

# Multivariate comparisons of rocky infratidal macrofaunal assemblages from replicate exploited and non-exploited localities on the Transkei coast of South Africa

Theresa Lasiak\*

Department of Zoology, University of Transkei, Private Bag X1 UNITRA, Umtata, Eastern Cape 5117, South Africa

**ABSTRACT:** Multivariate analyses, in the form of dendrograms, MDS (multidimensional scaling) ordinations, 2-way crossed ANOSIMs (analyses of similarities) and SIMPER (similarity percentage) analyses, were used to examine the influence of human predators on rocky infratidal assemblages. Comparisons are based on mean macrofaunal abundance and biomass estimates obtained from samples collected at multiple sites within 3 'no-take' marine reserves and at 3 adjacent exploited localities on the Transkei coast of South Africa. The dendrogram and MDS derived from the abundance estimates revealed 2 major subdivisions, one representing the sites in the 2 southern localities, and the other the sites within the central and northern localities of Transkei. Similar trends were evident in analyses based on biomass estimates, the major exception being the presence of an outlying site. Temperate species which were either restricted to or attained higher abundances and biomasses in the southern region appeared to be primarily responsible for this sub-division of sites. Two-way crossed ANOSIMs indicated that there were significant differences in the assemblages found under the exploited and non-exploited treatments and between the 3 pairs of locations. Two-way SIMPER analyses suggested that the major differences in the assemblages under the 2 treatment regimes were the lower abundance and biomass of sessile filter feeders and microalgal grazers that are dependent on the primary substratum and the greater abundance of phytal-associated species under exploited conditions. These differences are in accordance with expectations based on our knowledge of the organisms targeted by shellfish-gatherers.

**KEY WORDS:** Exploitation · Shellfish · Impacts · South Africa · Multivariate analyses

## INTRODUCTION

The rocky intertidal biota along the Transkei coast, one of the former independent homelands of South Africa, is subject to intense subsistence exploitation and is also utilized to a lesser extent by recreational and commercial fishers (Hockey et al. 1988, Fielding et al. 1994, Lasiak 1997). The subsistence-gatherers take a wide range of organisms, but exhibit a marked preference for the brown mussel *Perna perna* and various species of patellid limpets (Bigalke 1973, Hockey &

Bosman 1986, Lasiak 1991, 1992, 1997). They have also been shown to be size-selective, generally gathering larger individuals (Siegfried et al. 1985, Hockey & Bosman 1986, Lasiak 1991, 1992). Although most of the organisms collected by the subsistence-gatherers are used as food, some are also collected for use as medicines or as bait, and, at some localities, oysters, mussels and rock lobsters are gathered for sale to local hotels and tourists (Bigalke 1973, Fielding et al. 1994). The recreational fishers collect mussels, oysters, and rock lobsters for personal consumption and organisms such as tunicates, limpets and mussel worms for use as bait. At present the only commercial form of exploitation permitted in the intertidal is harvesting of the alga

\*E-mail: lasiak@getafix.ut.ac.za

*Gelidium* for sale to 1 of 2 concessionaires (Fielding et al. 1994).

The regulations governing the exploitation of marine resources along the Transkei coast are rarely enforced, poorly advertised, and regularly flaunted, particularly by subsistence-gatherers who either are unaware of or do not recognize the validity of these rules. The fact that the quantity of shellfish removed by individual subsistence-gatherers is far in excess of the prescribed limits has prompted a number of workers to try and assess the impact of exploitation on intertidal biota (Siegfried et al. 1985, Hockey & Bosman 1986, Lasiak & Dye 1989, Lasiak 1991, 1992, Lasiak & Field 1995). Unfortunately several of these studies, like many of the foraging-effects studies conducted elsewhere (Moreno et al. 1986, Oliva & Castilla 1986, Duran et al. 1987, Castilla & Bustamente 1989, Godoy & Moreno 1989), are marred by inadequate spatial replication because they are based on comparisons of the biota at only 2 localities, one exploited and the other non-exploited. To assess the effect of human disturbances on biotic assemblages and populations, comparisons should preferably be based on samples taken from several replicate perturbed and unperturbed localities. Alternatively, samples from a single perturbed locality should be compared with those from several unperturbed control localities (Underwood 1989). The existence of 3 supposedly 'no-take' marine reserves

(Dwesa, Hluleka and Mkambati Nature Reserves) along the 273 km stretch of shoreline bordering the Transkei region provides an ideal opportunity to conduct a properly replicated study of the effects of human predators on intertidal biota. The following assessment of the effect of exploitation on rocky infratidal assemblages is based on multivariate comparisons of samples collected from several replicate shores situated within and adjacent to these 3 reserves. The data presented on the assemblages within and adjacent to the Dwesa Nature Reserve have been reported on previously in Lasiak & Field (1995).

## METHODS

**Study area.** The relative positions of the paired exploited and non-exploited localities selected for study are shown in Fig. 1. The non-impacted localities comprised 2 sites situated approximately 1 km apart in the Dwesa Nature Reserve (Sites D1 and D2), 1 site in the Hluleka Nature Reserve (Site H) and 3 sites situated approximately 3 km apart in the Mkambati Nature Reserve (Sites M1, M2 and M3). Although exploitation of intertidal biota within these areas has been limited since their establishment in the late 1970s, marine sanctuary status was only attained in October 1991 (Transkei Environmental Conservation

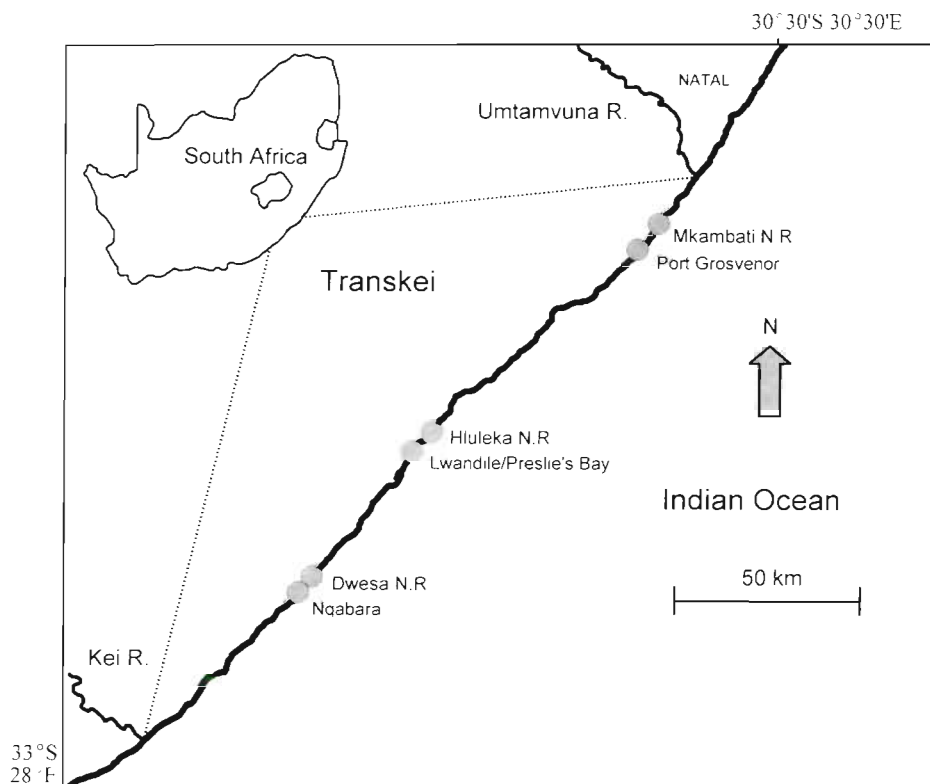


Fig. 1 Exploited (Nqabara, Lwandile, Port Grosvenor) and non-exploited (Dwesa, Hluleka and Mkambati nature reserves) localities on the Transkei coast of South Africa

Decree No. 9 of 1992). The exploited localities, which were each positioned to the south-west of these reserves, comprised 3 sites situated along a 4 km stretch of shore between the Nqabara River and Nqabara Point in southern Transkei (Sites N1, N2 and N3); 2 sites situated approximately 1 km apart in central Transkei (Sites LW and PB); and 3 sites situated along an 8 km stretch of shore between Lambasi and the Msikaba river in the vicinity of Port Grosvenor in northern Transkei (Sites G1, G2 and G3). As study sites were restricted to either gently sloping or slightly stepped rock platforms exposed to strong wave action, the relative proximity of these sites and localities was determined largely by the intervening coastal topography. Marked regional differences in underlying geological substrata precluded standardization on the basis of rock type; the sites in the northern region are located on quartzite, those in the central region are located on unmetamorphosed sandstone and those in the southern region are on either shale or mudstone platforms.

**Sampling procedure.** During equinoctial spring low tides, hammers and paint scrapers were used to remove between 7 and 10 haphazardly selected 0.5 m<sup>2</sup> quadrat samples of infratidal biota from each of the study sites. A combination of adverse sea conditions and limited personnel and storage facilities prevented simultaneous sampling at all study sites. Samples from the southern region were collected in March 1992; those from the central region and the Mkambati Nature Reserve were taken the following March; samples from the exploited northern sites were collected in September 1993. Although the possibility of temporal confounding cannot be entirely discounted, the results of a long-term monitoring programme along this coast indicate that there were no major changes in the community structure of rocky intertidal biota during the study period (Dye 1998). Samples were preserved in 10% formalin for subsequent laboratory analysis. The individual samples were then sorted, macrofauna was identified to species-level wherever possible, individuals were counted and the shell-free dry weights of the various species were determined after drying at 60°C. Heavily calcified species were decalcified in 1 M nitric acid prior to drying.

**Data analysis.** The data from the individual quadrat samples were used to estimate the mean number of individuals and the corresponding mean biomass for each of the macrofaunal species found at each of the study sites. These estimates were then input into 2 data matrices, one representing the mean abundance estimates for each of the 14 study sites and the other the corresponding biomass estimates. Owing to the limitations on the size of the data set that the multivariate programmes in the PRIMER v4.0 software package can

handle, a sub-set of each data matrix consisting of the 160 most important of the 248 species recorded was selected using the REDUCE routine. Following the recommendation of Field et al. (1982), the estimates in the resultant data matrices were double-root transformed prior to the computation of triangular similarity matrices based on the Bray-Curtis similarity measure. The results of the latter were then summarized diagrammatically in the form of dendrograms based on group-average sorting and in 2-dimensional non-metric multidimensional scaling (MDS) ordinations. Two-way crossed analyses of similarities (ANOSIM) randomization tests were used to test for differences between locations and treatments (Clarke 1993). The principal species contributing to the division of sites into the major clusters evident in the dendrogram and MDS were identified by means of 1-way similarity percentages analyses (SIMPER) (Clarke 1993). The principal species responsible for discrimination between the exploited and non-exploited treatments were identified by means of 2-way similarity percentage analyses (SIMPER2) (Platell et al. in press).

## RESULTS

The 2-way crossed ANOSIM tests based on the similarity measures derived from the abundance and biomass estimates revealed highly significant differences among locations (averaged across all treatment groups) and between the exploited and non-exploited treatments (averaged across all location groups) (Table 1). Significant differences are also evident between each pair of locations.

Two major sub-divisions are evident in the dendrogram derived from the abundance estimates; Cluster I comprises the 5 sites in the southern region and Cluster II the other sites (Fig. 2). Cluster I subsequently splits into 2 groups, one representing the 2 non-exploited sites (D1 and D2) within the Dwesa Nature Reserve and the other the 3 exploited sites (N1, N2 and N3) at Nqabara. Cluster II splits into 2 sub-clusters: Sub-cluster IIa comprises all the sites in the northern region and Sub-cluster IIb represents those in the central region. Two major groupings are evident within each of these sub-clusters. One of the groups in Sub-cluster IIa represents the 3 non-exploited sites (M1, M2 and M3) in the Mkambati Nature Reserve and the other the 3 exploited sites (G1, G2 and G3) situated in the vicinity of Port Grosvenor. One of the groups in Sub-cluster IIb comprises the non-exploited site (H) in the Hluleka Nature Reserve and the exploited site Preslie's Bay (PB), and the other represents the exploited site Lwandile (LW). Although similar groupings of sites are apparent in the corresponding MDS

Table 1. Results of 2-way crossed ANOSIM randomization tests based on similarity measures derived from macrofaunal abundance and biomass estimates. (a) Results of global tests on the effect of location and treatment and (b) results of pairwise tests on the effect of location (\* significance at  $p < 0.05$ ). R: R-statistic. S: southern, C: central, N: northern

(a) Parameter	Source of variation			
	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) Parameter	S and C locations		S and N locations		C and 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*

ordination it is also evident that in each region the non-exploited sites are located above and to the right of the corresponding exploited sites (Fig. 2b).

Inspection of the original data matrix reveals that 133 of the 248 macrofaunal species identified during this study were common to Clusters I and II, 39 species were restricted to the sites in the southern region, and 76 species were absent from this region. The 20 most important species responsible for discriminating between Clusters I and II, on the basis of average abundances, are listed in Table 2. Two of these species, the gastropod *Turbo sarmaticus* and the amphipod *Palinotus natalensis*, were restricted to the southern region, and 2 others, a small unidentified turbinid gastropod and the reef-worm *Idanthyrsus pennatus*, were restricted to the central and northern sites. Twelve species attained higher average abundances, and 4 attained lower average abundances, in the southern region than at the sites to the north. The species which either were restricted to or attained higher abundances in the southern region comprised 4 ubiquitous, 6 cold temperate, 3 warm temperate, and 1 subtropical form. The species which either were restricted to or were more abundant in the north comprised 1 ubiquitous, 1 cold temperate and 4 subtropical forms.

Two major clusters and one outlier, the exploited site Lwandile (LW), are evident in the dendrogram based on the biomass estimates (Fig. 3a). As is the case for the abundance based dendrogram, Cluster I

splits into 2 groups, one representing the exploited sites and the other the 2 non-exploited sites in the southern region. Cluster II initially splits into 2 sub-clusters; Sub-cluster IIa represents the 3 non-exploited sites in the Mkambati Nature Reserve, and Sub-cluster IIb comprises the 3 exploited sites in the northern region and the 2 remaining sites in the central region. The groupings evident in the MDS ordination (Fig. 3b) are similar to those outlined by the dendrogram except for the fact that Hluleka (H) is positioned between the sites at Mkambati and Port Grosvenor in the MDS but in the dendrogram it is grouped with Preslie's Bay (PB), one of the exploited central sites. As is the case with the

ordination based on abundances, the non-exploited sites are clearly situated above and to the right of their exploited counterparts.

The major species responsible for discriminating between Clusters I and II, on the basis of average

Table 2. Major species, ranked in order of importance, contributing to the average dissimilarities between Clusters I and II as determined by similarity percentages (SIMPER) analyses based on mean abundance estimates. Letters indicate the geographic distribution range of the species. U: ubiquitous, C: cold temperate, W: warm temperate and S: subtropical.  $\delta_i$  and  $\Sigma\delta_i$  are the individual and cumulative contributions, respectively, to the average dissimilarity

Species	Average abundance		Contribution to dissimilarity	
	I	II	$\delta_i$	$\Sigma\delta_i$
<i>Pentacta doliolum</i> (C)	294.92	5.30	3.31	3.31
<i>Turbo</i> sp. (S)	0.0	10.85	1.79	5.10
<i>Parechinus angulosus</i> (C)	29.62	0.80	1.70	6.80
<i>Pseudactinia flagellifera</i> (C)	23.24	0.81	1.46	8.26
<i>Perna perna</i> (U)	128.56	49.24	1.44	9.70
<i>Burnupena cincta</i> (C)	3.42	0.03	1.43	11.13
<i>Anthothoe stimpsoni</i> (C)	30.56	11.05	1.27	12.40
<i>Patella aphanes</i> (S)	1.82	18.95	1.22	13.63
<i>Bunodactis reynaudi</i> (C)	2.44	8.65	1.21	14.84
<i>Idanthyrsus pennatus</i> (S)	0.0	2.17	1.17	16.00
<i>Palinotus natalensis</i> (S)	1.14	0.0	1.15	17.15
<i>Tricolia capensis</i> (U)	117.78	140.23	1.10	18.25
<i>Burnupena pubescens</i> (C)	2.52	0.04	1.05	19.30
<i>Eurythoe</i> sp. (S)	1.14	2.70	1.04	20.34
<i>Burnupena lagenaria</i> (W)	6.52	0.80	1.03	21.37
<i>Turbo sarmaticus</i> (W)	1.64	0.0	1.02	22.39
<i>Pyura stolonifera</i> (U)	8.96	0.97	1.01	23.40
<i>Patiriella exigua</i> (U)	4.68	1.40	0.98	24.38
<i>Pseudonereis variegata</i> (U)	137.18	47.0	0.98	25.35
<i>Haliotis spadicea</i> (W)	1.92	0.06	0.96	26.31
Average % dissimilarity				34.22

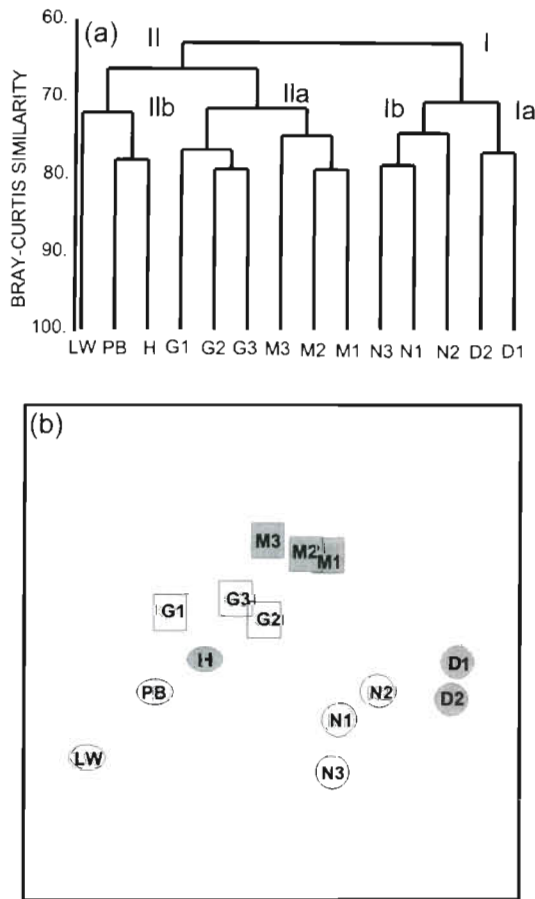


Fig. 2. (a) Dendrogram and (b) MDS ordination based on Bray-Curtis indices of similarity derived from root-root transformed mean macrofaunal abundance estimates (circles, ovals and squares represent study sites in the southern, central and northern region of Transkei respectively; open and shaded symbols represent exploited and non-exploited sites respectively); D1, D2: Dwesa Nature Reserve sites; N1, N2, N3: Nqabara sites; H: Hluleka Nature Reserve; LW: Lwandile; PB: Preslie's Bay; M1, M2, M3: Mkambati Nature Reserve sites; G1, G2, G3: Port Grosvenor sites

biomasses, are listed in Table 3. Three of these species, *Burnupena cincta*, *Burnupena pubescens* and *Chiton tulipa*, were restricted to and 2 others, *Onitochiton literatus* and *Idanthyrsus pennatus*, were absent from the southern region. Twelve species attained greater average biomasses and 3 attained lower average biomasses at the southern sites than at the sites grouped together in Cluster II. The species which either were restricted to or attained higher biomasses in the southern region comprised 3 ubiquitous, 6 cold temperate, 5 warm temperate and 1 subtropical form. The species which either were restricted to or attained higher biomasses in the central and northern regions comprised 2 cold temperate and 3 subtropical forms.

The 20 highest-ranked species responsible for discriminating, on the basis of abundances, between the exploited and non-exploited sites are listed in Table 4. Three molluscs, *Perna perna*, *Patella granularis* and *Patella cochlear*, 2 barnacles, *Chthamalus dentatus* and *Tetraclita serrata*, the sea anemone *Pseudactinia flagellifera* and the cushion star *Patiriella exigua* attained higher average abundances within the reserve treatment. Only 2 of these species, *P. perna* and *P. cochlear*, are targeted by shellfish-gatherers. Four amphipods, *Paramoera capensis*, *Elasmopus japonicus*, *Lysianassa ceratina* and *Podocerus* sp., 2 molluscs, *Haminoea natalensis* and *Brachidontes semistriatus*, 2 polychaetes, *Thelepus* sp. and *Lumbrineris coccinea*, the sea anemone *Bunodactis reynaudi*, the brittle star *Ophionereis porrecta* and the isopod *Cymodoce pustulata* were more abundant in the exploited treatment. Two species, an unidentified polychaete and the sponge *Sycon* sp., were absent from the reserve treatment. These 20 species ac-

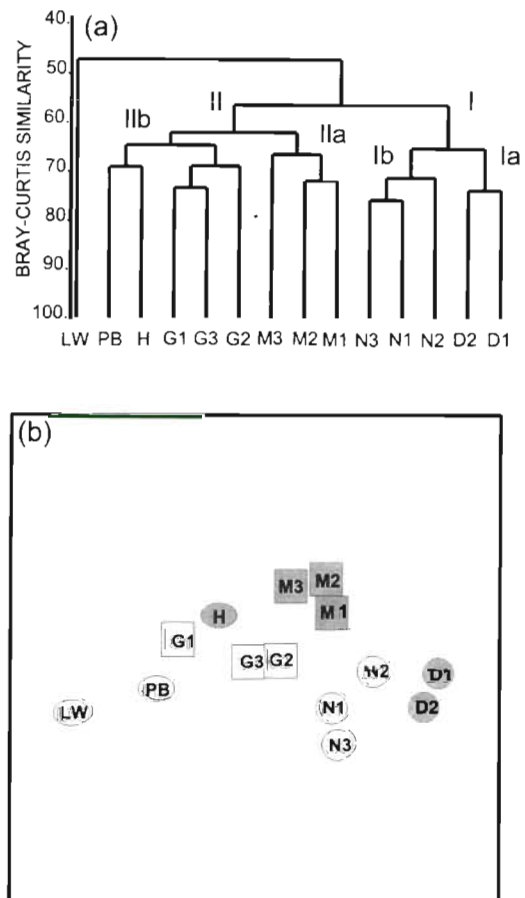


Fig. 3. (a) Dendrogram and (b) MDS ordination based on Bray-Curtis indices of similarity derived from root-root transformed mean macrofaunal biomass estimates (symbols as in Fig. 2)

counted for 26.4% of the average dissimilarity ( $\delta = 25.8\%$ ) between the 2 treatments.

The 20 most highly ranked species discriminating, on the basis of biomass, between the exploited and non-exploited treatments are also listed in Table 4. These species accounted for 35.9% of the average dissimilarity ( $\delta = 34.1\%$ ) between the 2 treatments. Five species, the bivalve *Brachidontes semistriatus*, the barnacle *Octomeris angulosus*, the sea anemone *Bunodactis reynaudi*, the opisthobranch *Haminoea natalensis* and the chiton *Dinoplax validofossus*, attained higher biomasses within the exploited treatment. The other 15 species either attained higher biomasses, or were present only, within marine reserves. This group included 9 molluscs (*Perna perna*\*, *Haliotis spadicea*\*, *Patella longicosta*\*, *Patella cochlear*\*, *Patella miniata*\*, *Oxysteles tabularis*, *Burnupena lagenaria*\*, *Patella aphanes* and *Patella granularis*), 2 echinoderms (*Pentacta doliolum* and *Parechinus angulosus*), 2 barnacles (*Tetraclita serrata* and *Chthamalus dentatus*), the sea anemone *Pseudactinia flagellifera* and the crab *Plagusia chabrus*. The 6 molluscs marked by asterisks are species taken regularly by shellfish-gatherers.

Table 3. Major species, ranked in order of importance, contributing to the average dissimilarities between Clusters I and II as determined by similarity percentages (SIMPER) analyses based on mean biomass estimates. Letters indicate the geographic distribution range of the species. U: ubiquitous, C: cold temperate, W: warm temperate and S: subtropical.  $\delta_i$  and  $\Sigma\delta_i$  are the individual and cumulative contributions, respectively, to the average dissimilarity

Species	Average abundance		Contribution to dissimilarity	
	I	II	$\delta_i$	$\Sigma\delta_i$
<i>Perna perna</i> (U)	135.9	14.3	4.86	4.86
<i>Pentacta doliolum</i> (C)	6.81	0.05	3.53	8.39
<i>Haliotis spadicea</i> (W)	2.86	0.36	2.69	11.08
<i>Parechinus angulosus</i> (C)	2.64	0.04	2.60	13.68
<i>Burnupena cincta</i> (C)	0.35	0.0	2.19	15.87
<i>Pseudactinia flagellifera</i> (C)	1.25	0.02	1.89	17.76
<i>Chiton tulipa</i> (W)	0.26	0.0	1.84	19.60
<i>Onitochiton literatus</i> (S)	0.0	0.29	1.69	21.29
<i>Burnupena lagenaria</i> (W)	0.66	0.14	1.54	22.83
<i>Thais capensis</i> (W)	0.24	0.01	1.52	24.35
<i>Pyura stolonifera</i> (U)	0.27	0.04	1.49	25.84
<i>Octomeris angulosus</i> (C)	0.01	0.35	1.49	27.33
<i>Patirella exigua</i> (U)	0.13	0.01	1.40	28.73
<i>Burnupena pubescens</i> (C)	0.08	0.0	1.25	29.97
<i>Patella cochlear</i> (C)	0.13	0.45	1.23	31.20
<i>Patella barbara</i> (C)	1.68	0.40	1.21	32.42
<i>Idanthysus pennatus</i> (S)	0.0	0.04	1.21	33.63
<i>Patella aphanes</i> (S)	0.03	0.35	1.21	34.83
<i>Patella tabularis</i> (W)	0.23	0.03	1.12	35.95
<i>Patella miniata sanguinans</i> (S)	1.45	0.69	1.10	37.05
Average % dissimilarity				41.57

## DISCUSSION

The dendrograms and MDS ordinations derived from the data collected during the present study indicate that the rocky infratidal macrofaunal assemblages at Hluleka, Lwandile and Preslie's Bay share much greater affinities with their counterparts in the northern than in the southern region of Transkei. As the southern part of the Transkei coast is regarded as a transition zone between the warm temperate south-coast province and the sub-tropical east-coast province (Kilburn & Rippey 1982), a biogeographical gradient appears to be the most likely explanation for the differences observed. This viewpoint is supported by the results of the SIMPER analyses, which indicate that species which either were restricted to or attained greater numbers or biomasses in the southern region made the greatest contribution to the difference in community structure between the southern and central and northern regions of Transkei combined. The fact that temperate species contributed more to the dissimilarities observed than subtropical species is somewhat surprising because previous work indicates that, as one moves north along the Transkei coast, the change

in the number of warm-water (i.e. sub-tropical) species exceeds the changes in the number of south-coast (i.e. warm temperate) and cold water species combined (Stephenson 1944). The most likely explanation for this discrepancy is the difference in species attributes used in the 2 studies; Stephenson's analyses were based on presence/absence data whereas the SIMPER analyses were based on the abundances and biomasses of the 160 most important species selected by the REDUCE routine. An improvement in our knowledge of the distributional range of species over the past 50 yr may also be a contributing factor. Inspection of the original data matrix, however, does indicate that a larger proportion of the species present in the central and northern regions were absent from the southern region than vice versa (76 species versus 39 species). The fact that temperate species made a greater contribution than subtropical species to the difference in community structure suggests that they may be less tolerant of the changes in sea temperature encountered along the Transkei coast. Regional differences in geological substrata and exploitation intensity along the Transkei coast may also contribute to the differences in these assemblages

Table 4. Major species, ranked in order of importance, contributing to the average dissimilarities between the protected (I) and exploited (II) sites as determined by 2-way similarity percentages (SIMPER2) analyses based on mean abundance and biomass estimates.  $\delta_i$  and  $\Sigma\delta_i$  are the individual and cumulative contributions, respectively, to the average dissimilarity. Species marked by (\*) were identified by Lasiak & Field (1995) as major discriminators of exploited and non-exploited communities in southern Transkei

Species	Average abundance		Dissimilarity contribution		Species	Average biomass		Dissimilarity contribution	
	I	II	$\delta_i$	$\Sigma\delta_i$		I	II	$\delta_i$	$\Sigma\delta_i$
<i>Perna perna</i> *	153.42	20.68	0.59	2.31	<i>Perna perna</i> *	124.17	6.19	2.18	6.38
<i>Paramoera capensis</i> *	0.44	11.39	0.43	3.97	<i>Haliotis spadicea</i> *	2.62	0.19	0.95	9.16
<i>Pseudactinia flagellifera</i> *	20.18	0.30	0.41	5.57	<i>Pseudactinia flagellifera</i> *	1.05	0.01	0.64	11.03
<i>Haminoea natalensis</i>	0.25	2.71	0.37	7.02	<i>Patella longicosta</i> *	2.15	0.58	0.63	12.88
<i>Patella granularis</i>	5.37	0.45	0.37	8.46	<i>Patella granularis</i>	0.21	0.0	0.61	14.68
<i>Bunodactis reynaudi</i>	3.04	8.98	0.36	9.87	<i>Tetraclita serrata</i> *	0.24	0.01	0.58	16.37
<i>Brachidontes semistriatus</i>	5.75	22.99	0.35	11.24	<i>Patella cochlear</i> *	0.49	0.17	0.58	18.07
<i>Ophionereis porrecta</i> *	32.59	84.07	0.34	12.57	<i>Pentacta doliolum</i> *	4.59	0.86	0.55	19.68
<i>Elasmopus japonicus</i> *	105.8	220.15	0.33	13.83	<i>Patella miniata</i> *	1.34	0.60	0.54	21.26
<i>Lysianassa ceratina</i> *	18.92	55.98	0.31	15.03	<i>Parechinus angulosus</i> *	1.79	0.36	0.53	22.81
<i>Chthamalus dentatus</i> *	3.03	0.18	0.31	16.22	<i>Oxystele tabularis</i> *	0.73	0.13	0.53	24.36
<i>Tetraclita serrata</i> *	4.22	0.27	0.30	17.40	<i>Brachidontes semistriatus</i>	0.01	0.15	0.50	25.83
<i>Sycon</i> sp.	0.0	0.75	0.30	18.58	<i>Octomeris angulosus</i>	0.18	0.22	0.48	27.23
<i>Patella cochlear</i>	6.78	2.82	0.30	19.75	<i>Burnupena lagenaria</i> *	0.42	0.24	0.47	28.61
<i>Thelepus</i> sp.	0.10	1.26	0.30	20.92	<i>Bunodactis reynaudi</i>	0.02	0.09	0.47	29.98
<i>Patiriella exigua</i> *	3.44	1.92	0.30	22.07	<i>Plagusia chabrus</i>	0.08	0.0	0.46	31.33
<i>Lumbinereis coccinea</i> *	0.20	2.55	0.28	23.18	<i>Haminoea natalensis</i>	0.0	0.02	0.41	32.52
<i>Podocerus</i> sp.	0.03	1.04	0.28	24.28	<i>Patella aphanes</i>	0.42	0.05	0.39	33.67
<i>Cymodoceella pustulata</i>	2.02	7.25	0.28	25.36	<i>Dinoplax validofossus</i>	0.04	0.10	0.39	33.67
Unidentified polychaete sp. U	0.0	0.48	0.27	26.41	<i>Chthamalus dentatus</i>	0.03	0.0	0.38	35.93
Average % dissimilarity				25.77	Average % dissimilarity				34.14

(Hockey et al. 1988, Lasiak 1997). The effect of these factors, however, cannot be determined with the sampling design used in the present study.

Few attempts have been made to compare the community-level attributes of exploited and non-exploited assemblages (Hockey & Bosman 1986, Lasiak & Field 1995). The results of the present study are only really comparable with those of Lasiak & Field (1995), as only they have made use of analytical techniques similar to and examined the same assemblages as those used in the present study. Hockey & Bosman (1986) used correspondence analysis to compare the community structure of lower balanoid zone assemblages at paired exploited and non-exploited sites in southern and central Transkei. Their analyses indicated that the assemblages at the exploited sites were more similar than those at the corresponding non-exploited sites. They concluded that selective predation was responsible for the convergence of exploited communities towards a common state, and attributed the considerable variation in community structure they observed amongst their non-exploited sites to the fact that these newly protected sites had yet to reach an equilibrium state.

The clear-cut separation of the exploited and non-exploited sites evident in the MDS ordinations produced from data collected during the present study

suggests that there are marked differences in the community structure of the exploited and non-exploited treatments. This was confirmed by the results of the 2-way crossed ANOSIM tests. The 2-way SIMPER analysis based on abundance estimates indicates that the major reasons for the differences between infratidal macrofaunal assemblages subject to these 2 treatments are the lower average abundance of 4 sessile species, *Perna perna*, *Pseudactinia flagellifera*, *Chthamalus dentatus* and *Tetraclita serrata*, and 3 small grazers, *Patella granularis*, *Patella cochlear* and *Patiriella exigua*, and higher average abundance of small phytal-associated species, such as the opisthobranch *Haminoea natalensis*, the brittle star *Ophionereis porrecta* and various amphipods, in exploited areas. Similar analyses based on biomass estimates indicate that 15 major discriminators attained a lower average biomass under exploited conditions. This group comprised 8 grazers, *Haliotis spadicea*, *Patella longicosta*, *Patella cochlear*, *Patella miniata*, *Parechinus angulosus*, *Oxystele tabularis*, *Patella aphanes* and *Patella granularis*, 4 filter-feeders, *Perna perna*, *Tetraclita serrata*, *Pentacta doliolum* and *Chthamalus dentatus*, 2 scavengers, *Burnupena lagenaria* and *Plagusia chabrus*, and the carnivore *Pseudactinia flagellifera*. Ten of the 20 highest-ranked discriminators high-

lighted by the 2-way SIMPER analysis based on abundance estimates and 11 of those identified by similar analyses based on biomass estimates (species marked with an asterisk in Table 4) have been identified previously by Lasiak & Field (1995) as being responsible for differences in exploited and non-exploited assemblages in the southern region of Transkei. In both studies, 2 species, *Perna perna* and *Pseudactinia flagellifera*, feature amongst the top 5 discriminators defined on the basis of both biomass and abundance estimates. The brittle star *Ophionereis porrecta* and the abalone *Haliotis spadicea* also featured consistently amongst the top 5 discriminators. The lack of representation of exploited species amongst the major discriminators was somewhat of a surprise because exploitation is known to lead to a marked reduction in both the abundance and biomass of target species (see Siegfried 1994 for review).

The differences in the community structure of the exploited and non-exploited infratidal macrofaunal assemblages reported above are in line with the effects one would have hypothesized simply from a knowledge of the organisms targeted by shellfish-gatherers and an understanding of the influence of these species on other low-shore biotic components. The removal of the brown mussel *Perna perna* and large grazing gastropods, such as patellid limpets, for example, is known to result in the domination of primary space by algae (Lambert & Steinke 1986, Dye 1992, 1995). The resultant change in the pattern of space occupancy on the shore is expected to have negative implications for a number of species; the reduction in the availability of primary space will lead to a decline in the settlement of sessile fauna and curtail the feeding activities of microalgal grazers, and the sessile faunal components already present are likely to become over-grown and even smothered by macroalgae. The total loss and/or reduction in size of mussel clumps resulting from exploitation is likely to have a deleterious effect on the large number of species which make use of this microhabitat as a source of food, shelter or attachment (Seed & Suchanek 1992). The species most likely to benefit from these changes are those which are normally found in association with or feed on macroalgae. The abundance and biomass of the adversely affected species is consequently expected to be markedly lower, while that of the species which benefit is expected to be much higher, at exploited localities.

The present study suggests that zoogeographic trends may have a much greater influence on infratidal community structure than the intense shellfish-gathering which takes place along the Transkei coast. This probably reflects the fact that zoogeographic differences are due primarily to the appearance/disappearance of species able/unable to tolerate the change in

the temperature regime along the Transkei coast; but, the differences between exploited and non-exploited localities are due to changes in abundance and biomass rather than the elimination/introduction of species.

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#### LITERATURE CITED

- Bigalke EH (1973) The exploitation of shellfish by coastal tribesmen of Transkei. *Ann Cape Prov Mus (Nat Hist)* 9: 159–175
- Castilla JC, Bustamente RH (1989) Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillea antarctica* (Phaeophyta, Durvilleales). *Mar Ecol Prog Ser* 50:203–214
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Duran LR, Castilla JC, Oliva D (1987) Intensity of human predation on rocky shores at Las Cruces in central Chile. *Environ Conserv* 14:143–149
- Dye AH (1992) Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish gathering. *Neth J Sea Res* 30:209–217
- Dye AH (1995) The effects of excluding limpets from the lower balanoid zone of rocky shores in Transkei, South Africa. *S Afr J Mar Sci* 15:9–15
- Dye AH (1998) Community-level analyses of long-term changes in rocky littoral fauna from South Africa. *Mar Ecol Prog Ser* 164:47–57
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Fielding PJ, Robertson WD, Dye AH, Tomalin BJ, van der Elst RP, Beckley LE, Mann BQ, Birnie S, Schleyer MH, Lasiak TA (1994) Transkei coastal fisheries resources. *Oceanogr Res Inst Durban Spec Publ* No. 3
- Godoy C, Moreno CA (1989) Indirect effects of human exclusion from the rocky intertidal in southern Chile: a case of cross-linkage between herbivores. *Oikos* 54:101–106
- Hockey PAR, Bosman AL (1986) Man as an intertidal predator in Transkei: disturbance, convergence and management of a natural food resource. *Oikos* 46:3–14
- Hockey PAR, Bosman AL, Siegfried WR (1988) Patterns and correlates of shellfish exploitation by coastal people in Transkei: an enigma of protein production. *J Appl Ecol* 25: 353–363
- Kilburn R, Rippey E (1982) *Sea shells of southern africa*. MacMillan, Johannesburg
- Lambert G, Steinke TD (1986) Effects of destroying juxtaposed mussel-dominated and coralline algal communities at Umdoni Park, Natal coast, South Africa. *S Afr J Mar Sci* 4:203–217
- Lasiak TA (1991) The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal people of Transkei, southern Africa. *Biol Conserv* 56:245–264
- Lasiak TA (1992) Contemporary shellfish-gathering practices of indigenous coastal people in Transkei: implications for



- the interpretation of the archaeological record. *S Afr J Sci* 88:19–28
- Lasiak TA (1997) Temporal and spatial variations in the pattern of shoreline utilization in a region subject to subsistence exploitation. *Environ Studies* 52:21–46
- Lasiak TA, Dye AH (1989) The ecology of the brown mussel *Perna perna* in Transkei: implications for the management of a traditional food resource. *Biol Conserv* 47:245–257
- Lasiak TA, Field JG (1995) Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. *J Exp Mar Biol Ecol* 185:33–53
- Moreno CA, Lunecke KM, Lepez MI (1986) The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblages. *Oikos* 46:359–364
- Oliva D, Castilla JC (1986) The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *PSZN I: Mar Ecol* 7:201–217
- Platell ME, Potter IC, Clarke KR (in press) Resource partitioning by four species of elasmobranch (Batoidea: Urolophidae) in coastal waters of temperate Australia. *Mar Biol*
- Seed R, Suchanek TH (1992) Population and community ecology of *Mytilus*. In: Gosling E (ed) *The mussel Mytilus: ecology, physiology, genetics and culture*. Elsevier, Amsterdam, p 87–169
- Siegfried WR (1994) *Rocky shores: exploitation in Chile and South Africa*. Springer-Verlag, Berlin
- Siegfried WR, Hockey PAR, Crowe AA (1985) Exploitation and conservation of brown mussel stocks by coastal people in Transkei. *Environ Conserv* 12:303–307
- Stephenson TA (1944) The constitution of the intertidal fauna and flora of South Africa. Part II. *Ann Natal Mus* 10: 261–358
- Underwood AJ (1989) The analysis of stress in natural populations. *Biol J Linn Soc* 37:51–78

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