Siphonariid limpets were generally present in larger numbers than patellid limpets, but at sites with more high elevation rock and/or less sand-inundation of rock surfaces the order was reversed. Littorinids, siphonariid limpets and patellid limpets were among the ten most abundant gastropod species at every study site (Table 31).

8.3.2.8 Cover-abundance of macroalgae per site

The cover-abundance of Rhodophyta, Chlorophyta and Phaeophyta, percentage of bare rock and area occupied by sessile macrofauna varied widely from site to site (Figure 65). Percentage cover by macroalgae ranged between 30% and 140% with a mean of 80% ± 7% cover-abundance. Rhodophyta dominated rock surfaces at most study sites, attaining cover abundance values from just under 25% to over 120%, with a mean percentage cover-abundance of 70% ± 7%. Percentage cover of Chlorophyta ranged from 2% to 30%, with a mean percentage cover-abundance of 9% ± 1.4%, and occurred as epiphytes of coralline algae, pioneers on newly exposed surfaces and established swards of Caulerpa on sand-inundated rock. Phaeophyta, though present at every site, never attained cover values above 6% and had a mean cover-abundance of about 1% ± 0.3%.

At sites with a limited extent of intertidal rock, total macroalgal abundance, and rhodophycean abundance in particular, was reduced. The highest percentages of bare rock were recorded at sites with much elevated rock surface, i.e. the high ridge site category. Two sites in the low ridge site category (BCN/Beacon Rock and BRK/Bird Rock) which, unlike others in the same category, had much bare rock surface, each had a tall shore normal ridge at the spring low tide mark. Two other sites with a high proportion of bare rock surface, PBE (Pollock North) in the low ridge group and CRW (Cape Recife West) in the high ridge group, both had beach erosion events a few days before sampling during which bed rock and beach lag was uncovered.
Figure 64. Gastropod abundance (ind m$^{-1}$ of integrated transect) and density (ind m$^{-2}$ of integrated transect). Littorinid numbers are plotted on the secondary y-axis. Sites are arranged according to site configuration: high ridges (WLW – MAB), low ridges (BCN – PBE), high platform (TST – HPE), low platform (CRE – MPB). Site codes are explained in Table 3 of Chapter 4.
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Table 31. The ten most abundant gastropod species per site. Species are arranged according to decreasing abundance (ind m⁻¹ of integrated transect). Taxon codes are explained in Addendum 4.
Figure 65. Cover-abundance of macroalgae and macrofauna as well as bare area on the rock substrate as a percentage of an integrated site transect. Macroalgal cover-abundance over 100% is due to inclusion of epiphytic algae in total cover-abundance. Sites are arranged according to site configuration: high ridge sites: WLW – MAB; low ridge sites: BCN – PBE; high platform sites: TST – HPE; low platform sites: CRE – MPB. Site codes are explained in Table 3 of Chapter 4.
The most abundant macroalgal species (Table 32) were all red seaweeds and were generally species that were abundant in the upper and lower turf assemblages that occupied a large intertidal area at most sites. Two coralline species, *Arthrocardia flabellata* and *A. filicula* were often the most abundant. Both were prominent members of short midlittoral algal turfs and reached highest abundance in sheltered midlittoral conditions without high sand cover. Species of *Polysiphonia* were among the more abundant, but never among the dominant species and, from its occurrence, appeared to have a wider range of tolerance for the degree of wave action in midlittoral reaches than the coralline dominants.

Due to the limited extent of the infralittoral fringe, macroalgae that favour those conditions were never among the dominants, with the exception of sand and wave-tolerant *Caulerpa filiformis* and *Hypnea spicifera*, which reached higher abundance at sites offering the conditions conducive to their establishment and persistence, e.g. Hougham Park West (HPW) and East (HPE), Cape Recife West (CRW), Kleinemonde East (KME).

8.3.2.9 Cover-abundance of sessile macrofauna on rock surfaces per site

Percentage cover by macrofauna varied from 4% to 40%, averaging 19.4% ± 2.29% per site (Figure 66). The total extent of sessile macrofauna across the intertidal was closely tied up with the amount of available rock at suitable elevations. Sites with a limited rock component as well as those with a smaller proportion of steeply angled intertidal rock substrate and/or lower wave action, i.e. those with high or low elevation platforms or only low elevation ridges, had a much lower mean abundance of sessile rock macrofauna than those with tall wave exposed rock faces, i.e. high ridge sites.

Cirripedia (barnacle species *Chthamalus dentatus*, *Tetraclita serrata* and *Octomeris angulosa*) were the most abundant sessile filter-feeders (Figure 66, Table 32) and had a very variable distribution and extent, ranging in cover-abundance from 1% (at Cannon Rocks/CNR) to 24% (at Beacon Rock/BCN) with an average cover-abundance of 9% ± 1.62 % per site. Cirripedia were more broadly distributed across the intertidal rock than any of the other sessile taxa which would have contributed to their cover-abundance values.

Bivalves and poriferans each occupied up to about 15% of rock area per site. The dominant bivalve, *Perna perna*, mostly limited to elevated positions in the low midlittoral, attained higher abundance at sites with much wave-exposed rock.

Porifera were restricted to low elevation rock surfaces in the mid to low intertidal and subtidal areas. At sites with much sheltered low midtidal rock surfaces (Table 32) not prone to sand-inundation, the encrusting sponge *Hymeniacedon perlevis* had increased cover. Average
Figure 66. Cover-abundance (% cover) of sessile macrofauna on rock substrate at each study site. Sites are arranged according to site configuration: high ridge sites (WLW – MAB), low ridge sites (BCN – PBE), high platform sites (TST – HPE), low platform sites (CRE – MPB). Site codes are explained in Table 3 of Chapter 4.
Table 32. The most abundant species of macroalgae and sessile macrofauna at each site. Species are arranged according to decreasing abundance (percentage cover referenced to a single integrated transect per site). Those given in bold print give a cumulative 75% of estimated cover-abundance of rock substrate per site. The remaining species listed contribute approximately an additional 20%. The mixed substrate shore biotic type code (A, B or C) as well as the mixed substrate shore configuration code is provided with the site code. Configuration legend: 1 h/s = high ridge sites, 1 m/s = low ridge sites, 2 h/s = high platform sites, 2 m/s = low platform sites. Biotic type legend: Biotic type A = *Jania-Corallina-Polysiphonia* turfs, Biotic type B = *Polysiphonia-Tayloriella-Caulacanthus* turfs, Biotic type C = *Arthrocardia-Laurencia* turfs. Taxon codes are explained in Addenda 3 and 4. Site codes are given in Table 3, Chapter 4.

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Table 32 (cont.). The most abundant species of macroalgae and sessile macrofauna at each site. Species are arranged according to decreasing abundance (percentage cover referenced to a single integrated transect per site). Those given in bold print give a cumulative 75% of estimated cover-abundance of rock substrate per site. The remaining species listed contribute approximately an additional 20%. The mixed substrate shore biotic type code (A, B or C) as well as the mixed substrate shore configuration code is provided with the site code. Configuration legend: 1 h/s = high ridge sites, 1 m/s = low ridge sites, 2 h/s = high platform sites, 2 m/s = low platform sites. Biotic type legend: Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs. Taxon codes are explained in Addenda 3 and 4. Site codes are given in Table 3, Chapter 4.

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Table 32 (cont.). The most abundant species of macroalgae and sessile macrofauna at each site. Species are arranged according to decreasing abundance (percentage cover referenced to a single integrated transect per site). Those given in bold print give a cumulative 75% of estimated cover-abundance of rock substrate per site. The remaining species listed contribute approximately an additional 20%. The mixed substrate shore biotic type code (A, B or C) as well as the mixed substrate shore configuration code is provided with the site code.

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</tr>
<tr>
<td>Chth_den 0.50</td>
<td>Pter_clo 0.59</td>
<td>Caul_ust 0.30</td>
<td>Tetr_ser 0.61</td>
<td>Cera_are 0.35</td>
<td>Chon_tee 0.97</td>
<td>Hild_lec 0.74</td>
<td>Giga_min 0.08</td>
</tr>
<tr>
<td>Spon_yen 0.47</td>
<td>Bld_min 0.53</td>
<td>Hyme_per 0.25</td>
<td>Clio_cel 0.49</td>
<td>Chyl_cap 0.35</td>
<td>Caul_zey 0.96</td>
<td>Octo_ang 0.73</td>
<td>Cora_off 0.07</td>
</tr>
<tr>
<td>Caul_fil 0.41</td>
<td>Peta_fas 0.37</td>
<td>Dict_lig 0.23</td>
<td>Acro_acr 0.21</td>
<td>Codi_dut 0.35</td>
<td>Jani_adh 0.92</td>
<td>Poly_sco 0.63</td>
<td>Arth_car 0.06</td>
</tr>
<tr>
<td>Poly_sp 0.37</td>
<td>Ptil_pol 0.34</td>
<td>Jani_adh 0.22</td>
<td>Clad_spp 0.20</td>
<td>Caul_fil 0.28</td>
<td>Cera_are 0.84</td>
<td>Pyur_sto 0.60</td>
<td>Caul_fil 0.06</td>
</tr>
<tr>
<td>Octo_ang 0.32</td>
<td>Dict_lig 0.34</td>
<td>Ulva_sp 0.22</td>
<td>Lept_tier 0.18</td>
<td>Giga_min 0.15</td>
<td>Hete_are 0.84</td>
<td>Clio_cel 0.52</td>
<td>Arth_dut 0.06</td>
</tr>
<tr>
<td>Clad_spp 0.29</td>
<td>Octo_ang 0.30</td>
<td>Giga_min 0.19</td>
<td>Iyen_ste 0.13</td>
<td>Hild_lec 0.14</td>
<td>Jani_ver 0.84</td>
<td>Tetr_ser 0.43</td>
<td>Hild_lec 0.05</td>
</tr>
<tr>
<td>Hypn_spi 0.27</td>
<td>Spon_yen 0.30</td>
<td>Ulva_ri 0.18</td>
<td>Arth_dut 0.11</td>
<td>Gunn_cap 0.12</td>
<td>Laur_pum 0.74</td>
<td>Spir_kra 0.43</td>
<td>Pter_cae 0.04</td>
</tr>
</tbody>
</table>
bivalve cover in samples was 4.14% ± 1.09% and for sponges 4.62% ± 1.27%. Polychaetes maintained low abundance (under 3% cover) though present at most sites. Ascidiacea, Anthozoa and Bryozoa were sparsely distributed and rarely detected, attaining combined cover-abundance values below 1% per site. In the case of Ascideacea undersampling the infratidal fringe due to unfavourable wave conditions played a role.

8.3.2.10 Cover-abundance of macroalgae per physical shore type

Phaeophyta were poorly represented and highly variable in occurrence compared to other algal divisions. These algae were significantly more abundant at high platform shores (Table 33) than low ridge shores (Kruskal-Wallis ANOVA: Phaeophyta: H = 8.841, p = 0.031, N = 4, 20). The Rhodophyta reached the highest cover at low platform sites (Figure 67), where they formed extensive mid-to-low intertidal algal turfs. Relatively high abundance of Chlorophyta at high platform sites can be linked to Caulerpa filiformis abundance combined with high cover by pioneer green algae on newly colonized rock.

Cover-abundance of the other two macroalgal types as well as the sessile macrofauna and the extent of bare rock did not change significantly from one physical mixed substrate shore type to the next (Chlorophyta: H = 4.005, p = 0.260, N = 4, 20; Rhodophyta: H = 7.105, p = 0.068, N = 4, 20; Sessile macrofauna: H = 4.762, p = 0.190, N = 4, 20; Bare rock: H = 6.891, p = 0.075, N = 4, 20).

Table 33. Results of post hoc test for significant differences in abundance of Phaeophyta at sites grouped according to different shore configuration types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values.

<table>
<thead>
<tr>
<th>Phaeophyta:</th>
<th>High ridges</th>
<th>Low ridges</th>
<th>High platform</th>
<th>Low platform</th>
</tr>
</thead>
<tbody>
<tr>
<td>High ridges</td>
<td>-</td>
<td>1.000</td>
<td>0.252</td>
<td>0.333</td>
</tr>
<tr>
<td>Low ridges</td>
<td>-</td>
<td>-</td>
<td><strong>0.048</strong></td>
<td>0.180</td>
</tr>
<tr>
<td>High platform</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.000</td>
</tr>
</tbody>
</table>

8.3.2.11 Cover-abundance of sessile macrofauna on rock surfaces per physical shore type

Barnacles were clearly the most prominent sessile animals at ridge sites, reaching their highest abundance at high ridge sites, but were much reduced in number and extent at platform sites (Figure 68). Mussels covered a greater surface area at high ridge and high platform sites with sufficient suitably elevated rock in the lower intertidal than at low ridge and low platform sites with little elevated surface. Sponges, on the other hand, had higher relative cover-abundance at sites with much low wave-protected rock surface, such as
Willows Beach (WLW) and Avalanche (AVA), both high ridge sites, and Cape Recife East (CRE), Miller’s Beach (MLS) and Humewood (HWD), all low platform sites, than those with wave-exposed rock surfaces, whether platforms, e.g. Three Sisters (TST), or ridges, e.g. Kleinemonde East (KME), where their cover-abundance was greatly reduced.

Cover-abundance of bivalves differed significantly between physical mixed substrate shore types (Kruskal-Wallis ANOVA: Bivalves: $H = 8.333$, $p = 0.032$, $N = 4, 20$; Table 34). Other sessile macrofauna had similar cover-abundance levels regardless of shore configuration (Kruskal-Wallis ANOVA: Polychaetes: $H = 1.799$, $p = 0.615$, $N = 4, 20$; Cirripedes: $H = 5.303$, $p = 0.150$, $N = 4, 20$; Porifera: $H = 5.071$, $p = 0.166$, $N = 4, 20$).

Table 34. Results of post hoc test for significant differences in abundance of bivalves at sites grouped according to different shore configuration types. Multiple Comparisons of mean ranks: $p$ values (2-tailed). Tests are significant at $p < 0.05$. Significant differences are indicated by bold italicized $p$-values.

<table>
<thead>
<tr>
<th>Bivalves:</th>
<th>High ridges</th>
<th>Low ridges</th>
<th>High platform</th>
<th>Low platform</th>
</tr>
</thead>
<tbody>
<tr>
<td>High ridges</td>
<td></td>
<td>0.859</td>
<td>1.000</td>
<td>0.682</td>
</tr>
<tr>
<td>Low ridges</td>
<td></td>
<td></td>
<td>0.100</td>
<td>1.000</td>
</tr>
<tr>
<td>High platform</td>
<td></td>
<td></td>
<td></td>
<td>0.081</td>
</tr>
</tbody>
</table>

8.3.2.12 Cover-abundance of macroalgae per biotic shore type

Biotic type A and biotic type C were highly dominated by red algae (Figure 69), whereas in Biotic type B, the sessile macrofauna occupied more area and the rhodophytes proportionally less. This was significantly more than in the communities of biotic type C (Kruskal-Wallis ANOVA: Sessile macrofauna: $H = 11.704$, $p = 0.002$, $N = 3, 20$; Table 35).

The amount of bare rock (uncolonized or kept ‘bare’ by grazing limpets) was variable. While phaeophytes were proportionally poorly represented in all three the biotic types, their highest relative abundance was reached at sites of biotic groups A and C. These algae were present in extremely low abundance in the biotic type B. Variations in the cover-abundance of Phaeophyta, Chlorophyta and Rhodophyta, as well as the amount of bare rock were not significant (Kruskal-Wallis ANOVA: Phaeophyta: $H = 4.322$, $p = 0.115$, $N = 3, 20$; Chlorophyta: $H = 2.714$, $p = 0.260$, $N = 3, 20$; Rhodophyta: $H = 1.788$, $p = 0.408$, $N = 3, 20$; Bare rock: $H = 2.174$, $p = 0.337$, $N = 3, 20$).
Figure 67. The mean percentage cover of macroalgae, sessile fauna and bare rock at sites grouped according to mixed substrate shore configurations.
Figure 68. The mean percentage cover (first data label) and percentage contribution to total sessile macrofauna cover (second data label) of dominant sessile macrofauna (Cirripedes, Bivalves and Porifera) at sites grouped according to mixed substrate shore configurations.
Table 3. Results of post hoc test for significant differences in abundance of sessile macrofauna at sites grouped according to different biotic mixed substrate shore types. Multiple Comparisons of mean ranks: p values (2-tailed). Tests are significant at p < 0.05. Significant differences are indicated by bold italicized p-values. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.

<table>
<thead>
<tr>
<th>Sessile macrofauna</th>
<th>Biotic type A</th>
<th>Biotic type B</th>
<th>Biotic type C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biotic type A</td>
<td>-</td>
<td>0.002</td>
<td>0.440</td>
</tr>
<tr>
<td>Biotic type B</td>
<td>-</td>
<td>-</td>
<td>0.044</td>
</tr>
<tr>
<td>Biotic type C</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

8.3.2.13 Cover-abundance of sessile macrofauna on rock surfaces per biotic shore type

Cirripedes were the most abundant in all three biotic types, reaching highest actual cover in biotic type B (Figure 70). Bivalves occupied roughly the same relative proportion of area in all three biotic types. Cirripedes and Porifera showed opposite trends in relative cover-abundance: cirripedes being dominant in biotic type A and poriferans in biotic type C.

Changes in cover-abundance of sessile macrofaunal taxa from one mixed substrate shore biotic type to the next were not significant (Kruskal-Wallis ANOVA: Polychaetes: $H = 0.688$, $p = 0.708$, $N = 3, 20$; Bivalves: $H = 2.794$, $p = 0.226$, $N = 3, 20$; Cirripedes: $H = 4.551$, $p = 0.102$, $N = 3, 20$; Porifera: $H = 2.448$, $p = 0.294$, $N = 3, 20$).
Figure 69. The mean percentage cover of macroalgae, sessile fauna and bare rock in mixed substrate shore biotic types. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.
Figure 70. The mean percentage cover (first data label) and percentage contribution to total sessile macrofauna cover (second data label) of dominant sessile macrofauna (Cirripedes, Bivalves and Porifera) in mixed substrate shore biotic types. Biotic type A = Jania-Corallina-Polysiphonia turfs, Biotic type B = Polysiphonia-Tayloriella-Caulacanthus turfs, Biotic type C = Arthrocardia-Laurencia turfs.
CHAPTER 9  Macrobenthic assemblages of intertidal zones

9.1 Introduction

Biotic intertidal zonation is a phenomenon of both rocky and sandy shores (Brown and McLachlan 1990), but is given expression differently, perhaps because of the contrasting manner in which hard and soft substrata interact with incident waves. A firm, hard surface, such as rock, would generally resist the force exerted on it by waves and reflect wave energy (Sunamura 1992). Sediment, on the other hand, is largely malleable, absorbing wave forces, allowing water to be pumped through it and the sediment itself may also become entrained and moved elsewhere by passing waves, resulting in the changeable shore profiles observed at sandy beaches (Short 1999). Bare rock surfaces generally do not retain water, whereas sediments do. A cross-shore moisture gradient is set up in beach deposits, linked to the water table level (Brown and McLachlan 1990; McLachlan and Jaramillo 1995), as well as across the rocky intertidal substrate, in this instance linked to rock surface elevation. On rock substrate, the moisture gradient is more complex as rock topography modifies conditions through the added factors of aspect, slope and surface relief, to name a few (Norton 1985).

The phenomenon of zonation on rocky shores was the topic of very early studies and global patterns have been described in detail, e.g. Stephenson and Stephenson (1972). Biotic zones are not that obvious in sediment and there is still no agreement on a universal system of zonation (Brown and McLachlan 1990; Field and Griffiths 1991; McLachlan and Jaramillo 1995; Giménez and Yannicelli 1997; Brown 2001). Despite patchy distribution patterns and local variations in the floral and faunal composition of intertidal biota, zonation patterns on the shores of the world do exhibit great consistency and are regarded as indicators of particular environmental conditions (e.g. Ballantine 1961; Pollock and Hummon 1971; Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Giménez and Yannicelli 1997; Brown 2001; Bayed 2003).

Tidal periodicity is not the leading factor in bringing about the conditions that prevail at different elevations between tidemarks, as patterns of zonation are also seen on tideless shores, but tidal amplitude plays a role in the horizontal and vertical extent of the zones (Stephenson and Stephenson 1972; Russell 1991; Giménez and Yannicelli 1997). Near-shore and intertidal topography, combined with the degree of wave action at the shore, modify the effects of tidal reach and, in turn, the distribution ranges and patterns of the intertidal biota (Lobban et al. 1985; Norton 1985; Brown and McLachlan 1990; Russell 1991).
On a rocky shore the intertidal zone is subject to strong environmental gradients over a very short distance (Norton 1985; Russell 1991). Light conditions, temperature and moisture levels change quite markedly moving from the spring low tide mark to the spring high tide mark, where physical conditions ultimately reign supreme as a structuring agency of biotic assemblages (Hawkins and Hartnoll 1985; Russell 1991).

On beaches, too, there is a progressive change from predominantly marine conditions near the lower end of the shore to more terrestrial conditions as one approaches the drift line, that sets up a gradient of conditions to which the benthic infauna respond (Eltringham 1971; Field and Griffiths 1991; Brown 2001). Macrofauna in sandy beaches distribute themselves in response to the spatial and temporal moisture regimes imposed by tide and beach dimensions resulting in two basic assemblages, i.e. the high shore air-breathing and low-shore water-breathing groups (see Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brown 2000). Beach infauna are, however, notoriously patchy in distribution, both spatially and temporally, which further complicates detection of zonation patterns (Brazeiro 1999; Schoeman et al. 2005).

The question of whether there are universally defined associations in sandy beaches is still not settled. The recognition of assemblages revealed by sampling is of necessity a subjective process if done by means of kite diagrams. Cluster analysis flags up groupings, but cannot show whether a group arises from a homogenous assemblage or a random combination of overlapping boundaries (Brazeiro 1999). The middle zone is particularly problematic in this way, as it may be interpreted either as a boundary area for biota primarily associated with the upper or lower shore zones or as an assemblage with a distinct and constant character. This issue was highlighted by Brazeiro (1999) who favoured the idea of a zone of overlap.

In spite of this, there should be some broad cross-shore trends linked to prevailing habitat conditions that can be trusted and form the basis of biotopes for beach infauna. On a mixed substrate shore the rock outcrops introduce topographic variation which locally modifies the overall moisture and wave gradient (Short 1999) and should influence the cross-shore distribution of biota (Brown et al.1991) in as much as it has been shown for subtidal sedimentary assemblages in the vicinity of submerged hard structures (Ambrose and Anderson 1990; Posey and Ambrose 1994; Barros et al. 2001).

The intertidal zones of South African rocky shores have been described in many authoritative texts, e.g. Stephenson and Stephenson (1972), Brown and Jarman (1978), Branch and Branch (1981). The consistency with which particular species occur in the same intertidal subzone or biotope around the coast can be taken as being indicative of an
environmental requirement by the organism and also a range of tolerance for conditions prevailing in that subzone (Connor et al. 1997). Biotopes have found application in the classification (e.g. Hill et al. 1998; Tittley and Neto 2000; Lombard et al. 2004) and long-term monitoring (e.g. Hill et al. 1998; Diez et al. 1999) of marine hard substrate communities.

9.2 Cross-shore trends in the numbers of species in sampling strata of sediment and hard substrate

9.2.1 Total and mean numbers of species per sampling stratum

There was a definite trend in the total numbers of species recorded from each sampling stratum in the sediment and on rock surfaces (Figure 71). The highest numbers of species were recorded from the infralittoral fringe samples of the rock surface (R8, R7) and sediment (S5), as well as the eulittoral algal turfs (R5, R3). The lowest total was recorded from a supralittoral fringe stratum (R0) on the rock surface.

The mean numbers of species in these sampling strata were much lower than the totals obtained as assemblages of these sites varied greatly in composition even though the numbers of species were not that variable. The mean number of species in the infralittoral fringe sampling strata (S5 and S4) of sediment exceeded that of the upper shore sampling strata by good measure (Kruskal-Wallis ANOVA: \( H = 40.130, p < 0.001, N = 6,120 \), post hoc by multiple comparisons, p values, Table 36). The mean species count in each of the eulittoral and infralittoral fringe sampling strata on the rock surface was appreciably higher than that of the Porphyra stratum of the supralittoral fringe; all but the infralittoral macroalgae comprised more species on average than the Afrolittorina stratum of the supralittoral fringe (Kruskal-Wallis ANOVA: \( H = 91.862, p < 0.001, N = 9,180 \), post hoc by multiple comparisons, p values, Table 37). There was also a significant difference in the mean number of species associated with the Perna stratum (higher) as compared to infralittoral fringe algae (Kruskal-Wallis ANOVA: \( H = 91.862, p < 0.001, N = 9,180 \), post hoc by multiple comparisons, p values, Table 37).

9.2.2 Total and mean numbers of macroalgal and macrofaunal species per sampling stratum on hard substrate

The contribution to the number of species in each hard substrate sampling stratum by macrofauna and macroalgae varied according to a pattern that appeared to be related to the intertidal elevation range of the particular sampling stratum (Figure 72). In the supralittoral fringe (R0 and R1) as well as elevated positions in the upper (R2) and mid- to low mid littoral (R4 and R6), more species of macrofauna were recorded than macroalgae. In the algal turfs (R3 and R5) of lower rock surfaces in the eulittoral zone, as well as in the sublittoral fringe
Figure 71. Total and mean (± 1 SE) number of species in sampling strata on rock and in sediment. S0 to S5 are sampling strata of the sediment. R0 to R8 are sampling strata of the rock surfaces. The stratum codes are explained in Table 4 (Chapter 4).

Figure 72. The mean number (± 1 SE) of macrofaunal and macroalgal species in each hard substrate sampling stratum.
(R7 and R8), a greater number of macroalgal than macrofaunal species were recorded on average. Significant differences were found between the mean numbers of macroalgal and macrofaunal taxa in all strata except for R0 and R3 (Mann-Whitney U-test. Table 38).

Table 36. Results of post hoc test for significant differences in the mean numbers of species in soft substrate sampling strata S0 to S5 of all sites. Multiple comparisons of mean ranks: p-values (2 tailed). Tests are significant for p < 0.05. Significant differences are indicated in bold italicized p-values.

<table>
<thead>
<tr>
<th></th>
<th>S0</th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
<th>S4</th>
<th>S5</th>
</tr>
</thead>
<tbody>
<tr>
<td>S0</td>
<td>1.000</td>
<td>1.000</td>
<td>0.444</td>
<td><strong>0.002</strong></td>
<td><strong>0.001</strong></td>
<td></td>
</tr>
<tr>
<td>S1</td>
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<td>1.000</td>
<td>0.035</td>
<td><strong>0.001</strong></td>
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<td></td>
</tr>
<tr>
<td>S2</td>
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<td>0.040</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>S3</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S4</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 37. Results of post hoc test for significant differences in the mean numbers of species in hard substrate sampling strata R0 to R8 of all sites. Multiple comparisons of mean ranks: p-values (2 tailed). Tests are significant for p < 0.05. Significant differences are indicated in bold italicized p-values.

<table>
<thead>
<tr>
<th></th>
<th>R0</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>R4</th>
<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
</tr>
</thead>
<tbody>
<tr>
<td>R0</td>
<td>1.000</td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td></td>
</tr>
<tr>
<td>R1</td>
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<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td>0.297</td>
<td></td>
</tr>
<tr>
<td>R2</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.524</td>
<td>1.000</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R3</td>
<td>1.000</td>
<td>1.000</td>
<td>0.580</td>
<td>1.000</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R4</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td><strong>0.191</strong></td>
<td></td>
<td></td>
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</tr>
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<td>R5</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.940</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 38. Results of statistical comparison of mean macroalgal and macrofaunal species richness in each rock substrate sampling stratum (R0 to R8) (n = 20). Mann-Whitney U-test. Results are significant at p < 0.05 for 2*1-sided p. Significant differences are indicated in bold italics.

<table>
<thead>
<tr>
<th>R0</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>R4</th>
<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>U</strong></td>
<td>166.0</td>
<td>34.5</td>
<td>40.5</td>
<td>134.0</td>
<td>55.0</td>
<td>92.0</td>
<td>51.0</td>
<td>113.5</td>
</tr>
<tr>
<td><strong>p</strong></td>
<td>0.369</td>
<td><strong>0.001</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.076</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.003</strong></td>
<td><strong>0.001</strong></td>
<td><strong>0.018</strong></td>
</tr>
</tbody>
</table>
9.3 Cross-shore trends in community composition and abundance

9.3.1 Sites of biotic type A (Jania-Corallina-Polysiphonia turfs)

9.3.1.1 Kleinemonde East (KME)

The cluster analysis (Figure 73A) indicated greatest similarity between the supralittoral fringe on rock (R0, R1) and macrobenthic assemblages of elevated midlittoral surfaces, the upper barnacle zone (R2) and Gelidium pristoides zone (R4). The grouping of the midlittoral algal turf (R3, R5) with the infralittoral fringe (R8) reflected the considerable degree of overlap in the cross-shore distribution of macroalgal taxa of these assemblages. Similarly, the assemblages of the cochlear zone (R7) and Perna perna zone (R6) had much in common. Unlike the rock surface assemblages, those of the sediment did not show a regular response to the environmental gradient: the only expected result being the greater degree of dissimilarity between the infralittoral sediment macrofauna close to the low tide swash line (S5) and the rest.

Sediment macrofauna abundance decreased from the low to high shore (Figure 73B) with polychaetes and crustaceans in roughly equal numbers. A polychaete, Gonadiopsis incerta, was most abundant, occupying the low shore, followed by Eurydice longicornis, a mid to high shore dominant, and Gastroscus psammodytes, abundant at the swashline. Talorchestia spp and Excirolana latipes occurred only on the high shore and Exosphaeroma hylecoetes on the midshore. Swashline species, for example, Gastroscus psammodytes, Exosphaeroma estuarium, Bullia rhodostoma, Lumbrineris heteropoda difficilis, L. tetraura, L. cavitrons, Pisionidens indica, Scoloplos johnstonei, were mostly absent from mid to highshore strata. Formicidae occurred at all strata except S5.

The supralittoral fringe on rock (Figure 73C) was truncated and Porphyra capensis occurred in low abundance in both the supralittoral fringe and upper barnacle zone (R2). The littorinid Afrolittorina knysnaensis, though numerically dominant, was less numerous than at other sites of this configuration and biotic type. Algae of the upper barnacle zone (R2) also comprised Ulva rigida, Leptophytum spp and Nothogenia erinacea (more common than P. capensis). Rhodomelopsis africana and Jania verrucosa dominated the midlittoral turf (R3 and R5), joined in lower midlittoral turf by Hypnea spicifera, the most abundant species of the infralittoral fringe. These three species together occupied nearly
Figure 73. KME, Kleinemonde East. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
80% of midlittoral and infralittoral surfaces. *Chylocladia capensis* was abundant in the lower midlittoral turf, *Leptophyton* spp in all midlittoral and low shore strata, and *Caulerpa filiformis* in the infralittoral fringe. *Gelidium pristoides* was widely distributed over strata on raised rock surfaces, at similar levels of abundance as at other sites with wave-exposed rock surfaces, found in conjunction with *Nothogenia erinacea, U. rigida, Leptophyton* spp, *Hildenbrandia lecannellieri, Polysiphonia incompta, Ralfsia verrucosa, Chylocladia capensis*.

The cochlear zone (Figure 73D) was well-developed with high abundance of *Spongitis yendoi, Gelidium micropterum* and other encrusting corallines, all of which suffered some overgrowth by infralittoral and lower midtidal turf species (*Rhodomelopsis africana, Hypnea spicifera, Chylocladia capensis, Caulerpa filiformis, Codium duthieae, Acrosorium acrospermum, Calithamnion stuposum*). The reefworm *Gunnaria capensis*, at least an order of magnitude more abundant than other sessile fauna, was widespread across the intertidal dominating upper rock surfaces. *Siphonaria concinna, S. serrata, Scutellastra granularis* and *Cymbula oculus* were widespread cross-shore. *Scutellastra cochlear* was confined to rock surfaces of the infralittoral fringe.

9.3.1.2 Hougham Park East (HPE)

According to the cluster analysis (Figure 74A), the supralittoral fringe (R1), which was strongly truncated, upper barnacle zone (R2) and upper algal turf (R3) formed an assemblage distinct from all others. Here, the remaining rock surface assemblages formed a diverse cluster which was also indicative of the considerable overlap between assemblages. The sediment macrofauna assemblages were similarly diverse: clusters suggest a bimodal distribution of important species (S1 with S3, S4 and S5), not a gradual transition along the intertidal gradient.

Macrofaunal abundance in sediment (Figure 74B) was greatest in the lower midlittoral (S3) and on the low shore (S4 and S5). Isopods, mainly *Exosphaeroma estuarium* and *Eurydice longicornis*, were numerical dominants: the former highly abundant with a midshore peak and the latter abundant on the low shore. *Exosphaeroma estuarium* and the polychaete *Caulleriella capensis* were numerical dominants in low midlittoral sediment which supported a diverse assemblage of macrofauna, i.e. crustaceans (*E. longicornis, Exciorolana latipes, Exciorolana natalensis* and *Tanaidae* sp1), molluscs (*Acanthochitona garnoti, Siphonaria concinna, Siphonaria* sp1, *Barbatia obliquata, Bullia digitalis, Akera soluta, Kellia rotunda*) and polychaetes (e.g. *Chaetzone setosa, Dodecaceria capensis*). *Exciorolana latipes*, distributed from the high to lower midlittoral zones, occurred with rocky shore amphipods *Jassa falcata* and *Aora anomala* in upper midshore sediment. *Talorchestia* spp, *Exciorolana latipes*
and *E. natalensis* as well as small numbers of isopod (*Lathrippa capensis*) and rocky shore amphipod (*Ischyrocerus anguipes, Aora anomala*) species were only seen in high shore sediment.

Except for *E. estuarium* and *E. longicornis*, low shore species did not appear above midtidal level. The rocky shore species *Acanthochitona garnoti* and *Syllis armillaris* were among the most abundant in the glassy zone (S4), though not confined to it, while *Pseudonereis variegata*, *Perioculodes longimanus*, *Barbatia obliquata* and *Nematoneiris unicornis* were among those only found in S4. *Exosphaeroma estuarium* and the polychaetes *Lumbrineris cavifrons* and *L. heteropoda difficilis* were numerical dominants at the lowtide swashline (S5) with *Syllis armillaris* and *E. longicornis*. Other common and abundant species noted in S5 included *Lysidice natalensis, Tanystylum brevipes, Trypanosyllis zebra, Tricola capensis* as well as *Corophium* sp1, *Tanaidae* sp and *Asellota* sp1, some of these also found at rocky shores. *Bullia digitalis* occurred in higher numbers in the midshore than low shore where it was found together with two other *Bullia* species, i.e. *B. pura* and *B. rhodostoma*.

A sparse turf community consisting of the turf-form of *Gelidium pristoides, Bostrychia intricata* and *Chaetomorpha aerea* occurred in stead of *Porphyra capensis* on supralittoral rock (Figure 74C). *Gelidium pristoides* was among the five most abundant algae at this site, extending its range widely across the midlittoral shore in the form of a low turf mixed with sand-tolerant turf-forming taxa like *Tayloriella tenebrosa, Arthrocardia flabellata* and *Leptophytum* spp. The infralittoral fringe formed over a broad area and the macroalgae of that zone were the most abundant. *Caulerpa filiformis* was the dominant species, extending into mid-tidal reaches, with *Hypnea spicifera* and *Corallina officinalis*, while another abundant alga, *Rhodomelopsis africana*, was limited to the lower reaches of the shore. *Spongites yendoi, Pterosiphonia cloiophylla, Plocamium corallorrhiza* and *Codium duthieae* occurred in the lower midtidal turf and infratidal fringe. The major algae of the cochlear zone, *S. yendoi* and *Gelidium micropterum* were found with both *Scutellastra cochlear* (R7) and *Perna perna* (R6).

Sessile filter-feeders were abundant (Figure 74C), dominated by the presence of *Octomeris angulosa, Perna perna* and *Chthamalus dentatus* on mid to lower intertidal surfaces: *O. angulosa* reached peak abundance with *G. pristoides, P. perna* did so in its own sampling stratum on the low shore and *C. dentatus* reached highest abundance in the high shore barnacle stratum (R2) and with *P. perna* on the low shore.
Figure 74. HPE, Hougham Park East. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
Hymeniacidon perlevis, Spirobranchus (Pomatoleios) kraussii, Gunnaria capensis and Choromytilus meridionalis were common on mid to low intertidal surfaces, but not among the dominant species.

Though the supralittoral fringe was reduced in vertical extent, Afrolittorina knysnaensis was still the most numerous gastropod (Figure 74D), with a cross-shore distribution from the supralittoral fringe onto midlittoral turf (R3). The other highly abundant gastropods were Siphonaria capensis, S. concinna, both occurring widely across the shore on sand-inundated rock, Scutellastra granularis, on elevated rock surfaces and A. africana in upper midlittoral reaches. S. cochlear was much reduced in abundance compared to sites with appreciable raised rock surface on the low shore, and its range extended shoreward from the usual position of the cochlear zone, apparently in competition with S. longicosta on lower intertidal surfaces. More individuals of S. cochlear occupied space among patches of P. perna than in the cochlear zone itself, but did not extend further up the shore.

9.3.1.3 Cannon Rocks (CNR)

The cluster analysis of this site (Figure 75A) revealed the great degree of similarity between rock surface assemblages, where only the infralittoral fringe (R8) and cochlear (R7) zones separated well from midshore strata. Beach macrofauna species separated into two distinct groupings representing the high shore and mid to low shore assemblages.

Macrofaunal abundance (Figure 75B) in sediment peaked close to the swashline (S5). Polychaetes were numerically dominant, particularly in low shore sediment. The most abundant macrofaunal species overall was Lumbrineris heteropoda difficilis. High shore sediment (S0 and S1) yielded insects not found elsewhere on the shore (Bledius spp, Abraeus sp., Telmatogoton sp.), as well as beach isopods (numerous Excirolana natalensis and a few E. latipes) and small numbers of aranaeoids (Amaerobioides africanus and Tanystylum brevipes). Iathrippa capensis and Telmatogoton minor were the only macrofauna species present in S2 samples, Eurydice longicornis was only found in lower mid shore (S3) samples together with low numbers of the amphipod Lysianassa ceratina, and Bullia rhodostoma occured in low numbers in both high and low shore samples. A diverse assemblage of species occurred with Lumbrineris heteropoda difficilis on the low shore in somewhat lower numbers. These comprised polychaetes (Pisionidens indica, Scoloplos johnstonei, Lumbrineris tetraura, Neanthes wileyi and Spio
filicornis), amphipods (Amaryllis macrophthalmal (endemic), Urothoe grimaldi, Guernea rhomba and Caprella danilevski) and isopods (Ischyromene huttoni and Anatanais gracilis) often seen at rocky shores.

On rock substratum, the supralittoral fringe was extremely truncated: no Porphyra capensis (R0) occurred and R1 was reduced to the extent that there was no substrate where littorinids alone were numerical dominants (Figure 75C and D). The entire rock surface was covered by algal growth, except where sessile fauna occupied space. Corallina officinalis was the most prevalent, together with Plocamium corallorhiza, Leptophytum spp, Hildenbrandia lecannellieri and Arthrocardia flabellata. The two encrusting species and A. flabellata were widespread across the shore, while the two larger dominants were for most part confined to lower midtidal turf and infralittoral fringe zones, the two most extensive assemblages. Caulerpa filiformis formed very visible patches on besanded rock surfaces at a lower midtidal to infralittoral fringe elevation. Slightly less abundant species associated with the above included Arthrocardia filicula, Polysiphonia incompta, Tayloriella tenebrosa and Plocamium beckeri. Gelidium pristoides (R4) was much reduced in abundance, occurring occasionally in the midlittoral as part of an algal turf dominated by small corallines. Algae of the cochlear zone (Spongites yendoi and Gelidium micropterum) were extremely poorly represented, suffering much overgrowth by infralittoral fringe and low turf algae. All sessile filter-feeders normally abundant on rocky shores were greatly reduced in extent at this site. Only Octomeris angulosa occurred in appreciable abundance on midlittoral rock surfaces. Other sessile forms occurred as small aggregates on midlittoral rock surfaces, mostly overgrown by algal turf.

Although the supralittoral fringe at this site was basically non-existent, Afrolittorina knysnaensis still persisted as the numerical dominant, though at much lower densities than at sites with taller rock surfaces (Figure 75D). The most abundant gastropods after A. knysnaensis were Siphonaria capensis, S. concinna, A. africana and Scutellastra granularis, all frequenting midlittoral rock substrate. Burnupena pubescens was abundant in the low midlittoral turf. The abundance of Scutellastra cochlear was severely suppressed, hardly reaching 10% of the density recorded at study sites with tall rock surfaces in the lower intertidal. S. cochlear occurred on the upper surfaces of small embedded boulders and in moist depressions towards the middle of the platform where no sand deposits were found.
Figure 75. CNR, Cannon Rocks. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
Cluster analysis of samples (Figure 76A) showed greater similarity between the truncated supralittoral fringe (R1) on rock and the midlittoral turfs, whereas the three strata associated with elevated rock surfaces (R2, R4 and R6) were more closely associated and had elements in common with the infralittoral strata (R7 and R8). The sediment macrofauna assemblages were not grouped according to a clear cross-shore trend, as the low and upper shore assemblages showed greatest similarity.

Total macrofaunal abundance (Figure 76B) in sediment was highest in the lower midlittoral. Crustacea (isopods) were the most abundant group with *Eurydice longicornis* the most abundant species. The wrackline samples were empty, but other high shore samples yielded low numbers of Formicidae and *Nerinides gilchrist*, a polychaete also found at the low tide swash. Insects were also found in the upper midlittoral, while lower midlittoral sediment had abundant *Eurydice longicornis* with *Excirolana latipes* and polychaete species (*Notomastus aberans, Scololepis squamata, Lumbrineris latreilli*). Low shore samples contained small numbers of *S. squamata, Nerinides gilchrist, E. longicornis, Jassa falcata, Tharyx filibranchia, Lineus sp, Parheteromastus tenuis, Urothoe serrulidactylis* and *Bullia rhodostoma*.

The low rock plate was very narrow at this site and upper intertidal zones (R0, R1 and R2) reduced. *Porphyra capensis* was not recorded and algae occurring with littorinids (R1) were characteristic of midlittoral turfs, i.e. *Arthrocardia filicula, Ophidocladus simplisciusculus, Pterocladella caespitosa* (Figure 76C). The 5 dominant algae were *Jania verrucosa, Arthrocardia flabellata, Leptophytum spp, Halimeda cuneata* and *Plocamium beckeri*, all abundant in the infralittoral fringe (R8). Other common species of the R8 stratum included *Laurencia natalensis, L. flexuosa, Plocamium rigidum, P. corallorhiza* and *Caulerpa filiformis*. The midlittoral turfs were dominated by *J. verrucosa* with *Leptophytum spp, A. flabellata, A. filicula* and smaller quantities of *Gigartina minima*. *Gelidium pristoides* was present in extremely low quantities and hardly distinguishable as a separate sampling stratum. *Spongites yendoi* was present in low quantities only in the cochlear stratum and *Gelidium micropterum* was absent.

Sessile filter-feeders were limited in extent. *Perna perna* occurred in midlittoral strata (Figure 76C), *Chthamalus dentatus* in the upper midlittoral to low supralittoral fringe, *Octomeris angulosa* in the upper barnacle stratum (R2) and with *P. perna* (R6). *Choromytilus meridionalis* was present in low numbers in the lower midlittoral and *Hymeniacidon perlevis* only occurred in the low midlittoral turf and infralittoral fringe.
Figure 76. MPB, Pollock South. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
Afrolittorina knysnaensis and A. africana were less abundant (Figure 76D) than at sites with more supralittoral rock, but still more numerous than other gastropods, occurring mostly as a densely populated narrow band in the supralittoral fringe/upper midlittoral zone, where they were found among C. dentatus, but also in the midlittoral zone at lower densities. Siphonaria capensis, S. concinna, Scutellastra granularis and Oxystele tigrina were the most common gastropods after the littorinids and were present in rather low numbers in midlittoral strata, with some Burnupena lagenaria, Nucella dubia and B. cincta. Even here there was a slight vertical shore partitioning between the siphonariids and the patellid limpet.

9.3.1.5 Pollock North (PBE)

In the cluster analysis, beach macrofauna samples grouped according to a cross-shore gradient (Figure 77A). Analysis of samples from rock surfaces reflected the low diversity of assemblages, grouping according to absence of presence of resilient pioneer algal species.

High polychaete abundance, particularly Scololepis squamata, was the major contributor to sediment macrofauna abundance in the low shore stratum S5 (Figure 77B). However, Eurydice longicornis, widely distributed across shore, was the most abundant species. Insects (particularly Formicidae) were found in the high shore strata (S0 and S1). Midlittoral strata contained predominantly Eurydice longicornis, polychaetes (e.g. Cirratulus africanus, Notomastus aberans, Timarete tenticulata) with low amounts of insects (Ichneumonidae sp, Cecidomyidae sp) and the gastropod Bullia rhodostoma. The low shore sediments of S4 and S5 yielded mostly Scololepis squamata and Spio filicornis, but with smaller populations of other species, e.g. Eurydice kensleyi, Urothoe pinnata, Gastroscus psammodytes, Bullia digitalis, Cerebratulus sp, Prionospio sexoculata, Nephtys capensis, Scoloplos johnstonei.

The rock substratum was limited to the midlittoral zone. As at other sites with no or limited rock for the establishment of supralittoral fringe biota, Porphyra capensis was not found (Figure 77C) and the littorinid sampling stratum was extremely curtailed. Only Ulva species occurred in R1 and was clearly part of a pioneer sere. The most abundant macroalgae were turf forming species that occurred mainly in the lower midlittoral turf (R5), i.e. Pterocladia caespitosa, Polysiphonia incompta, Jania verrucosa, Gigartina minima, as well as an ephemeral pioneer species, Ulva prolifera forming the upper midlittoral turf (R3) with smaller quantities of algae commonly found in turfs, e.g. Blidingia minima, U. rigida, Caulacanthus ustulatus, Cladophora spp. Gelidium pristoides was found from R2 (upper barnacle stratum) to R5 in low abundance, and
Figure 77. PBE, Pollock North. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
in both the tufted and low branching forms. The upper barnacle stratum (R2) was reduced in extent. The barnacle was also recorded in midlittoral strata and was the most abundant sessile filter-feeder. The diversity of sessile fauna was very low compared to other sites and those present did not attain appreciable levels of abundance. Aside from *Chthamalus dentatus*, the sessile fauna consisted of small amounts of *Octomeris angulosa*, *Perna perna* and *Spirobranchus kraussii* on the elevated surfaces of rock and *Choromytilus meridionalis*, *Mytilus galloprovincialis* and *Hymeniacidon perlevis* with low midlittoral turf on low or partly buried rock surfaces. Both littorinids were present and occurred in all sampling strata on rock (Figure 77D), reaching densities comparable to that of other sites with a truncated supralittoral fringe, numbers still exceeding those of other gastropods. The next most common gastropods (though in low numbers) were *Siphonaria capensis*, *S. concinna* and in smaller numbers *Scutellastra granularis* and *Siphonaria serrata*, all usually common and abundant in the midlittoral zone of rocky shores. Gastropod diversity was, however, much reduced compared to other sites.

9.3.2 Sites of biotic type B (*Polysiphonia-Tayloriella-Caulacanthus* turfs)

9.3.2.1 Avalanche (AVA)

The cluster analysis of these samples revealed a strong response to the cross shore vertical and horizontal gradients impinging on the rock surface biota (Figure 78A), as there was a clear separation between assemblages of upper shore / high elevation samples and those of the alga turfs and infralittoral fringe that both tended to occur on low rock surfaces. Sediment macrofauna assemblages, on the other hand, showed a much less regular pattern where the only clear separation was between the wrack line and the remaining zones.

Most of the sediment macrofaunal taxa at this site had a bimodal distribution across-shore (Figure 78B): present in upper intertidal (S1 and S2) and lower intertidal sediment (S4 and S5), with no macrofauna in lower midlittoral (S3) samples from sand patches among rock substrate. Polychaetes were numerically dominant. The wrackline yielded insect species (Muscidae sp1) and other high shore sediment a range of taxa including various polychaetes (e.g. *Scololepis squamata*, *Notomastus aberans*) and isopods (*Exosphaeroma hylecoetes*, *Eurydice longicornis*). The most abundant taxon overall was the polychaete *Scololepis squamata* which exhibited highest abundance at the low tide swash (S5). Other abundant taxa with a similar distribution trend were nemertine *Cerebratulus* sp, polychaete species *Scoloplos johnstonei*, *Notomastus aberans*, *Lumbrineris heteropoda difficilis*, *Scoloplos uniramus*, as well as isopods *Eurydice longicornis* and *Exosphaeroma hylecoetes* and a
Figure 78. AVA, Avalanche. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
turf-associated bivalve *Barbatia obliquata*. Although assemblages in the glassy zone (S4) were more diverse than at the swashline (S5), the numerical dominance of *S. squamata* together with taxa only found in the infralittoral fringe samples (*Nerinides gilchrist*, *Urothoe pinnata*, low numbers of *Bullia digitalis* and *B. pura*) resulted in S5 having the greatest overall abundance of macrofauna. Taxa that were only seen in the glassy zone included the nemertine *Lineus* sp, endemic isopods *Zuzara furcifer* and *Exosphaeroma laeviusculum* and a number of polychaete species (e.g. *Spio filicornis*, *Cirratulus africanus*, *Nephys dibranchis*).

Small quantities of algae persisting on supralittoral fringe rock, in place of *Porphyra capensis*, comprised *Caulacanthus ustulatus*, encrusting corallines and *Ulva* sp. (Figure 78C). Midlittoral rock surfaces were predominantly covered by macroalgal turf formations. The 5 most abundant turf macroalgae were *Arthrocardia filicula* and *Polysiphonia incompta*, of both upper and lower midlittoral turfs, *Tayloriella tenebrosa*, which occurred in midlittoral and infralittoral turfs, and *Gigartina minima* and *Jania adhaerens*, common in all intertidal turfs of this site. Many other well-known species of algal turfs occurred in somewhat smaller quantities with the dominants listed, e.g. *Arthrocardia flabellata*, *Caulacanthus ustulatus*, *Ceramium* spp, *Jania verrucosa*, *J. crassa*, *Arthrocardia duthieae*, *Bostrychia intricata* and *Chylocladia capensis*.

*Gelidium pristoides*, a midshore dominant of most rocky shores, was present in low quantities as isolated clumps or a creeping, branching form (apparently due to severe grazing by limpets according to Stephenson and Stephenson (1972)) with few associated algae and mostly confined to midshore rock surfaces of various elevations. The sand-inundated infralittoral fringe was dominated by the filamentous turf alga *Tayloriella tenebrosa*, with smaller quantities of *Plocamium corallorhiza*, *Halimeda cuneata*, *J. crassa*, *A. duthieae*, *Plocamium beckeri* and *Hypnea rosea*. *Spongites yendoi* covered over 50% of the “cochlear zone”, but was overgrown to quite some extent by algae of the infralittoral fringe and low midlittoral turfs.

The dominant sessile animal was the encrusting sponge *Hymeniacidon perlevis*, which covered between 15% and 43% of midlittoral rock (Figure 78C) and was also found in small quantities on more elevated surfaces. *Chthamalus dentatus*, *Octomeris angulosa*, *Perna perna* and *Tetraclita serrata* were next most abundant in decending order. *P. perna* was mostly confined to a narrow zone in the lower intertidal, with few small individuals settling in higher shore positions. Although *Choromytilus meridionalis*, a mussel known to be sediment-tolerant, occurred in
much smaller quantities than *P. perna*, it was still among the 10 most abundant sessile fauna and as at other sites occupied low midlittoral rock surfaces prone to sand-inundation.

*Afrolittorina knysnaensis* was present in several shore zones (Figure 78D), reaching highest abundance among *Chthamalus dentatus* on upper midlittoral rock surfaces. *Scutellastra granularis* occurred in midlittoral strata favouring those that coincided with elevated rock substrate, whereas *Siphonaria capensis* was broadly distributed across the shore from the littorinid-dominated supralittoral fringe to the low midlittoral turf. *Scutellastra cochlear* confined to the low shore, occurring only in its own biotope. A diverse assemblage of gastropods accompanied the dominants in different sampling strata, some broadly distributed across the shore, most notably *Afrolittorina africana*, *Siphonaria concinna*, *Burnupena lagenaria* and *Oxystele tigrina*.

9.3.2.2 Maitlands Inner (MAA)

According to the cluster analysis, upper and midshore assemblages on the rock surfaces showed a high degree of similarity (Figure 79A), clearly due to wide cross-shore distribution of mid-shore turf dominants. The character of the low shore sampling strata (R6, R7 and R8) differed markedly from midshore turfs, with strong dominance by a few sand-tolerant species, but also a more diverse assemblage. Sediment macrofauna assemblages showed three distinct and separate clusters corresponding to a cross-shore gradient.

Overall macrofauna abundance in sediment was highest at the low tide swashline (S5) (Figure 79B). Polychaetes were most abundant and concentrated at the low shore. The most abundant species overall was *Fabricia capensis*, a colonial polychaete confined to the filamentous algal turfs of sand-inundated low intertidal rock. Insects, *Bledius* spp, were highly dominant in high shore sediment (S1). Otherwise, the wrackline and high shore sediment (S0 and S1) yielded low numbers of *Excirolana natatesis*, *Exosphaeroma hylecoetes*, *Talorchestia* spp. and *Floresorchestia anomala*. Low numbers of *Excirolana natatesis* also occurred in the upper midlittoral (S2). *Donax burnupi* occurred in a band coinciding with the mid- and low shore (S3 and S4). *Eurydice longicornis*, abundant at the low tide swashline, extended its range into midlittoral strata. The swashline assemblage was characterised by high abundance of *Fabricia capensis*, *Scoloplos* spp, *Eurydice longicornis* and *Gastrosaccus psammodytes*. *Barbatia obliquata*, *Lumbrineris heteropoda heteropoda*, *L. heteropoda difficilis*, *Scoloplos johnstonei*, *Bullia rhodostoma* and *Excirolana latipes* occurred there in much lower numbers.
Figure 79. MAA, Maitlands Inner. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
Porphyra capensis and Hildenbrandia lecannellieri were the only algae seen in the supralittoral fringe on rock substratum where they were sparsely distributed (Figure 79C). Arthrocardia flabellata reached high dominance in midshore turfs, with Corallina officinalis, as a basiophyte for abundant Ulva rigida. As there were large areas of recently colonized midlittoral rock surface, pioneer abundance was high. Two or more unidentified Cladophora species, Blidingia minima and Ulva prolifera formed the basis of the pioneer sere in midlittoral turf. Algae of the established communities comprised Caulacanthus ustulatus, H. lecannellieri, Ralfsia verrucosa, Leptophyrum spp, Jania spp, Centroceras clavatulum and Pterocladiella caespitosa; the latter also part of the pioneer sere. Gelidium pristoides was most abundant in the midlittoral reaches, but extended up and down the shore at much lower densities, occurring with turf communities and also taking on the turf form occasionally. The infralittoral fringe was dominated by Caulerpa filiformis with somewhat less abundant Hypnea spicifera, Codium duthieae, Hypnea viridis and Arthrocardia filicula. The cochlear zone alga Spongites yendoi was abundant only in that sampling stratum, extensively overgrown by H. spicifera, C. filiformis, H. viridis, various Arthrocardia spp and filamentous species (Ophidocladus simplisciusculus, Pterosiphonia cloiophylla). Gelidium micropterum was present in low abundance, also suffering overgrowth.

Perna perna was the dominant sessile filterfeeder (Figure 79C), occurring in highest densities in R6, but also in substantial quantities with Scutellastra cochlear, among algae of the infralittoral fringe and with G. pristoides in the midshore. Other commonly found sessile macrofauna were Chthamalus dentatus from the supralittoral fringe down to midtidal levels, and Tetracita serrata, Octomeris angulosa and Mytilus galloprovincialis, all mostly in the midlittoral.

The five most abundant gastropods (Figure 79D) were Afrolittorina knysnaensis, Scutellastra granularis, Oxystele tigrina, O. variegata and Siphonaria concinna. As at other study sites, Scutellastra granularis appeared to favor elevated rock surfaces. Other gastropods occurring with midlittoral assemblages in appreciable abundance included Siphonaria capensis, Burnupena cincta, Nucella dubia and Siphonaria serrata. The littorinids, widespread across the intertidal, were absent from the infralittoral fringe. Other species (with the exception of S. concinna and Nucella dubia) occurred only in the midlittoral zone. Scutellastra cochlear numbers were low and it was not found outside of the cochlear sampling stratum which was limited in extent.
9.3.2.3 Maitlands Outer (MAB)

For this site, adjacent and similar to MAA, but with fewer and lower rock outcrops, the cluster analysis (Figure 80A) reflects the greater degree of intermingling and lower diversity of rock-bound assemblages on mid-to low shore rock (R3, R5, R8), which separated well from assemblages on elevated and high-shore rock. The sediment macrofauna separated into two clusters on the presence or absence of *Excirolana natalensis*.

The highest macrofauna abundance (Figure 80B) in sediment was recorded from the swashline (S5). Crustacea were the most abundant occurring in high densities throughout the intertidal. The most abundant species overall were: amphipod *Urothoe pinnata* and isopods *Excirolana natalensis* and *Eurydice longicornis*. The high shore dominant *Excirolana natalensis* decreased in number towards the low tide mark. *Eurydice longicornis* and *Exosphaeroma hylecoetes* found in most of the sampling strata were highly abundant in the midlittoral also inhabited by *Excirolana latipes*, *Urothoe pinnata*, species associated with macroalgae (*Barbatia obliquata* and *Amaryllis macrophthalma*) and various polychaete species in low numbers. *Donax burnupi* occurred in a band above and below the water table outcrop (S3 and S4). *Lumbrineris heteropoda heteropoda* and *Urothoe pinnata* were highly abundant and dominant on the low shore where *Tellina gilchristi*, *Haploscoloplos* sp, *Exosphaeroma estuarium*, *Bullia rhodostoma* and *Gastrosaccus psammodytes* occurred in low numbers.

The supralittoral fringe was reduced due to a lack of suitable rock surface (Figure 80C). There were few *Porphyra capensis* in association with *Hildenbrandia lecannellieri*, *Ralfsia verrucosa* and *Bostrychia intricata*. *Ulva prolifera* was highly abundant in R3 as part of a pioneer sere on newly colonized rock. *Polysiphonia urbana* dominated stable midlittoral and low shore sand-inundated turfs. Low quantities of *Gelidium pristoides* formed a midshore community with *Ulva rigida*, *Caulacanthus ustulatus*, *Ralfsia verrucosa* and *Gigartina minima*, that was also found in R6 with *Perna perna*. It also occurred with low intertidal turf (R5) dominants. *Hypnea spicifera* was dominant in the sand-inundated infralittoral fringe mingled with patches of *Caulerpa filiformis* and *Jania verrucosa*. Other infralittoral algae included *Arthrocardia flabellata*, *Ulva rigida*, *Corallina officinalis* and *J. crassa*. *Spongites yendoi* and *Gelidium micropterum* of the cochlear stratum were partly overgrown by larger algae of the infralittoral fringe (e.g. *Jania verrucosa*) and lower midlittoral turf (*Polysiphonia urbana*, *Arthrocardia flabellata*) as well as *Streblocladia tenuissima* which was only seen in R7.
Figure 80. MAB, Maitlands Outer. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
*Perna perna*, the predominant sessile filterfeeder, occurred in highest densities (Figure 80C) on mid and low shore rock (R4 and R6) with *G. pristoides*, but also extended into the upper midlittoral and the infratidal fringe strata where it occurred with *Scutellastra cochlear* and among algae. Other sessile filter feeders were much less abundant: *Chthamalus dentatus* and *Octomeris angulosa* occurring from the supralittoral fringe into the midlittoral zone, *Tetraclita serrata* on midlittoral surfaces, *Hymeniacidon perlevis* on low midlittoral rock and both *Choromytilus meridionalis* and *Mytilus galloprovincialis* in the midlittoral zone.

*Afrolittorina knysnaensis* was the most abundant gastropod (Figure 80D) and widespread across the intertidal, being absent only from the infralittoral fringe. Its abundance appeared to be less suppressed than that of other gastropods: *Siphonaria concinna, Scutellastra granularis* and *Oxystele tigrina* occurring mostly in the midlittoral zone. *Scutellastra cochlear* was present in low numbers and was not found beyond the cochlear sampling stratum. Other gastropods of appreciable abundance in mid to low intertidal assemblages include *A. africana, O. variegata, Nucella dubia, Burnupena cincta* and *B. lagenaria.*

9.3.2.4 Beacon Rock (BCN)

In the cluster analysis (Figure 81A) the infralittoral fringe (R8) and cochlear zone (R7) separated well from other rock-bound assemblages, all of which were of much lower diversity. There was also a clear separation between the midlittoral turfs (R3, R5) and assemblages of elevated rock surfaces. Sediment macrofauna grouped in a pattern corresponding to a cross-shore gradient, forming clear low shore (S4, S5) and midshore (S2, S3) clusters.

Macrofauna abundance in sediment was greatest in the narrow mid-to low shore (Figure 81B). Crustacean and polychaete taxa shared dominance. *Eurydice longicornis* and *Scololepis squamata* were the most abundant species, followed by *Exosphaeroma hylecoetes, Notomastus aberans, Urothoe pinnata* and *Nerinides gilchrist.* *Eurydice longicornis* was most abundant and the numerical dominant in lower midtidal sediment (S3). A common seaweed amphipod, *Hyale grandicornis* was the only taxon in high shore sediment of S1 and also occurred in the midlittoral (S3). *Urothoe pinnata* and *Nerinides gilchrist* exhibited a bimodal cross-shore distribution and were found at the wrackline and at the low tide swashline where they more abundant. *Scololepis squamata, E. hylecoetes* and *N. aberans* only occurred in low- to midlittoral sediment. *Scoloplos johnstonei, Eurydice kensleyi* (endemic), *Excirolana latipes* and *Spiro flicornis* were present in low numbers in the
Figure 81. BCN, Beacon Rock. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and A. knysnaensis are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
midshore (S2 and S3). Numerically low ranking species confined to the low shore (S4 and S5) included polychaetes *Scoloplos* spp, *Cirratulus chrysoderma, Lumbrineris tetraura, L. heteropoda difficilis, Timarete tenticulata*, amphipods *Urothoe serrulidactylis* and *Perioculodes longimanus* and mysid *Gastrosaccus psammodytes.*

Less than 50% of the rock surface was covered by macroalgae (Figure 81C). Having much rock surface in the supralittoral fringe, this site supported *Porphyra capensis* which reached 3% cover. A few hardy species (*Caulacanthus ustulatus, Bostrychia intricata, Leptophytum* spp, *Cladophora* spp, *Ulva rigida*) persisted in the supralittoral in very small quantities (ca. 6% cover in total). *Gelidium pristoides* and the encrusting algae *Leptophytum* spp and *Hildenbrandia lecannellieri* were equally abundant on midlittoral elevated surfaces which were mostly bare. *Polysiphonia incompta* was the spatial dominant in the midlittoral turf that occurred mainly as a fringe around the sand-inundated bases of midlittoral rock with *Amphiroa rigida. Tayloriella tenebrosa* was the most abundant infralittoral alga together with *Plocamium beckeri, Plocamium rigidum* and *Jania verrucosa.* The algae characteristic of the cochlear zone, *Spongites yendoi* and *Gelidium micropterum* were accompanied by other encrusting and turf-like forms, but no major overgrowth by infralittoral fringe algae was noted.

At this site sessile macrofauna were the spatial dominants (Figure 81C). *Octomeris angulosa* was the most abundant species on elevated surfaces from the upper to lower reaches of the midlittoral. *Hymeniacidon perlevis* dominated low rock surfaces in the mid to low intertidal. *Perna perna* and *Chthamalus dentatus* were widely distributed across the upper midlittoral in lower abundance, with *P. perna* slightly more prominent towards the low intertidal where it competed with *Hymeniacidon perlevis* and the invasive mussel *Mytilus galloprovincialis.* The indigenous sand-tolerant mussel *Choromytilus meridionalis* was present in low quantities on midlittoral surfaces.

As at other sites, *Afrolittorina knysnaensis* was the most abundant gastropod (Figure 81D). It was widely spread over the intertidal and reached highest abundance in the midlittoral with *G. pristoides* (R4). *Afrolittorina africana* was present in high numbers compared to other sites in the upper shore reaches. *Scutellastra granularis, Siphonaria concinna* and *S. capensis* all on midlittoral substratum, were dominants at roughly equally abundance. Other slightly less numerous gastropods in midlittoral reaches included, *Siphonaria serrata, Oxystele tigrina, O. variegata* and *Burnupena lagenaria. Scutellastra cochlear* was among the 5 most abundant and dominated only in its zone where it attained high densities.
9.3.2.5 Humewood (HWD)

In the cluster analysis (Figure 82A), rock substratum assemblages exhibited clear groupings in response to the intertidal gradient: the supralittoral fringe (R0, R1) and the upper midlittoral strata (R2, R4) separating early from the midlittoral and infralittoral fringe turfs (R3, R5, R8), while *Perna perna* (R6) and cochlear (R7) zones also formed a distinct cluster. The sediment macrofauna assemblage at the beach toe (S5) was the most diverse and separated well from other beach strata, all reduced in cross-shore width, which showed more commonality in dominant taxa, probably due to a considerable amount of overlap.

Sediment macrofauna exhibited a midshore (S3) peak in overall abundance (Figure 82B) and polychaetes were highly dominant. *Notomastus aberans*, the overall numerical dominant, had a wide cross-shore distribution, while *Timarete tenticulata* and *Scololepis squamata*, were concentrated in mid to low shore sediment. The wrackline was sparsely populated. Only two taxa were found, namely, *Excirolana latipes* and an oniscid isopod, both of which also inhabited midshore sediment. The upper zones of two cross-shore beach transects were truncated due to coastal armouring. High shore sediment (S1) yielded abundant *Eurydice longicornis* and *Notomastus aberans*, with smaller numbers of *Excirolana natalensis* and the rocky shore amphipod *Paramoera capensis*. Only *E. natalensis* was absent from lower sediments. Midshore sediment (S2 and S3) supported a diverse assemblage of polychaetes, isopods and amphipods including *Notomastus aberans* (numerical dominant), *E. longicornis, Paramoera capensis* and *Urothoe pinnata*, all with a wider cross-shore range, *Eurydice kensleyi, Zuzara furcifer* and *Notomastus latericeus* only recorded in the midlittoral, and *Exosphaeroma hylecoetes, Scololepis squamata, Timarete tenticulata, Cerebratulus* sp, *Lumbrineris* spp, *Scoloplos johnstonei, Nephtys capensis*, also found in shallow sediment among rocks on the low shore.

Low shore sediment above the swashline yielded a diverse assemblage of organisms comprised of numerical dominants *S. squamata, N. aberans, E. hylecoetes* and *E. longicornis* and in slightly lower numbers *Lumbrineris heteropoda difficilis, Nerinides gilchrist, Cerebratulus* sp, *Paramoera capensis, Scoloplos johnstonei, Nephtys capensis, N. dibranchis* and *Gastroscosus psammodytes*. At the swashline (S5), the most abundant species *N. aberans, Timarete tenticulata, E. longicornis* and *Exosphaeroma hylecoetes*, with *Lumbrineris tetraura, Cerebratulus* sp, *Scoloplos johnstonei, Urothoe pinnata, Nephtys capensis, N. dibranchis, Spio filicornis, Urothoe serrulidactylis* and *Bullia rhodostoma* in lower numbers.
The rock substratum biota was dominated by small corallines mostly confined to midlittoral turfs (R3 and R5) (Figure 82C). The supralittoral fringe was well developed on tall rock surfaces: macroalgae present in small quantities were *Porphyra capensis*, *Ectocarpus* sp and *Ulotrix flacca*. The upper midlittoral turf (R3) was the most extensive. *Arthrocardia flabellata*, reaching 80% cover in that stratum and also common in other lower shore substrata, was the most abundant alga. Other midlittoral taxa in turf included *Leptophytm* spp, *Jania crassa*, *Tayloriella tenebrosa*, *Laurencia natalensis*, *Corallina officinalis* and *Gelidium pristoides*. On the low shore *Gigartina minima*, *Pterosiphonia cloiophylla*, *Plocamium corallorhiza* and less abundant algae were added (*Arthrocardia filicula*, *A. carinata*, *Spongites yendoi*, *Polysiphonia scopolorum* and *Halimeda cuneata*). *Gelidium pristoides* was not among the most abundant, but reached about 20% cover in R4, the midlittoral *Gelidium* zone, where it occurred with encrusting (e.g. *Hildenbrandia lecannellieri*, *Leptophytm* spp, *Ralfsia verrucosa*) and turf-forming algae (*Arthrocardia* spp mentioned) and also extended into the coralline turfs (R3 and R5) where it took on a turf-like growth form. In the cochlear zone (R7) *S. yendoi* and *Gelidium micropterum* were locally abundant at 60% and 20% cover respectively. Extensive overgrowth by turf-forming algae (*Gigartina minima*, *A. filicula*, *A. flabellata*, *Pterocladiella caespitosa*, *Jania verrucosa*) and encrusting algae (*R. verrucosa*, *Hildenbrandia rubra*) was evident.

The encrusting sponge *Hymeniacidon perlevis* was among the spatial dominants (Figure 82C) covering over much of the mid to low midlittoral and extending into the infralittoral fringe. *Perna perna* dominated in its own stratum but also extended into adjacent strata in smaller numbers giving it a greater than expected importance at this site. Other rocky shore filter-feeders (*Octomeris angulosa*, *Spirobranchus krausii*, *Tetraclita serrata*, *Chthamalus dentatus*) were present in low numbers.

Littorinids (*Afrolittorina knysnaensis* and *A. africana*) were widely distributed in intertidal zones (Figure 82D). The two most common siphonariids (*S. capensis* and *S. concinna*) had a midlittoral distribution and tended to occupy the same surfaces as *Scutellastra granularis*. *Scutellastra cochlear* was common and abundant in its own zone in the infralittoral fringe, showing no range extension upshore.
Figure 82. HWD, Humewood. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and _A. knysnaensis_ are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
9.3.3 The sites of biotic type C (*Arthrocardia-Laurencia* turfs)

9.3.3.1 Willows Beach (WLW)

In the cluster analysis (Figure 83A), the associations of rock substratum assemblages grouped in relation to the intertidal gradient. The infralittoral fringe and cochlear zone (R8 and R7, respectively) separated early from other rock substratum assemblages, which formed three clusters linked to the intertidal habitat occupied, i.e. upper rock surface assemblages (R2, R4 and R6), midlittoral turfs (R3, R5) and supralittoral fringe (R0, R1). Sediment macrofauna assemblages formed two clusters that corresponded to low and upper shore zones.

Sediment macrofauna, mainly polychaetes, decreased in abundance by two orders of magnitude from the narrow beach toe (S4) above the rocky intertidal towards the wrackline (Figure 83B). An oligochaete, *Marionina* sp., normally of meiofaunal size range, was the most abundant in high and low shore sediment (data not shown). The next most abundant taxa, *Exosphaeroma hylecoetes* and *Nerinides gilchrist*, decreased sharply in abundance from the low towards high shore, occurring with *Kellia rotunda*, a bivalve associated with rocky and sandy environments, across much of the shore and with *Talorchestia* spp in the dry upshore sediment. The mid- to low shore sediment also yielded several taxa normally found in phytal habitats on rocky shores, e.g. *Tricola capensis*, *Hyale grandicornis* and *Perinereis capensis*.

The composition of the rock surface biota corresponded to a typical rocky shore assemblage (Figure 83C). Elevated rock surfaces (strata R0, R1, R2, R4 and R6) were typically bare for most part, probably due to a combination of grazing by limpets and adverse conditions. *Porphyra capensis* (in R0) was sparsely, but widely distributed over rock substratum in the supralittoral range where small quantities of *Bostrychia intricata*, *Hildenbrandia lecannellieri* and *Cladophora* spp were found in crevices and moist depressions. The most abundant algal taxa at this site were those dominant in midlittoral turfs which were extensive at this site: *Arthrocardia flabellata*, *Leptophyrum* spp, *Cladophora* spp, *Hildenbrandia lecannellieri*, *Bldingia minima*, *Codium lucasi*. *Gelidium pristoides* was among the most abundant at this site, occurring mostly on midlittoral and infralittoral surfaces and in two different forms: where it was regularly grazed, it merely consisted of flat branching fronds and where it escaped grazing it had the more familiar tufted appearance. The most abundant infralittoral fringe algae were *G. pristoides*, *Arthrocardia carinata*, *Laurencia natalensis*, *Leptophyrum* spp, *Amphiroa ephedraea*, all others occurring in much smaller abundance.
Figure 83. WLW, Willows Beach. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
The two most typical species of the cochlear zone, *Spongites yendoi* and *Gelidium micropterum* were highly abundant in the cochlear zone (R7), but were not found outside of it. Several small turf-like and other encrusting species were associated with the cochlear zone. The encrusting sponge *Hymeniacidon perlevis* dominated the upper midlittoral turf substratum (R3) and was abundant on low shore surfaces. The filter-feeders normally associated with rocky shores were not as well-represented as expected. *Chthamalus dentatus* was more common than other barnacles, i.e. *Tetraclita serrata* and *Octomeris angulosa*, occurring with it on exposed surfaces in the upper-, mid- and low shore. *Perna perna* was also not very abundant, occurring only on the low shore in elevated positions on rocks.

*Afrolittorina knysnaensis*, hugely abundant at WLW, occurred widely across the intertidal (Figure 83D) its numbers dropping off towards the low shore. *Scutellastra cochlear* was the most abundant limpet, reaching high densities in the cochlear zone to which it was restricted. Other highly abundant gastropods included *Scutellastra granularis*, confined to elevated surfaces across the shore, and three false limpets with a less restricted cross-shore distribution, *Siphonaria concinna*, *S. serrata* and *S. capensis*, but apparently favouring sheltered surfaces.

### 9.3.3.2 Kini Bay (KNB)

In the cluster analysis (Figure 84A), rock substratum assemblages also grouped in accordance with the intertidal gradient: the infralittoral fringe (R8), cochlear zone (R7) and *Perna* zone (R6) formed one diverse cluster that separated early from other rock substratum assemblages mainly due to the complete absence of *Afrolittorina knysnaensis*. Midlittoral turfs (R3, R5) were distinct from the assemblages or upper rock surfaces, i.e. the midlittoral strata R2 and R4, and supralittoral fringe strata (R0, R1). Sediment macrofauna assemblages formed two clusters corresponding to low and upper shore zones.

Overall abundance of sediment macrofauna was the highest of all study sites even without the hugely abundant “mega-meiofauna” *Polygordius* and *Marionina* (omitted from Figure 84B) with greatest numbers recorded in low shore sediment. Amphipods were numerical dominants, mainly due to high numbers of *Zygomaera emarginata*, the most abundant, *Paramoera capensis* and *Incratella inermis*, all known rocky shore species. High polychaete numbers were mainly due to *Trypanosyllis zebra*, also known from rocky habitats, in beach toe sediment. The isopod *Exciorolana (Pontogeloides) latipes*, known to frequent sandy beach, was a common component of all the intertidal zones at this site, reaching its highest numbers in midlittoral strata. Abundance at the wrackline and high shore exceeded that of other sites by an order of magnitude and
was mainly due to high numbers of the staphylinid beetle *Bledius* spp (most abundant), *Marionina, Talorchestia* spp and *Excirolana natalensis*, with taxa found only in wrackline and high shore sediment (various insect species, *Platorchestia platensis, Tylos capensis and Eorhynchus rectipalma*, Enchytraeidae spp *Floresorchestia anomala* and *Namanereis quadriceps*). Midlittoral sediment also yielded abundant *Paramoera capensis* with Enchytraeidae spp., *Akera soluta* and isopods *Excirolana latipes* and *E. natalensis*. Together with the beach toe dominants, there were several other crustacean (e.g. *E. latipes*, Janiriidae spp) and polychaete species (*Sphaerosyllis sublaevis*), some confined to the low shore, e.g. *Syllis armillaris* and *Cyathura estuaria*.

On the rock substratum, the supralittoral fringe was characterised by sparsely distributed *Porphyra capensis* (Figure 84C) and small aggregates of *Bostrychia intricata, Leptophyrum*, *Hildenbrandia lecannellieri*, and *Chaetomorpha* spp in moist depressions. The most abundant algal taxa at this site were: *Leptophyrum* spp, highest abundance in the infralittoral fringe, *Jania subulata, Gelidium pristoides and Hildenbrandia lecannellieri*, abundant in the midlittoral sampling strata, *J. subulata* in the algal turfs and the other two on higher rock surfaces; and *Arthrocardia filicina* and *A. carinata*, dominant in the low midlittoral turf and infralittoral fringe, respectively. Algae associated with *Chthamalus dentatus* (R2) included *Iyengeria stellata, Bidingia minima*, a turf-like form of *G. pristoides, Caulacanthus ustulatus, Ralfsia verrucosa* and *Jania* spp. Several encrusting algae (*R. verrucosa, Leptophytm* spp, *L. ferox, H. lecannellieri*) and a small turf-forming coralline (A. *flabellata*) occurred with *G. pristoides* (R4) on high surfaces. The typical algae of the cochlear zone, *Spongites yendoi* and *Gelidium micropterum*, were abundant in that sampling stratum, showing little sign of overgrowth. *Gelidium pristoides* was fairly abundant in R7, encrusting forms *H. lecannellieri* and *R. verrucosa* were present as well as *J. adhaerens, Caulacanthus ustulatus, Dasya scoparia* and *Ulva rigid*. *Octomeris angulosa* was the most abundant sessile filter-feeder, reaching high abundance in the R2 (upper barnacle stratum) of the upper midlittoral and R6 (*Perna* stratum) on the low shore. The second most abundant filter-feeder was *Perna perna* which reached very high abundance on tall ridges of the low shore. *Tetraclita serrata* occurred with *O. angulosa* and was dominant with *G. pristoides* in the midlittoral stratum S4. On low elevation rock surfaces of the midlittoral turf strata, the poriferan *Hymeniacidon perlevis* was an abundant species. Aside from the supralittoral fringe, *Afrolittorina knysnaensis* occurred prolifically across a broad cross-section of midlittoral assemblages.
Figure 8.4. KNB, Kini Bay. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
Scutellastra cochlear was also abundant reaching high densities in the cochlear zone and extending its range into R6, where it lived side-by-side with *P. perna* banks in much lower numbers. Three species (*Siphonaria concinna*, *A. africana* and *Scutellastra granularis*) shared dominance in the midlittoral zones, *A. africana* being more numerous in the supralittoral and upper midlittoral, whereas *S. concinna* was abundant on the midlittoral turfs (R3 and R5) and *S. granularis* in lower sampling strata. Other mobile gastropods that reached appreciable levels of abundance at this site included *Siphonaria serrata* and *S. capensis* (midlittoral zones), *Scutellastra longispina*, *Burnupena lagenaria* and *Oxystele tigrina* (low shore zones).

9.3.3.3 Cape Recife West (CRW)

The cluster analysis (Figure 85A) showed an unusual grouping of rock substratum assemblages. The infralittoral fringe algae (R8), cochlear zone (R7), lower midlittoral turf (R5) and *Gelidium pristoides* assemblage (R4) formed a cluster that separated immediately from remaining rock-bound assemblages. In the sister cluster, the supralittoral fringe (R0, R1) showed a high degree of similarity and separated early from the cluster composed of upper (R2, R3) and lower midlittoral (R6) assemblages. Sediment macrofauna separated into three clusters corresponding to the low (S4, S5), mid (S2, S3) and upper (S0, S1) shore.

Sediment macrofauna were most numerous at the low tide swash line (S5), decreasing towards the high shore (Figure 85B). The overall composition resembled that of sandy beaches in general, as crustaceans, polychaetes and molluscs were all numerically important. The isopod *Eurydice longicornis* was most abundant reaching highest density in midlittoral sediment (S2 and S3), while polychaetes reached highest abundance at and near the low tide swash (e.g. *Lumbrineris heteropoda difficilis*, *Lumbrineris tetraura*, *Scoloplos johnstonei*). Some taxa were confined to particular shore zones, which contributed to the distinction between low, mid and upper shore assemblages, e.g. isopods *Excirolana latipes* and *Excirolana natalensis*, amphipods *Floresorchestia anomala* and *Talorchestia* spp, as well as insect species of Neanuridae, Curculionidae and Cynipidae were found only in or near the wrack line, whereas *Cerebratulus* sp, a few *Lumbrineris* spp, *Notomastus aberans* and *Bullia rhodostoma* occurred in midlittoral sands, and several species (e.g. *Scoloplos* spp, *Scololepis squamata*, *Pseudonereis variegata*, *Atylus swammerdami*, *Hyale grandicornis*, *Tanaidae* sp, *Eurydice kensleyi*, *Gastrosaccus psammodytes*) did not
extend their range further upshore than the low tide swash, where the most diverse assemblage occurred. *Bullia rhodostoma*, the only molluscan species recorded, occurred in both low and midshore samples.

The macroalgae and sessile macrofauna of rock surfaces reach highest level of cover and abundance (Figure 85C) in upper midlittoral turf (R3) and low midlittoral assemblages (R6, R7 and R8). The supralittoral fringe (R0, R1) supported a low cover of *P. capensis* on tall rocks, with *Bostrychia intricata, Ulva rigida* and encrusting *Hildenbrandia lecannellieri*. The upper and lower midlittoral algal turfs (R3 and R5) were the most extensive, composed mainly of spatial dominants *Arthrocardia flabellata, A. duthieae, Polysiphonia incompta, A. filicina, Jania verrucosa* and *Caulacanthus ustulatus* as well as *Laurencia pumila, Leptophyllum spp, Jania adhaerens, H. lecannellieri, G. pristoides* and *B. intricata*. A number of these species were elements the infralittoral fringe with *Caulerpa filiformis* in sandy areas of the infralittoral fringe. *G. pristoides* was not among the most abundant, but colonized mid- and low midlittoral surfaces at various heights, often as a turf or the low branching form. *Spongites yendoi* and other encrusting forms in the cochlear zone (R7) were marginally overgrown by larger infralittoral fringe algae.

Compared to sites with much raised attachment surface in the lower intertidal, sessile filter-feeder abundance on rock was reduced (Figure 85C). Dominant sessile macrofauna were indicative of a high degree of wave exposure. *Octomeris angulosa*, reaching highest percentage cover in the upper barnacle zone R2, *Perna perna*, very abundant in the R6, but also with a wider cross-shore extent in other sampling strata, *Chthamalus dentatus*, less abundant, but with a wide distribution across-shore in midlittoral strata, *Hymeniacidon perlevis*, found only on lower midlittoral and low shore sheltered surfaces, and *Tetraclita serrata*, on raised midlittoral and low shore surfaces with *G. pristoides* and *P. perna*, respectively.

The littorinid *Afrolittorina knysnaensis* reached highest densities in upper intertidal zones (Figure 85D) with *A. africana*, fairly abundant at this site. *Scutellastra cochlear* was the second most numerous gastropod, occurring in very high densities in R7 and smaller numbers with *P. perna* in R6. Other numerical dominants include *Siphonaria concinna, S. capensis* and *Scutellastra granularis*, all frequenting midlittoral to low shore surfaces. *Scutellastra granularis* was, however, absent from the turf sampling strata R3 and R5 which occupied frequently sand-inundated midlittoral low elevation rock. Somewhat less abundant gastropod species found in the lower intertidal included *Siphonaria serrata, Oxystele tigrina, O. variegata, Scutellastra longicosta, Siphonaria oculus*. 

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Figure 85. CRW, Cape Recife West. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
9.3.3.4 Bird Rock (BRK)

In the classification (Figure 86A) the cluster consisting of the infralittoral fringe (R8) and cochlear zone (R7) separated very early from other rock-bound assemblages which, in contrast, displayed a fair degree of similarity clearly due to the high abundance of encrusting algae (Leptophytum spp) at this site. The high shore sediment macrofauna (S0, S1) formed a distinct grouping, whereas mid to low shore assemblages combined in one cluster, perhaps due to dominance of particular polychaete species.

Sediment macrofauna abundance (Figure 86B) peaked in mid- to low shore sand (S4 and S3). Polychaetes were the overall numerical dominants across all intertidal zones, but the haustorid amphipod Urothoe pinnata was the most abundant species overall, followed by the isopod Exosphaeroma hylocoetes and spionid Scololepis squamata. Scoloplos johnstonei, Notomastus aberans and Nerinides gilchrist were bimodally distributed, being numerical dominants at both the wrack line and low tide swash to infralittoral sand. The wrackline assemblage was further characterised by low numbers of Excirolana natalensis, unidentified insects (Muscidae sp1, Formicidae, Cixiidae and Tenebrionidae) and oligochaetes (Enchytraeidae). The midshore assemblage was comprised of high numbers of S. squamata, U. pinnata and Eurydice longicornis, as well as taxa only recorded from midshore samples (S2, S3), e.g. Nemertea, amphipods Ampelisca spinimana and Zygoamaera emarginata (endemic). Several numerically lower ranking taxa were only seen in or near the swash line, e.g. Spio filicornis, Scoloplos spp, Prionospio sp1, Scoloplos uniramus, Lumbrineris spp, Lineus sp., Aonides oxycephala, Nephtys spp and Orbinia angrapequensis.

The midlittoral and infralittoral algal turfs produced the highest overall cover-abundance on rock surfaces (Figure 86C). Porphyra capensis occurred in low quantities (as normally expected at a rocky shore) and was joined by several hardy algae in the supralittoral fringe, e.g. Leptophytum spp, G. pristoides, Ulva spp, Cladophora spp. The articulated coralline Arthrocardia filicula was the most abundant macroalga at this site, followed by Hildenbrandia lecanellieri, Bostrychia intricata, and a filamentous alga Ophidocladus simpliciusculus, all dominant in the extensive upper midlittoral turf (R3). Small, coralline and tough, encrusting species occurred with the midlittoral dominant, Gelidium pristoides, among the 5 most abundant overall, on elevated midlittoral surfaces (see R4). In the infralittoral fringe, dominance was shared almost equally by Arthrocardia flabellata, Halimeda cuneata and P. corallorhiza with smaller quantities of Amphiroa anceps. The 5 most abundant sessile macrofauna (Figure 86C) were Chthamalus dentatus (mainly upper midlittoral rock), the opportunistic barnacle Notomegabalanus algicola,
Figure 86. BRK, Bird Rock. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and A. knysnaensis are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
also on midlittoral surfaces, *Octomeris angulosa* on mid to low substrata, *Hymeniacidon perlevis* extensively covering lower mid-intertidal rock substratum, and *Spirobranchus (Pomatoleios) kraussii* forming small aggregates on midlittoral rock.

The littorinid *Afrolittorina knysnaensis* was present in highest abundance, peaking on upper midlittoral surfaces (Figure 86D). Other abundant molluscs in decreasing order were *Scutellastra cochlear*, reaching high densities only in the infralittoral fringe, *Siphonaria concinna*, *A. africana* and *Scutellastra granularis*, all wide-spread and abundant across intertidal zones. Other gastropod species that attained appreciable density in midlittoral reaches include *Siphonaria capensis*, *Burnupena lagenaria*, *Oxystele tigrina*, *Siphonaria serrata* and *Nucella dubia*.

9.3.3.5 Aston Bay (ASB)

Classification (Figure 87A) revealed the high degree of similarity between the supralittoral fringe (R1 only) and the assemblages of midlittoral elevated rock surfaces (R2, R4). Unusually, the midlittoral turf assemblages (R3, R5) had much in common with the low shore *Perna* (R6) and cochlear (R7) zones, leaving only the infralittoral fringe algae (R8) to form an isolated cluster with little in common with the remaining rock surface assemblages. Extremely low species richness and abundance of macrofauna in sediment (lowest of all sites) produced only three recognizable assemblages, clustered in the classification as S1 and S4-S5.

Sediment macrofauna was found in only three shore zones: near the neap high mark (S1) and on either side of the low tide swash line (S4 and S5). Numbers were highest at the beach step (Figure 87B). Three polychaete species (*Brania rhopalophora*, *Nerinides gilchrist* and *Scoloplos uniramus*) contributed most to overall abundance. *Excirolana latipes* was the only species at S1, but low shore sediments at S4 and S5 yielded low numbers of polychaetes (*Brania rhopalophora*, *Nerinides gilchrist*, *Scoloplos uniramus*, *Magelona* sp and other *Scoloplos* spp), amphipods (*Colomastix pusilla* and *Perioculodes longimanus*) and the mysid *Gastrosaccus psammodytes*.

The rock surface assemblages consisted mostly of macroalgae that produced a high degree of cover throughout all intertidal levels except the supralittoral fringe (Figure 87C). The supralittoral fringe was strongly truncated: *Porphyra capensis* was not recorded here, the littorinid stratum (R1) reduced in vertical extent and only small turf-like algae (e.g. *Bostrychia intricata*) persisted in R1. Macroalgae predominated on mid to low shore rock surfaces (close to 100% cover). The short turf-forming geniculate coralline *Arthrocardia flabellata*, which occurred in all intertidal
subzones except with *Gelidium* (R4) and reached its highest level of dominance in low midlittoral turf (R5), was most abundant overall. *Laurencia natalensis* was most abundant in the turfs associated with low midlittoral rock surfaces (R5), *Perna* (R6) and the infralittoral fringe (R8), while the turf-forming filamentous alga *Tayloriella tenebrosa*, dominated upper midshore turfs (R3) and the coralline *Arthrocardia filicina* reached high abundance with *Perna* (R6) and in the infralittoral fringe (R8). *Laurencia pumila* and the encrusting alga *Ralfsia verrucosa* were also common constituents of the midlittoral turf stratum R5. *Gelidium pristoides*, the midshore dominant of most rocky shores, was fairly well represented, though not a dominant at this shore type, and spread widely cross-shore interspersed with turf algae and taking on a turf-like growth habit itself. The *Scutellastra cochlear* zone (R7) was dominated by the encrusting alga *Spongites yendoi*, together with species more often associated with the infralittoral fringe and low intertidal turfs. The infralittoral fringe was dominated by *L. natalensis* and *Plocamium corallorhiza* and further characterised by the roughly equal presence of several other large macroalgae including *Caulerpa filiformis* and various articulated corallines (*A. flabellata, A. filicina, Amphiroa beauvoisii, Corallina officinalis, Halimeda cuneata*).

There was a low overall abundance of sessile filter-feeders (Figure 87C). The sponge *Hymeniacidon perlevis* and barnacle *Chthamalus dentatus* were most common, each occupying less than 2% of the transect area, *H. perlevis* favouring low midshore surfaces with algal turf (R3, R4, R5) and *C. dentatus* found in elevated positions across the intertidal. Most of the other sessile fauna occupied less than 1% of transect area. *Perna perna* (R6) occurred in small clumps in the lower intertidal, overgrown by macroalgae. Small numbers of *Choromytilus meridionalis* occupied low midlittoral surfaces with sand-inundation (in R1, R2).

Gastropod abundance was suppressed compared to sites with extensive rock surface. *Afrolittorina knysnaensis*, confined to elevated rock surfaces (R1, R2 and R4), was the most abundant gastropod (Figure 87D). *Siphonaria capensis, S. concinna* and *S. serrata*, were widely distributed across-shore, while *Scutellastra granularis*, a midshore dominant of rocky shores, was strictly confined to elevated midshores surfaces (R2, R4, R6). *Scutellastra cochlear* occurred on isolated rock surfaces in its own zone only.
Figure 87. ASB, Aston Bay. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
9.3.3.6 Paradise Beach (PDB)

This site was physically similar to Aston Bay (ASB) and had a greatly reduced supralittoral fringe also lacking *Porphyra capensis* (R0). Classification of intertidal samples indicated a greater level of integration between midlittoral and upper shore assemblages of rock surfaces than at ASB (Figure 88A). The midlittoral turfs (R3 and R5) overlapped with the *Gelidium* zone (R4) having more species in common. The low shore biota (infralittoral fringe algae, cochlear zone and *Perna* zone) formed a cluster distinct from other rock-bound assemblages. The diverse beach macrofauna community separated into two clusters corresponding to a high shore-wrackline assemblage (S0, S1), mainly due to high enchytraeid abundance, and a low to midshore association consisting of a diverse range of taxa. The S2-S5 cluster resulted from a bimodal intertidal distribution of *Scololepis squamata*.

Beach macrofauna abundance was highest at the beach toe and infralittoral sediment (Figure 88B). Polychaetes were numerical dominants together with enchytraeid oligochaetes and amphipods. *Scololepis squamata* was the most abundant species overall. High shore sediment (S0, S1) yielded mainly abundant Enchytraeidae spp. and *Talorchestia* spp. Midshore sediment (S2, S3) supported assemblages characterised by abundant *Excirolana latipes, Eurydice longicornis, Excirolana latipes, Capitellidae, Gonadiopsis incerta* and *Scololepis squamata* with smaller numbers of *Urothoe serrulidactylis, U. tumorosa* and *Scoloplos johnstonei*. Low numbers of *Bulla rhodostoma* occurred in midlittoral sediment (S3). A few species (e.g. *Scoloplos* spp, *Lumbrineris heteropoda heteropoda, Mediomastus capensis*) extended their range upshore from below the swash line (S5) only as far as the glassy zone/zones or resurgence (S4) where they were still abundant. Other species separated the two intertidal subzones, occurring only in one or the other, e.g. *Urothoe pinnata, Spio filicornis, Cerebratulus* sp, *Lumbrineris heteropoda difficilis* (only in infralittoral/swashline sediment) and *Paraonis gracilis oculata, Cirratulus africanus* and *Notomastus latericeus* (only in S4). As at ASB, the highly abundant macroalgal assemblages covered midlittoral and low intertidal rock surfaces extensively (Figure 88C). Algae of the reduced supralittoral fringe comprised *Leptophytum* spp and *Ulva rigida*, indicative of frequent inundation. Encrusting species (*Leptophytum* spp, *Ralfsia verrucosa, Hildenbrandia lecannellieri*) were also associated with *Chthamalus dentatus* (R2) together with a small, sand-tolerant turf alga *Gelidium reptans*. The 5 most abundant macroalgae consisted of four associated mainly with midlittoral sampling strata (*Arthrocardia*
filicula, Laurencia natalensis, Arthrocardia flabellata and Laurencia pumila) and one that was infralittoral (Codium duthieae). The infralittoral fringe was composed of a number of species in notable quantities, e.g. C. filiformis, P. corallorhiza, Amphiroa beauvoisii.

Gelidium pristoides occurred in small quantities and its distribution was restricted to the uppermost midlittoral rock surface where even there it was in competition with algal turfs. Algae found in association with G. pristoides include encrusting forms (Leptophytum spp, R. verrucosa, H. lecannelli) and turf elements (e.g. A. filicula, A. flabellata, L. natalensis, L. pumila, G. minima, C. ustulatus). The cochlear zone algae showed a similar trend to other study sites were rock height in the infralittoral was reduced, i.e. S. yendoi was a dominant element, while G. micropterum was present only in small amounts. Neither alga was found beyond R7.

The most abundant sessile animal was H. perlevis, which occurred mainly on low midlittoral rock surfaces. C. dentatus, S. krausii, C. meridionalis and T. serrata were present in low abundance on midlittoral rock surfaces. Filter-feeders often associated with wave exposed conditions had very low abundance, i.e. P. perna and O. angulosa. Other sessile fauna of note includes B. reynaudi, a sand-tolerant sea anemone.

The littorinid A. knysnaensis was still the most abundant gastropod, the numbers lower than at a shore with tall supralittoral rocks. The abundance of A. africana, however, appeared to be severely suppressed as it was only occasionally found. Siphonariids S. concinna and S. capensis occurred in roughly equal abundance from the littorinid zone to low shore strata. All other mobile gastropods occurred on much lower numbers. Of these Scutellastra cochlear was relatively the most abundant, although the densities attained in the cochlear zone was low. Scutellastra granularis numbers were very low compared to other sites. Other gastropods species that were commonly recorded at low abundance include O. tigrina, O.variegata, S. longispina, S. serrata, S. tabularis and Haminoea alfredensis.
Figure 88. PDB, Paradise Beach. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
9.3.3.7 Hougham Park West (HPW)

In the classification (Figure 89A) the cluster consisting of the infralittoral fringe (R8) and cochlear zone (R7) separated very early from other rock-bound assemblages which all had in common a pioneer species, *Blidingia minima*, that colonized newly exposed rock substratum and occurred as an epiphyte on algal turf species. As at a number of other sites, the sediment macrofauna formed two major clusters representing the assemblages of the high shore sediment (S0, S1) and the mid to low shore assemblages that were similar in composition.

Sediment macrofaunal abundance (Figure 89B) decreased sharply from the low tide swash line upshore. A large form of the meiofaunal polychaete *Polygordius* (data not shown) was highly abundant in the coarse sediment of this beach. Crustaceans were numerical dominants overall, the most abundant taxon being *Exosphaeroma estuariurn*, which occurred widely across the shore with other crustacean species, e.g. *Eorchestia rectipalma*, *Excirolana natalensis* in high shore sediment and *E. natalensis*, *Ischyromene huttoni* and *Isaeopsis tenax* and the midge *Telmatogeton minor* in the midlittoral. The low shore sediment yielded a more diverse assemblage which included Capitellidae, the bivalve *Brachidontes* sp, the isopod *Lanocira* sp1, polychaete *Cirratulus africanus*, chiton *Acanthochitona garnoti* and *Cerebratulus* sp. in the resurgence zone (S4) and *Exosphaeroma hylecoetes*, *Scoloplos johnstonei*, *Siphonaria concinna*, *Eunice cincta*, *Zuzara furcifer* (endemic), *Gastrosaccus psammodytes*, confined to the swashline/beach toe (S5).

Overall cover abundance on rock surfaces increased towards the low shore (Figure 89C). Although there was much rock surface at HWS, forming shaded overhangs, *Porphyra capensis* was rare in the supralittoral fringe, which rather comprised fairly abundant *Blidingia minima*, as well as *Cladophora* spp, *Petalonia fasciata*, *B. intricata* and *Ulva rigida*. The 5 most abundant algae were *Hypnea spicifera*, *Tayloriella tenebrosa*, *Polysiphonia incompta*, *Gigartina minima* and *Polysiphonia urbana*. *Hypnea spicifera* dominated the lower midtidal turf and infralittoral fringe with *Caulerpa filiformis*, *Rhodomelespia africana* and *Plocamium corallorhiza*, abundant only on the low shore. Macroalgae that occurred on the low shore in smaller quantities include *Pterosiphonia cloiophylla*, *Spongites yendoi* and *Corallina officinalis*. *Polysiphonia incompta*, *T. tenebrosa*, *Gigartina minima* and *Leptophytum* spp shared dominance in the turfs of midtidal to lower midlittoral zones (R4, R5 and R6) as the three most abundant macroalgae with a complement of less abundant species (*U. rigida*, *Pterocladiella caespitosa*, *Chylocladia capensis*, *B. minima*, *P. fasciata*). In the upper midlittoral turf, *B. intricata* was the most abundant species mixed with small quantities of lower
Figure 89. HPW, Hougham Park West. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
midlittoral turf dominants. The midlittoral alga, *Gelidium pristoides*, was present in very low abundance, occurring as a short turf-form with *Chthamalus dentatus*, and among midlittoral turf algae. The cochlear zone (R7) was indistinct as *S. yendoi*, the encrusting alga normally indicative of it, though abundant on the low shore, was extensively overgrown by the large turf-forming algae of the infralittoral fringe.

*Perna perna* was the dominant sessile filter-feeder (Figure 89C), extending into the infralittoral fringe and midtidal surfaces. Two other bivalve species, *Choromytilus meridionalis* and *Mytilus galloprovincialis* were present in upper midlittoral zones but at very low abundance. *Octomeris angulosa*, usually indicative of wave-exposed conditions, was most abundant in upper midlittoral reaches, with lower quantities of *C. dentatus* above midtidal level and *Hymeniacidon perlevis* and the reefworm *Gunnarea capensis* in the lower.

Two littorinids, *Afrolittorina knysnaensis* and *A. africana*, *Siphonaria capensis* and *S. concinna* were the most abundant gastropods (Figure 89D) and extended across most of the intertidal. *Scutellastra cochlear* occurred in somewhat lower densities confined to the cochlear zone (R7). Other gastropods common on midlittoral surfaces included *Siphonaria serrata, S. oculus, Scutellastra granularis, Helcion concolor* and * Oxystele tigrina*.

9.3.3.8 Three Sisters (TST)

Classification of samples (Figure 90A) also resulted in a separation of low shore (R6, R7 and R8) from midlittoral assemblages which formed a separate cluster from the supralittoral fringe (R0, R1). The infralittoral fringe macroalgal turf (R8) was, however, placed closer to midlittoral turfs due to upward range extensions of some infralittoral species and the extensive cross-shore distribution of *Gelidium pristoides*, *Ulva rigida* and several small wave- and sand-tolerant turf-forming species (notably, *Bostrychia intricata, Gigartina minima* and *Jania crassa*) at this site.

Sediment macrofauna separated into three clusters corresponding to the low (S4, S5), mid (S2, S3) and upper (S0, S1) shore.

Beach macrofaunal abundance (Figure 90B) decreased upshore from the low tide swash sediment with a slight midlittoral peak. Polychaetes were the most abundant, followed by isopods. *Scoloplos uniramus* and *Pseudonereis variegata* were the most abundant polychaete species overall. *Exosphaeroma hylecoetes* and *Eurydice longicornis* were the most common isopods both widely distributed across the shore, with highest numbers of *E. hylecoetes* in midlittoral sediment (S3) and *E. longicornis* in mid- to low littoral strata (S3 and S4). *Excirolana natalensis*
Figure 90. TST, Three Sisters. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
occurred between the wrackline and upper midlittoral sand (S0, S1 and S2), reaching its highest abundance on the high shore (S1) with *Excirolana latipes*. Midlittoral sediment (S3) further yielded an abundance of polychaetes, notably *Scoloplos uniramus, Pseudonereis variegata, Lumbrineris caviotrons, L. heteropoda heteropoda* and *Orbinia angrapequensis*. Many polychaete species did not occur further upshore from the swashline/infralittoral sediment, e.g. *Lumbrineris tetraura, Scololepis squamata, Scoloplos johnstonei, Lumbrineris tetraura, Notomastus aberans, Paradoneis lyra*. Those that did were present in much lower numbers, e.g. *Scoloplos uniramus, Pseudonereis variegata* also reach its greatest densities. Swashline sediment also yielded low numbers of the hipid *Emerita austroafricana*.

Midlittoral and infratlltoral fringe rock substrata were extensively covered by a diverse algal turf and cover abundance was unusually high even in the supralittoral fringe habitat (Figure 90C). There was extensive supralittoral rock surface (cliff) with a shaded overhang. *Porphyra capensis* reached about 3% cover with *Hildenbrandia lecannellieri* and *Leptophytum* spp and shaded surfaces supported an assemblage dominated by *Bostrychia intricata*, with smaller quantities of *Ulva rigida, U. prolifera, Blidingia minima* and *Cladophora* spp. *Gelidium pristoides* (character species for R4) was the most abundant alga overall, occurring throughout the midlittoral (in its own stratum) as well as the low and upper intertidal reaches as tufts, the turf growth form and occasionally the low branching (grazed) form. *Ulva rigida, Caulacanthus ustulatus, Leptophytum* spp, dominated the mid to low eulittoral. An unidentified *Jania* sp. was highly dominant with *Gelidium reptans* and *Pterocladiella caespitosa* in upper midlittoral turf which covered an extensive cross-shore area. Additional common turf elements included *B. intricata, Gigartina minima, Arthrocardia carinata* and *Jania crassa*. Dominant infralittoral fringe algae comprised *Caulerpa filiformis* and *Hypnea spicifera*. Other species of the infralittoral association present in much lower abundance included *Halimeda cuneata, Rhodomelopsis africana, Amphiroa beauvoisii* and *Ecklonia radiata*. The cochlear zone (R7) was poorly represented, perhaps because of undersampling at this site due to unsafe conditions. *Spongites yendoi* was locally dominant, so some degree overgrown by larger forms, and *Gelidium micropterum* occurred in low abundance. The most abundant sessile filter-feeder was *Perna perna*, dominant and extensive in the wave-exposed lower eulittoral. Other sessile taxa abundant on eulittoral rock substratum included *Spirobranchus kraussii, Tetaclita serrata, Chthamalus dentatus, Octomeris angulosa* and *Gunnarea capensis*.
The most abundant gastropod (Figure 90D) was *Afrolittorina knysnaensis*, followed by *Scutellastra granularis*, *Siphonaria capensis*, *A. africana* and *Siphonaria concinna*, these co-occurring across the intertidal from the supralittoral fringe to low eulittoral turf (R5). Except for *A. africana*, these molluscs occurred widely throughout the midlittoral. *Scutellastra cochlear* was represented by rather low numbers.

9.3.3.9 Cape Recife East (CRE)

Classification resulted in a pattern common to other mixed substrate sites with an extensive rock component, where the infralittoral fringe (R8), cochlear zone (R7) and *Perna* zone (R6) formed a cluster separating early from remaining rock-bound assemblages (Figure 91A). In the second cluster, the upper and lower eulittoral turfs (R3 and R5) were associated and the assemblages of elevated rock surfaces midlittoral rock surfaces (R2, R4) had more common with the limited supralittoral fringe (R1). The sediement macrofauna assemblages formed three clusters corresponding to the low (S4, S5), mid (S2, S3) and upper shore (S0, S1). The low shore cluster exhibited a high level of dissimilarity to the mid- and upper shore clusters due to a highly diverse assemblage of species mainly confined to that shore elevation.

Beach macrofaunal abundance (Figure 91B) decreased upshore from the beach toe (S5) with a slight peak towards the wrackline (S1). Polychaetes were most abundant, followed by amphipods, both taxa concentrated at the low shore, while high shore stations were dominated by oligochaetes. Molluscs were absent. *Scololepis squamata* was the overall numerical dominant, highly abundant at the beach toe. Aside from oligochaetes (Enchytraeidae spp) high shore sand yielded polychaete species (e.g. *Scololepis squamata*, *Scoloplos johnstonei*), insects (*Abraeus* sp1, *Telmatogeton minor*, *Melyridae* spp) and the amphipod *Urothoe serrulidactylus*. Midshore sediment (S2 and S3) harboured *Eurydice longicornis* (most abundant) with smaller numbers of the rocky shore amphipod *Cyproidea ornata* and polychaete *Scoloplos uniramus*. The numerical dominants in low shore sediment (S4 and S5) were *S. squamata*, *U. serruridactylus* and *S. johnstonei*. Other taxa found in somewhat lower numbers included the polychaetes *Mediomastus capensis*, *Nerinides gilchrist*, *Capitella capitata*, *Pseudonereis variegata*, *Neanthes willeyi* and *Prionospio* sp., isopods *Exosphaeroma hylecoetes*, *E. laeviusculum*, *Eurydice longicornis* and *Ischyromene magna*, amphipods *Cyproidea ornata*, *Atylus swammerdamei* and *Lysianassa ceratina*, known from sandy gravel as well as phytal habitats.

Overall cover-abundance was high (Figure 91C) except in the upper eulittoral barnacle stratum (R2) and the elevated midlittoral *Gelidium* stratum (R4). *Porphyra capensis* was absent, leaving only the R1 or littorinid sampling stratum, which was also much reduced, mainly due to a
Figure 91. CRE, Cape Recife East. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
smaller vertical extent of rock compared to sites of other configurations. Macroalgae of the supralittoral fringe comprised *Bostrychia intricata*, *Gelidium reptans* and *Hildenbrandia lecannellieri*, all in very small quantities. As at other low platform sites, midlittoral (R3 and R5) and infralittoral fringe (R8) macroalgal turfs were extensive. The 5 most abundant macroalgal species in these assemblages were *Arthrocardia flabellata*, *Laurencia natalensis*, *Hildenbrandia lecannellieri*, *A. filicula* and *Leptophytum* spp. Other species associated with these included *Jania adhaerens* and *Ulva prolifera*, mainly in the upper midlittoral turf (R3), *Laurencia pumila*, *G. pristoides*, *Acrosorium acrospermum*, *Caulacanthus ustulatus* and *Codium lucassii*, added in the lower midlittoral turf (R5), and *Arthrocardia duthieae*, *Plocamium corallorhiza* and *Dictyota dichotoma* added in the infralittoral fringe.

*G. pristoides* (R4 stratum) occurred as discrete clumps or in the low branching form on elevated midlittoral surface, but was much reduced in extent compared to rocky shores with high midlittoral rock surfaces. Encrusting algae (*H. lecannellieri*, *Leptophytum* spp and *Ralfsia verrucosa*) and short corallines (*A. flabellata*, *A. filicula*) were associated with *G. pristoides* on elevated surfaces. The cochlear zone (R7) was confined to raised surfaces of rock in the infratidal fringe zone, with much of it overgrown by turf-forming macroalgae, e.g. *A. filicula*, *A. duthieae*, *C. ustulatus*, *Hypnea viridis*. *Spongites yendoi* and *Gelidium micropterum* were present in low quantities. As at the similar site, CNR, sessile filter-feeder abundance was low, but perhaps less reduced by comparison. *Hymeniacidon perlevis* occurred mainly on upper midtidal surfaces with algal turf (R3) and also appeared in low shore assemblages (R5, R7 and R8). Sessile filter-feeders normally abundant on high rocky shores were reduced in number, and *Octomeris angulosa*, *Tetraclita serrata* and the mussel *Perna perna* much more so than *Chthamalus dentatus*. Small aggregates on lower eu-littoral rock surfaces were overgrown by algal turf. *P. perna* also occurred among *Scutellastra cochlear* in the cochlear zone (R7). The sand-tolerant bivalve *Choromytilus meridionalis* was not recorded here.

Though it was the most abundant at this site, *Afrolittorina knysnaensis* numbers were lower compared to other sites, tailing off rapidly towards the low shore (Figure 91D). The other gastropods of numerical importance included *Siphonaria concinna*, *S. capensis* and *S. serrata*, all abundant across the midlittoral, and *Scutellastra cochlear*, densely packed in the limited cochlear zone. The cochlear stratum (R7) appeared to overlap with the *Perna* stratum (R6), as the two species occurred together in both sampling strata where one of them is the dominant. Other molluscs that were fairly abundant in the midlittoral zone comprise *A. africana*, *Scutellastra granularis*, *Cymbula oculus* and *S. longicosta*. 

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9.3.3.10 Miller's Beach (MLS)

The cluster analysis produced clear separations of the infralittoral, eulittoral and supralittoral rock surface assemblages (Figure 92A). The supralittoral fringe was much reduced in extent (only R1), midlittoral turfs extensive and similar in composition (R3, R5) in contrast to the assemblages of raised rock surfaces (R4, R6) and the infralittoral fringe (R8) and cochlear zone (R7). Following the trend at mixed substrate sites with limited, water-logged beaches, clusters formed by sediment macrofauna reflected bimodal cross-shore distribution patterns, hence the pairing of the swashline-beach toe (S5) and upper midlittoral (S2) assemblages.

Macrofauna abundance in sediment diminished upshore from the swash line/infralittoral level with a smaller midlittoral peak in numbers (Figure 92B). This highly diverse assemblage lacked highly dominant species. Polychaetes were the most abundant group and most abundant species, after *Polygordius*, was the colonial *Fabricia capensis*. Crustacea (amphipods) were the next most abundant mainly because of high numbers of the amphipods *Urothoe pinnata* and *U. serrulidactylis*. The wrackline (S0) was dominated by insects, the most abundant of which was an unidentified species of Orsellinae (Hemiptera). Several species were common in both upper and low shore sediments, notably, *Excirolana natalensis*, *Paramoera capensis* (a rocky shore amphipod), *Eurydice longicornis*, *Scoloplos* species, *Urothoe pinnata*, *Pseudonereis variegata*, *Urothoe serrulidactylis*, *Scololepis squamata*, *Notomastus aberans*, *Exosphaeroma hylecoetes*, *Donax burnupi* and *Cerebratulus* sp.

The shore sediment (S4 and S5) harboured diverse assemblages. *Urothoe serrulidactylis* was the most abundant species in S4, followed by three species of roughly the same abundance (*Urothoe pinnata*, *Exosphaeroma hylecoetes* and *Scoloplos johnstonei*) and in lower numbers *Cerebratulus* sp, *Scololepis squamata* and *Lumbrineris heteropoda heteropoda*, as well as *Eurydice longicornis*, *Excirolana natalensis*, *Paramoera capensis*, *Hyale grandicornis* and a few polychaete species, e.g. *Arabella iricolor*, *Marphysa depressa*, *Pseudonereis variegata*.

*Fabricia capensis* and *Urothoe pinnata* were close numerical dominants of S5, the sediments at the beach toe and of sand patches over rock substrate. Somewhat less abundant species included *Urothoe serrulidactylis*, *Cirratulus chrysoderma* and *Timarete tenticulata*. Lower numbers of *Cerebratulus* sp, *Exosphaeroma hylecoetes*, *Syllis armillaris*, *Scoloplos johnstonei*, *Paramoera capensis*, *Nerinides gilchrist* and *Eurydice longicornis*, as well as polychaetes (e.g. nephtids and spionids) and species not usually associated with beach sediments (e.g. *Acanthochiton garnoti*, *Anthostella stephensoni*, *Cymbula miniata*) were recorded from this fine sand.
Figure 92. MLS, Miller’s Beach. Cluster analysis of samples (A), abundance of macrofauna in sediment (B), cover-abundance of macroalgae and sessile macrofauna on rock substrate (C) and gastropods (D). Overall abundance (solid black line) and *A. knysnaensis* are shown on the secondary y-axis (right). Abundance of other species (bars) is shown on the primary y-axis.
The mid-low eulittoral and infralittoral rock platform at this site was almost completely covered in algal turf, only elevated midlittoral rock surfaces (R4, R6) and the upper barnacle stratum (R2) had bare areas (Figure 92C). *Porphyra capensis* was absent from this site and the littorinid stratum (R1) reduced in vertical extent. The upper balanoid zone (R2) had mostly encrusting forms like *Ralfsia verrucosa*, *Hildenbrandia lecannelli*eri and *Leptophyllum* spp. The midlittoral turfs (R3 and R5) were most extensive, so that prominent members of these two turfs, i.e. *Arthrocardia flabellata*, *Polysiphonia urbana*, *A. filicula*, *Leptophyllum* spp. and *Jania crassa* were the also overall numerical dominants. The most common species of the low shore (R5 to R8) were *A. filicula*, *J. subulata*, *Halimeda cuneata*, *Dictyota dichotoma*, *Plocamium corallorhiza*, *Laurencia pumila* and *Corallina officinalis*. *Gelidium pristoides* was much reduced in quantity but widespread intertidally, occurring in appreciable amounts only on raised rock surfaces in midtidal reaches, in low amounts among upper midlittoral turf algae, with *Perna perna* in R6 and in the infralittoral fringe (R8). The algae of the cochlear zone (*Spongites yendoi* and *Gelidium micropterum*) were restricted to the tops of embedded boulders, occurring with algae of the infralittoral fringe (*Arthrocardia carinata*, *A. filicula*, *Laurencia pumila* and *C. officinalis*) and were partly overgrown.

*Hymeniacidon perlevis* was the dominant sessile animal (Figure 92C), growing over much of the mid to low midlittoral and extended into the infralittoral fringe. *Chthamalus dentatus* was fairly common on upper to midlittoral raised rock surfaces, together with *Spirobranchus kraussii*. Some of the usual rocky shore filter-feeders (*P. perna*, *Octomeris angulosa*, *Tetraclita serrata*) were present in very low numbers: *P. perna* in its own and adjacent strata at a midlittoral elevation and the two barnacles in the upper and lower midlittoral.

The most abundant gastropods (Figure 92D) were littorinids *Afrolittorina knysnaensis* and *A. africana*, the siphonariid limpets *S. capensis* and *S. concinna*, and trochids *Oxystele variegata* and *O. tigrina*. The littorinids had an extremely wide cross-shore distribution, while the siphonariids and trochids were only seen in midlittoral reaches, occupying the same surfaces as *Scutellastra granularis*, *Burnupena lagenaria* and *Siphonaria. serrata*. *Scutellastra cochlear* was found in low numbers with the algae characteristic of the cochlear zone.
CHAPTER 10 Geographical distribution of mixed substrate shores along a section of the Eastern Cape coast

10.1 The extent of mixed substrate shores, sandy beaches and sand-free rocky shores

The greater proportion of the 380.4 km section of coast between Kruis River mouth and Great Fish Point, i.e. 40% (150 km), consisted of mixed substrate shores as defined in this study (Table 39). When each mixed substrate shore configuration type is taken as a separate shore type on a par with sandy and rocky shores, i.e. six shore types in total, the purely sandy shores occupied the greater proportion of the coast, followed by purely rocky shores and the high ridge mixed substrate configuration (i.e. ridges throughout the intertidal mixed with sand deposits), while the two platform configurations and the low shore ridges were uncommon.

Table 39. The overall length and proportion of shoreline taken up by each mixed substrate shore configuration, as well as purely rocky and purely sandy shores. HWS = spring high tide level, LWS = spring low tide level, MSL = mean sea level.

<table>
<thead>
<tr>
<th>Type</th>
<th>Distance (km)</th>
<th>Percentage of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandy beaches with no visible outcrops of rock.</td>
<td>136.251</td>
<td>35.82</td>
</tr>
<tr>
<td>Rocky shore (platform/ridges) with no visible sand deposits</td>
<td>92.576</td>
<td>24.34</td>
</tr>
<tr>
<td>Ridges between HWS and LWS with sand deposits (Configuration 1 h/s).</td>
<td>54.983</td>
<td>14.46</td>
</tr>
<tr>
<td>Ridges below MSL with a sandy beach (Configuration 1 m/s).</td>
<td>35.348</td>
<td>9.29</td>
</tr>
<tr>
<td>Platform between HWS and LWS with sand deposits or beach (Configuration 2 h/s).</td>
<td>34.062</td>
<td>8.95</td>
</tr>
<tr>
<td>Platform below MSL with a sandy beach (Configuration 2 m/s)</td>
<td>27.151</td>
<td>7.14</td>
</tr>
</tbody>
</table>

10.2 Distribution of mixed substrate shores in relation to sandy beaches and sand-free rocky shores

Mixed substrate shores rarely extended for more than a few kilometres of coastline in one stretch before being replaced by either a different mixed configuration, rocky shore section or a sandy beach (Figures 93 to 96). Some sections of mixed substrate shore were only a few tens of metres in length. Intermingling of shore types occurred mainly along straight sections of coast and near rocky points, while the embayed portions were composed of sandy beaches for most part.
Figure 93. The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 24° 00' 00" and E 24° 45' 00".
Figure 94. The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 24° 45' 00" and E 25° 35' 00".
Figure 95. The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 25° 35' 00" and E 26° 25' 00".
Figure 96. The distribution of mixed substrate shores, purely rocky and purely sandy shores. Study sites are labelled in bold print. The section between E 26° 25' 00" and E 27° 15' 00".
About 70% of the high ridge mixed substrate sections occurred between sand-free rocky shores in wave exposed positions, about 10% between a rocky stretch and sandy beach in embayments and the remainder associated with high or low platform sections on either embayed or open coast.

Low ridge mixed sections (shale) were rarely found with sand-free rocky shores (about 2% of shores), but commonly with sandy beaches in embayments (about 70% of low ridge shores) and adjacent to high ridge or high platform shores outside of embayments. Along this stretch of coast it was not found next to low platform shores.

The remains of aeolianite platforms with a supralittoral cliff (high platform shores) occurred adjacent to rocky shores and high ridge mixed substrate shores along wave-exposed sections of coast outside of embayments (about 10% of high platforms). The remaining high platforms were associated with either a sandy beach-dune system or low platforms with sand in roughly equal proportions. Although sections of platform may have been sufficiently steep and high to be without sand deposits, this was difficult to determine even at the resolution used.

The majority of low platform shores occurred east of Algoa Bay. There were only two very short sections of this form of mixed substrate configuration in the stretch of coast west of Cape Recife, but the longest continuous section of low platform shore occurred immediately east of Cape Recife (study sites CRE/ Cape Recife East, MLS/Miller's Beach and MPB/Pollock South) within Algoa Bay. At four localities (less than 20%), low platforms had a high ridge mixed substrate shore on one side, but in the majority of cases (roughly 50:50) they were flanked by a sandy beach or high platform shore on one or both ends. All these platforms were backed by narrow associated sandy beach-dune systems.
Chapter 11 Discussion

The shore configurations of this study relate to hypothetical physical categories envisaged by Bally et al. (1984) and Brown et al. (1991) for the southern African subcontinent. Study sites range from almost sand-free rocky shores to practically rock-free sandy shores. Careful prior observation of spatial and temporal variation reduced error in site choice. Even so, there were study sites difficult to classify on a structural basis due to the combination of rock type (ridge with platform at Humewood) and placement (shore linear ridges instead of shore normal at Beacon Rock and Bird Rock). In such cases the site was placed in a configuration category that best corresponded to its most prominent rock formation in stead of creating a new category. The more common error of misinterpreting a mixed substrate shore as rocky or sandy was eliminated (e.g. McLachlan et al. (1977, 1981), Carter (1986), Munnik (1987), Fischer (1989), Van Zyl and Robertson (1991), Dobkins (1992), Bustamante et al. (1995), McLachlan and McGwynne (1986), McGwynne et al. (1988)).

Study sites are comparable to those of Dower (1989), representative of the coastline between Cape St Francis and Great Fish Point (see Marker 1988) and structurally similar to mixed substrate shores, some interpreted as sandy or rocky coasts, in other parts of the globe (e.g. Stephenson and Stephenson (1972), Littler and Murray (1975), Daly and Mathieson (1977), Hay (1981), Littler and Littler (1981), Stewart (1982, 1983), Taylor and Littler (1982), Littler et al. (1983), Taylor and Hay (1984), Littler et al. (1991), Brown et al. (1991), Airoldi (2001), Hubbard and Dugan (2003), Schiel et al. (2006)).

11.1 Physical attributes of mixed substrate shores

11.1.1 Hard (rocky) substrata

The hardness of rock determines its susceptibility to erosion (Sunamura 1992): resistant rock types form prominent and rugged hard surfaces. Shore profile data of this study showed that sandstone-quartzite rock produced a rugged, irregular intertidal rock substratum and occupied a much greater range of elevations compared to shale and aeolianite shores. High ridge shores were broken to a greater degree by shore-normal gulleys than sediment-free rocky shores. Gulley width plays a role in the degree to which onshore sand transport takes place. Substantial intertidal sand deposits typically occurred at shores with wider gulleys. Shale formed low, narrow and very wide set ridges limited to the lower half of the intertidal zone. The reduced prominence of the rock component compared to sand gave the appearance of a truly mixed habitat, where the shore was mostly sandy.
The aeolianite platforms, at most slightly tilted with no sign of deformation (see Marker 1988) were featureless except where a cliff still persisted, differed greatly with regard to their cross-shore extent, but tended to occur as continuous expanses of rock with attached sandy beaches in the upper and/or lower reaches of the shore. Wide platforms provide much sand-free rock substratum reminiscent of a rocky shore, whereas the narrow platforms are more easily identified as mixed habitats.

11.1.2 Soft (sandy) substrata

11.1.2.1 Width and depth of sand deposits in relation to shore configuration

Study sites represent a continuum, with narrow, strongly geologically-controlled beaches at one end and wider, deeper sandy beaches with only small, isolated rock outcrops at the other. Between these two extremes there is a range of beach configurations increasing in width and continuity, and with different degrees and forms of geological control by adjacent hard substrata (see Jackson et al. 2005). The best developed beaches may have depths approaching that of sandy beaches in the bay, up to 4 m deep according to Lubke (1988), as copious amounts sand are available on bay bottoms (Bremner 1983; Tinley 1985). The most sediment-deficient beaches probably consist of thin veneers 10s of cm deep. Beach macrofauna, however, usually do not occur at depths greater than 30 to 35 cm (Eleftheriou and Holme 1984) which implies that they may only be significantly affected when the beach veneer is extremely thin (< 30 cm).

The main factors affecting availability of sand for beach accretion were distance from updrift dunes or sandy beaches and the degree to which the rock component (as cross-shore or long-shore rock extent, range of rock height ratings which infers complexity) controlled alongshore and cross-shore transport. The narrowest beaches occurred at study sites with wide and/or very rugged (high rock height rating) rocky traverses that were not adjacent to sandy shores, whereas those in close proximity to continuous sandy beaches and/or backed by dunes had wider beaches, regardless of configuration type. Rugged, complex rock traverses greatly reduce wave energy at the seaward edge, consequently, cross-shore transport of sediment is inhibited (e.g. Koehl et al. 1993; Jeffery and Underwood 2000) and limited sediment deposition occurs in the lee of the rocky traverse to form a shallow or narrow beach (Hoppley 1982; Muñoz-Pérez et al. 1999; Short 1999; Schiel et al. 2006; Jackson et al. 2005). A low cross-shore rock traverse (as platform or ridges) reduces wave energy without much interference with sand transport and allows more substantial (wider and deeper) beaches to form. Low relief, narrow rock traverses, on the other hand, appears
to control beach development via increased mobility of sediment due to an elevated water table (see Short 1999).

Shallow patches of sand occurred more often at wave-exposed high and low platforms and ridge shores with a high rate of sediment movement. Cross-shore sediment depth variation showed two main trends: depth decreasing towards the beach toe or towards the midshore reaches. Variations could only be detected at sites with thinner sand veneers. Sediment-deficient reflective beaches tend to exhibit the first, as beach erosion is limited to the lower tidal reaches (Bird 1983; Short 1999). The most plausible explanation for reduced depth in middle reaches is greater beach mobility due to increased saturation when the bed rock lies just below the surface of sediment (Short 1999).

Beach width and depth data suggest a spatial (and potentially functional) connection between at least some types of mixed substrate shores, sandy beaches and active dunes via wave processes driving on shore and along shore sand fluxes (see Tinley 1985, Bate and Campbell 1998). Deeper investigation could shed light on the dynamics of temporal change in sediment load on mixed substrate shores.

11.1.2.2 Sediment characteristics in relation to shore configuration

The sediment (particle size and type) of which a beach is composed is largely a geological inheritance and not a consequence of wave height regime (Short 1999). Sandy beaches and mixed substrate shores of the Eastern Cape coast all receive sediment, mostly derived from the drowning of the coastal plain sand dunes and beaches during the previous marine transgression, from nearshore bottoms (Bremner 1983; Tinley 1985). The South African coastline is mid-latitudinal which implies moderate to high swell conditions, quartzitic sands as well as carbonitic sediment and the full range of beach types (reflective to dissipative) (Short 1999). The predominant sediment type at study sites was quartzitic fine or medium sand with a negligible very fine fraction, resembling that of sandy beaches along St Francis Bay and Algoa Bay, e.g. McLachlan (1977a), McLachlan (1983b), McLachlan et al. (1984), Nel (2000), Schoeman et al. (2003). As all sites experienced at least moderate wave action and on a continuous basis, the loss of fines could be partly due to winnowing by wave action (King 1972) and partly geological control (Koehl et al. 1993; Jeffery and Underwood 2000; Jackson et al. 2005) modifying cross-shore sediment transport.

Sediment grain size composition differed across-shore, most sites showing a coarsening of sediment towards the low end of the shore, a characteristic associated with reflective beaches (Short 1999), but that may also be the remains of past storm activity (Bird 1983;
Jackson et al. 2005). A second trend was for sediments to be coarsest in midtidal reaches which implies higher wave energy (King 1972) and ties in with greater beach mobility (see Short 1999).

Carbonate content, though variable, was comparable to previous data of the region (McLachlan 1977a; Wooldridge et al. 1981; McLachlan et al. 1984) and relatively high, indicating an increased marine component in sediment (Bremner 1983; Tinley 1985). At these study sites, elevated carbonate content may result from resuspension and shore-ward transport of carbonate-rich particles from the bay bottom by local wind-driven upwelling.

Organic matter content of sediment was low except at some wave-sheltered beaches, where it was markedly increased. Values were in the same range as previously recorded bay data (1.02% to 3.41%: McLachlan et al. 1984). Low organic content is indicative of an active wave environment as particulate organic matter is easily resuspended and winnowed out by wave action (Brown and McLachlan 1990). Increased organic particulate matter could be due to added allochtonous matter (Garner pers.obs. 2006, 2008) or derived from biological activities in sediment (Brown and McLachlan 1990).

11.2 Dynamic attributes of mixed substrate shores

At all study sites, even rocky locations (also see McLachlan et al. 1984), wave shoaling and breaking occurred before arrival at the swashline/shoreline and resulted in a surf zone. The bottom topography in the nearshore region of Algoa and St Francis Bay allows the formation of surf zones ranging from 50 m to 500 m wide (see McLachlan et al. 1984). The widest surf zones at these sites form either over an extensive gently sloping soft bottom with or without low rock outcrops or entirely over a shallow hard bottom. In the latter case, the shallowness of the water relative to wave height and the gentle shoreward slope enable the formation of a surf zone over the rock platform (see Cowell et al. 1999; Sunamura 1992; Aagaard and Masselink 1999). The narrowest surf zones occurred at high ridge sites with continuous longshore intertidal rock and a high rock height rating. At these sites, the shore slope was also most likely steeper and wave breaking postponed almost to landfall. Unfortunately much of the nearshore morphology along the rocky sections of the two bays has not been investigated.

On sandy shores waves dissipate their energy in the outer surf zone (with a reduction in wave height) due to bottom-roughness of the sand bottom and then again as wave swash (Wang and Kraus 2005). In much the same way as a sand-bottomed surf zone, a rocky traverse causes dissipation and loss of wave energy (height) (Wang and Kraus 2005) and brings about low wave conditions on midlittoral and upper shore rock surfaces and sediment
deposits. Mixed substrate shore surf zones uniquely overlie both the sand prism and rocky traverse. This changes as the tide rises, a factor which exerts an influence on wave-beach interaction, wave energy dissipation patterns and water circulation within the surf zone, given that the rock traverse reduces wave energy more rapidly than a sand bottom (Hopley 1982; Lobban et al. 1985; Koehl et al. 1993).

Due to their low intertidal position, shape and low height, surf wave dissipation occurred mainly at the seaward ends of low ridges at low tides, but on a higher tide they were submerged and the surf zone was active on the beach. At high platform study sites narrow shore platforms extended no further seaward than the lower intertidal and the near-shore surf zone was sand-bottomed. At higher tidal levels, the surf zone also enveloped the rock plate where wave attenuation was usually intensified as a result of increased bottom-roughness due to algal turf (Roberts et al. 1975; Jokiel and Morrissey 1993; Short 1999; Peterson et al. 2004), but this was limited to a short distance and much of the wave energy was dissipated in the swash zone on the beach itself (Wang and Kraus 2005).

At study sites with wide sand-bottomed surf zones and limited intertidal rock expanses, after initial wave energy dissipation in the outer surf zone, additional attenuation took place as waves traversed intertidal rock surfaces. At those with hard-bottomed surf zones, i.e., wide, low platforms, wave energy dissipation simply continued over the rock traverse as wave shoaling and breaking occurred in the shallow water over the shore platform. Bottom-roughness was enhanced by the carpet of subtidal algal turf and potholes in the rock plate (see Roberts et al. 1975; Koehl et al. 1993).

Physical shore data of this study identified the range of rock heights relative to sea level (reflected in rock height rating, a measure of ruggedness or complexity) as an important variable in the control of water and wave action. At high ridge sites wave height was sharply reduced over a relatively short distance as compared to low ridge and platform sites, as irregular rock surfaces greatly increased bottom-roughness. A greater proportion of tall rock increases wave collision, reflection and wave splash (see Gaylord 2000). Increased rock height and bottom-roughness, especially at the seaward side of the shore greatly enhanced energy loss before waves entered midshore reaches (see Roberts et al. 1975; Koehl et al. 1993; Muñóz-Pérez et al. 1999; Short 1999; Larson and Kraus 2000) simply because of a greater extent of interaction between the hard substrate and incident waves (Larson and Kraus 2000; Gaylord 2000). In addition, rocky ledges and reefs form channels which control water flow patterns (see Roberts et al. 1975; Koehl et al. 1993) and affect transport processes and settlement patterns of biota (Koehl et al. 1993; Jeffery and Underwood 2000).
At low ridge sites, shore normal ridges had the same effect as groynes: changed nearshore surf zone circulation, sediment transport patterns and updrift accumulations or sand patches within the surf zone (Short 1999; Larson and Kraus 2000; Garner, pers. obs. 2006, 2007, 2008).

Wave-exposed sites with adequate sediment supply and rapid onshore-offshore, as well as along shore sediment transport, showed marked variations in the beach gradient (Garner, pers. obs. 2006, 2007, 2010). Shores with greater intertidal rock height produced steeper beaches, a testament to the attenuating effect of the rock section (see Muñóz-Pérez et al. 1999; Short 1999). Although coarse sediment tends to produce a steep gradient regardless of wave conditions because of greater infiltration rates and net onshore transport (Short 1999; Defeo and McLachlan 2005), the formation of a very steep, coarse-grained beach at a wave exposed shore, e.g. at Kini Bay (KNB), must indicate extremely effective wave attenuation that results from a combination of ruggedness (high rock height rating), rock pools and cross-as well as longshore extent of the rock traverse.

Wave-exposed sandy beaches of Algoa Bay and St. Francis Bay are in an intermediate morphodynamic state (McLachlan 1983b; Short and Masselink 1999). Study site beach states differed from those of adjacent sandy shores under a similar wave regime (Nel 2000; Schoeman et al. 2003). Hard structures (e.g. natural rock reefs or platforms and man-made structures) can have a marked influence on the characteristics of a beach by modifying wave processes and elevating the water table: factors that affect sediment mobility and transport (Short 1999; Jackson et al. 2005). This varies with wave regime and topographic features of the shore (see Short 1999).

Overall, attenuation at low ridge sites gave rise to an intermediate-reflective beach (see Short and Wright 1983). At high ridge shores beaches experienced little wave activity and were mostly reflective to reflective-intermediate (see Short 1999). High platform shore beaches were reflective and stable in upper reaches, but highly mobile and more intermediate in midlittoral reaches with rapid beach profile and sediment distribution changes over time (Short 1999). At these sites the shallow sediments that overlie the shore platform are easily lifted off and moved along when immersed during wave swashes as the rock platform makes the beach less stable by reducing permeability (Short 1999). Beaches at wave-sheltered low platform sites showed features of the dissipative state. Here the wave energy dissipation resulting from a specific combination of bottom topography relative to incident wave height and a fine-grained, low gradient beach (slopes between 1/15 (4°) and 1/50 (1°)), resulted in gentle, smooth swashes on the beachface, much like that of dissipative sandy beaches.
The degree of wave action at any shore is the most significant parameter controlling physical and biological attributes of the ecosystem. Mixed substrate shores have often been characterized as wave sheltered (e.g. Stephenson and Stephenson 1972), but more recent assessments have recognized a range of wave exposures (e.g. Lombard et al. 2004). Direct measurement of wave force and water movement is always difficult, whether at a beach or a rocky shore. The alternative is to derive wave exposure from other physical and/or biotic variables sensitive to changes in wave regime. McLachlan’s (1980) exposure rating, developed for sandy beaches, was applied to the mixed substrate shores in this study to investigate the effect of intertidal hard substrate on beach exposure rating. The difference between the rating calculated for full shore width (including rock traverses) and beach width only, gave the degree to which rock reduced wave exposure of the beach component.

Study sites with high rock height ratings (mostly high ridge sites) showed the greatest degree in reduction of wave exposure, e.g. from E (exposed) to S (sheltered). These data contrasted with highly wave-exposed narrow platform sites lacking surface complexity where the rock height rating was unaffected. Exposure rating also showed no reduction at the study sites with a small midtidal rock outcrop. Clearly the rock component exerted no influence on surf zone processes. A similar effect was seen at wave exposed low platform sites where the low elevation of the rock plate greatly reduced its potential to attenuate waves: exposure rating was unchanged and beach indices indicated a reflective rather than intermediate state as was evident in the field. On the other hand, there were also low platform study sites where a definite reduction in exposure rating of the beach was measured, resulting from a specific degree of wave attenuation by the platform due to its length, width and height compared to tidal range. The fine grained beaches at these sites have previously been described as wave-sheltered (also see McLachlan et al. 1977, McGwynne et al. 1988; Munnik 1987) and have slopes between 1/15 (4°) and 1/50 (1°), indicative of moderate wave energy and intermediate or dissipative conditions (Flemming and Fricke 1983; Short 1999; Jackson et al. 2005). From a biological point of view this could imply a stable environment with a tendency towards stagnation and anoxia as flow rates slow down (McLachlan 1983; Brown and McLachlan 1990).

Clearly both morphodynamic state and wave exposure of the beach are influenced by the presence of hard substrate. By imposing control over wave processes, the presence of hard structures reduces the predictive value of sandy beach indices like Dean’s parameter (Short 1999, Sunamura 1992, Jackson et al. 2005). Beach state indices (Dean’s parameter and BSI) of several study sites disagreed following a trend reported by Jackson et al. (2005) for geologically controlled Irish beaches. At sandy beaches, beach slope is strongly linked to beach state and significantly influences the living conditions of infauna by determining
percolation rates, oxygenation and desiccation patterns (Brown and McLachlan 1990). At these study sites the relationship between beach slope, beach state and shore configuration variables, i.e. cross-shore or mid-longshore rock and rock height rating, is complex and requires further investigation.

11.3 Biotic classification based on macrobenthic assemblages

The macrobenthic assemblages associated with sediment and hard surfaces formed the basis for a biotic classification of mixed substrate shores, systems that are virtually unknown, but well-represented in the South African context. This approach provided a means by which to overcome the often bewildering structural variation of these systems and to rather regard the response of the macrobenthos to time-integrated effects of interactions between physical and dynamic parameters of their environment.

The use of macrobenthos to characterise intertidal habitats and indicate environmental gradients is based on the precept that taxa respond to environmental factors in a predictable manner. By implication they can be used as indicators of a particular environmental driver or suite of parameters that independently or interactively determine the overall habitat conditions of intertidal communities (e.g. Ballantine 1961). Although particular species or assemblages of the sandy or rocky intertidal have known and consistent habitat preferences (Day 1974; McQuaid and Branch 1985; Nel et al. 1999; McArdle and McLachlan 1991, 1992; McLachlan and Jaramillo 1995; Brown 1996) these have so far been used on a case by case basis to suggest or verify environmental gradients in either sandy or rocky habitats and not become part of a broadly-based approach incorporating multiple species responses to indicate prevailing habitat conditions. Sand-inundation effects on the rock substrata and the influence of hard substrata on conditions in the sediment are environmental factors that affect the biota of mixed substrate shores in addition to the conditions universally associated with the intertidal habitat across biogeographical regions, i.e wave energy, desiccation gradients, sediment grain size, shore or beach slope, rock topography.

The presence of a prevalent taxon or taxa in a sampling zone was perceived to be indicative of particular environmental conditions, e.g. high or low flow rates, different levels of desiccation or oxygenation levels, mindful that most species have tolerance ranges that go wider than the range essential for life (Vermeij 1978). A major change in the abundance of such a taxon relative to others may signify a major difference in the required physical conditions. This is the basis of any biotic classification (e.g. Ballantine 1961, Lewis 1964).

On most of the world’s rocky coasts it has been possible to identify species that indicate high wave exposure (Ballantine 1961; Lewis 1964; McQuaid and Branch 1985) and indicators for
beach state linked to wave exposure have been identified (McLachlan and Jaramillo 1995). The same cannot be said of sheltered conditions on rocky shores (Blamey and Branch 2009), but in sandy habitats, polychaete dominance has been linked to wave shelter (Brown 2001). While the prevalence of macroalgae and changes in their physiognomy, have often been taken as indicative of shelter (Norton et al. 1981), on rock surfaces it may rather be the absence of wave-exposure dependent species that could signify an increase in wave shelter. If it works, the same argument could then be applied to other environmental factors, e.g. the presence of sediment around rock-bound communities.

The majority of the taxa that served as visual cues for recognizing the proposed mixed substrate shore biotic types inhabited the eulittoral zone. This is convenient for further study and future identification of subgroups in the three initial biotic types: the low shore becomes immersed much sooner than on rocky shores as there are not enough high rock formations in the lower intertidal reaches to “hold the tide and waves back”.

The mixed substrate shore biotic types identified in this study showed no particular affinity for any of the shore configuration types used in the physical shore classification. In the DCCA of all species, sites grouped in response to drivers that acted across configuration and not to shore configuration (ridges or platforms) *per se*. Classifying mixed substrate shores according to geology or configuration alone therefore does not provide a means by which to separate them according to functionality.

These meta-communities responded to combinations of environmental parameters that comprised dimensional shore components, i.e. rock height, width and long-shore extent of the rock traverse, sand inundation of rock, as well as dynamic factors, i.e. wave exposure and wave energy. The latter a major driver of intertidal communities for which previous biotic classifications (e.g. Ballantine 1961, Lewis 1964, Hill et al. 1998; Tittley and Neto 2000) and other studies (e.g. McQuaid et al. 1985) have successfully identified indicators. Ultimately, it appears, these communities respond to a time-integrated wave energy gradient that is brought about by the different degrees of structural control exerted on wave and water movement patterns by the intertidal and perhaps even subtidal hard structures. A reduction in rock outcrops within the surf zone results in a less pronounced cross-shore gradient in wave energy loss and consequently a more wave-exposed, sandy eulittoral zone.

The three potentially valid biotic types recognized, Type A (*Jania-Corallina-Polysiphonia* turfs), Type B (*Polysiphonia-Tayloriella-Caulacanthus* turfs), and, Type C (*Arthrocardia-Laurencia* turfs), were found to represent different positions along two gradients in particular: wave action/exposure and sand-inundation. Biotic type A represents a range of eulittoral wave-exposures, greater degrees of inundation of rock by medium to coarse-grained
sediment, but potentially more rapid sediment movement. Biotic type C represents the most wave-sheltered midlittoral, least sand-inundation but also finer grain sizes and greater beach stability. Biotic type B represents intermediate situations with regard to midlittoral wave energy, sand-inundation and grain sizes.

The number of species in each of the three mixed substrate shore biotic types identified in this study was similar, but composition and abundance patterns were sufficiently different to distinguish among them. However, their physiognomy was also indicative of change, as the same species could be small and delicate at a biotic type C locality and robust in A or B. Biotic type C had more species in common with local rocky shore communities than the other two and the least in common with purely sandy beaches. It may represent a transitional biotope between ‘true’ rocky shore and ‘true’ mixed substrate shore communities.

Within each broadly-described biotic type of this study there were potential “subtypes” linked to particular sites that were not replicated and that in all likelihood represented responses to other gradients that impinged on them, e.g. sediment grain size and swash climate. The fact that there were some site-linked responses does not imply that the shore configuration is more important than indicated by the DCCA. Structural variability of the coast will always introduce small-scale variation that could serve to enhance or suppress diversity and locally modify the general pattern (Lewis 1964; Stephenson and Stephenson 1972) by increasing or decreasing habitat variability at a scale relevant to the organism (Kostylev et al. 2005). Structural control of surf zone processes and wave energy transformation by hard substrate significantly had similar attenuation effects on waves (see Short 1999, Jackson et al. 2005) explaining how the macrobenthos of structurally dissimilar study sites could show an almost identical biotic response to the same variable in the DCCA.

11.4 Species richness, composition and abundance trends in macrobenthic assemblages

11.4.1 The general perspective: one shore, two substrata

This study is the first to report quantitative abundance data from South African mixed substrate shore sites, comprising the biotic assemblages of both sediment and hard substrate. Trends in species richness, composition and abundance of the macrobenthic assemblages of mixed substrate shores show some commonality with their equivalents from purely sandy or rocky shores, but sufficient difference to set them apart. Neither the macrobenthic assemblages of the rock surfaces nor those of the beach deposits showed evidence of reduced diversity and abundance that could be linked to the proximity of the other substratum type. For both reasons, based on statistically tested data, the null
hypothesis with reference to community composition is rejected. The macrobenthic assemblages of mixed substrate shores differ sufficiently in composition from those of purely sandy beaches and rocky shores to be characterized as unique.

The overall number of species and the taxonomic composition (animal phyla and macroalgal divisions) compared well to previous mixed substrate shore studies in South Africa (Dower 1989, McQuaid and Dower 1990, Brown et al. 1991). In line with previous species richness comparisons of rocky shores and sandy beaches (Brown and Jarman 1987; Field and Griffiths 1991; Brown 2001), rock substratum biota contributed more to overall species richness per site than beach macrofauna.

The high number of shared species on rock surfaces at ridge (sandstone-quartzite or shale) and aeolianite platform shores (over 50% for sediment fauna and over 80% for rock substrate fauna) shows that geology alone does not determine species richness and composition, a finding supported by previous work on mixed substrate shores (McQuaid and Branch 1984; Dower 1989). Rather, it could be effects resulting from the interaction between water, hard structures and sediment that influence overall habitat conditions. In this study, platform shores in general harboured significantly more species than ridge shores, a finding that opposes that of Dower (1989). However, only the low ridge and high platform shores of this study differed significantly in richness, purely due to the macroalgae. The reasons for this may be two-fold: first, the high platform shores offer much greater continuity in hard surface habitat compared to low ridge shores, affecting colonization rates (Sousa 1984, 1985), and, second, they are flat, which retards drainage and keep surfaces and interstices moist for longer, so enabling a variety of biota from lower elevations to extend their range into midlittoral reaches enriching those communities (Townsend and Lawson 1972; Lobban et al. 1985; Russell 1991; McLachlan and Jaramillo 1995). Intermittent sand-inundation further allows species with different levels of sand-tolerance to co-exist successfully as the habitat is diversified (Connell 1978; Sousa 1984, 1985; Connell and Keough 1985), but sand also enhances moisture retention which alone could explain increased numbers of species and abundance (Hay 1981) on horizontal surfaces as compared to ridge shores. The high platforms were also narrow, reducing the extent of surface exposed to heat and desiccation.

11.4.2 The macrofauna of the sediment

The sediments of mixed substrate shores have previously not attracted the attention of beach ecologists. These habitats have been perceived as species-poor and unable to support the population sizes associated with sandy beaches (Bally et al. 1984; Brown et al. 1991), consequently, very little is known about their macrofaunal assemblages. Organisms found in sand associated with rock have, however, been featured in various field guides (e.g.
Day 1967a,b 1974; Griffiths 1976; Kensley 1978; Branch et al. 2005, 2010) and identified in two previous works on mixed substrate shores, Brown et al. (1991) and Dower (1989). Neither study provided further quantified data useful for comparison. Sediment macrofauna data of this study is compared only to sandy beach studies.

11.4.2.1 Species richness and overall abundance compared to other studies

Macrofaunal species richness and total abundance of this study was lower than that of Western Cape beaches in Bally (1981), but on average higher than South African sandy and mixed shores (Table 40) with a comparable range of slopes, grain sizes and exposures (McLachlan 1977; Dye et al. 1981; McLachlan et al. 1981; Wooldridge et al. 1981; Dower 1989; Nel 2000; Schoeman et al. 2003; Todkill unpub.). Study sites under similar wave attack as nearby sandy beaches were up to 3 times more species rich (compared to data of McArdle and McLachlan (1991, 1992); McLachlan (1977a,b); Nel (2000); Schoeman et al. (2003)).

Species richness and total abundance also exceeded expectations according to globally based estimates of Defeo and McLachlan (2005) and McLachlan and Dorvlo (2005) for temperate reflective-intermediate beaches and beaches with fine to medium sand, as well as those with a similar width range to these study sites (see McLachlan and Dorvlo 2007). Total abundance and density compared well with some studies from other parts of the world on intermediate beaches, e.g. Hacking (1998), Rodill and Lastra (2004), but were appreciably lower than those reported from temperate dissipative beaches (e.g. Degraer et al. 1999, 2003; Janssen and Mulder 2005) and others with a similar granulometry and beach state as these sites, e.g. Lercari and Defeo (2003).

11.4.2.2 Species richness and overall abundance in relation to environmental variables

Macrofaunal species richness and taxonomic diversity, abundance and density usually increase with flatter slope, greater beach width, finer sand, lower wave height and slower swash on the beach face, all of which are linked to dissipative conditions in the surf zone (McLachlan 1990; McLachlan et al.1993; Brown and McLachlan 1990; Brown 2001; Dugan et al. 1994; Defeo and McLachlan 2005; McLachlan and Dorvlo 2005, 2007). These same variables also confer greater beach habitat complexity (Hacking 1998) and variability (McLachlan and Dorvlo 2005). Change in the above community parameters is also linked to a number of indices of beach state (Defeo and McLachlan 2005; McLachlan and Dorvlo 2005).
Table 40. Species richness compared to relevant previous studies. An asterisk (*) indicates a mixed substrate shore that was sampled as a sandy shore. Possible shore configurations derived from site information are given in brackets. The numbers given in brackets include insects. 
N = number of study sites. Regions: Eastern Cape = 1, Western Cape = 2.

<table>
<thead>
<tr>
<th>Author(s) and date of publication</th>
<th>Reg.</th>
<th>Mesh size (mm)</th>
<th>N</th>
<th>Total (n)</th>
<th>Mean</th>
<th>Range (n)</th>
<th>Shore type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Garner (unpub, this study)</td>
<td>1</td>
<td>1</td>
<td>20</td>
<td>166 (196)</td>
<td>32</td>
<td>10 - 52 (10 - 55)</td>
<td>20 mixed (high ridge, low ridge, high platform, low platform)</td>
</tr>
<tr>
<td>Dower (1989)</td>
<td>1</td>
<td>1</td>
<td>10</td>
<td>26</td>
<td>11</td>
<td>3 - 18</td>
<td>10 mixed (low ridge, high platform, low platform)</td>
</tr>
<tr>
<td>Todkill (unpub.)</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>15</td>
<td>8</td>
<td>7 - 9</td>
<td>3 mixed (high ridge, low ridge, low platform)</td>
</tr>
<tr>
<td>McLachlan (1977)</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>12</td>
<td>9</td>
<td>4 - 11</td>
<td>4 sandy</td>
</tr>
<tr>
<td>Dye et al. (1981)</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>14</td>
<td>4</td>
<td>1 - 10</td>
<td>4 sandy</td>
</tr>
<tr>
<td>McLachlan et al. (1981)</td>
<td>2</td>
<td>4</td>
<td>5</td>
<td>14</td>
<td>10</td>
<td>7 - 12</td>
<td>5 sandy</td>
</tr>
<tr>
<td>Wooldridge et al. (1981)</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>24</td>
<td>8</td>
<td>3 - 15</td>
<td>3 sandy, 1 mixed* (low platform)</td>
</tr>
<tr>
<td>McGwynne et al. (1988)</td>
<td>1</td>
<td>-</td>
<td>2</td>
<td>zero</td>
<td>-</td>
<td>-</td>
<td>2 mixed* (high ridge)</td>
</tr>
<tr>
<td>Nel (2000)</td>
<td>1,2</td>
<td>1</td>
<td>14</td>
<td>42</td>
<td>18</td>
<td>5 - 21</td>
<td>14 sandy</td>
</tr>
<tr>
<td>Jaramillo et al. (1995)</td>
<td>1</td>
<td>1</td>
<td>11</td>
<td>11</td>
<td>11</td>
<td>11</td>
<td>1 sandy</td>
</tr>
<tr>
<td>Brown (1971)</td>
<td>2</td>
<td>?</td>
<td>6</td>
<td>26</td>
<td>18</td>
<td>12 - 21</td>
<td>3 sandy, 3 mixed* (low ridge)</td>
</tr>
<tr>
<td>Schoeman et al. (2003)</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>28</td>
<td>16</td>
<td>12 - 21</td>
<td>3 sandy</td>
</tr>
</tbody>
</table>
In this study, beach macrofauna species richness did not vary significantly with shore configuration, assumed to provide habitat structure and affect processes, or biotic shore type, assumed to represent the community response to conditions. Although species numbers varied from site to site, there was no trend that could be linked to the occurrence of platforms, ridges or community composition. Species richness also showed no trend with sediment depth, grain size, beach slope, the extent of rock across shore or any of the beach indices calculated, but was significantly correlated with the extent of rock in a shore linear direction. This was telling, as a greater long-shore extent of rock could potentially greatly modify conditions on an upshore beach.

Study sites with platforms and closely-spaced ridges had reflective beaches, yet none with the low numbers of species expected of such a beach type. It appears that the hard substrate and algal growth ameliorate wave conditions and afford a degree of wave-shelter that allows more species to co-exist than otherwise expected (Roberts et al. 1975; Jokiel and Morrissey 1993; Koehl et al. 1993; Short 1999; Peterson et al. 2004). There could also be additional food input linked directly or indirectly to algal primary production. In addition, sand-tolerant species were probably added from the rock-bound communities (see Hacking 1998). A continuous rock expanse could also change drainage patterns through sediment, elevating the water table (Short 1999) as seen at dissipative beaches (Brown and McLachlan 1990). Although the water table was not investigated in this study, there was ample evidence of water table elevation as a result of a shallow rock bottom under the sediment. If would thus be possible for delicate forms such as polychaetes to maintain a presence on the beachface and so enrich the macrofaunal assemblage.

Abundance of the sedimentary assemblages increased significantly (p< 0.05) with grain size, beach slope and the amount of long shore rock, but showed no relationship with other shore variables and indices calculated. These findings are contrary to abundance trends at sandy beaches. This was partly due to increased numbers of *Polygordius* (of macrofaunal size) in coarse sediment of study sites with steep reflective beaches, e.g. platform and high ridge shores. Polygordiid polychaetes are often found in large concentrations in coarse-grained intertidal and subtidal sediments (Ramey et al. 2006).

With site data grouped as mixed substrate shore biotic types, the mean number of beach macrofauna species (30 to 32 species) and abundance were higher than the usual range for intermediate sandy beaches, approaching levels normally expected of dissipative beaches (Bally 1981, Hacking 1998; Brown 2001, Degraer et al. 1999, 2003; Janssen 2005). Macrofauna abundance levels were indicative of wave-sheltered conditions normally due to wave energy dissipation in the surf zone (Brown and McLachlan 1990, McArdle and
McLachlan 1991) and compared rather to that of sublittoral sediment (McLachlan et al. 1984), but with a similar degree of variability to assemblages in medium to fine sediments of intermediate beaches.

Results therefore show that species richness and overall abundance of sediment macrofauna increase at mixed substrate shores of this study most probably in response to sedimentary habitat conditions brought about by hard substrate, regardless of actual configuration, where the greater continuity of a shore linear rock component more significantly influences important variables such as drainage patterns, saturation, sediment grain size, depth and beach slope. This effect may be enhanced by biological activity of hard substrate biota.

11.4.2.3 Overall taxonomic composition compared to other studies

Polychaetes, crustaceans and molluscs constitute the majority of marine macrofauna species in sandy beaches worldwide, with crustaceans and molluscs usually the most diverse (Brown 2001; Defeo and McLachlan 2005).

The proportional contribution of polychaetes, crustaceans (as isopods and amphipods) and molluscs (bivalves and gastropods) to total species richness at study sites differed markedly from the norm at sandy beaches. Here, polychaetes exhibited increased diversity (up to 40% of species), while molluscs were clearly under-represented (about 7%). These findings contrast sharply with the most common trend at South African sandy beaches: gastropods or crustaceans are usually the most diverse (30% and 70% of species), while polychaetes contribute up to 20% (McLachlan 1977b; Dye et al. 1981; McLachlan et al. 1981; Wooldridge et al. 1981; Nel 2000). Eastern Cape intermediate beaches are especially rich in mollusc species (Nel 2000): their suppressed diversity at mixed substrate shores is of some importance. On balance, in two other studies of South African sandy beaches, crustaceans and polychaetes each made up in the region of 40% of species and molluscs 20% (Brown 1971; Schoeman et al. 2003).

11.4.2.4 Overall taxonomic composition in relation to environmental variables

From locality data, it is possible that both Brown (1971) and Schoeman et al. (2003) may have included sheltered or low energy intermediate beach habitat. High polychaete diversity indicative of wave sheltered intermediate/dissipative beaches was also reported by Nel (2000) on the Eastern Cape coast. From the community composition of study sites it would seem that, hard substrate aside, the sediment macrofauna assemblages live for most part in conditions where wave action is neither harsh nor highly energetic.
The influence of hard substrate on community composition is illustrated by sites in close proximity to sand beaches under similar wave attack. At mixed substrate sites Maitlands Inner (MAA) and Maitlands Outer (MAB), polychaetes and crustacean species contributed 30% each, molluscs about 10% and other species the rest of the total species count. At the adjacent Maitlands beach, polychaetes, crustaceans and molluscs contributed roughly 30% each (Schoeman et al. 2003). *Donax serra* and *D. sordidus* (Schoeman et al. 2003) were replaced by *D burnupi* at the mixed substrate sites. *Bullia rhodostoma* was present in lower numbers. Polychaetes had a similar composition at the mixed and sandy beach sites, with addition of *Fabricia capensis*, a colonial polychaete also found in sediment among algal turfs. The beach isopod *Tylos capensis* was absent from all three sites (see Schoeman et al. 2003). Similarly, Humewood (HWD) and Miller’s Beach (MLS) had an increased proportion of polychaete and reduction in mollusc species compared to the adjacent Kings’ Beach with similar changes in species composition and the loss of *B. rhodostoma* at MLS (Schoeman et al. 2003). At Hougham Park West (HPW) and East (HPE) the only notable change compared to nearby Sundays River Beach (see McLachlan 1977; Schoeman et al. 2003), was a reduction in mollusc diversity, absence of donacids, and loss of *B. rhodostoma* at HPW.

Site-site variation in the numbers of species of polychaetes and crustaceans relative to each other could not be significantly linked to a change in site configuration. Polychaetes and crustaceans contributed roughly similar numbers of species throughout. At both types of ridge site and the low platform sites the number of polychaete species increased slightly and mollusc diversity was lower. These changes could be a response to the effects mentioned earlier in relation to shore linear rock extent for platforms and ridges, but could also simply be due to an unfavourable shift in surf-wave conditions at low ridge sites (see Short 1999). Numbers of mollusc and insect species also showed variation potentially linked to site variables unrelated to hard substrate effects on sediment: the number of insect species increased at sites with dunes nearby and mollusc diversity was boosted by addition of taxa from algal turfs. The relationships between major taxonomic groups and specific site variables and indices were tested statistically (data not shown), but was inconclusive.

Overall taxonomic composition varied little within the proposed biotic types, but variation between biotic types could be indicative of environmental conditions. Reduced crustacean and mollusc diversity relative to polychaetes in biotic type C (*Arthrocardia-Laurencia* turf) is probably a response to reduced wave activity on the beach, but may also be due to greater grain size of beach sediments or another variable related to site conditions as most of these sites had a substantial rock component which impeded sediment transport and produced a sheltered eulittoral zone. High annelid diversity and abundance are also known indications of
wave sheltered conditions (Brown 2001) or dissipative beaches (McLachlan and Jaramillo 1995). In biotic type A, polychaete diversity was lower compared to other groups. This biotic type was associated with more wave-exposed beach conditions than the other two. Biotic type B, on the other hand, had more crustacean species and was linked to intermediate wave conditions.

11.4.2.5 Abundance and community composition in relation to environmental variables

These study sites were characterised by a huge polychaete presence, numerical dominants at most sites, and irrespective of physical shore type, but reaching highest numbers in wave-sheltered sediment. Isopods and amphipods, however, were also of some numerical importance, featuring more strongly at wave-exposed localities across configuration types. Unlike sandy beaches, oligochaetes became important at some of these localities, mainly in wave-sheltered sediment. As with their species richness, abundance of gastropods and donacid bivalves was strongly suppressed: a clear indication that conditions at mixed substrate shores fell outside the tolerance range of most beach molluscs. This was also the case with mysids, common elements of beach communities. The usual beach molluscs were replaced by chitons, bivalves and gastropods associated with sand-covered algal turf.

The general community composition of proposed biotic types showed a trend that clearly separated them: at biotic type C polychaetes, isopods and amphipods were highly abundant compared to all other taxa, in biotic type B, bivalves were important along with those three groups, and in biotic type A, molluscs and insects also reached prominence. This trend can potentially be linked to a gradient in intertidal habitat conditions (previously discussed) and substrate availability.

The presence or absence of particular taxa says much about conditions at mixed substrate sites as opposed to sandy beaches. Sediment macrofauna species at these study sites were of three kinds: typical sandy beach species (either greatly increased, greatly decreased or at roughly same abundance as at a beach), species of very low prominence at sandy beaches that gained importance in these habitats and species not found at sandy beaches (from rock surfaces). The last two types made out a unique feature of these sedimentary assemblages. In the majority of cases where rocky shore species were found, it was ascertained that they were live specimens and therefore potential inhabitants although this could only be finally affirmed by a focused study. A third category of significance would be the sandy beach species completely eliminated from these sediments if it could be conclusively shown that their absence was not a sampling artifact.
A number of isopods and amphipods, common at sandy beaches, were also abundant at these study sites and are clearly able to extend their range to mixed substrate shores. These include species of *Euridyce*, *Excirolana* and *Exosphaeroma*, usually recorded at energetic sandy beaches (McLachlan 1977; Dye et al. 1981; McLachlan et al. 1981; Wooldridge et al. 1981; Nel 2000), but with previous records from Western Cape beaches with a rock component (Brown 1971; Brown et al. 1991). Low shore haustorid amphipods (*Urothoe* spp) and wrackline talitrids (*Talorchestia* spp) (Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brown 2001) were present at most of these study sites and have both previously been recorded from the sediment of mixed and rocky shores (Day 1974).

Rocky shore species (never present at sandy beaches) that frequently occurred in the sediment of these study sites include the amphipods *Zygomaera emarginata*, known to occur in sand among rocks and algal turfs (Griffiths 1976), and *Paramoera capensis*, probably the most common amphipod of rocky shores (Day 1974; Branch et al. 2010).

Mysids (*Gastrosaccus*), surf zone dwellers with known sensitivity to grain size (Nel et al. 1999), appear to have been excluded from localities where rock platforms or ridges disconnect the surf zone and beach sediment or modify surf zone processes for part of the tidal cycle. Mixed substrate shores interrupt an otherwise sandy coast, as is often seen in the alternation of sandy bays and rocky headlands, breaking habitat continuity and may well lead to local extinctions (see Merriam and Wegner 1992). In the marine environment, species with planktonic stages ensure connectivity among their populations, but water-borne propagules of infauna are highly dependent on wave action for reaching a favourable situation and could be prevented from doing so if water movement is modified sufficiently by rocks (Koehl et al. 1993).

Three *Bullia* species (*B. rhodostoma*, *B. digitalis* and *B. pura*) were recorded from study sites. The most abundant and most frequent was *B. rhodostoma*, often found at sandy beaches. The non-surfing form of this species has previously been observed at mixed substrate shores in the Western Cape (Brown et al. 1991). Surfing behaviour was not observed in specimens found in this study. This gastropod was recorded at several study sites with substantial intertidal rock, but, like the other two, absent from sites with more than 80% shore-linear rock, e.g. Willows Beach (WLW), Kini Bay (KNB), Cape Recife East (CRE), Hougham Park West (HPW) that disconnect the surf zone from the beach sufficiently to preclude normal interaction (see Short 1999). Although it has a wider habitat tolerance than anticipated in terms of surf-wave activity, present data suggests a cut-off point for *B. rhodostoma* perhaps in the region of 60% shore linear rock extent, but this may be a local effect and would require more investigation. The other sandy beach species, *B. digitalis* is
also known to occur at sandy shores with a rock component (Brown et al. 1991), but was less common in the present study.

The mussel found most often in sediments of these study sites, *Barbatia obliquata*, is known from rocky shores where they attach to rocks in sandy pools (Day 1974, Branch et al. 2010). In this study it occurred in wave-sheltered sediment overlying algal turf of the infralittoral fringe and lower eulittoral zone. The sandy beach clams at these study sites were *Donax burnupi* and *Tellina gilchristi*, both in low numbers. Low bivalve abundance is linked to competition avoidance behaviour when food input is low and has been observed in species of *Tellina* elsewhere, but not reported in South African tellinids (Brown and McLachlan 1990).

The absence of burrowing bivalves from present sites, particularly the iconic South African beach clam, *Donax serra*, is noteworthy. *Donax serra* aggregates on sections of intermediate beach where the beach surface is regular, flat and swashes long and slow (Brown and McLachlan 1990; McLachlan et al. 1995). At mixed substrate shores, rock introduces irregularity into the swash movement and cause waves to lose energy, both phenomena could cause the swash to become a less predictable or less reliable food vehicle and lead to the exclusion of this species (McArdle and McLachlan 1991; McLachlan et al. 1995), but inadequate sediment depth, a shallow anoxic layer or unsuitable grain sizes (Nel et al. 2001) could also play a role. The absence of *D. serra* suggests that it is potentially vulnerable to beach erosion, as it appears to be unable to establish itself on shallow beaches and those with a degree of geological control. Conversion of sandy beaches to mixed substrate habitats could lead to local extinction of this species of economic importance. Absence of preferred habitat conditions has lead to disjunct distribution of *Emerita brasiliensis* (Lercari and Defeo 1999; Soares 2003; Defeo and Cardoso 2004) and is implicated in the elimination of many sandy beach species from steep, coarse reflective beaches (Brown and McLachlan 1990; Brown 2001; Defeo and McLachlan 2005).

A chiton species (*Acanthochiton garnoti*) found at a number of study sites is primarily associated with rock substrata, is known to be sediment tolerant and has previously been recorded at mixed substrate shores (Brown et al. 1991). Whether it could be regarded as an indicator for a particular set of environmental conditions associated with mixed substrate shores will require further investigation. In this study it was found in sediment adjacent to algal turf of the eulittoral zone.

The abundance of insects was highly variable and the trends based on site configuration not really informative. Not enough is known about the distribution trends of the insect species found in this study to comment on their importance. This can probably be rectified by a
focussed sampling campaign, as the role of insects in beach ecology should not be ignored (Hacking 1998) and at mixed substrate shores, the attendant insect species may well be different from those of purely sandy beaches. This is exemplified by the discovery of a weevil species new to science, and still to be described, in samples from one of the high ridge sites (S. Proschetz, pers. com. 2010).

Although capitellids (e.g. Notomastus aberrans), spionids (e.g. Scololepis squamata), orbiniids (e.g. Scoloplos) and polygordiids were among the most abundant polychaetes at these sites, representatives of other families, e.g. cirratulids, nereids, nephtyids, sylids and eunicids were encountered regularly. Many of the polychaete species recorded have previously been described only from sandy beaches, but some are known to occur in sediments caught in gulleys on rocky shores, so they may actually be typical of shores combining both substrata (Day 1967a,b, 1974; Brown 1996; Brown et al. 1991). High polychaete abundance is associated with wave sheltered beaches (Brown 1971, 2001; Brown and McLachlan 1990; Stephenson 1999) as well as dissipative conditions (McLachlan and Jaramillo 1995; Degraer et al. 1999, 2003) and has been linked to sediment disturbances (Brown and McLachlan 1990) and the proximity of reefs in soft bottoms (Barros et al. 2001).

The appearance of sizable populations of oligochaetes together with polychaetes have recently been reported from heterogeneous intertidal sediments of mixed substrate shores, i.e. fine to medium sand with a coarse fraction of pebbles (Parapar et al. 2009), and also formed part of assemblages under macroalgal wrack (Griffiths et al. 1983; McGwynne et al. 1988; Colombini and Chelazzi 2003). In the present study, large numbers of oligochaetes were found in medium sand with or without much coarse material. There was, however, a difference in the species that predominated at the different sites, where Marionina (normally part of meiofauna) predominated in coarse sediment and an enchytraeid species in fine sediments. This segregation of habitats could be attributed to a response to sediment grain-size, wave action, oxygenation or moisture retention ability of the sediment (Brown 1983). In all those situations the sediment was sheltered from major wave action.

11.4.2.6 Hard substrate as an agent of change

There have as yet been no studies of the effects of the presence of permanent hard structures on the community descriptors of beach sediments. Studies done on the infauna of subtidal sediments near natural and artificial hard structures have shown changes in the composition and abundance of infauna linked to sediment characteristics and distance from the reef (e.g. Davis et al. 1982; Ambrose and Anderson 1990; Posey and Ambrose 1994; Barros et al. 2001). In the above-mentioned studies assemblages were characterized by
high abundance of polychaetes as compared to other fauna. In a pattern similar to present mixed substrate study sites, high numerical dominance by polychaetes and crustaceans was the norm at beaches with associated protective hard structures (dykes and groynes) which reportedly modified the wave environment (Degraer et al. 2003; Bayed 2003).

Considering the multivariate nature of factors controlling the distribution of macrofaunal assemblages in sediment, community composition (high polychaete diversity and numerical dominance with species added from rock substrata combined with suppressed mollusc diversity and exclusion or replacement of sandy beach taxa) described for mixed substrate sites of the present study, most likely arose from the combined influence of a range of environmental parameters (see Brown and McLachlan 1990) of which wave-shelter and the hydrodynamics imposed by hard substrata are important components.

Various studies have considered the effects of disturbance on sandy beach macrofauna species composition, distribution and abundance patterns. Fresh-water flows (e.g. Lercari and Defeo 1999, 2003), beach nourishment (e.g. Peterson et al. 2000), beach grooming (e.g. Peterson et al. 2000), ORV impacts (Stephenson 1999), artisanal harvesting (e.g. Schoeman 1996, 1997, Schoeman et al. 2000), oil spills and organic matter pollution (Brown and McLachlan 1990), as well as more natural forms of disturbance such a bioturbation (Brown and McLachlan 1990; Short and Hesp 1999), are among the factors investigated. A high presence of capitellid and cirratulid polychaetes, known opportunists, is usually associated with such situations and they tend to persist for as long as the environmental conditions favour their dominance: periods which could stretch over years (Brown and McLachlan 1990).

If the sediments of mixed substrate shores are indeed ‘intermediately disturbed beaches’ as a result of factors such as irregular wave action and water movement and additional organic input from resident rock surface biota, it may well lead to polychaete domination in the long term in the same way that sediment-tolerant species persist on rock surfaces in spite of not being competitive dominants (Sears and Wilce 1975; Airoldi 2003).

### 11.4.3 The macrobenthos of rock surfaces

The total number of species (macrofauna and macroalgae) for mixed substrate sites of this study was in the same range as reported for South African rocky shores with or without known sand-inundation, taking into account the variation introduced by methodology and bioregion (McLachlan et al. 1981; McQuaid and Branch 1985; McQuaid et al. 1985; Munnik 1987; Fischer 1989; McQuaid and Dower 1990; Brown et al. 1991; Dobkins 1992). Several taxa were common to both shore types. At South African rocky shores, macrofauna species
richness usually exceeds that of macroalgae. At these study sites macrofaunal species richness was sufficiently reduced compared to rocky shores, e.g. McLachlan et al. (1981), Brown and Jarman (1978), McQuaid and Branch (1985), Fisher (1989), to reverse the trend. Macroalgal species richness fell in the upper range of previous regional phycological surveys, e.g. Brown and Jarman (1978), Bolton and Anderson (1997), and other rocky and mixed substrate shore studies, e.g. Beckley and McLachlan (1980), McLachlan et al. (1981), Munnik (1987), Anderson and Stegenga (1989), Dower (1989), Dobkins (1992).

Macrofaunal species richness per site neither changed substantially with shore configuration and proposed biotic type, nor with gradients in environmental parameters (sand-inundation, wave exposure, extent of the rock traverse or any of the calculated indices). The number of macroalgal species exceeded macrofaunal species in each of the physical shore types and proposed mixed substrate shore biotic types, and by the greatest margin at high platform shores and biotic type A (Jania-Corallina-Polysiphonia turfs) and C (Arthrocardia-Laurencia turfs).

11.4.3.1 Taxonomic composition and abundance of sessile macrofauna

Overall mussel abundance (Perna perna, Choromytilus meridionalis, Mytilus galloprovencialis) was much lower than at rocky shores, while barnacles (Chthamalus dentata, Octomeris angulosa, Tetractita serrata) had a similar abundance level (e.g. McLachlan et al. 1981; Beckley and McLachlan 1980; McQuaid and Branch 1985; Gibbons and Griffiths 1986). Dye (1998), however, demonstrated huge annual, biennial and longer-term fluctuations in population density and cover of sessile rocky shore species. Snapshot sampling as was done in the present study could well have caught particular populations at a high or low point, giving a skewed representation of their abundance.

High abundance of mussels and barnacles (specifically Octomeris angulosa) has been linked to greater wave exposure (Velimerov et al. 1977; Underwood 1981; McQuaid and Branch 1984, 1985; McQuaid et al. 1985; Norton 1985). The highest abundance of mussels and barnacles was recorded at sites with a high rock height rating where wave splash was more probable and/or water movement vigorous (but see Gaylord 2000), ensuring a regular supply of food and propagules (Koehl et al. 1993; McQuaid and Lindsay 2007). Perna perna quickly becomes recruitment- and food-limited at wave-sheltered sites where both wave force and velocity and water flow rates are reduced (McQuaid and Lindsay 2007). A similar response may be the reason for the reduction in the abundance of Octomeris angulosa and Tetractita serrata (often with P. perna) at sites with low rock height ratings. Low abundance of P. perna at mixed substrate sites is most likely due to low availability of substratum with a suitable wave climate, rather than inundation by sand, which has been thought to be a kill
factor. Recent genetic work suggests that east coast populations of this mussel may be sand-tolerant (Zardi et al. 2008, 2011), which may explain their apparent state of health at wave-exposed mixed substrate sites with rapid on-off sand movement (biotic type A).

A shift to encrusting sponges and loss of poriferan species has been associated with increased sedimentation (Brown et al. 1991; Carballo 2006). In the present study, an encrusting sponge, _Hymeniacidon perlevis_ was usually the only poriferan recorded and became abundant on sand-influenced and sand-free rock alike, which suggests tolerance to sand-inundation. It was rare at high platform sites with sand-inundation, a probable response to an unfavourable wave action regime which also explains its lack of importance in biotic type A, as this species reached highest abundance on wave-sheltered low elevation rock surfaces in the mid to low intertidal (especially biotic type C sites).

11.4.3.2 Taxonomic composition and abundance of macroalgae

The floral composition (i.e. the number of species belonging to Phaeophyta, Chlorophyta and Rhodophyta) of macroalgae at study sites agreed with previous studies of the region (Munnik 1987; Dower 1989) as well as the southeast coast ratio, i.e. 13%P: 17%C: 70%R (Seagrief 1988; Bolton and Anderson 1997) and followed the pattern for the South African coast (Bolton and Anderson 1997). The (R + C)/P ratio (Cheney 1977) for present study sites was below the South coast algal flora (Bolton 1986) and Eastern Cape flora (Seagrief 1988) ratio’s, but close to previously calculated ratio’s for local rocky shore assemblages (Munnik 1987). This indicates strong tropical floristic affinities (sew Cheney 1977; Bolton 1986) similar to rocky shore localities of the south and east coast of South Africa (Brown and Jarman 1978; Bolton 1986; Bolton and Anderson 1997). High platform sites had the lowest ratio, indicative of a relative increase in brown algae in that wave-exposed situation, even with greater rhodophyte diversity. Elevated (R + C)/P ratio at low ridge and low platform sites could then reflect a greater degree of midlittoral wave shelter.

The (R + C)/P ratio is particularly sensitive to a change in the number of phaeophytes, which often seem to be less common in rocky shore communities of the Eastern Cape and could easily be overlooked. If they are under-represented in the samples of a particular study site, the ratio shifts in favour of tropical species and is therefore perhaps more meaningful when used on a regional scale, rather than for comparison of localities. As the mixed substrate shore biotic types were community based rather than locality based, the (R + C)/P ratio and %P:%C:%R ratio is more meaningful. Biotic type A (_Jania-Corallina-Polysiphonia_ turfs) had a much higher (R + C)/P ratio and greater proportion of red seaweed species compared to the other two. Biotic type C (_Arthrocardia-Laurencia_ turfs) sat at the opposite end of the scale. All three had a low number of phaeophyte species. Differences in the proportion of reds to...
greens to browns show a potential response to wave exposure and sand-tolerance, as many red seaweeds are sediment-tolerant. Biotic type C typified sheltered eulittoral conditions with lower sediment loads on rock, whereas biotic types A and B, both more sand-influenced, have rapid accretion-erosion cycles linked to wave climate, A more so than B.

The majority of species at these mixed substrate sites had their centre of distribution in the south or east coast (Simons 1976; Bolton 1986), e.g. the red algae Acrosorium maculatum, Gelidium abbottorum, G. pristoides, Gigartina pistillata, Hypnea spicifera, Laurencia flexuosa and L. glomerata, Plocamium beckeri and Polysiphonia incompta; greens Codium duthieae, Valonia macrophysa and Ulva rigida, and browns Anthophycus longifolius, Colpomenia sinuosa, Dictyota dichotoma, Ecklonia radiata and E. biruncinata, Endarachne binghamiae, Sargassum incisifolium and Zonaria subarticulata. A few cold-water species e.g. Arthrocardia filicula, Hildenbrandia lecannellieri, Leathesia marina, Nothogenia erinacea, Plocamium rigidum, Petalonia fascia, Splachnidium rugosum (Bolton 1986; Brown and Jarman 1978) and some with tropical affinities, e.g. Halimeda cuneata, Caulerpa filiformis and C. racemosa, Codium platylobium, Padina sp, Dictyopteris spp, were also consistently found (Stephenson and Stephenson 1972; Simons 1976; Brown and Jarman 1978).

Rhodophytes were consistently the most abundant, dominating eulittoral and infralittoral rock surfaces. There are very few Southern African studies that have paid attention to the assemblages on sand-influenced rock surfaces, yet the prevalence of red macroalgae is a theme common to all (see Munnik (1987), Anderson and Stegenga (1989), Dower (1989), Fischer (1989), Engledow (1998)). Other evidence of their spatial dominance on besanded rock surfaces comes from biogeographical texts (e.g. Brown and Jarman (1978), Bolton and Anderson (1997)) and field guides (e.g. Stegenga et al. (1997), De Clerck et al. (2005)). Stephenson and Stephenson (1972) remarked on the prevalence of red and green seaweeds on the rocky intertidal adjacent to sandy areas on South African shores. However, a high number of species and high abundance of red macroalgae and paucity of browns, as at the present sites, also typify the warm temperate flora of the south and east coast (Brown and Jarman 1967; Bolton and Anderson 1997) that has a substantial tropical component, species that may be pre-adapted for the presence of sediment.

At the present study sites, red algae mostly formed dense turfs on primary substrate. These species exhibited structural features such as crustose or rhizomatous holdfasts (seen in algal turfs of sand-stressed rocky shores elsewhere) that confer exceptional ability to withstand sand-inundation, enable them to survive long periods of burial under sand and, in this way, retain long-term dominance of hard substrate (Hay 1981; Taylor and Littler 1982; Taylor and Hay 1984; Stewart 1982, 1983, 1989; D'Antonio 1986; Airoldi et al. 1996;
Anderson et al. 2008). The growth form of most turf species at these study sites consisted of many uprights (also see Hay 1981; Taylor and Hay 1984; Stewart 1982, 1983, 1989; D’Antonio 1986) which confer advantages related to herbivory and cropping by foraging fish (Hay 1981; Taylor and Hay 1984). Removal of algal tissue is generally limited to the tips of fronds and promotes branching regrowth which produces the complex and densely interlocking structure of turf (Taylor and Hay 1984). In the present study evidence of cropping (possibly by fish foraging for invertebrates) was seen in turf-forming algae of a wide range of sizes.

At these sites, an increase in chlorophyte abundance and diversity could be linked to the development of new seral stages after disturbance (see Airoldi 2003), a high degree of epiphytism in species of Ulva, Chaetomorpha and Rhizoclonium and, the ability of sand-loving Caulerpa filiformis to dominate in extensive swards on the low shore. The majority of green seaweeds in this study are pioneers, ephemerals and opportunistic species known for their ability to rapidly colonize bare substrate (Daly and Mathieson 1977; Littler et al. 1983; Robles 1982; Jernakoff 1985; Boaventura et al. 2002). Species of Ulva and Enteromorpha were highly abundant as epiphytes on coralline algal turfs (see Hay 1981) and pioneers at sites with rapid sediment movement and high wave energy where they quickly became established on newly opened substrate after storm-wave activity (Garner, pers.obs. 2006, 2007, 2008). Opportunistic colonization of intermittently besanded surfaces by algae (see Daly and Mathieson 1977; Littler et al. 1983; Robles 1982; Jernakoff 1985; Boaventura et al. 2002) has been attributed to sand-tolerance in their propagules (Robles 1982).

A common sight at South African mixed substrate shores of the south and east coasts, Caulerpa filiformis colonizes rock bases under a shallow deposit of sand. It appears to favour a combination of deep sand and moderate wave action. Like its congener, C. taxifolia, it appears to be resistant to anoxic conditions that arise in sediments it has colonized (Gribben et al. 2008), remains alive even after lengthy burial (Garner, pers. obs. 2007, 2008) and probably continues growth while buried (Williams et al. 1985). Halimeda cuneata occurred with C. filiformis at sites with more wave-sheltered low tide sediment. It, too, appears to be tolerant to low oxygen levels and survives lengthy periods of variable sand-inundation (Garner, pers.obs. 2007, 2008).

An increase in green and red algae with a concomitant reduction or even elimination of brown algae (Brown et al. 1991; review in Airoldi 2003; Balata et al. 2007; Eriksson and Johanssen 2005; Schiel et al. 2006; Shepherd et al. 2009) is a well-known trend at sand-stressed rock substrata and has been linked to intolerance of sand at settlement stages rather than maturity (see Devinny and Volse 1978). Large cold-water kelps are thought to be
intolerant of sand (Stegenga et al. 1997), perhaps because of their origin, but in South African kelps intolerance to sediment has not been shown inconclusively (Bolton 1986). At these study sites, brown algae were often partly sand inundated without ill effects (e.g. *Ecklonia biruncinata, Sargassum incisifolia, Dictyota, Dictyopteris*).

11.4.3.3 Abundance and composition of motile macrofauna (gastropods)

Limpets, notably patellids and siphonariids contributed most of the gastropod species, as well as significantly more to the total species count than any other macrofaunal taxon of rock substratum. There are very few community studies involving molluscs of rock surfaces and available data could not be used for direct comparison of species richness (e.g. McLachlan et al. (1981), McQuaid and Branch (1985), Munnik (1987), Dower (1989)). The gastropod fauna of these mixed substrate sites was similar in taxonomic composition, at least with regard to dominants, than rocky and mixed substrate shores of the Eastern Cape coast (McLachlan et al. 1981; Munnik 1987; Dower 1989). Only *Scutellastra cochlear* seemed to become eliminated from these shores.

Littorinid abundance and density, though highly variable, exceeded that of other gastropod taxa mostly by a factor of 10. At most sites littorinid abundance compared well with previous studies of the region (McLachlan et al. 1981; Munnik 1987; Dower 1989). Their abundance was only markedly reduced at study sites with low rock height ratings (see Brown et al. 1991) and less extensive cross-shore rock surface combined with a lack of midlittoral wave shelter, i.e. low ridge sites and some platform sites (see Stephenson and Stephenson 1972). Under wave attack many of these small gastropods become dislodged and isolated from their natural habitat. They do not seem to be able to survive in sediment.

Limpets commonly occur at both wave-exposed and sheltered rocky shores of the world (Branch 1981; Branch and Branch 1981; Branch 1985). Both patellid and siphonariid limpets were more abundant at these study sites than at rocky and other mixed substrate shores of the region (e.g. Dower 1989; Fischer 1989; Munnik 1987). Siphonariid density exceeded patellids at all sites with more substantial beaches and a greater degree of sand-inundation on rock, particularly low ridge and platform sites: not surprising in view of their known tolerance of anoxic conditions associated with sand-inundation (Marshall and McQuaid 1985). The presence of sand did not, however, completely eliminate patellid limpets as proposed by Marshall and McQuaid (1989) on the basis of their lack of physiological adaptation to anoxia.

The infralittoral limpet *Scutellastra cochlear* presents a special problem. It is ubiquitous on South African rocky shores, forming the ‘cochlear zone’ and among the most abundant at
densities up to 2600 ind/m² (Branch and Branch 1981; McQuaid and Branch 1985). In this study it reached a population density comparable to their population numbers at rocky shores at only one site, Willows Beach (WLW), a wave-exposed high ridge shore with minimal sand. At all other sites, their numbers were greatly reduced and the extent of the cochlear zone curtailed. There are many factors that influence the population sizes of intertidal limpets and these have been thoroughly reviewed (see Branch 1981; 1985). The apparent decline or complete absence of *S. cochlear* could be due to any number of reasons. Branch (1981, 1985) mentions encroachment by large algae and inadequate wave action, amongst others, both factors that could play a role at present study sites. The elimination of *S. cochlear* has further consequences, as the entire algal assemblage associated with it, starting with the highly productive *Gelidium micropterum*, disintegrates and disappears within weeks of the complete removal of the limpet (Branch 1981). McQuaid and Branch (1985) reported its absence from a soft erodable rock substratum and its replacement by *Scutellastra barbara*, a faster growing infralittoral species. At present sites, *S. barbara* was present at similar or lower densities compared to *S. cochlear*, but there was no evidence of replacement of the other species except at Cannon Rocks (CNR) where *S. cochlear* was particularly suppressed and loss of individuals was evident as part of the algal community still remained. *Scutellastra longicosta*, however, also invades vacated *S. cochlear* territories even where *S. cochlear* densities are high (Branch 1981), a phenomenon observed at present sites.

Of the mollusc species associated with hard substrate, one bivalve (*Barbatia obliquata*), one chiton (*Acanthochiton garnoti*), two patellids (*Cymbula miniata* and *C. oculus*), one key-hole limpet (*Fissurella mutabilis*) and one siphonarid (*Siphonaria concinna*) were occasionally also found in sediment samples. Other gastropods of rock substrate found in sandy areas on occasion were *Burnupena cincta* and *Tricola capensis*. One can only speculate about the reasons for the appearance of gastropods in sediment samples: they may have actively entered the sandy area perhaps in search of food, e.g. *B. cincta* (Brown et al. 1991), or simply been dislodged from the rock substrate.

11.4.3.4 Sediment as an agent of change

Although temporal variability of sediment was not a focus area of the present study, frequent visits to sites confirmed sedimentation regimes ranging from fairly rapid sediment accretion-erosion cycles at some sites to no alteration of sediment level at others, where rock adjacent to sandy areas did not experience any appreciable inundation by sand. Change, if any, occurred over a matter of days, weeks or months, but there was no evidence of massive seasonal inundation linked to an oscillating wind-wave regime as reported in many other
studies of sediment-stressed rocky shores, e.g. Daly and Mathieson (1977), Airoldi (2003) and references within, Anderson et al. (2008), and seasonal beaches, e.g. Hubbard and Dugan (2003).

The presence of sand can play a pivotal role as a disturbance agent, shaping patterns of abundance in the communities of intertidal rock surfaces by suppressing or eliminating intolerant species and favouring sand-tolerant species (Robles 1982; Taylor and Littler 1982; Marshall and McQuaid 1989; Carballo 2006; Anderson et al. 2008). Sediment alone may place a lower limit on distribution of sessile fauna (see Daly and Mathieson 1977) and eliminate all but the most tolerant species from low surfaces (see Daly and Mathieson 1977; Engledow and Bolton 1994; Zardi et al. 2008, 2011) especially at higher inundation volumes (Engledow and Bolton 1994).

Epilithic macrobiota have different levels of ability to survive periods of burial, so much so that some species are said to be psammophobic (sand-avoiding) (McQuaid and Dower 1990). In contrast psammophilic organisms “prefer” habitats with sediment deposits and are advantaged by its presence (Day 1974; McQuaid and Dower 1990). Beach macrofauna would fall in this category. While sessile forms such as barnacles and mussels are unable to escape inundation and can only survive long-term burial if they have an innate tolerance (Chapman 1943; Stephenson 1943; Littler et al. 1983; Brown 1996; Sloan and Irlandi 2008; Zardi et al. 2011), individuals of motile sediment-intolerant species on rock surfaces could avoid burial by migrating away (Littler et al. 1983) or habitually occupy elevated positions (Marshall and McQuaid 1989).

In this study, the lowest numbers of rock macrofauna and macroalgal species were recorded from sites having only isolated rock outcrops. This finding concurred with Brown et al. (1991) who reported low species richness for Western Cape mixed substrate shores with a similar ratio of sand to rock. Any of a number of factors could be implicated, e.g. isolation (Sousa 1984, 1985), limited substrate (Sousa 1984), shore elevation (Sousa 1984, 1985; Brown et al. 1991), periodic sand inundation (Littler and Littler 1981; Littler et al. 1983; Branch et al. 1990), low recruitment due to effects of sediment on settlement (De Vinny and Volse 1978; Lobban et al. 1985; Schiel et al. 2006), reduced available light due to suspended sediment (Lobban et al. 1985), scouring by sand (Daly and Mathieson 1977; Brown et al. 1991) and anoxia during inundation (Lobban et al. 1985; Brown et al. 1991).

At a low outcrop it may be difficult to avoid being swept off and buried in the sediment. Macrobiota persisting on an isolated rocky outcrop in a beach, probably do so with the aid of morphological and physiological attributes that help them survive environmental stressors such as anoxia (Marshall and McQuaid 1989, Airoldi 2003), scouring (Kendrick 1991), light
deprivation (Lobban et al. 1985; Anderson et al. 2008) and thus they have a refuge from competition and other biotic interactions to which they are less well adapted (Hay 1981; D’Antonio 1986; Airoldi 2003).

The present study sites simultaneously represented a gradient in substrate availability and the impact by sand. It is logical to surmise that entire assemblages of macroalgae and associated macrofauna were eliminated where they were not provided with substratum to colonize. Even with suitable rock surface, factors such as suspended or deposited sediment could have eliminated some species at a vulnerable life stage, while permitting colonization by pre-adapted sediment-tolerant taxa. The degree of sediment tolerance or a need for it appears to be a significant differential in these systems. On-shore transport of propagules was not impaired at these shores as newly exposed substrate was rapidly colonized, after which succession ensued. This enhanced diversity, even if it was only a temporary or seasonal effect (see Sousa 1979). However, long-term dominance of substratum was more likely the result of pre-adapted life cycle features (e.g. tetrasporophytes in turf-forming rhodophyceans), a feature of these communities that signifies long-term stability in spite of an appearance of instability due to changes in sediment load.

Spatial and temporal variability in sedimentation of a hard substrate (e.g. periodic burial and uncovering of rock substrate) modulates competitive outcomes, with potentially negative consequences for algal community diversity (Daly and Mathieson 1977; Littler and Littler 1981; Engledow and Bolton 1994; Airoldi and Cinelli 1997; Airoldi 2003; Balata et al. 2007; Eriksson and Johansson 2005; Anderson et al. 2008). However, at an appropriate intensity and/or frequency of disturbance, the habitat heterogeneity (patchiness) introduced could lead to greater diversity of assemblages (Sousa 1979; Littler and Littler 1981; McQuaid and Dower 1990). The composition of the developing assemblage will depend on timing of the disturbance event (Petrakis and Dudgeon 2005) and prevailing environmental conditions (Van Zyl and Robertson 1991).

Why are macroalgae dominant and macrofauna suppressed at these sites? Macroalgae and sessile macrofauna compete for space on rock substrate. Spatial dominance by one of the other has been attributed mainly to differences in tolerance to wave action (Velimerov et al. 1977; Underwood 1981; Norton 1985). In wave-sheltered situations macroalgae usually become more abundant (not necessarily more diverse) (Velimerov et al. 1977; Underwood 1981; Norton 1985). They compete more successfully for space on lower intertidal surfaces (McQuaid and Branch 1984, 1985; McQuaid et al. 1985) and in the presence of sediment (Vermeij 1978; Littler et al. 1983; Engledow and Bolton 1994) than sessile filter feeders. This would explain dominance of rock surfaces by algae with simultaneous reduction in sessile
macrofauna at study sites where eulittoral rock surfaces were wave-sheltered and below midtidal elevation. At others, reduced drainage of rock surfaces due to a gentle inclination (e.g. platforms) enhanced by sediment cover facilitated upward range extension by more resistant infralittoral biota and their epiphytes bringing a concomitant increase in abundance and diversity (see Hay 1981; Norton 1985; D’Antonio 1986; McLachlan and Jaramillo 1995; Trowbridge 1992; Engledow and Bolton 1994; Menge et al. 1994). Moist conditions enhance colonization and growth after settlement so that they soon reach a size at which they escape grazing by herbivores. In this way the colonization of primary substratum by sessile macrofauna is prevented. The correlation of mobile herbivores with bare areas on upper rock surfaces of study sites with high rock height ratings where sessile filter feeders were often abundant, but algae very few, confirms this notion.

11.5 Macrobenthic assemblages of intertidal zones

11.5.1 A general perspective: one shore, two substrata

The macrobenthos of the intertidal habitat are subject to strong gradients in insolation and desiccation, among others (Stephenson 1943, Russell 1991). In this baseline investigation of intertidal zonation at mixed substrate shores, each sampling stratum represented an intertidal assemblage or biotope associated with a particular zone or subzone.

At study sites with height limited rock, i.e. most of the low ridge and low platform shores, but even to an extent at the high platform shores, integration of subzones (zonal overlap) was evident as species from lower zones or subzones became integrated with those of upper rock surfaces. Further vertical range extension of a species or assemblage occupying the uppermost surfaces of the rock substrate was prevented, but not invasion by elements from a lower intertidal biotope into the upper assemblage.

On rock surfaces and in sediment this phenomenon could be a response to a favourable moisture gradient (see Townsend and Lawson 1972; Lobban et al. 1985; Russell 1991; Brown 2001), but tidal migrations by motile macrofauna could have played a role in sediment (McLachlan and Jaramillo 1995; Brown 2001). Both phenomena result in blurring of zonation patterns: species from lower reaches “invade” higher elevations on the shore, making the zonal transitions less apparent, so that adjacent zones melt together (Russell 1991; McLachlan and Jaramillo 1995; Brown 2001). Zonal overlap or integration could thus lead to enhanced species richness because of an edge effect on a very small scale (Odum 1971; Holland and Risser 1991). Stephenson and Stephenson (1972) reported similar patterns at shores with low gradient intertidal rock: the zones became more extended in a horizontal direction, intergrading extensively and losing their identity. Increased species richness at
sites with low relief rock substrate could therefore be a consequence of zonal overlap, where taxa from lower strata creep into the relatively higher positions. Since elevated water level facilitates this process, it may be evidence of slow sea level rise, as at almost all sites where this zonal overlap as well as fouling of biota by encrusting algae was observed, the extent of overlap was roughly of the same magnitude, amounting to roughly 15 cm in height.

Classification revealed the composition of these communities and how they related to one another in terms of their response to intertidal gradients. It further showed that the response of macrobenthos to intertidal gradients was independent of shore configuration and biotic community type, although the species composition of the macrobenthic assemblages reflected affinities of each particular community type.

In classification by cluster analysis, assemblages (samples) are sorted on the basis of dissimilarity/similarity. Normally one would deal with samples of comparable communities, e.g. only sediment macrofauna. In these analyses, samples from two habitat-forming substrata in the same environment were analysed simultaneously. Careful interpretation was required: where there was a great degree of dissimilarity between, for instance, two rock surface samples, one may well end up being grouped with samples from sediment in the same cluster. Normally that may be interpreted as similarity between the samples in the cluster, but in this case it was necessary to see it rather as evidence of dissimilarity between biotopes or clusters on the same substratum. Although a few species of macrofaunal normally associated with the rock surface or phyal habitat were recorded from sediment samples, there were no records of macroalgae and sessile macrofauna in sediment. Although macrofauna found in sediment samples (and normally psammophilic) were discovered inside algal turfs inspected to identify algae, they were not inumerated, as turf macrofauna were excluded from the original study plan due to time and funding constraints. This aspect will require follow up. Macrofauna of the phyal habitat were found in sediments and if the opposite is true it strengthens the argument for trophic linkage of these two habitats, a potential topic for further study.

The macrobenthos associated with sampling strata or biotopes in sediment and on rock surfaces exhibited distributions that seemed to be a response in the first place to the normal intertidal environmental gradient (landward loss of moisture, increased irradiation and heat). Wide intermediate sandy beaches and rugged, tall wave-exposed rocky shores probably represent the benchmarks for regularity in the distribution and full development of these assemblages. The communities of such shores have been described repeatedly in many studies. Their intertidal zonation patterns are known and widely accepted. A secondary pattern or trend was deviation from the regular response as a result of the influence of the
other substratum type on wave action, water flow rate and patterns, drainage, oxygenation and desiccation, on the one hand, and substrate availability and settlement processes on the other. At these study sites, the degree to which the intertidal zonation pattern on rock surfaces or in sediment resembled the ‘ideal’ appeared to be tied up with substrate availability and wave action.

11.5.2 Composition and distribution trends of macrofauna in intertidal biotopes/subzones of sediment

In sediment the overall cross-shore distribution trend in beach macrofauna reflected the three biotic zones proposed by McLachlan and Jaramillo (1995), and, relative to tidemarks, the Stephenson zonation scheme developed in the first place for rocky shores, while physical zones could also be identified as described in Pollock and Hummond (1971) and McLachlan and Jaramillo (1995). The biotic zonation patterns at study sites were indicative of a range of beach states, from reflective to low-energy dissipative (McLachlan and Jaramillo 1995). The overall reduction in species richness from the low to high shore in sediment followed the well-described trend at sandy shores (see Brown and McLachlan 1990; Field and Griffiths 1991; McLachlan and Jaramillo 1995; Brown 2001).

Abundance exhibited one of two overall cross-shore trends: a gradual decrease from the spring low tide mark (LWS) to the spring high tide mark (HWS), with a small peak at the driftline at localities where abundance of terrestrial species (enchytrid oligochaetes, insects) and semi-terrestrial taxa (talitrid amphipods) was boosted by wrack deposits (see McLachlan and Jaramillo 1995), or a bimodal distribution with a pronounced infralittoral and subequal upper midlittoral peak. The second trend did not concur with the usual pattern in South African sandy beaches (Brown and McLachlan 1990; Nel 2000; Brown 2001; Dreyer 2008), all microtidal and intermediate, and also differed from morphodynamically similar wave-dominated beaches elsewhere (McLachlan and Jaramillo 1995; Defeo and McLachlan 2005). At 30% of sites mid-shore abundance was greater than in low shore strata. This pattern was remarkably similar to previously reported trends at dissipative beaches (see Giménez and Yannicelli 1997; Degraer et al. 1999, 2003). This may be an outcome of extensive overlap between upper and lower assemblages (see Brazeiro 1999), in view of the limited width of these beaches, leading to an abundant and enriched assemblage composed of species actually centred in the upper or lower reaches and not forming a uniquely midlittoral association as proposed by McLachlan and Jaramillo (1995) (see Brazeiro 1999).

As in sandy beaches (Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brazeiro 1999), macrofauna in mixed substrate shore sediments had patchy distribution patterns as
25% to 50% of samples yielded no material. Sample yield ranged from impoverished to very rich in individuals and species, suggesting that the organisms formed aggregations.

There were few semi-terrestrial crustacean and insect species per site at the supralittoral boundary of the beach (wrackline) except where there was an input of organic matter in the form of wrack (see Field and Griffiths 1991; Brown 2001; Colombini and Chelazzi 2005). Total and mean species richness of the eulittoral zone in the mixed substrate shore beaches, were intermediate to that of the supralittoral and infralittoral fringe assemblages. High species richness at the low tide swash elevation compared to the mid and upper beach deposits followed the trend at sandy beaches (Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brown 2001; McLachlan and Dorvlo 2005). The mean number of infralittoral species recorded was similar to that of some dissipative beaches (cf. Bayed 2003; Degraer et al. 1999; Janssen 2005), but also highly variable, an attribute that has been associated with communities of fine to medium sands, with a low slope and low wave height on the beach face, i.e. wave sheltered conditions (McLachlan and Dorvlo 2005). Variability is also characteristic of communities at ecotone boundaries as microhabitats are more variable and may not fall within the tolerance range of some species (Gosz 1991).

A range of potential drivers of distribution have been identified for sandy beach macrofauna, e.g. food concentrations (Brown and McLachlan 1990), an environmental gradient (Dugan et al. 1994; Giménez and Yannicelli 1997), a response to wave action (McLachlan and Dorvlo 2005), swash pattern (Brown and McLachlan 1990; McArdle and McLachlan 1991, 1992), swash zone position (Giménez and Yannicelli 1997), sediment characteristics (Brown and McLachlan 1990; Nel 1995; Rodill and Lastra 2004), sediment moisture (McLachlan and Jaramillo 1995; Brazeiro 1999; Degraer et al. 2003) or even biological interactions (Brown and McLachlan 1990; Defeo et al. 1997). Slow recolonization of disturbed patches is not excluded, especially since capitellid and spionid polychaetes were often dominant elements of these assemblages (Levin 1984). While there have been attempts to refine knowledge of the spatial scales at which patchiness in sandy beach fauna occurs, it remains to be seen whether the spatial scale here is comparable to sandy beach macrofauna (Schoeman et al. 2003). Mixed substrate shore research has not reached the point where such questions could reasonably be asked and answered.

At these sites the extent and placement of the rock traverse was an additional factor exerting an influence on distribution patterns of biota in sediment. Samples from sandy patches among rocks often yielded a very low abundance of macrofauna or were devoid of material, perhaps as consequence of the hard substratum modifying or impeding transport processes (Koehl et al. 1993; Jeffrey and Underwood 2000). Larvae or adult infauna swept along in
turbulent wave bores could easily be deposited on the rock surfaces where their chances of survival are reduced. Disturbance (human foot traffic, sediment removal) combined with slow recruitment and colonization could also play a role in the absence or sparseness of biota in midlittoral sand patches (Levin 1984). Dugan and Hubbard (2010) reported the effective loss of the supralittoral fringe and upper midlittoral zones due to placement of hard structures (coastal armouring). The presence of rock outcrops and platforms are, however, also known to retard drainage, increasing moisture levels (Short 1999) and allowing delicate forms like polychaetes to extend their range upwards (McLachlan and Jaramillo 1995; Degraer et al. 2003).

At over half of the study sites, the shore configuration caused the beach deposit to be cut off from the sandy subtidal region for part of the tidal cycle and reduced the amount of time during which the tide and waves influenced the beach, a phenomenon typical of platform beaches (Short 1999). Infauna arranged themselves along the intertidal moisture gradient in a way similar to active sandy beaches and produced distinct intertidal associations. Assemblages differed from those of sandy beaches with an equivalent morphodynamic state in that some of the typical sandy beach species were absent and other taxa, often not usually associated with sandy beaches, added.

The low shore, between the water table outcrop and low tide swash line, corresponding to the sublittoral zone of McLachlan and Jaramillo (1995) (or infralittoral fringe of Stephenson, Salvat’s zones of resurgence and saturation, sampling strata S4 and S5 of this study) was dominated by large populations of polychaetes (mainly spionids, orbiniids, capitellids, cirratulids, eunicids and nereids) and haustorid amphipod species, many associated with sandy beaches (McLachlan and Jaramillo 1995), but some species with a known association with the sediment deposits of mixed and rocky shores (Day 1967a,b, 1974; Brown 1971; Griffiths 1976; Brown et al. 1991, Brown 1996; Branch et al. 2005, 2010). A few species often typical of intermediate to dissipative beaches, i.e. mysids, glycerids, hippids, phoxocephalids, nephtyids and donacids (McLachlan and Jaramillo 1995), were conspicuously absent from these assemblages at some study sites.

In mid-shore reaches, i.e. the littoral zone of McLachlan and Jaramillo (1995) (Stephenson’s midlittoral zone, Salvat’s retention zone, sampling strata S2 and S3 of this study), cirolanid isopods and polychaetes (mainly spionids, orbiniids, capitellids) were mostly the dominant organisms. According to McLachlan and Jaramillo (1995) cirolanids, spionids and ophelids usually occur in the middle zone. Ophelids were absent from these shores.

At the upper end of the shore, in the vicinity of spring high tide level, i.e. the supralittoral zone of McLachlan and Jaramillo (1995) (Stephenson’s supralittoral fringe, Salvat’s drying
zone, sampling strata S0 and S1 of this study), the assemblage usually comprised of insects, talitrid amphipods and oniscid isopods, showing good correspondence with McLachlan and Jaramillo (1995). At these shores, macrofauna from the midshore (or even lower), e.g. cirolanids, capitellids, sphaeromatid isopods and haustorids regularly appeared in samples of the upper shore reaches. Overlap between adjacent zones was evident from cross-shore distribution and abundance trends of taxa and low levels of dissimilarity in adjacent sampling strata. Whether this was a transitory condition or permanent is question for future research.

Overlap of the assemblages of adjacent zones was described by McLachlan and Jaramillo (1995) and not unusual in sandy beaches. Similar trends have been demonstrated in studies of microtidal dissipative and intermediate beaches elsewhere, e.g. Giménez and Yannicelli (1997), Brazeiro (1999), and in South Africa (Nel 2000; Dreyer 2008). Giménez and Yannicelli (1997) and Dreyer (2008) found that the assemblages of adjacent zones changed over time due to the response of species to altered environmental gradients. Beach fauna are known to be highly mobile and rarely confined to just one zone or level on a beach (Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brown 2001).

At study sites of mixed substrate shore biotic types A and B where the rock component was less extensive or of such a configuration that normal surf-beach interaction occurred throughout most of the tidal cycle, beaches were intermediate-reflective and the macrofaunal assemblages exhibited a cross-shore distribution commonly seen at sandy beaches of similar morphodynamic state and moderate to high wave exposure (see “Brown’s zones” in Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brown 2001). Assemblages were characterized by high abundance of cirolanid and exosphaeromatid isopods in midtidal reaches and the spionid *Scololepis squamata* abundant in both mid- and lower zones and in addition an abundant insect assemblage in upper shore sediment.

At sites with lower beach gradients, low and high shore strata had more in common with each other than with mid-shore strata. This is not unusual at sandy beaches either and appears to be linked to beach slope and moisture levels: a more gradual slope is associated with increased moisture levels in the sediment making it possible for some low-shore taxa to persist higher up on the shore and increase similarity with upper shore strata (Giménez and Yannicelli 1997; Degraer et al. 1999, 2003).

The beach sediments of sites of mixed substrate shore biotic type C (*Arthrocardia – Laurencia* turfs) were the most wave-sheltered. This was the case also at sites where the rock traverse was exposed to direct wave action and together with macroalgal turfs (Schiel et al 2006) attenuated wave energy at an appropriate rate. Dissipative beaches are normally
high energy systems, but their beach sediment are sheltered from heavy wave action as wave energy is mostly expended in the outer broad, flat and shallow surf zone (Short 1999). Together with fine sediment and slow drainage, these sheltered conditions favour delicate life forms, such as polychaetes. Many of the polychaetes found in the infralittoral fringe zone are at the upper limit of their range, being predominantly subtidal in distribution (McLachlan and Jaramillo 1995). At dissipative beaches subtidal forms are able to colonize the lower reaches of the beach more so than at any other type because of the elevated water table brought about by the fine sediment and gentle slope (Brown and McLachlan 1990; Short 1999; McLachlan and Jaramillo 1995). Some of these are characteristic of sheltered conditions and not found in wave-exposed situations (McLachlan and Jaramillo 1995). The occurrence of haustorids and a varied assemblage of polychaetes (e.g. eunicids, spionids, orbinids, nereids, syllids, cirratulids) as well as nephtyids, *Gastrosaccus* and a phoxocephalid (*Paraphoxus*) in low shore sediments of sites of biotic type C, strongly suggest intermediate to dissipative conditions (see McLachlan and Jaramillo 1995).

Although none of these beaches had the width of dissipative sandy beaches, the composition of the assemblages had much in common with such beaches (see Giménez and Yannicelli 1997; Degraer et al. 1999, 2003), perhaps because of the great degree of shelter afforded the beach deposits of these sites by the adjacent sea-ward rock platform. Adding to species richness were polychaetes, amphipods and isopods that have previously only been associated with algae and sediments of rocky shores. The close proximity of sand to rock-bound communities made it possible for sediment-tolerant phytal inhabitants to further enrich the assemblages of the sediment. Among these were several rare and endemic species. Cluster analyses demonstrated varied interrelations between assemblages of the low-, mid- and upper shore zones. Giménez and Yannicelli (1997) and Degraer et al. (1999, 2003) demonstrated similarly complex patterns in dissipative sandy beaches.

### 11.5.3 Composition and distribution trends in macrobenthos of rock surface intertidal biotopes/subzones

The cross-shore zonation pattern on rock surfaces followed the pattern on rocky shores of the Agulhas Marine Province (Bolton and Anderson 1997, Brown and Jarman 1978) or south coast (Branch and Branch 1981) and consisted mainly of algal turfs, a common sight on south and east coast rocky shores (Bolton and Anderson 1997). Macrobenthic assemblages of study sites with high rock height ratings strongly resembled sediment-free rocky shores in composition and cross-shore distribution trends and differed markedly from those lacking in high rock surfaces.
The overall reduction in species richness from the low to high shore on rock surfaces followed the well-described trend at rocky shores (see Stephenson 1943; Lewis 1964; Stephenson and Stephenson 1972; Brown and Jarman 1987; Russell 1991) with the exception that in the infralittoral fringe zone there consistently was a significant reversal in the normal pattern of species richness on hard substrate, i.e. the cochlear zone harboured more species than the infralittoral fringe macroalgal assemblages due to enhanced macroalgal diversity.

11.5.3.1 The supralittoral fringe

The supralittoral fringe (Littorina zone in many studies) was represented by two sampling strata based on the presence or absence of *Porphyra capensis*. The alga is an annual, appearing in late spring and disappearing in late summer and constitutes an “island” of different microclimate compared to adjacent bare rock (Russell 1991). Like *Afrolittorina* (Brown and Jarman 1978; Underwood 1981; Russell 1991), it is adapted to the harsh conditions (strong solar radiation and severe desiccation) of the supralittoral fringe that place an upper limit on the distribution of most macroalgae and macrofauna of rocky shores (Norton 1985).

*Porphyra capensis* widely occurs in the Eastern Cape (Agulhas Marine Province) (Bolton and Anderson 1997) on high relief rocky shores (Beckley and McLachlan 1980; Fischer 1989; Munnik 1989; Olivier 1989; Van Zyl and Robertson 1991; Dobkins 1992), but has not yet been reported from shores with low aeolianite platforms or low rock ridges (Dower 1989; Munnik 1989; Dobkins 1992). Unless due to a sampling artifact, *Porphyra capensis* appears to be excluded from shores of biotic type A, characterised by a high degree of sand-inundation of rock substrate which suppresses development of the supralittoral fringe (see Stephenson and Stephenson 1972; Brown et al. 1991).

*Afrolittorina knysnaensis*, the most prominent and abundant in the supralittoral fringe, but not restricted to it, is found widely across the eulittoral zone, e.g. Fischer (1987), Munnik (1987). It may be less vulnerable to a reduction in high shore rock surface than *P. capensis*. The abundance of *A. knysnaensis* appeared to be suppressed only at sites of biotic type A and reached its lowest abundance where turbulent surf, sand scour and possibly sand-blasting may all have contributed to reducing their numbers (see Brown et al. 1991).

The supralittoral fringe was best developed at sites with high rock surfaces, exhibiting low species richness similar to that of rocky shores (see Brown and Jarman 1978; Bolton and Anderson 1997). At sites with low relief rock substrate, the supralittoral fringe was indistinct from eulittoral zones and species richness in the supralittoral fringe greatly exceeded that of
rocky shores and other mixed substrate shore data (see McQuaid et al. 1985; Dower 1989). This was probably a response to special micro-climactic conditions (shade, increased moisture) brought about by a combination of rock topography interacting with wave action, aspect and rock surface properties and facilitated upward range extension of more delicate species (Townsend and Lawson 1972).

11.5.3.2 The eulittoral

Overall species diversity in the eulittoral communities associated with *Chthamalus stellatus* (R2), upper midtidal turf (R3), *Gelidium pristoides* (R4), lower midtidal turf (R5), and *Perna perna* (R6) was similar and compared well to lower shore zones. The eulittoral zone sees interaction with waves and tidal flows on a daily basis. The different ways in which waves impinge on intertidal surfaces probably play a major role in determining distribution trends of eulittoral biotopes. Wave sheltered low midlittoral surfaces with a carpet of tightly-packed algal turf are immersed sooner (see Koehl et al. 1993; Jeffrey and Underwood 2000) and subject to surges of passing bores and currents, whereas waves continue to batter the elevated surfaces for a much longer period over a tidal cycle (Gaylord 2000).

Macroalgal species richness was only slightly lower in biotopes of upper rock surfaces compared to low surface algal turfs. On upper surfaces, a combination of predation and harsh environment usually prevents successful colonization of algae. Much of the variation in the number of species recorded in eulittoral biotopes is probably a response to local micro-habitat conditions brought about by any number of environmental factors including rock topography, substrate orientation, substrate surface characteristics, exposure to wave action, intertidal water flow patterns and sediment deposition patterns, as well as biological interactions, i.e. competition and predation. Both *Gelidium pristoides* and *Perna perna* have been described as bio-engineer species capable of strongly modifying the micro-climate around them (Gibbons and Griffiths 1986; Gibbons 1988c, d; Hammond and Griffiths 2004) and creating benign patches or islands in a generally hostile environment. This allows colonization by other algae and species of macrofauna, increasing the species richness of the biotope they characterise. In this study, there were more species associated with these two character taxa at localities where there was evidence of zonal overlap, perhaps because of improved moisture conditions which allowed more algae to grow to a size where they escaped predation by the limpets usually associated with these zones.

On elevated rock surfaces of sites in mixed substrate shore biotic type C, the upper balanoid (upper midlittoral) zone, the most obvious and abundant organisms were the barnacles *Chthamalus dentatus*, *Tetraclita serrata* and *Octomeris angulosa*. The barnacles were joined by small turf-like *Bostrychia intricata* as well as resistant encrusting forms like *Hildenbrandia*
lecannellieri adapted to the drying conditions (Underwood et al. 1983; Russell 1991). This agreed with descriptions of the upper balanoid at rocky shores in texts mentioned above as well as previous studies (Fischer 1987; Munnik 1987). Numbers of species associated with Chthamalus stellatus were similar to Eastern Cape rocky shores (Brown and Jarman 1987).

Elevated midlittoral rock surfaces were dominated by Gelidium pristoides with Arthrocardia flabellata in close association (also see Munnik 1987), while encrusting algae (Leptophytum spp, H. lecannellieri, Ralfsia verrucosa) and the barnacles T. serrata and C. dentatus also typically occurred. The prevalence and abundance of G. pristoides on midlittoral rock surfaces of Eastern Cape rocky shores is well documented (see Carter 1986, 1988; Carter and Anderson 1991) and the species has been recorded at many rocky and mixed shore sites in the Eastern Cape (e.g. Beckley an McLachlan 1980; Dower 1989; Fischer 1989; Munnik 1989; Olivier 1989; Dobkins 1992). The alga thrives under a cycle of vigorous wave action and water movement during inundation with exposure to air and drying at low tides. The ability to photosynthesize rapidly after a period of drying has been demonstrated in other algal species with similar habitat preferences (Norton 1985).

Though present at every site, the extent of G. pristoides was reduced at sites with limited rock above midtidal elevation. The upper limit of G. pristoides is determined by physical factors and the lower limit by competition and predation (Carter and Anderson 1991) and between these boundaries it appears to depend on the availability of midtidal surfaces that experience a degree of wave splash as well as rapid water movement during the period of immersion. Sand-inundation of G. pristoides was observed at a number of sites, but there was no indication that the degree of sand inundation had negative consequences for G. pristoides.

Perna perna has a highly variable distribution (Erlandsson and McQuaid 2004) determined most strongly by wave action via food availability and propagule distribution patterns (McQuaid and Lindsay 2007). At sites with few elevated low shore rock surfaces and/or reduced wave action on those surfaces P. perna occurred as small patches. Its relatively low position allowed much overgrowth by species of lower intertidal elevations resulting in high species counts in the associated biotope.

This was the case at most sites in biotic type C where both Octomeris angulosa and Perna perna had low abundance. Munnik (1989) reported P. perna absent from Cape Recife East (CRE), but in this study a few isolated patches were located. Three sites of biotic type C were more wave exposed and exhibited a variation on the typical eulittoral zone pattern of biotic type C in that these sites were rather dominated by a combination of Perna perna and Octomeris angulosa on low eulittoral rock surfaces and the turf among the sessile filter-
feeders had a greater proportion of encrusting algae (Leptophytum, Ralfsia verrucosa, Hildenbrandia lecannellieri) with small quantities of Arthrocardia filicula or A. flabellata and Bostrychia intricata. Both P. perna and O. angulosa have been associated with moderately wave-exposed rocky shores (e.g. McLachlan et al. 1981; Branch and Branch 1981; McQuaid and Branch 1985; Brown and Jarman 1987; Lubke 1988).

At sites of biotic type B, the mussels present, i.e. Choromytilus meridionalis, Mytilus galloprovencialis and P. perna, are now all known to have a degree of sand-tolerance (see Day 1974; Zardi et al. 2008, 2011), although in P. perna this has only been shown for the east coast strain (Zardi et al. 2006, 2011). Despite regular sand-inundation and intermittent complete burial, sessile filter-feeders with a preference for moderate wave action (P. perna and O. angulosa) were present in notable quantities at biotic type B sites, limited perhaps only by the amount of available substrate, as algae compete for attachment space. Sites where rock height was limited to more or less midtidal elevation, midlittoral turfs formed the dominant biotic component of hard substratum. The turfs experienced regular sand-inundation and also accumulated fine sediment at all sites, a factor that is though to enhance their ability to withstand desiccation (Hay 1981; Norton et al. 1981). Competition for primary space in the turfs prevents new colonists from becoming established, particularly since the dominant species on those substrata are pre-adapted to retain their space.

Species richness in the two “dwarf” algal turfs (R3 and R5) was often the highest of rock surface biotopes, but due to incomplete data on turfs in other studies, comparison was made difficult. “Turfs” are often lumped under the identity of a few easily recognized species (e.g. Beckley and McLachlan 1980; McLachlan et al. 1981, Munnik 1989; Dobkins 1992), perhaps because the process of identifying the many, tiny forms that make up a huge proportion of the turf (and contribute greatly to species richness) can be a rather time-consuming and often exasperating task. Also in this study, the algal turfs have by no means been identified exhaustively, as dominant forms were sought.

The majority of sites representing biotic type C of this study had a strongly wave-sheltered eulittoral zone. At these sites, the extensive short turf of the upper midlittoral (R3) consisted almost exclusively of Arthrocardia flabellata. The composition of the turf was the same at sites with high rock ridges and those with only low ridges. Associated algae include Leptophytum spp, H. lecannellieri, Cladophora spp, Blidingia minima, and Pterocladiella caespitosa. The encrusting sponge Hymeniacidon perlevis was a consistent element of the turf. The lower eulittoral turf (R5) consisted mostly of Arthrocardia flabellata with a smaller Arthrocardia filicula component, alternating with Leptophytum spp, Laurencia natalensis, Codium lucasii ssp capense, and other coralline species. At three sites of biotic type C,
where the eulittoral was more wave-exposed, the dominant macroalgal species in the eulittoral zone was a robust form of the filamentous species, *Polysiphonia urbana*, with smaller amounts of the coralline turf species.

At the sites of biotic type B where sand-inundation of rock surface assemblages was more common than at those of of biotic type C, midlittoral coralline turfs had a higher admixture of fine filamentous species (e.g. *Polysiphonia incompta*) and gelatinous turf algae (*Caulacanthus ustulatus*) of green pioneer algae (e.g. *U. prolifera, U. rigida, Cladophora spp, B. minima*).

Sites of of biotic type A were the most sandy in midlittoral reaches of all the study sites and had low relief rock surfaces where the distinction between the assemblages of upper rock surfaces and lower rock surfaces was less clear as algae from lower turfs "invaded" the assemblages of upper rock surfaces. This observation concurs with the Stephenson’s (1972) on low relief shores. The midlittoral assemblages of the sites in this community showed a great deal of dissimilarity among themselves. The upper midlittoral turfs contrasted with those of other communities in the increase in abundance and number of species normally found in lower intertidal zones. Articulated corallines were still among the dominant taxa, but a range of macroalgae from lower midlittoral and infralittoral fringe strata were added to the assemblage, e.g. *Plocamium corallorhiza, Dictyota dichotoma, Rhodomelopsis africana, Caulerpa filiformis* and *Tayloriella tenebrosa*.

11.5.3.3 The infralittoral fringe

Although the cochlear zone (R7) and infralittoral macroalgal fringe (R8) made out a very small proportion of the cross-shore continuum, the total number of species in these two subzones was the highest. The mean species richness, on the other hand, was similar to that of the eulittoral strata. The infralittoral algal fringe (R8) was less rich in macroalgal species than at rocky shores and also appeared to harbour fewer motile and sessile animal species (see McQuaid and Branch 1984, 1985; Gibbons and Griffiths 1986). The latter could be an artifact of the sampling method (photographs) as small individuals might have been concealed by algal fronds. Since this study mainly concentrated on dominant taxa, these were not taken into account.

The cochlear zone usually has fewer macroalgae than the infralittoral macroalgal zone, because of grazing by limpets (McQuaid and Branch 1984,1985; Gibbons and Griffiths 1986). In this study this trend was reversed, as reflected in both the total and mean number of species. At most of the study sites the cochlear zone was overgrown by a variety of algae increasing the number of species associated with this zone.
The cochlear zone being on low shore exposed rock surfaces come under wave attack as soon as the tide rises, and is often among the first surfaces on which waves make landfall. The organisms of this zone are adapted to the wave regime as their body shapes and physiognomy suggest, and reap the benefits of the water-borne nutrients and high aeration levels (Branch 1981, Gaylord 2000). A change in the wave regime could eliminate the key species in this zone, *S. cochlear*. It is known to have a preference for moderate to heavy wave action, but is unable to remain where wave action become extremely heavy or too mild (Branch 1985; McQuaid and Branch 1984, 1985). Within weeks of its disappearance, the nature of the algal assemblage changes and the characteristic algae disappear and are replaced by infralittoral turf algae (Branch 1981).

Normally easily identified by the presence of *Scutellastra cochlear* and the accompanying encrusting algae *Spongites yendoi* and *Gelidium micropterum* and/or *Herposiphonia heringii* (Bolton and Anderson 1997), this zone was present at sites of all three of biotic types. It was most extensive at sites of biotic type C, in line with previous accounts of south coast rocky shores, e.g. Stephenson and Stephenson (1972), Brown and Jarman (1978), Seagrief (1988), Bolton and Anderson (1989). At sites of biotic type B it was less well-presented and at sites of biotic type A the least. At sites where the cochlear subzone appeared to be suppressed, the main differences noticeable were: greatly reduced area, possibly tied up with a reduction in the provision of suitable rock surface in the infralittoral fringe, decrease in the cover-abundance of the character algae, a marked increase in the abundance of low turf-forming (e.g. *Caulacanthus ustulatus*, *Chylocladia capensis*, *Polysiphonia urbana*, *Streblocladia tenuissima*) and encrusting species (*Ralfsia verrucosa*), “fouling” the cochlear surface area, and, an invasion by larger competitors for space from the lower infralittoral fringe (*J. verrucosa*, *H. spicifera*) and opportunistic species (*U. rigida*) overgrowing the dominant non-geniculate corallines. At Cannon Rocks (CNR) the cochlear zone was recognized mainly from the algae typically present. Munnik (1989) reported *S. cochlear* absent from Cape Recife East (CRE), but in this study a few isolated patches were found. In a similar fashion, the near absence of *S. cochlear* at CNR may be a sampling artifact.

Stephenson and Stephenson (1972) proposed that the cochlear zone disappeared entirely from wave sheltered shores and was gradually replaced by an algal turf. This observation has somehow led to an assumption that all mixed substrate shores are sheltered and would thus lose the cochlear zone, e.g. a reduction in the cochlear zone has been attributed to wave-shelter (Munnik 1987) and sand-intolerance (Dower 1989). Although no specific evidence to the contrary has emerged from this study, it is doubtful that the mere presence of sand is enough to eliminate the cochlear zone. It appears that it may rather be the lack of rock surface of a suitable orientation and adequate wave energy input that inhibits the
development of this zone. Species are often eliminated from potentially suitable habitat due to boundary impermeability (Gosz 1991), difficult physiological gradients (Ray and Hayden 1992), a too small patch size (Pickett and White 1985) and high variability in microhabitat which makes settlement more unsure (Gosz 1991). A slight rise in sea level could also wholly immerse the cochlear zone at sites with a low relief, exacerbating an already limiting situation.

The infralittoral fringe macroalgal assemblage was well represented in all three mixed substrate shore biotic types and exhibited the greatest degree of variation of the intertidal biotopes studied. A large number of the species recorded have perennating long-lived basal crusts or spreading rhizomatous holdfasts capable of regeneration after disturbance by vegetative growth (see Hay 1981; Norton et al. 1981; Norton 1985; Bolton and Anderson 1997; Anderson et al. 2008). Several common and abundant species of present sites have been associated with rocky shores of the region, e.g. Plocamium corallorhiza, Gelidium abbotiorum, Amphiroa and Arthrocardia spp, Laurencia spp, Jania spp, Dictyota spp and Pterosiphonia cloiophylla (Bolton and Anderson 1997; Beckley and McLachlan 1979; McLachlan et al. 1981; Munnik 1987; Fischer 1987). Caulerpa filiformis was listed as sand-tolerant (Anderson and Stegenga 1989; Bolton and Anderson 1997).

At low ridge sites, the number of infralittoral fringe species was well below that of the other physical shore types, which suggested that the separation of rock substrate by stretches of sediment amounted to a form of natural habitat fragmentation (Merriam and Wegner 1992) where isolated rock ridges had less chance of gaining new recruits from distant assemblages (see Sousa 1979). Many of the macroalgae occupying the infratidal zone form turfs, pre-empting space and thereby reduce the chances that new individuals become established (Stewart 1983; Sousa 1985; D’Antonio 1986). Sand-tolerant rhizomatous alga species (e.g. Hypnea spicifera and Caulerpa filiformis) that abounded at sites of biotic types A and B are thus not dependent on the successful settlement of new propagules and have a competitive advantage.

The infralittoral fringe of biotic type C was characterised by the dominance of macroalgae recorded in previous studies, e.g. Beckley and McLachlan (1979), McLachlan et al. (1981), Munnik (1987), Fischer (1987), Anderson and Stegenga (1989) and Bolton and Anderson (1997). These were Gelidium abbotiorum, Laurencia spp., particularly L. natalensis, Arthrocardia spp., Amphiroa spp, and Plocamium corallorhiza. The most common brown alga was Stypopodium. As these sites have been characterised as sheltered inshore, the presence of this assemblage is probably indicative of a preference for mild wave action. At some sites the assemblage also included sand-tolerant species that were not found in wave-
exposed sand-influenced sites, e.g. *Halimeda cuneata*. The more wave-exposed sites of biotic type C had a greater admixture of either large coralline species (*Amphiroa, Arthrocardia*) and brown algae (*Sargassum, Ecklonia*) or large sized filamentous taxa (*Rhodomelopsis, Polysiphonia* spp) and a different brown alga (*Dictyopteris*).

The sites of biotic type B differed from those of biotic type C in that the dominant species were filamentous turf algae, e.g. *Tayloriella tenebrosa, Polysiphonia* spp. as well as larger sand-tolerant species, forming a continuous turf dominating low shore rock surfaces with *Arthrocardia* spp. and *Jania* spp., e.g. *Caulerpa filiformis* and *Hypnea spicifera* (Bolton and Anderson 1997; Stegenga et al. 1997). Therefore, taking into account that there was considerable natural variability along any coast, it appears that these sites, though retaining most of the elements of “proper” rocky shore communities, also have additional taxa that could only have gained a foothold because of the influence of sand on these communities.

The infralittoral fringe of biotic type A, had a high proportion of corallines that are sand tolerant, e.g. *Jania* spp, *Arthrocardia* and *Corallina*, mixed with other sand-tolerant species, e.g. *Dictyota* spp, *Plocamium* spp, *Caulerpa* and *Hypnea*.

**11.5.4 Classification of the assemblages of intertidal biotopes/subzones**

High ridge sites, the closest to sediment-free rocky shores in structure and dynamics, provided a range of conditions enabling development of the full range of intertidal subzones on rock surfaces with their attendant macrobenthic assemblages and exhibited very clear differentiation into infralittoral fringe (R7, R8), low surface eulittoral (R3, R5), high surface eulittoral (R2, R4, R6) and supralittoral fringe (R0, R1). In biotopes that exhibited a degree of intermingling and overlap, it was evident from the grouping in the cluster analysis, where taxa from the upper eulittoral zone and supralittoral fringe were mixed and so too infralittoral and low eulittoral taxa. At mixed substrate study sites where rock surfaces were discontinuous (e.g. low ridge sites) and/or of low elevation, a particular biotope or assemblage would simply be absent from the study locality or shore section where the appropriate substratum was not offered (see Stephenson and Stephenson 1972). An extreme example of this is the site with a single midtidal rock outcrop where an impoverished version of other midlittoral biotopes was found on the rock substrate. For some species the tolerance range within which they could become established and sustain themselves were rather narrow which meant elimination from a locality where these specific conditions were not fully met, e.g. *Porphyra capensis, Scutellastra cochlear, Gelidium micropterum*. Those with wider tolerance ranges became the ubiquitous species found perhaps at rocky shores as well. Others (possibly *Caulerpa filiformis, Plocamium beckerii, Halimeda cuneata, Tayloriella tenebrosa*) with a tolerance range for which the optimum coincides with a
particular set of conditions offered by a mixed substrate situation, e.g. moderate wave action, deep medium to fine sand around hard substrate and suitable oxygenation, could well reach their greatest abundance at particular mixed substrate shores and be eliminated from sediment-free rocky shores.

The infralittoral fringe zone (R7 and R8) most often split off together and joined the sister clade consisting of sediment samples, but this simply illustrated the high degree of dissimilarity between those samples and the rest of the assemblages on rock surfaces. This could mostly be attributed to a completely different set of macroalgae dominating low intertidal rock surfaces, often times with sand-inundation. The two alternative patterns, i.e. R6 joining R7 and R8, or R8 left behind with R5, were indicative of the degree and type of zonal overlap observed at these sites, both of which can be ascribed to water movement patterns on the one hand and sediment load on the other. The two eulittoral algal turf biotopes (R3 and R5) were closely similar at study sites with a greater degree of wave shelter over midlittoral low surfaces compared to infralittoral. The exception to the rule being where in response to greater wave activity and limited rock substrate, there was greater overlap between the lower turf assemblage (R5) and either R8 or another, increasing dissimilarity between the two midlittoral turfs.

For sediment macrofauna, the requirements probably hinged on a balance between surf-wave activity, sediment water-retention /moisture levels and oxygenation, as well as sediment grain size. There again, at study sites where the particular suite of conditions were not met, it led to elimination of the taxon from the locality (see Brown and McLachlan 1990; Brown et al. 1991). Wider searches would need to be done to establish the extent of elimination of particularly some typical beach macrofauna species of importance, e.g. *Bullia* spp or *Donax serra*.

According to the cluster analyses, zonation patterns in sediment ranged from highly regular groupings that appeared to follow the usual cross-shore gradients in sediment to highly irregular groupings indicative of bimodal cross-shore distribution patterns in dominant species. This was the case at some, but not all sites with wide, substantial beaches without rocks intruding in the subaerial beach. In these analyses, subclusters of sediment samples grouped according to a regular cross-shore intertidal gradient: the infralittoral fringe / low shore (S5- S4), eulittoral zone / midshore (S3-S2) and supralittoral fringe / high shore (S1-S0) assemblages. This pattern contrasted sharply with the pattern described above. The distinction between the three clusters was linked to distribution of dominant beach macrofauna: polychaetes were the most abundant and diverse in low shore strata, crustaceans (cirolanids and sphaeromatids) held the mid- and high shore and insects were
common in high shore samples. The low shore assemblage (sampling stratum S5) was highly different from those of the mid- and upper shore at a number of sites as it separated from other sediment samples at a high level of dissimilarity.

Clearly the presence of rock in the sand over a wider cross-shore extent modified important habitat conditions, e.g. drainage patterns and water flow which in turn influences propagule transport. Low shore taxa were able to become established much higher up on the shore than would be the case at a rock-free sandy beach. Addition of macrofauna, particularly infralittoral polychaetes, to midlittoral sediment, increased the abundance and diversity of those assemblages. The underlying environmental factor responsible for this pattern could have been an elevated water table due to underlying rock substrate, which enabled the upward migration of delicate forms usually confined to lower elevations.

The cluster analysis and DCCA demonstrated the importance of sediment grain size. Three sites of biotic type C, TST (Three Sisters), KNB (Kini Bay) and HPW (Hougham Park west) had beach deposits with a high coarse fraction. From the literature, the sediment deposits at these sites should have been devoid of macrofaunal life due to coarse grain size and steep slopes (Brown and McLachlan 1990; McLachlan and Jaramillo 1995; Brown 2000). In accordance with McLachlan and Jaramillo (1995) these sites had reflective beaches, i.e. only two recognizable zones, the supralittoral fringe and the eulittoral, with a partially developed or no infralittoral fringe. Instead of being depauperate, these sites supported a varied and abundant fauna that included taxa not usually associated with sandy beaches (e.g. Hyale, Pseudonereis, Zygomaera, Paramoera, Caulleriella, Acanthochiton, Siphonaria and Barbatia) together with some that are typical of South African sandy beaches (e.g. Tylos, Talarcestia, Exosphaeroma, Excirolana) and species of very large-sized Polygordius and Marionina usually associated with coarse-grained (Brown and McLachlan 1990), sheltered (Parapar et al. 2009) and heterogeneous intertidal sediments (Ramey et al. 2006). Cluster analyses demonstrated a clear distinction between upper and lower beach zones based on species composition and abundance, but simultaneously a high degree of similarity among mid- to lower zones, a trend that was probably linked to the degree of contraction in zones due to limited beach size and / or steep slope.

The observations and quantitative data obtained from the cross-shore analysis offers much potential material to investigate experimentally. The effects of the two crucial environmental variables (substrate availability and water movement regime) need to be separated and the life stage at which their effects are significant established. One can only speculate on the nature of the drivers that result in overlapping subzones or biotopes. More investigation is required to discover the nature and reasons for the process involved.
11.6 The extent and distribution of mixed substrate shore types in the Eastern Cape.

The present system of mixed substrate shore configurations was based on the pioneering schemes proposed by Bally et al. (1984) and Brown et al. (1991) and was an attempt at introducing a greater degree of objectivity into the classification. Descriptive terms such as “many”, “few”, “isolated”, “scattered” were avoided as far as possible, as these were subjective terms that could introduce unnecessary bias. The present scheme accommodated shore configurations commonly found on the southeast coast (Marker 1988), but also occurring more widely along the South African coast (Bally et al. 1984; Brown et al. 1991) where they give rise to mixed substrate shores in areas with an adequate supply of mobile sand (Marker 1988). Only boulder shores were not incorporated in this system, as they were rare along the southeastern coastline (Marker 1988; Coetzee 1991).

The distribution of the different configurations was dictated by coastal geomorphology and geology (see Marker 1988) and differed, sometimes considerably, from previous assessments of the coast, e.g. the coastal sensitivity map of Jackson and Lipschitz (1984). Earlier mapping of shores employed three basic categories, sandy, rocky and mixed shores, as the purpose of their work was not to investigate fine-scale structural features of the coast (e.g. Lombard et al. 2004). In this study, the focus was on obtaining that type of detail where possible as the null hypothesis was that communities responded to all mixed substrate shore configurations equally, not showing a definite affiliation to a particular physical type.

Multivariate analysis of community data identified several biotic communities none of which related specifically to a configuration category. There were by implication different functional types of mixed substrate shores based on changes in species composition and abundance. These differences were not necessarily linked to a particular configuration type, but rather to the water movement regime that resulted from structural control exerted over wave action by the rock platforms and reefs at these study sites, a phenomenon studied with reference to sandy beaches (Short 1999; Jackson et al. 2005). However, even on rocky shores, the low shore rocks are known to attenuate wave action and bring about sheltered mid-littoral conditions (Stephenson and Stephenson 1972; McQuaid et al. 1985; Blamey and Branch 2009).

The exact extent of these biotic shore types was not determined in this study as biotic types could not be discerned at the resolution available, but may be possible using other techniques. *Arthrocardia-Laurencia* turf (mixed substrate biotic type C) was potentially the most wide-spread as it occurred at study sites of all four configuration types with wave-
sheltered mid-littoral conditions and smaller sand component. High ridges tend to create sheltered mid-littoral conditions regardless of the degree of wave exposure and this biotic type may also occupy rocky shore eulittoral surfaces (as at Willows Beach) and potentially take up about 50% of the coastal section investigated.

*Jania*-Corallina-Polysiphonia turf (mixed substrate biotic type A) occurred at one low ridge site and platform sites of both types, the common factors being a wave-exposed eulittoral zone and well-developed intermediate beach. *Polysiphonia-Tayloriella-Caulacanthus* turf (mixed substrate biotic type B) occurred at low platform and both types of ridge shore with a well-developed more sheltered beach and lower wave energy than at sites supporting biotic type A. Both these biotic types appear to be requiring a combination of conditions that is not available extensively along the surveyed section of coast. They should therefore be more limited in distribution, occupying less than 10% each and occurring as short, discontinuous entities along the coast.

Based on its wide association with different physical shore configurations, the *Arthrocardia-Laurencia* community was identified as potentially most wide-spread. Previous studies of Eastern Cape rocky shores and the rock substrate communities of mixed substrate shores of different physical configurations (ridges and platforms) have also indicated the prevalence of those taxa on eulittoral rock surfaces (Beckley and McLachlan 1980; McLachlan et al. 1981; Munnik 1987; Olivier 1989).

### 11.7 Conservation status of mixed substrate shores

A few major assessments of the South African coast, e.g. Jackson and Lipschitz (1984), Campbell and Bate (1997), Lombard et al. (2004), Harris et al. (2011), provided a knowledge base for strategic placement of marine protected areas (MPAs) in order to maximise protection of important processes, functions, habitat- and biodiversity. Some of these focussed on a particular significant physical attribute, e.g. substrate (Jackson and Lipschitz 1984), dynamic parameter, e.g. surf zones (Harris et al. 2011), or biotic component, e.g. surf zone diatoms (Campbell and Bate 1997), in order to detect common patterns in system functionality and structure. In the hierarchical classification of the coast by Lombard et al. (2004) broad-scale biotic features were employed together with physical (substrate) and dynamic (wave action) attributes, and biotopes recognized as the lowest tier of classification that can be used in characterising shore types.

Frachetti et al. (2005) and Blamey and Branch (2009) pointed out that unless small-scale habitat features were given due consideration, many MPAs could completely ‘miss the point’.
In some studies, the biotope approach was applied to address small-scale variations in biotic responses, but also prevent unnecessary subdivision on physical grounds where biota showed a similar response to conditions that appeared to the human eye to be different, e.g. Hill et al. (1998), Tittley and Neto (2000). The results of the present study concurred showing that small-scale physical variations (i.e. shore configuration) were not necessarily accompanied by parallel variations in biotic components, in a similar dynamic environment (i.e. wave action regime).

The recommended minimum targets for protecting and maintaining the integrity of marine biodiversity components is 20 – 30% of each kind of habitat (WPC 2003). Along highly variable sections of the Eastern Cape coast, such as the section mapped in this study, several shore types or habitats potentially occurred along a 50 km stretch of coastline that corresponded to a planning unit in the broad-scale planning approach of the South African National Spatial Biodiversity Assessment 2004.

Using an irreplaceability analysis and minimum set analyses of species data Lombard et al. (2004) identified candidate coastal areas to be considered for future protect in order to meet the minimum conservation target for marine species. Among these there were three sections of the south-east coast with high irreplaceability values (0.8 – 1). These were: (a) the coastline to the west and east of Cape St Francis; (b) Algoa Bay (Cape Recife to approximately Sunday's River); and, (c) a section between Port Alfred and Great Fish Point. All three fall within the section of coastline mapped in this study. Study sites were located in two of them. Of the intertidal habitats identified by Lombard et al. (2004), some rocky and mixed shore habitat types (according to their definition) have protection within the limits of the Agulhas bioregion, although none of these fell within ‘no take’ MPAs. According to Lombard et al. (2004), two rocky shore habitat types (very exposed and sheltered), three mixed shore habitat types (very exposed, exposed and sheltered) as well as all the sandy beach habitat types did not reach protection targets in the Agulhas bioregion. This meant that most of the coastline mapped in this study, and all the study sites except for one (WLW - Willows), represented intertidal habitat types that should be candidates for potential inclusion in additional protected areas.

Shellfish (mussels, oysters, chitons, various gastropods, including limpets) is heavily exploited along large sections of the southeast coast (Dobkins 1992; Lasiak and Field 1995) and this has been implicated in diversity loss (McLachlan et al. 1981) and changed community structure (Lasiak and Field 1995). At these sites it may have led to a strong reduction in the populations of sought-after molluscs, e.g. Turbo sarmaticus, which exhibit
strong seasonality in reproductive behaviour (Lombard 1977). At lower numbers the likelihood of finding individuals in sampling quadrats or even during a general search is reduced. Abundance of ‘non-patellid’ gastropods such as Oxystele, Burnupena and Turbo, was an order of magnitude or more below the numbers previously reported at the same localities (Munnik 1987; Fischer 1989). These data make a case for the protection of a representative portion of the coast and introduction of selective no-take zones to give these communities a chance to recover and provide a sustainable yield in the future.
Chapter 12 Conclusions

There have been two opposing viewpoints regarding the nature of mixed substrate shore communities: according to one perspective they are regarded as species-poor and of low significance (see Bally et al. 1984), while the opposite point of view is that they are more diverse than equivalent rocky shores and sandy beaches put together (McQuaid and Dower 1990) and may comprise of a unique and abundant biota (Brown 1996).

The former view was not without basis, even in the absence of empirical data on beach communities. The beaches of mixed substrate shores do not have the appearance of “normal” permanent sandy beaches because of rock substrate interrupting the continuity of the sand prism. The normal wave-beach interactions which determine the very nature of sandy beach systems (see Brown and McLachlan 1990) could therefore be disrupted. According to their cross-shore gradient and width, they can be expected to be species-poor (Defeo and McLachlan 2005; McLachlan and Dorvlo 2007). Sediment instability, i.e. ephemeral deposits and the rapid erosion-accretion cycle at some of these beaches amount to frequent disturbance and has been linked to low species richness (Connell and Keough 1985; Stephen (1929) in McQuaid and Dower 1990).

From the literature, communities of the rock substrate tend to convert to a more simplified community structure (low diversity, low biomass) when subjected to sand-inundation on a regular basis (see Airoldi 2003 and references within). Severe and/or frequent inundation acts as a disturbance as it leads to loss of biomass (sensu Pickett and White 1985), whereas a more “chronic” form of inundation acts as a stressor (sensu Grime 1977) by suppressing production. Both effects may result in a loss of sediment-intolerant species of the climax community and replacement by sediment-tolerant forms without necessarily enhancing community diversity.

The view that mixed substrate shores should harbour more diverse assemblages than either rocky or sandy shores is also not without support. Fairly undisturbed climax communities could become dominated by just a few highly successful species through the ecological mechanism of competitive exclusion (see Paine 1966; Sousa 1979). Frequent small random disturbances enhance micro-scale habitat diversification as various seral stages co-exist in the same environment (Sousa 1985). At a mixed substrate shore, shifting sediment patches could cause short-term physiological stress and mortality by inducing anoxia and reducing light availability under the sand patch. Short-term alternation of conditions could lead to the co-existence of competitors with slightly different abilities, where the extent to which they
dominate a substrate is determined by temporary shifts in the most significant environmental drivers.

Heterogeneous habitats provide opportunities for fugitive (e.g. species typical of early seral stages) and refugee species (those limited to spatial refuges) to co-exist with dominants (Connell 1985), instead of being excluded by them. At mixed substrate shores, living conditions offered by the two major substrate types are potentially influenced by their proximity to each other. In both habitat types this could enhance the ability of pioneers/fugitives and refugee species to co-exist with climax species and even replace them. Post disturbance, convergence of a successional series to a particular climax is not a given and different dominance outcomes may be possible in relation to site-specific factors, keeping in mind that the response of a species population in any location is closely tied up with the response of each individual in the situation (Connell and Slatyer 1977; Connell and Keough 1985; Westoby et al. 1989). Mixed substrate shores are known to have high temporal and spatial variability, which make them ultimately suitable as “evolutionary corridors” through which biota, particularly molluscs, adapt to newly offered substrata (Brown 1996) – in this way uniquely adapted assemblages could result.

From the literature (e.g. Stephenson and Stephenson 1972; Daly and Mathieson 1977; Stewart 1982; Littler et al. 1983; D’Antonio 1986; Sunamura 1992; Roy et al. 1994; John and Lawson 1991; Short 1999; Knox 2000; Hubbard and Dugan 2003; Jackson et al. 2005) it is clear that globally mixed substrate shores have structural attributes in common which stem from similar geological and geomorphological features of the coastline. From the findings of Sunamura (1992), Roy et al. (1994) and Short (1999), and more recently Jackson et al. (2005), mixed substrate shores should form where the gradient of the shore platform, sediment budget and sea level combines to give a section of coast where sediment accumulation is allowed by a low enough shore gradient and sediment supply sufficient to partially inundate the rock base between tide marks.

Two basic physiognomies appeared to be possible at these study sites depending on whether the hard substrate (i.e. rock) was in the form of a more or less horizontal platform of recent sedimentary rock or composed of older formations (e.g. sandstone, granite, quartzite, shale) that have undergone transformation and have a broken irregular structure. The thickness of the sand veneer depends on supply which in turn may be linked to the proximity of a source (dune field, river, eroding cliffs) and the nearshore sea bottom topography, as sediment reaches the shore mainly by along shore transport (Storlazzi and Field 2000). Waves interacting with immovable hard substrata and moveable sediment on a micro-scale produce habitat conditions particular to each site, but also in common with shores of a
similar degree of wave exposure. Elevated rock surfaces are conducive to more wave splash and spray, which implies a different type of wave and water motion than over low-lying surfaces (Stephenson and Stephenson 1972; Gaylord 2000). Shallow sediment over rock surfaces and adjacent to rock bases are more likely to be entrained and moved off than that of deeper deposits (Short 1999).

Gradients in the environmental parameters rock substrate height, cross-shore extent of the rock and sandy substrata, long shore extent of the rock and sandy substrates within the study site, sediment grain size, the degree of sand-inundation of rock substrate and wave exposure were represented in the study sites.

12.1 Community descriptors of macrobenthic assemblages in relation to mixed substrate shore configurations (physical shore types)

Variations in three community descriptors (species richness per site, species composition of assemblages and abundance) of the macrobenthic assemblages (sediment macrofauna, macroalgae, sessile macrofauna and gastropod fauna of rock surfaces) of mixed substrate shores were not consistently related to the shore configuration types used in this study as a basis for a physical shore classification in line with earlier mixed substrate shore classification systems.

The macroalgae were the only biotic assemblage that appeared to demonstrate a response to shore configuration as these assemblages were richer in species at platform sites than ridge sites. The increased species richness of sediment macrofauna at some low platform sites was a response to wave shelter and beach slope rather than the physical configuration of the shore, as the number of species was lower at low platforms with wave exposed steep beaches than those with low gradient, sheltered beaches.

12.2 Species richness compared to sandy beaches and rocky shores

While shore configuration may influence species richness and composition through substrate continuity and interaction with wave energy, the effect on either rock-bound or sand-bound communities was not as pronounced as expected.

The macrofaunal communities in sediments of these mixed substrate sites were more species rich than South African intermediate sandy beach communities to which they were compared. The species richness of macrofauna in sediments rather approached that of dissipative and sheltered beaches (McLachlan and Jaramillo 1995; McLachlan and Dorvlo 2005).
The species richness per site of macrofaunal and macroalgal assemblages of the rock substrate at these mixed substrate shores was in the same range as those of previous rocky shore studies.

Ordination of sites demonstrated that $\beta$ – diversity of macroalgal and sediment macrofaunal assemblages was higher than that of the sessile macrofauna and gastropod assemblages of rock substrate.

**12.3 Community composition and abundance compared to sandy beaches and rocky shores**

The overall taxonomic and abundance composition of the sedimentary macrofauna differed from that of intermediate sandy beaches and harboured a greater range of taxa at phylum level.

Polychaetes were the numerical dominants of the sedimentary assemblages at all of these mixed substrate shores. Isopods reached higher levels of abundance at the more wave-exposed sites than at those that were wave-sheltered. Polychaetes comprised a greater variety of taxa than usually found at intermediate sandy beaches to which these sites were compared. The mollusc biota, particularly donacids, of these sediments were consistently much lower in both abundance and species number than those of sandy beaches of similar beach morphodynamic state.

The composition and high abundance of the polychaete assemblages (deposit-feeding forms like capitellids, orbiniid, spionids, cirratulids) were indicative of sheltered conditions (also seen at dissipative beaches), but also sedimentary environments regularly subjected to disturbance. The cosmopolitan spionid *Scololepis squamata* was present at most sites, but orbiniids (*Scoloplos*) and capitellids (*Notomastus*) often made out the bulk of the polychaetes. The most common isopods were cirolanids (*Eurydice longicornis, Excirolana latipes* and *E. natalensis*). Sphaeromatids were also abundant (*Exosphaeroma* spp.), but oniscid isopods rare. The most common amphipods were haustorids (*Urothoe pinnata* and *U. serrulidactylus*) and a number of species often associated with macroalgal turfs (*Paramoera capensis, Jassa falcata*), but talitrid amphipods were present in low abundance.

Rhodophytes were the most abundant and varied macroalgal division. Brown algae were lower in species and abundance than at rocky shores in South Africa. The reduction in species and cover-abundance of browns were more evident at wave-sheltered study sites. Green algae contributed comparatively more to total species richness and cover-abundance at sites with a greater degree of sediment inundation.
Macroalgal assemblages were dominated by a turf of small articulated corallines (*Arthrocardia* spp, *Jania* spp), filamentous species (*Polysiphonia* spp, *Tayloriella tenebrosa*), the encrusting sponge *Hymeniacidon perlevis* and infralittoral taxa with a known tolerance to sand (*Laurencia* spp, *Plocamium* spp, *Halimeda cuneata, Dictyota dichotoma*), but also more prevalent under mild wave conditions.

The algal assemblages showed progressive change attributable to the combined effect of greater wave exposure and increased resuspension-deposition of sand. Wave-sheltered rock surfaces were dominated by small articulated corallines (*Arthrocardia* spp, *Jania* spp) and encrusting species (*Leptophytum, Hildenbrandia, Codium lucassii* ssp *capense, Hymeniacidon perlevis*). At sites with sand deposition-resuspension and an active wave regime due to reduced attenuation by rocks, the corallines were increasingly joined by filamentous turf algae (*Polysiphonia* spp, *Tayloriella tenebrosa*) and robust sand-tolerant infralittoral turf species (*Hypnea spicifera, Caulerpa filiformis*).

The taxonomic composition and abundance trends of the sessile fauna at these mixed substrate shores were similar to that of South African rocky shores. The gastropod assemblages were less abundant compared to previous rock shore studies and showed evidence of suppression species richness.

**12.4 Trends in assemblages of intertidal zones**

The general cross-shore reduction in species richness from the low spring tide to high spring tide mark corresponded to that of both rocky and sandy shores.

At sites with only low elevation rock surface or limited rock surface the cochlear subzone was enriched by algae from the infralittoral algal fringe subzone causing the subzone to harbour more algal taxa than at topographically steeper shore, together with an appreciable reduction in the extent and development of the cochlear zone.

The cross-shore zonation patterns of macrofauna in beach sediments demonstrated an intergrading trend, as low shore biota were displaced higher up. This may have been a consequence of an elevated water table and further compounded by truncation of upper zones in the beaches of limited width. At these study sites the there was a marked midshore peak in macrofaunal abundance which curiously resembled that of dissipative beaches.
12.5 Ecological implications of patterns in species richness, composition, abundance and zonation

The overall taxonomic composition of assemblages in the sediment suggested a transitional (ecotonal) environment. Some species usually associated with normally functioning sandy beaches (e.g. nephtyids, glycerids, oniscids, donacids, mysids) were greatly reduced, while others (e.g. ciranalid isopods, haustorids, spionids) persisted, together with taxa that frequented both exposed and sheltered habitats (e.g. Bullia digitalis, Eteone siphodonta) or did not usually extend their range into surf-beaten beach sediments, preferring sheltered sediments instead (e.g. Arabella iricolor, Ampelisca spinimana). In addition, macrofauna from the phytal habitat provided by macroalgal turfs (e.g. Amaryllis macrophthalma, Pseudonereis variegata) extended their activities into the adjacent beach sands.

Although this study has not found taxa unique and specific to mixed substrate sediments, several rare and endemic taxa were recorded for which available information suggests a mixed substrate environment.

The zonation patterns of these shores intergraded to a greater degree than at shores with a steeper topography. As this was undoubtedly accompanied by a change in environmental conditions it may precipitate the loss of species with a preference for higher rock surfaces, e.g. patellid limpets.

12.6 Mixed substrate shore biotic classification

In this study three broad-based mixed substrate shore biotic types were identified using hierarchical cluster analysis and DCA. A DCCA was used to isolate major trends in the community data in response to gradients in a suite of environmental parameters common to these shores. The most notable responses in these mixed substrate shore biotic types were to gradients in wave energy, sediment grain size, the potential for sand-inundation of rock-substrate communities, sediment depth and the spatial attributes of the rock substrate (cross-shore extent, long-shore extent and rock height). These responses were clearly demonstrated to not be linked to shore configuration per se, but rather the degree of wave-substrate interaction that produced different levels of incident wave energy attenuation and change in the wave environment of the eulittoral zone.

Mixed substrate shore biotic type A (Jania-Corallina-Polysiphonia turfs) had a highly variable composition as a consequence of a strong infralittoral fringe component in the eulittoral communities of representative sites. This biotic type was characterised by an environment with a high degree of sand influence. Its strongest response was to environmental factors that potentially affected the assemblages of the beach component rather than the biota of
rock surfaces, i.e. sand depth of the beach, and the swash climate, but also to the degree of sand cover of rock substrate communities. The rock traverse had a limited intertidal extent and therefore a limited attenuating influence. The beaches were the most wave-exposed of all the sites and had a reflective-intermediate character, borne out by the isopod-dominated assemblages. The macroalgal communities of this biotic type were characterised by high abundance of infralittoral fringe taxa that were tolerant of sand inundation, e.g. Caulerpa, Hypnea, Corallina, mixed with turfs of sand-tolerant Polysiphonia and Jania. Gunnaria capensis was only indicator species that could be identified as common to all the members of this type (except one site, Pollock north (PBE), and with high fidelity.

The mixed substrate shore biotic type B (Polysiphonia-Tayloriella-Caulacanthus turfs) occupied in some respects an intermediate position between A and C in species composition and environmental conditions. The eulittoral communities of rock substrate had a strongly filamentous nature added to the fine coralline species that appeared to be ubiquitous on most intertidal rock surfaces, and was dominated by Polysiphonia spp. and Tayloriella. The infralittoral fringe was predominantly composed of highly sand-tolerant taxa also found in biotic type A, but with a greater filamentous and fine turf-forming element (Polysiphonia, Caulacanthus). Probably because of the prevailing intermediate surf-wave conditions these communities also had a higher abundance of Octomeris angulosus and Perna perna. No unique indicator species could be pin-pointed for this biotic type, but P. perna and O. angulosus was constantly more abundant at these sites than those of other biotic types.

Mixed substrate shore biotic type C (Arthrocardia-Laurencia turfs) represented in many ways the polar opposite of biotic type A. The site members of this biotic type demonstrated the greatest degree of cohesiveness of the three biotic types identified in this study. This biotic type was characterised by a strong intertidal wave attenuation gradient that was linked to the shore-normal extent of intertidal and subtidal rock traverses as both wave height and swash climate ameliorated with increased extent (structural control) by the hard substrate. This was the least sand-influenced mixed substrate shore biotic type. The beaches and eulittoral rock substrate communities of this biotic type were composed of biota that were highly indicative of wave-sheltered conditions. Midlittoral algal turfs were highly dominated by small, fine articulated coralline species (Arthrocardia spp) and towards the infralittoral fringe non-coralline turf forming and larger forms (Laurencia spp, Plocamium spp., Amphiroa spp.) were added. Although the macroalgal species with a high degree of sand tolerance were not excluded from these sites, they only appeared where infralittoral rock surfaces experienced sand-inundation on a regular basis. Beach sediments were highly dominated by a diverse assemblage of deposit-feeding polychaetes and in addition to some commonly occurring sandy beach cirolanid isopods, supported species highly characteristic of low
energy dissipative conditions. There were numerous indicator species for this biotic type, e.g. *Amphiroa* spp., *Scutellastra longicosta*, *Pseudonereis variegata*, *Codium* spp.

**12.7 The extent of mixed substrate shore types in the Eastern Cape**

The extent of the four mixed substrate shore configuration types, sandy beaches and rocky shores without detectable sand deposits of the physical shore classification were mapped along a section of the Eastern Cape coastline. Sandy beaches and (sand-free) rocky shores were the dominant shore types and tended to take up longer continuous sections of the coast than any of the four physical mixed substrate shore types. These were also not equally common along the stretch of coast assessed. The potentially most common and extensive mixed substrate shore biotic type is the *Arthrocardia-Laurencia* turf (type C) as it was associated with all four the physical mixed substrate shore types and probably also occurs on rocky shores. Biotic types B and C have less potential for a wide distribution as their environmental requirements and tolerance range necessitates a situation of moderate to high wave action and a copious supply of sand and their distribution may be restricted to such situation. The true extent of these three proposed biotic types need to be ground-truthed and related to the present distribution of MPAs in order to determine the need and potential for their inclusion.

**12.8 Final remarks and recommendations**

The macrobenthic assemblages at mixed substrate shores investigated in the present study exhibited a detectable trend in relation to substrate availability and wave activity. This study identified three broad-based biotic types that each potentially consist of subtypes or may with better definition be shown to comprise several valid types. Biotic type A was composed of a rather heterogeneous collection of sites that were similar in some respects, but may also each have been the sole representative of a valid mixed substrate biotic type. Further investigation of mixed substrate shores should focus on further refinement and definition of the communities of mixed substrate shores with a very limited intertidal rock traverse. Within biotic types B and C, the cluster analysis and DCA also suggested that these provisional broad-based biotic types were composed of subtypes that responded very specifically and differently to environmental gradients.

The gradient in substrate availability is not straightforward, but clearly shows that supply of suitable substrate and by implication habitat controls community composition. Quantification of the gradient presents difficulty. In this study, sand deposits around rock bases encouraged establishment of sand-tolerant algae *in loco* even if sand made out less than 10% of the shore, which demonstrates the importance of small-scale habitat variations in the
colonization of substratum. If the extent of rock-sand-interface is known, it could be useful in predicting community change where sand-inundation patterns change. These species respond to a time-integrated pattern of habitat interactions. It is possible that alternative states exist at these shores in response to variations in substrate proportions. Any study to clarify the relationship between sediment-load and the sand-tolerant species of these systems should focus strongly on the temporal dimension.

One of the environmental gradients not evaluated was the nature of the water table at these shores, a parameter that appeared to show much complexity in cross-shore gradient, but could play a very important role the cross-shore distribution of biota. This environmental parameter needs to be related to these communities.

This study proposes that mixed substrate shore types may differ in their functionality and relationships to other systems. How do these shores compare and relate to others on a biotic-functional level? The significance of eullittoral algal turf communities has been highlighted. As climax communities they will play a major role in the functionality of these systems. The high proportion of coralline algae infer low productivity and slow growth, but also great stability. There is therefore a need to investigate the functional aspects of these biotic types from a system point of view.

From a biodiversity angle, mixed substrate shore biotic types should be assessed and representative localities considered for inclusion in existing or future marine protected areas.
List of References


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Addendum 1: Additional references used


**Addendum 2: Data used to calculate beach exposure ratings**

Beach exposure rating interpreted according to McLachlan (1980). The rating of each contributing parameter is given individually. Median vs Slope is a rating based on beach slope (or shore slope) and median sediment particle size. Values in brackets are the ratings based on the full shore instead of beach only. E = exposed, ME = moderately exposed, VE = very exposed, S = sheltered, VS = very sheltered.

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## Addendum 3. Macroalgae Species List

C = Chlorophyta, P = Phaeophyta, R = Rhodophyta

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Addendum 5. Site photographs

Top left: Aston Bay; Top right: Avalanche; Bottom left: Beacon Rock; Bottom right: Bird Rock. (Photos: C.J. Garner)
Top left: Cannon Rocks; Top right: Cape Recife East; Bottom left: Cape Recife West; Bottom right: Hougham Park East. (Photos: C.J. Garner)
Top left: Hougham Park West; Top right: Humewood; Bottom left: Kini Bay; Bottom right: Maitlands Inner. (Photos: C.J. Garner)
Top left: Maitlands Outer; Top right: Miller’s Beach; Bottom left: Paradise Beach; Bottom right: Pollock North. (Photos: C.J. Garner)
Top left: Pollock South; Top right: Three Sisters; Bottom left: Willows Beach; Bottom right: Kleinemonde East. (Photos: C.J. Garner)