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The putative impact of exploitation on rocky infratidal macrofaunal assemblages: a multiple-area comparison

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The putative impact of subsistence foragers along the Transkei coast of South Africa was determined by comparing the community-level attributes of infratidal macrofaunal assemblages in three 'no-take' reserves with those at adjacent exploited localities. The objective of this study was to ascertain whether the differences in the assemblages found at exploited and non-exploited localities were consistent along this coast. Two-way ANOVAs indicated that the presence/absence of exploitation had no effect on univariate community measures. Macrofaunal biomass was the only measure which showed significant differences amongst locations and interaction effects. Abundance/biomass comparison curves revealed that all the exploited sites except one showed the configuration typical of moderately disturbed sites and that all the non-exploited sites except one showed the trend typical of undisturbed sites. Two-way crossed ANOSIM tests indicated that treatment and location both had significant effects on these assemblages and that there were also significant differences between each pair of locations. The latter probably reflects regional differences in species composition due to the fact that this coast lies at the junction of two zoogeographic marine provinces. The multidimensional scaling (MDS) ordinations derived from abundance and biomass estimates revealed two major clusters of sites, one representing sites in the southern region and the other sites within the central and northern regions. The non-exploited sites within each region were situated above and to the right of the corresponding exploited sites. Similarity percentage analyses (SIMPER) indicated that the major species contributing to the average dissimilarity between the exploited and non-exploited localities varied regionally. There was, however, a fair amount of consistency in terms of the functional groups highlighted by these analyses. Some of the species adversely affected by exploitation are dependent on primary substrata either for their food supplies or for attachment. Likewise many of the species which appeared to benefit from exploitation were phytal-associated forms.

INTRODUCTION

Owing to the paucity of non-impacted localities within particular geographic regions human foraging-effects studies have tended to take the form of spatial comparisons centred around exploited locations situated adjacent to individual marine reserves (Castilla & Duran, 1985; Hockey & Bosman, 1986; Oliva & Castilla, 1986; Castilla & Bustamente, 1989; Duran & Castilla, 1989; Godoy & Moreno, 1989; Keough et al., 1993; Lasiak & Field, 1995). Many of these studies are flawed by pseudoreplication because they are based on comparisons of the biota at only one pair of localities (Fairweather, 1991). As there may be a number of other equally plausible, but entirely unaccounted for, differences between the localities besides the presence/absence of exploitation differences in the biota cannot be attributed solely to the effects of exploitation.

The following assessment of the putative impact of shellfish gathering is based on the premise that alternative explanations for differences in the biota at exploited and non-exploited localities can be refuted by comparing multiple impacted and non-impacted localities, i.e. by repeating the 'experiment' in one or more independent settings (Underwood, 1989; Clarke, 1993). The existence of three 'no-take' marine reserves along a 273 km stretch of shoreline subject to intense subsistence exploitation on the Transkei coast of South Africa provides an opportunity to test the generality of such assessments over a regional scale. The primary objective of this study was to ascertain whether the differences in the community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in the central and northern regions of Transkei, South Africa are consistent with those reported recently in the southern region (Lasiak & Field, 1995). Such a finding would support the notion that shellfish gathering is the causative agent responsible for the differences in community structure.

MATERIALS AND METHODS

Study area

The non-exploited localities were determined primarily by the location of the Dwesa (32°18′S 28°50′E), Hluleka (31°50′S 29°19′E) and Mkambati (31°18′S 30°0′E) Nature Reserves as these are the only readily-accessible non-exploited shores along the Transkei coast (Figure 1). Three exploited localities, each of which was situated adjacent to the southern end of one of these reserves, were selected for comparison. The relative proximity of the exploited and non-exploited localities varied between 3 and 12 km, depending on coastal topography. Samples were collected from several sites at each locality. The study sites were

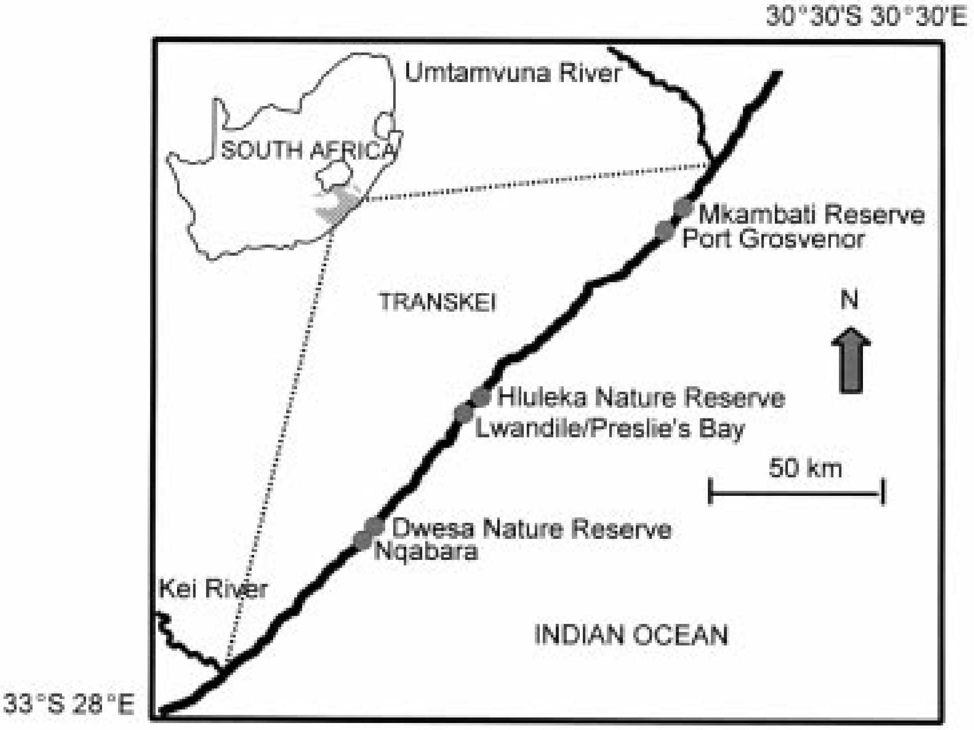

Figure 1. Map showing the location of the three 'no-take' reserves and the three exploited localites on the Transkei coast of South Africa.

restricted to either gently-sloping, or slightly-stepped, rock platforms exposed to strong wave action. Marked differences in the underlying geological substrata along the coast precluded standardization of sites on the basis of rock type. The sites in the northern region were located on quartzitic sandstone, those in the central region were located on unmetamorphosed sandstone; and those in southern Transkei were located on either shale or mudstone platforms.

The study sites in the southern region comprised two non-exploited sites (D1 and D2), situated approximately 1 km apart in the Dwesa Nature Reserve, and three exploited sites (N1, N2 and N3) situated along a 4 km stretch of shore between Nqabara Point and Nqabara River (Lasiak & Field, 1995). As the rugged coastal relief in central Transkei limited the number of potential study sites, sampling was restricted to one non-exploited site (H1) in the Hluleka Nature Reserve and two exploited sites, Lwandile (LW) and Preslies Bay (PB), situated approximately 1 km apart. The northern study sites comprised three non-exploited sites (M1, M2 and M3), each situated approximately 3 km apart, in the Mkambati Nature Reserve; and three exploited study sites (G1, G2 and G3) situated along an 8 km stretch of shore between Lambasi and the Msikaba River in the vicinity of Port Grosvenor (Figure 1).

Sampling procedure

Between seven and ten haphazardly-selected 0.5 m^2 quadrat samples of infratidal biota were collected from each of the study sites during equinoctial spring tides. The samples from the southern region were all taken in March 1992, those from the central region and the Mkambati Nature Reserve were collected the following March, but the exploited northern locality was not sampled until September 1993. Although there is a possibility that comparisons amongst localities may be subject to temporal confounding the results of a long-term monitoring programme suggest there were no significant changes in the community structure of rocky intertidal assemblages along the Transkei coast during the period in question (Dye, 1998). The 114 quadrat samples collected were preserved in 10% formalin for subsequent analysis. In the laboratory the individual samples were sorted, the macrofauna were identified to either species or genus level, then counted and their shell-free dry weights were determined after drying to constant weight at 60°C. Heavily-calcified species were decalcified with 1M nitric acid prior to drying.

Data analysis

In view of the primary objective of this study the analyses presented are based on similar univariate, graphical and multivariate techniques to those used by Lasiak & Field (1995) to contrast assemblages at exploited and non-exploited localities in southern Transkei. The individual species abundance estimates obtained from each of the quadrat samples were used to estimate the mean macrofaunal abundance, species diversity (Hill's N1 and N2) and evenness (Hill's E5 ratio) indices for each site (Ludwig & Reynolds, 1988). The mean number of macrofaunal species present and mean macrofaunal biomass at each site were also estimated. Mixed model two-way analyses of variance (ANOVA) were used to examine the influence of the random factor location (southern, central and northern region of Transkei) and the fixed factor treatment (exploited vs non-exploited) on these measures (Underwood, 1997).

The mean values of the measures from each site constituted the replicates used in these analyses. Prior to these analyses the correlation between means and standard deviations across the cells of the design was examined and appropriate data transformations selected (Clarke & Warwick, 1994). Post-hoc comparisons of significant effects were based on Tukey's Honestly Significant Difference (HSD) tests (StatSoft, 1995).

The abundance biomass comparison (ABC) technique was used to assess the disturbance status of each of the study sites. This method necessitates the juxtaposition of k-dominance curves for abundance and biomass; these curves were obtained by plotting the cumulative ranked macrofaunal abundance and biomass data against log species rank. According to the conceptual model underlying this technique the relative location of the two curves varies with the degree of disturbance. In the case of undisturbed commmunities the k-dominance curve for biomass should be located above the abundance curve, in moderately-disturbed communities the two curves will be more or less coincident, and in severely-disturbed communities the abundance curve should lie well above the biomass curve (Warwick, 1986).

Data matrices containing estimates of either the mean number of individuals or the corresponding mean biomass for each of the macrofaunal species found at each of the study sites were used to compute triangular similarity matrices based on the Bray−Curtis similarity measure. As the biological question of interest was the effect of exploitation on the entire assemblage the counts and biomass values were root-root transformed prior to the estimation of similarities, as recommended by Field et al. (1982). This transformation was preferred as it preserves information on the relative abundance or biomass of species and also ensures that commoner species are given greater weight than rare species (Clarke & Warwick, 1994). As the relative abundance of the exploited species varies markedly the use of a transformation which includes contributions from all species was deemed most appropriate. Two-way crossed analyses of similarities (ANOSIM) were used to test for differences amongst locations and between treatments. Two-dimensional ordinations based on the rank order of similarities of sites were produced by means of non-metric multidimensional scaling (MDS). The major species responsible for discriminating between samples from the exploited and non-exploited localities in each region were identifed by means of the similarity percentages (SIMPER) routine (Clarke, 1993). Owing to the limitations on the size of data set that the SIMPER program can handle a subset of the 125 most important species was selected using the REDUCE routine. To ensure the results of these analyses were comparable with the similarity percentages analyses reported in Lasiak & Field (1995) abundance and biomass estimates from individual quadrat samples were used rather than mean estimates for each site.

Table 1. *Results of mixed model two-way analyses of variance based on estimates of macrofaunal abundance and biomass, species richness, evenness and diversity (Hill's N1 and N2).*

Univariate measure	Source of variation	*F*-ratio	*P*
Abundance	Treatment	1.896	0.302
	Location	0.516	0.615
	Treatment × Location	1.044	0.396
Biomass	Treatment	2.685	0.243
	Location	10.550	0.006*
	Treatment × Location	4.889	0.041*
Species richness	Treatment	1.054	0.413
	Location	1.605	0.259
	Treatment × Location	2.860	0.116
Evenness	Treatment	5.593	0.142
	Location	2.183	0.175
	Treatment × Location	0.750	0.503
Diversity (N1)	Treatment	0.627	0.511
	Location	0.231	0.799
	Treatment × Location	1.598	0.261
Diversity (N2)	Treatment	1.900	0.302
	Location	0.659	0.543
	Treatment × Location	1.060	0.390

RESULTS

Mixed model two-way ANOVA indicated that treatment (exploited vs non-exploited) had no significant effect on any of the univariate community measures (Table 1, Figures 2 & 3). Macrofaunal biomass was the only measure to show significant differences amongst locations and a significant interaction between location and treatment. Tukey HSD tests indicated that the mean biomass of the samples from the southern location was significantly higher than that at the other locations and that the mean biomass of the samples from the non-exploited southern location (Dwesa Nature Reserve) was significantly higher than that recorded in any of the other location/treatment combinations (Table 1).

The ABC plots for the sites in the central and northern region (Figures 3 & 4) were generally comparable with those described previously for the sites in southern Transkei (Lasiak & Field, 1995). All of the non-exploited sites, except that at Hluleka, were categorized as

Table 2. *Results of two-way crossed ANOSIM tests based on Bray–Curtis similarity measures derived from both root–root transformed macrofaunal abundance and biomass estimates.*

A. *Results of global tests on the effect of location and treatment.*

	Source of variation			
Grouping	Locations		Treatments	
	R	*P*-level	R	*P*-level
Abundance	1.000	<0.001*	0.872	0.007*
Biomass	0.932	<0.001*	0.649	0.01*

B. *Results of pairwise tests on the effect of location.*

	Source of variation					
Grouping	S & C Locations		S & N Locations		C & N Locations	
	R	*P*-level	R	*P*-level	R	*P*-level
Abundance	1.000	0.01*	1.000	0.033*	1.000	0.025*
Biomass	0.933	0.01*	1.000	0.033*	0.761	0.025*

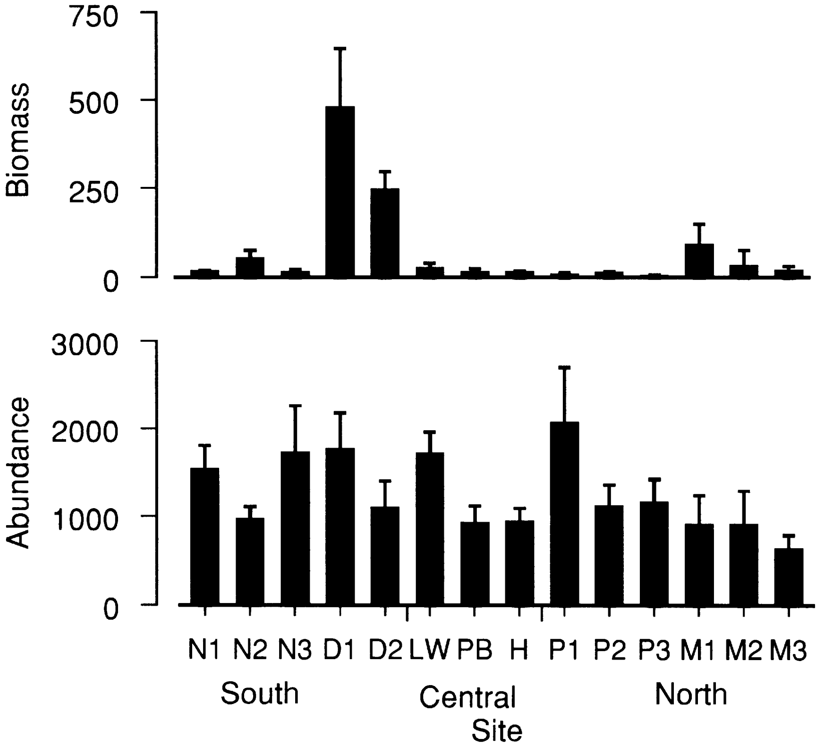

Figure 2. Mean (±SD) estimates of macrofaunal abundance and biomass recorded in 0.5 m^2 infratidal samples from each of the 14 study sites.

undisturbed as their biomass curves are located well above the abundance curves. All of the exploited sites, except N2 which showed the configuration typical of an undisturbed site, were categorized as moderately-disturbed sites. At three of these sites, namely N3, G1 and G3, the abundance curve lies slightly above the biomass curves whereas at the other exploited sites the converse applies.

The two-way crossed ANOSIM tests based on similarities derived from both abundance and biomass estimates revealed significant differences between treatments and amongst locations. Significant differences were also evident between all pairs of locations (Table 2).

Two distinct clusters of sites are evident in the MDS ordination derived from the mean abundance estimates (Figure 5A). The cluster on the right-hand side of the ordination comprises the five sites from the southern region whereas that on the right-hand side includes the sites in the central and northern region. The non-exploited sites within each region are generally located above and to the right of the corresponding exploited sites. Similar patterns are also evident in the MDS ordination derived from the mean biomass estimates, however, in this case the two clusters lie closer together (Figure 5B).

Similarity percentage (SIMPER) analyses based on abundance estimates indicated that the average dissimilarity between the samples from the non-exploited and exploited localities varied from 36.6 to 42.0% (Table 3). In the southern region, 11 of the 20 highest-ranked discriminators attained higher average abundances at the non-exploited locality. Eight of these are sessile suspension-feeders normally found attached to hard substrata, two of the others, *Patiriella exigua* and *Patella oculus* are sedentary grazers dependent on hard substrata, the remaining species, *Anachis kraussi*, is a small predatory gastropod. Six of the major discriminators which attained higher average abundances at the corresponding exploited locality are phytal-associated forms. Included within this group are the brittle-star, *Ophionereis porrecta*, the amphipods, *Paragrubia vorax*, *Lysianassa ceratina*, *Elasmopus japonicus* and *Paramoera capensis*, and the polychaete worm, *Lumbrinereis coccinea.* The holothurian *Pentacta doliolum*, the flatworm *Planocera* sp., and the carnivorous polychaete worm *Lumbrinereis tetraura* were the other discriminants which attained higher average abundances at the exploited locality. Only two of the species highlighted by this analysis, the brown mussel *Perna perna* and the limpet *Patella oculus*, are known to be exploited in this region (Lasiak, 1991, 1992). In the central region, ten of the 20 most highly-ranked discriminators attained higher average abundances at the non-exploited locality. This group comprised the sessile suspension-feeders, *Perna perna* and *Bunodactis reynaudi*, the grazing gastropods, *Oxystele tabularis*, *Patella longicosta*, *P. cochlear*, *P. aphanes* and *Fissurella natalensis*, the worms, *Syllis variegata* and *Notoplana* sp., and the amphipod *Stenothoe valida.* Eight of the major discriminators which attained higher average abundances at the corresponding exploited locality are phytal-associated species. Included within this group are the small grazing gastropods, *Tricolia capensis* and *Turbo* sp., the isopod *Cymodocella pustulata*, the amphipods *Paragrubia vorax*, *Podocerus* sp. and *Lysianassa ceratina* and the small bivalves *Neocardia africana* and *Gregariella petagnae.* The polychaete worm *Eunice antennata*, and the barnacle *Balanus venustus* are the other discriminators which attained higher average abundances at the exploited locality. Three of the major discriminators identified by this analysis, *Perna perna*, *Patella longicosta* and *P. cochlear*, are known to be exploited in the central region of Transkei (Dyantyi, 1995). In the northern region only five

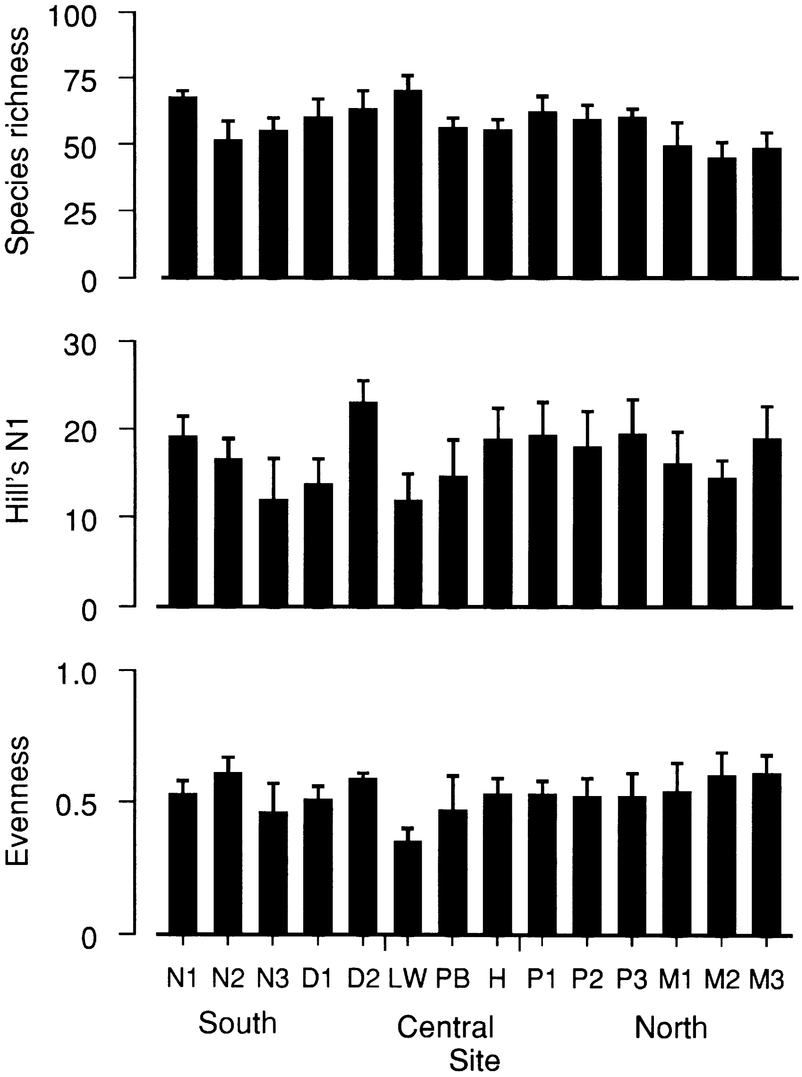

Figure 3. Mean (±SD) estimates of species diversity (Hill's N1), species richness and evenness of the macrofaunal assemblages at each of the 14 study sites.

of the twenty most-highly ranked discriminators attained higher average abundances at the non-exploited locality, they were the bivalve *Perna perna* and the grazing gastropods *Patella aphanes*, *P. cochlear*, *P. granularis* and *P. longicosta*. Seven of the discriminants which were more abundant at the exploited locality are normally found in association with algal beds. Included within this group are the amphipods *Paramoera capensis*, *Elasmopus japonicus*, and *Lysianassa ceratina*, the brittle star *Ophionereis porrecta*, the isopod *Sphaeramene poltylotos*, and the grazing gastropods *Turbo* sp. and *Haminoea natalensis* (Table 3). The bivalve *Brachidontes semistriatus*, the polychaete worm *Megalomma quadriloculatum*, the anemones *Bunodactis reynaudi*, and *Anthothoe stimpsoni*, the flatworm *Planocera* sp., the sipunculid *Phascolosoma* sp., the chiton *Acanthochiton garnoti* and the gastropod *Anachis kraussi* were the other major discriminants which attained higher average abundances at the exploited northern locality (Table 3). Only three of the major discriminators identified in the northern region, *Perna perna*, *Patella cochlear* and *P. longicosta*, are known to be exploited by shellfish gatherers in this region (Lasiak, 1997).

Comparisons of the principal discriminators across regions revealed surprisingly little overlap; the major exceptions being the brown mussel *Perna perna* and the amphipod *Lysianassa ceratina* which featured in all regions. Although 12 species were identified as principal discriminators in two of the three regions, only nine of these exhibited consistent trends. Three of these species, *Patella aphanes*, *P. cochlear* and *P. longicosta*, attained higher abundances at the non-exploited localities in the central and northern region. Four others, namely *Ophionereis porrecta*, *Elasmopus japonicus*, *Paramoera capensis* and *Planocera* sp. attained higher average abundances at the exploited localities in the southern and northern region. The two remaining species, the amphipod *Paragrubia vorax* and the gastropod *Turbo* sp., were more abundant at the exploited localities in the southern and central regions and in the central and northern regions respectively.

Similarity percentage (SIMPER) analyses based on biomass estimates indicated that the average dissimilarity between the non-exploited and exploited localities varied from 47.9 to 51.2% (Table 4). Eighteen of the most highly ranked discriminators in the southern region attained higher biomasses at the non-exploited locality. Nine of these species, namely the mussel *Perna perna,* the abalone *Haliotis spadicea*, the limpets, *Patella barbara*, *P. cochlear*, *P. longicosta*, *P. miniata sanguinans* and *P. oculus*,

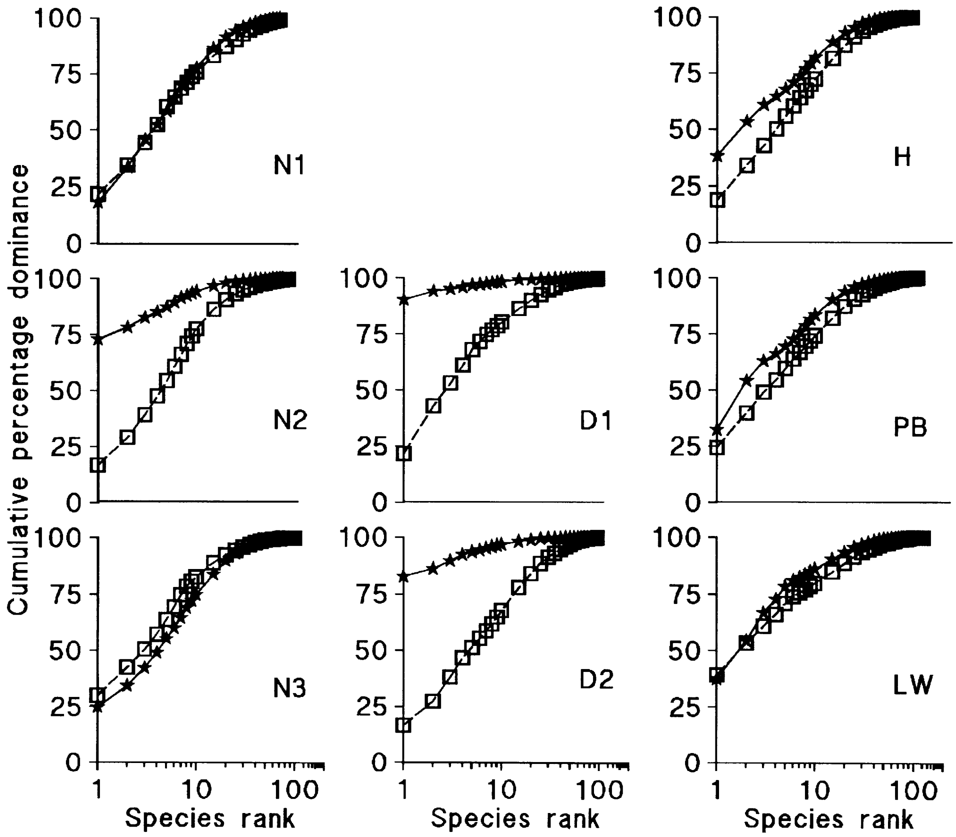

Figure 4. Abundance/biomass curves based on the infratidal macrofaunal samples collected from the study sites in the southern and central region of Transkei (□, abundance; ★, biomass).

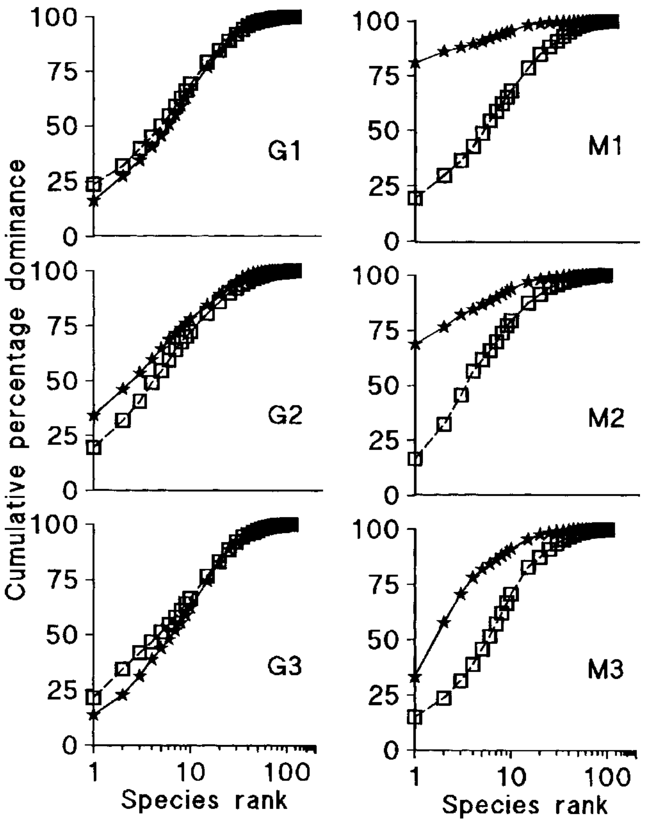

Figure 5. Abundance/biomass curves based on the infratidal macrofaunal samples collected from the study sites in the northern region of Transkei (□, abundance; ★, biomass).

and the coiled-gastropods *Burnupena lagenaria* and *B. cincta*, are known to be exploited by subsistence-collectors in this region (Lasiak, 1991, 1992). Five of the others, *Parechinus angulosus*, *Oxystele tabularis*, *Patiriella exigua*, *Chiton tulipa* and *Fissurella natalensis* are grazers dependent on primary substrata. Ten of the principal discriminators identified in the central region attained higher average biomasses at the non-exploited locality, five of these species, *Perna perna*, *Patella longicosta*, *P. miniata sanguinans*, *P. cochlear* and *Pyura stolonifera* are exploited by subsistence gatherers in this region (Dyantyi, 1995). Three of the others, *Oxystele tabularis*, *Fissurella natalensis* and *Patella aphanes* are small grazing gastropods dependent on hard substrata. Five of the species which attained higher biomasses at the exploited locality in central Transkei were sponges. Two others, the hydrozoan *Thecocarpus* sp. and the small gastropod *Tricolia capensis* are often found in association with algal beds. In the northern region 12 of the principal discriminators attained a higher average biomass at the exploited locality, five of these species are known to be exploited in this region. Five of the others, *Fissurella natalensis*, *Onitochiton literatus*, *Oxystele tabularis*, *Patella granularis* and *P. aphanes* are small grazing gastropods dependent on hard substrata. The crab *Dehaanius undulatus* which was the only discriminator to attain a higher average biomass at the exploited northern locality is regarded as a phytal-associated species. Four of the others, the bivalve *Brachidontes semistriatus*, the anemone *Bunodactis reynaudi*, and the polychaete worms *Idanthrysus pennatus*, and *Megalomma quadrioculatum* are sessile suspension-feeders.

Table 3. *Major species, ranked in order of importance, contributing to the average dissimilarities between samples from the non-exploited (group I) and exploited localities (group II) in each of the three regions of Transkei, as determined by SIMPER analyses based on root-root transformed numerical abundance estimates and the Bray–Curtis measure of dissimilarity.*

Southern region				Central region				Northern region			
Species	Av. ab. I	Av. ab. II	$\Sigma\delta_i$	Species	Av. ab. I	Av. ab. II	$\Sigma\delta_i$	Species	Av. ab. I	Av. ab. II	$\Sigma\delta_i$
Pseudactinia flagellifera	57.4*	0.5	3.0	*Perna perna*	42.7*	2.9	2.5	*Perna perna*	116.4*	16.2	2.2
Perna perna	264.4*	38.0	5.3	*Tricolia capensis*	178.3	449.3	4.8	*Brachidontes semistriatus*	1.5	48.4	4.4
Pomatoleios kraussi	17.3*	0.2	7.0	*Cymodocella pustulata*	0.4	9.3	6.6	*Paramoerca capensis*	0.3	27.5	6.2
Ophionereis porrecta	8.7	63.4	8.7	*Oxystele tabularis*	15.3*	3.6	8.3	*Ophionereis porrecta*	36.3	123.6	8.0
Balanus amphitrite	10.6*	0.6	10.3	*Neocardia africana*	3.0	45.8	10.0	*Megalomma quadrioculatum*	3.6	34.6	9.7
Chthamalus dentatus	5.2	0.0	12.0	*Bunodactis reynaudi*	14.7*	1.8	11.6	*Bunodactis reynaudi*	0.7	18.1	11.3
Tetraclita serrata	5.1*	0.3	13.5	*Eunice antennata*	0.7	9.5	13.2	*Turbo* sp.	1.6	15.9	12.8
Balanus venustus	24.6*	5.8	15.0	*Patella longicosta*	7.4*	1.3	14.7	*Anthothoe stimpsoni*	10.0	24.4	14.3
Paragrubia vorax	0.2	6.7	16.4	*Balanus venustus*	11.1	13.3	16.3	*Patella aphanes*	38.7*	16.0	15.7
Patiriella exigua	10.2*	1.0	17.9	*Patella cochlear*	4.9*	0.2	17.8	*Elasmopus japonicus*	112.9	323.9	17.1
Lysianassa ceratina	7.7	52.6	19.2	*Gregariella petagnae*	0.1	4.1	19.2	*Patella cochlear*	11.6*	4.3	18.5
Patella oculus	4.5	0.0	20.4	*Paragrubia vorax*	1.3	10.2	20.6	*Planocera* sp.	2.5	6.7	19.9
Elasmopus japonicus	76.0	139.9*	21.7	*Syllis variegata*	32.6*	8.3	22.0	*Patella granularis*	7.4*	0.9	21.2
Planocera sp.	0.3	4.9*	22.9	*Patella aphanes*	2.1*	1.9	23.3	*Sphaeramene polytylotos*	0.9	5.9	22.5
Pentacta doliolum	277.3	306.7*	24.1	*Notoplana* sp.	2.0*	0.0	24.6	*Haminoea natalensis*	0.0	3.7	23.8
Paramoera capensis	0.7	3.5*	25.3	*Podocerus* sp.	1.1	7.6	25.9	*Patella longicosta*	7.5*	1.4	25.1
Anachis kraussi	25.7	8.8	26.5	*Fissurella natalensis*	1.9*	0.5	27.1	*Phascolosoma* sp.	2.6	19.5	26.4
Gunnarea capensis	9.9	2.3	27.7	*Stenothoe valida*	3.7*	0.8	28.3	*Lysianassa ceratina*	26.5	51.0	27.7
Lumbrinereis tetraura	0.1	3.7*	28.8	*Turbo* sp.	4.4	19.1	29.5	*Acanthochiton garnoti*	6.8	31.9	29.0
Lumbrinereis coccinea	0.4	4.4*	29.9	*Lysianassa ceratina*	18.7	68.6	30.7	*Anachis kraussi*	1.1	4.3	30.2
Average percentage dissimilarity			41.3	Average percentage dissimilarity			36.6	Average percentage dissimilarity			42.0

Av. ab., average abundance at each locality, $\Sigma\delta_i$, cumulative contribution of the species to the average dissimilarity between the localities; *, species that were more abundant at the non-exploited localities.

Table 4. *Major species, ranked in order of importance, contributing to the average dissimilarities between samples from non-exploited (group I) and exploited localities (group II) in each of the three regions of Transkei, as determined by SIMPER analyses based on root–root transformed biomass estimates and the Bray–Curtis measure of dissimilarity.*

Southern region				Central region				Northern region			
Species	Av. b. I	Av. b. II	$\Sigma\delta_i$	Species	Av. b. I	Av. b. II	$\Sigma\delta_i$	Species	Av. b. I	Av. b. II	$\Sigma\delta_i$
Perna perna	318.0*	14.6	8.8	*Perna perna*	5.6*	0.2	5.6	*Perna perna*	34.4*	1.9	6.4
Haliotis spadicea	6.4*	0.5	12.7	*Patella longicosta*	2.3*	0.1	9.7	*Patella longicosta*	2.7*	0.2	10.0
Pseudactinia flagellifera	3.1*	<0.1	16.6	*Psammoclema* sp.	0.0	7.4	13.7	*Patella miniata sanguinans*	1.2*	0.3	13.0
Pentacta dolium	13.6*	2.3	19.3	*Polymastia* sp.	0.4	3.9	17.6	*Brachidontes semistriatus*	<0.1	0.4	15.5
Parechinus angulosus	5.3*	0.8	21.9	*Patella miniata sanguinans*	1.1*	<0.1	20.5	*Patella barbara*	0.6*	0.3	17.8
Patella barbara	1.7*	1.6	24.0	*Myriastra parvistella*	<0.1	0.6	23.2	*Patella cochlear*	0.8*	0.3	20.0
Tetraclita serrata	0.3*	<0.1	25.9	*Oxystele tabularis*	0.5*	<0.1	25.7	*Fissurella natalensis*	0.5*	0.4	22.2
Patella miniata sanguinans	1.6*	1.3	27.9	*Haliclona* sp.	0.2	1.1	28.1	*Onitochiton literatus*	0.5*	0.3	24.4
Thais capensis	0.6*	<0.1	29.8	*Patella cochlear*	0.4*	0.0	30.5	*Oxystele tabularis*	0.7*	0.1	26.6
Patella oculus	0.6*	<0.1	31.6	*Octomeris angulosus*	0.5	0.7	32.7	*Patella aphanes*	0.8*	0.1	28.5
Oxystele tabularis	0.9*	0.2	33.4	*Eunice antennata*	0.1	0.4	34.7	*Marphysa corallina*	2.0*	1.3	30.4
Burnupena lagenaria	1.0*	0.4	35.2	*Patella barbara*	0.2	0.3	36.6	*Patella granularis*	0.3*	<0.1	32.2
Patiriella exigua	0.3*	<0.1	36.9	*Fissurella natalensis*	0.2*	0.1	38.5	*Burnupena lagenaria*	0.2	0.2	34.0
Haliclona sp.	0.3*	0.1	38.5	*Dehaanius undulatus*	0.4*	0.3	40.4	*Bunodactis reynaudi*	0.0	0.2	35.7
Chiton tulipa	0.5*	0.1	40.1	*Bunodactis reynaudi*	0.1*	<0.1	41.9	*Dehaanius undulatus*	<0.1	0.1	37.4
Burnupena cincta	0.6*	0.2	41.7	*Pyura stolonifera*	0.3*	<0.1	43.4	*Anthothoe stimpsoni*	0.1*	0.1	38.9
Patella longicosta	1.3*	1.2	43.2	*Tricolia capensis*	0.6	1.0	44.8	*Lepidonotus durbanensis*	0.1	0.1	40.4
Fissurella natalensis	0.2*	0.1	44.7	*Patella aphanes*	0.1*	<0.1	46.1	*Phascolosoma* sp.	<0.1	0.1	41.8
Marphysa corallina	0.2	0.7	46.1	*Thecocarpus* sp.	0.0	0.1	47.4	*Idanthrysus pennatus*	<0.1	0.1	43.2
Patella cochlear	<0.1	0.2	47.2	*Stelleta herdmani*	0.0	1.6	48.7	*Megalomma quadriloculatum*	0.0	0.1	44.6
Average percentage dissimilarity			47.9	Average percentage dissimilarity			50.1	Average percentage dissimilarity			51.2

Av. b., average biomass at each locality, $\Sigma\delta_i$, cumulative contribution of the species to the average dissimilarity between the localities; *, species that attained higher biomasses at the non-exploited localities.

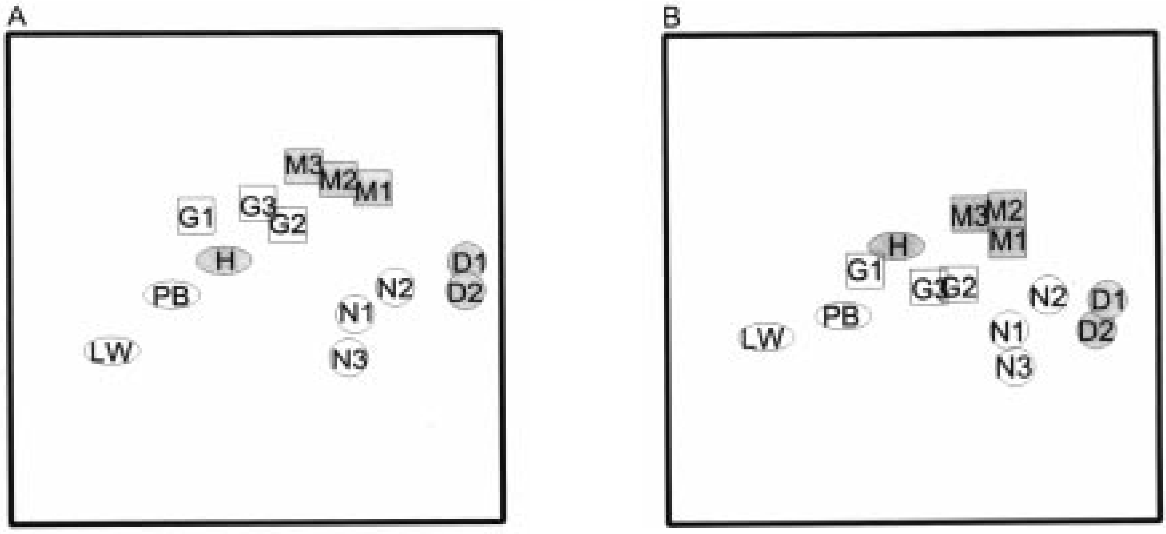

Figure 6. (A & B) MDS ordinations based on Bray–Curtis indices of similarity derived from root-root transformed mean macrofaunal abundance and biomass estimates respectively (circles, ovals and squares represent study sites in the southern, central and northern region of Transkei respectively; open and shaded areas represent exploited and non-exploited sites respectively; D1 & D2, Dwesa Nature Reserve sites 1 & 2; N1, N2 & N3, Nqabara sites 1, 2 & 3; H, Hluleka Nature Reserve; LW, Lwandile; PB, Preslie's Bay; M1, M2 & M3, Mkambati Nature Reserve sites 1, 2 & 3; G1, G2 & G3, Port Grosvenor sites 1, 2 & 3).

There was a much greater regional overlap between discriminator species identified on the basis of biomass than in terms of abundance; *Perna perna*, *Patella longicosta*, *P. miniata sanguinans*, *Fissurella natalensis* and *Oxystele tabularis* attained higher biomasses at the non-exploited localities in all three regions. Two other species, *Patella barbara*, and *P. cochlear*, identified as major discriminators in all three regions only attained higher biomasses at two of the non-exploited localities. Although six species were identified as major discriminators in two of the regions, only two of these, *Patella aphanes* and *Burnupena lagenaria*, showed a consistent trend, both attained a higher biomass at the non-exploited localities.

DISCUSSION

A valuable insight into the likely consequences of exploitation can be obtained simply by observing the gathering practices of the exploiters and having some knowledge of the literature dealing with the biology of, and interactions between, rocky shore organisms (Underwood, 1993). The rocky intertidal biota along the Transkei coast is subject to intense exploitation by the coastal inhabitants, mainly during spring low tides (Bigalke, 1973; Siegfried et al., 1985; Hockey & Bosman, 1986; Lasiak, 1992, 1997). Although most of the exploitation effort is directed at shellfish for personal consumption, in some areas there is also collection of algae, bait, rock lobsters, mussels and oysters for commercial gain (Fielding et al., 1994). The major organisms targeted by the subsistence-exploiters are the brown mussel *Perna perna*, the limpets *Patella barbara*, *Patella longicosta*, *Patella miniata* and *Patella oculus*, the abalone *Haliotis spadicea* and various large coiled-gastropods (Bigalke, 1973; Siegfried et al., 1985; Lasiak, 1991, 1992). Previous research along this coast suggests that the selective removal of patellid limpets results in a marked increase in macroalgal cover, and that this, in turn, reduces the availability of primary space for other species (Lasiak & White, 1993; Dye, 1995). The removal of entire mussel clumps is also likely to have a deleterious effect as large number of species make use of this important structural component as a source of food, shelter or site of attachment (Seed & Suchanek, 1992). There are consequently likely to be major differences both in the pattern of space occupancy and in the diversity of exploited and non-exploited assemblages.

Marked differences in the pattern of general space occupancy on exploited and non-exploited shores in Transkei have indeed been reported. Whereas non-exploited infratidal areas generally exhibit a well-defined mosaic structure with clumps of mussels, and tufts of coralline algae interspersed by patches of crustose algae and large patellid limpets, comparable exploited areas are usually dominated by extensive mats of algae which occupy most of the available space (Dye, 1992, 1993). In view of the above, and previous worker's observations of the influence of exploitation on species richness and diversity (Hockey & Bosman, 1986; Duran & Castilla, 1989), the failure of the present study to demonstrate significant treatment effects on these indices was somewhat surprising. Hockey & Bosman (1986) noted that non-exploited mid-shore assemblages in Transkei generally supported significantly lower species richness than their exploited counterparts. Duran & Castilla (1989) found that the exclusion of humans from a rocky shore in central Chile led initially to a gradual increase in the species diversity of mid-shore primary space occupiers, but after 21 months diversity began to decline, apparently reaching a plateau after 36 months. At a nearby persistently-exploited site species diversity remained close to zero throughout the three year study period.

Lasiak & Field (1995) suggested that the lack of response in such indices may be due to the loss of species from one locality type being countered by the gain of an equivalent number of species at the other locality.

Similarity percentage (SIMPER) analyses based on data from the central and northern regions, however, indicated that there were considerably less species absent (8 and 24 respectively), on average, from the exploited localities as compared with the non-exploited localities (57 and 41 respectively). The fact that these losses were not accompanied by differences in species richness points to marked differences in species composition between sites within treatment. An alternative explanation, which cannot be discounted without adequate pre-impact data, is the possibility that there may have been differences in the species composition of the localities prior to the cessation of exploitation within the reserves. Consideration also needs to be given to the problem of assessing species loss in assemblages containing many species with low abundance (GESAMP, 1995) and to the possibility that diversity may either increase, decrease or remain the same in the face of disturbance (Warwick & Clarke, 1993).

The present study indicates that the other univariate community measures were also insensitive to differences between exploited and non-exploited treatments. The lack of response in overall macrofaunal abundance and biomass is probably due to the fact that these indices obscure variations in the response of individual species. For example, some species may show a reduction in abundance/biomass in response to exploitation whilst others actually increase in numbers/biomass. Although the lack of a treatment effect on macrofaunal biomass appears to be contrary to the findings of Lasiak & Field (1995) the results of the Tukey HSD tests based on interactions between treatment and location show that the biomass of macrofauna in the Dwesa Nature Reserve is significantly higher than that observed at any of the other locations examined. In-depth examination of the species by site biomass data set suggests that the mussel *Perna perna* is primarily responsible for the elevated biomass in that reserve.

Although abundance/biomass comparisons and species diversity indices are based on the same information there are clearly substantial differences in their discriminatory abilities. This reflects the fact that ABC curves retain information on dominance patterns within samples whereas diversity indices reduce that information to a single value (Clarke, 1990). Although the difference in location of the abundance and biomass curves was not as marked at Hluleka as in the other reserves all of the non-exploited sites showed the response expected of undisturbed sites. Similarly, all the putatively impacted sites, except N2, showed the configuration typical of moderately disturbed sites. Lasiak & Field (1995) attributed the latter discrepancy to the fact that N2 tends to be less exploited than its adjacent counterparts because it is only accessible during calm conditions. The undisturbed assemblages were characterized by one or two large-bodied species, which dominated in terms of biomass but not in terms of numbers. At five of these sites, the community dominant, *Perna perna*, accounted for $>65\%$ of the overall biomass but only 10–25% of the total abundance. Although this species was also the biomass dominant at the other undisturbed sites, it was far less important, comprising between 30 and 40% of the biomass and $<5\%$ of the total individuals. The preferential removal of *P. perna* appears to be the major factor responsible for the reduction in inequality of importance of the numerical and biomass dominants evident at the exploited sites. Inspection of the original data matrices indicated that although *P. perna* was not numerically important it was the biomass dominant at three of the exploited sites, namely N1, N2 and P2. Elsewhere the holothurian *Pentacta doliolum*, the sponge *Psammoclema* sp. and the polychaete worm *Marphysa corallina* were the biomass dominants.

The results of the multivariate analyses paint a very different picture from that derived from the analyses based on univariate community measures. The clear-cut separation of the exploited and non-exploited sites within each particular region which is evident in the MDS ordinations implies that there are in fact substantial differences in the macrofaunal assemblages found under the two treatments. This was confirmed by the results of the two-way crossed ANOSIM tests which revealed significant differences between treatments and amongst locations. Marked differences in the multivariate structure of exploited and non-exploited lower balanoid zone assemblages along this coast have been reported previously by Hockey & Bosman (1986). Although these authors also noted substantial differences in the structure of the assemblages found at their non-exploited localities, their analyses suggested that the assemblages from the exploited localities were all similar in structure. As the Transkei coast is located at the junction of two marine biogeographic provinces (Kilburn & Rippey, 1982), the most likely explanation for the significant location effect is the associated regional differences in infratidal community structure. Regional variations in a number of other factors, e.g. underlying geological substrata (Hockey et al., 1988), standing stocks of exploited intertidal invertebrates (Fielding et al., 1994), and intensity of exploitation (Lasiak, 1997), may also contribute to the differences between locations.

Similarity percentage (SIMPER) analyses based on abundance suggested that the major reasons for the differences in community structure of the exploited and non-exploited localities were the lower abundance of species dependent on primary substrata and the greater abundance of phytal-associated species at the exploited localities. Similar analyses based on biomass estimates indicated that the biomasses of several grazers and large suspension-feeders were much lower at the exploited localities. Five of these were species favoured by shellfish gatherers, namely *Perna perna*, *Haliotis spadicea*, *Patella barbara*, *Patella miniata sanguinans* and *Patella oculus.* These responses can all be attributed to the influence of exploitation; the removal of mussels and the large grazing gastropods mentioned above, for example, both promote the domination of primary space by algae, this, in turn, either pre-empts settlement by sessile fauna or leads to their elimination via over-growth and smothering (Lasiak & Field, 1995). The consequent change in biogenic habitat structure also has implications for the associated fauna; a reduction in the size and/or elimination of mussel clumps undoubtedly has an adverse effect on the species associated with this microhabitat, similarly, a reduction in the availability of primary space has a negative impact on micro-algal grazers. Loss of these species may well be countered by benefits to phytal-associated species accrued from the increased algal cover. The relative lack of overlap in discriminatory species noted amongst the three regions probably reflects the zoogeographic gradient along the Transkei coast (Kilburn & Rippey, 1982).

Environmental impact assessments based on comparisons of multiple sets of putatively impacted and non-impacted localities assume that other potentially confounding variables are averaged out by replicating the design in several areas (Underwood, 1989). This means that, if the differences between the impacted and non-impacted localities are found to be consistent across areas, they can be attributed solely to the effects of that particular source of impact. In the present study the most consistent trends were those evident in the abundance/biomass comparisons and the multivariate analyses. The lack of consistency in the response of the univariate community level attributes suggests that the underlying assumption on which these analyses were based, i.e. that exploitation results in a change in the mean value of certain biological variables, may be flawed. Although the location of the Transkei coast within a zoogeographic transition zone and the associated replacement of some species along the coast by others undoubtedly confuses the issue it is evident from the SIMPER analyses that the functional groups affected by exploitation were the same all along the Transkei coast. The results of the SIMPER analyses also suggest that biomass may be a more sensitive and consistent indicator of the effects of exploitation than abundance.

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