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# Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei

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## Abstract

The rocky intertidal biota along the Transkei coast of southern Africa is subject to intense exploitation by the indigenous coastal inhabitants. To assess the putative ecological impact of such unconstrained foraging activities the infratidal macrofaunal assemblages at three exploited sites were contrasted with those at two adjacent non-exploited sites. Comparisons of community-level attributes were based on a variety of univariate, graphical and multivariate techniques. Two-way nested anovas revealed that trends in species richness and diversity were not consistent with the presence/absence of exploitation. The apparent conflict between these results and expectations based on Connell's intermediate disturbance hypothesis appear to be related to differences in the competitive abilities of "early" and "late" successional species on these shores. Macrofaunal biomass was the only univariate parameter to show significant treatment effects. Although the repeated pulse disturbance regime associated with exploitation differs from the sustained press regime imposed on pollution-impacted communities, their respective abundance/biomass curves show similar trends. Multivariate analyses, in the form of dendrograms, multidimensional scaling (MDS) ordinations and SIMPER routines, derived from Bray-Curtis measures of similarity based on abundance and biomass data, provided the most clear-cut discrimination between exploited and non-exploited sites. The difference in community structure appears to result from a reduction in the abundance of sessile filter-feeders, increase in abundance of certain seaweed-associated species, and decrease in biomass of exploited species and their associated fauna. Differences in community structure amongst sites within treatments were attributed to additional environmental variations. The putative effects of exploitation are also contrasted with those resulting from other forms of anthropogenic disturbance elsewhere.

*Keywords:* Community structure; Exploitation; Macrofauna; Rocky Shores; South Africa

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## 1. Introduction

The impact of man's recreational activities on coastal ecosystems is a matter of increasing concern. Human activities likely to impinge on the biota of rocky shores include the collection of organisms either for aquaria, as bait or for sustenance, fishing, snorkelling, over-turning of boulders, inspection of rock pools as well as general trampling over the rock platform. Whilst it is evident that such activities may lead to the removal and/or damage of a wide range of biota, the degree to which these activities affect intertidal populations and/or assemblages is still largely unknown. The most widely-reported impacts have been those which are exploitation-related (Moreno et al., 1984; Castilla & Duran, 1985; Hockey & Bosman, 1986; Oliva & Castilla, 1986; Duran et al., 1987; Ortega, 1987; Castilla & Bustamente, 1989; Duran & Castilla, 1989; Godoy & Moreno, 1989; Lasiak, 1991a; Keough et al., 1993).

Many of the above-mentioned studies, particularly those involving contrasts between exploited and non-exploited populations and/or communities, have been criticised because of inadequate spatial replication (Fairweather, 1991). The lack of within-shore replication means that observed differences can not be compared statistically neither can they be attributed unequivocally to the effects of human exploitation. To overcome this problem Underwood (1989) advocates the comparison of multiple areas of impacted and non-impacted sites. There is also a need for potentially-confounding physical and biotic variables to be controlled within set limits when selecting sites and faunistic samples (Clarke & Green, 1988). This argument is especially pertinent to rocky intertidal environments which are usually characterized by marked spatial heterogeneity.

The rocky intertidal biota along the Transkei coast of southern Africa is subject to intense exploitation by the indigenous coastal people. In particular, large quantities of shellfish are used to supplement the rather meagre maize-based diet on which these rural people depend. In addition to this, there is also limited commercial exploitation of various species of algae belonging to the genus *Gelidium*. The shellfish-gatherers have been shown to be selective, both in terms of species and size classes removed (Bigalke, 1973; Hockey & Bosman, 1986; Lasiak, 1991a). Analyses of shell middens indicate that the brown mussel *Perna perna* is the most important food item, accounting for $>80\%$ of the contents (Lasiak, 1991b). Other species favoured by the collectors include the limpets *Patella barbara*, *P. longicosta*, *P. miniata*, and *P. oculus*; the abalone *Haliotis spadicea*; and the coiled gastropods *Turbo sarmaticus* and *Burnupena cincta* (Lasiak, 1991a, 1992). The shellfish-gatherers also preferentially select larger individuals (Siegfried et al., 1985; Hockey & Bosman, 1986; Lasiak & Dye, 1989; Lasiak, 1991a). The impact of such exploitation on target populations has been well documented (Siegfried et al., 1985; Hockey & Bosman, 1986; Lasiak & Dye, 1989; Lasiak, 1991a,b, 1992, 1993a), comparatively little is known about the effects on community structure and functioning (Hockey & Bosman, 1986). The latter study, which contrasted three pairs of adjacent exploited and protected shores, focussed on differences in community structure within the balanoid zone. Observations of shellfish-gatherers on the shore, coupled with analyses of shell middens (Lasiak, 1992), however, indicate that the greatest exploitation effort is usually directed at the infratidal fringe, where most of the preferred prey are concentrated.

The primary objective of the current study was to assess the putative impact of subsistence exploitation on rocky infratidal assemblages by contrasting three exploited and two non-exploited sites. In order to minimize confounding influences associated with the marked geographic differences in exploitation effort and underlying geological substrata along the Transkei coast (Hockey et al., 1988), and the position of Transkei

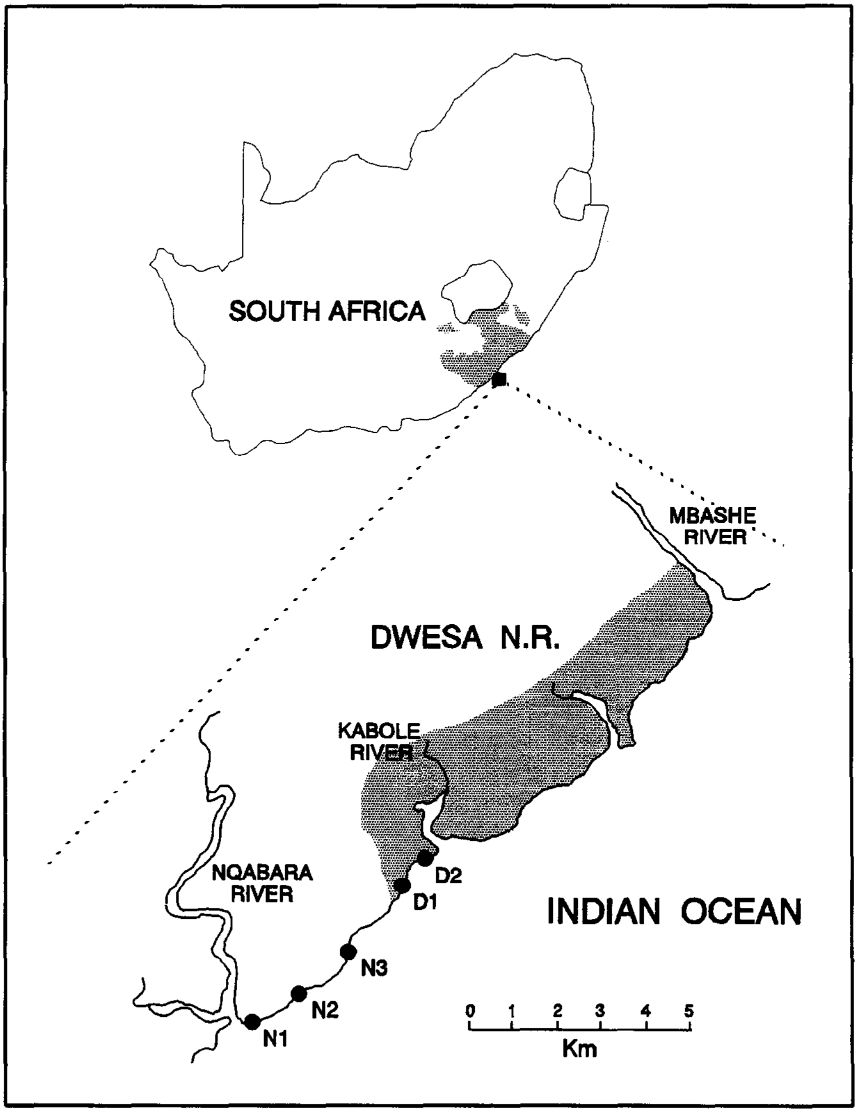


Fig. 1. Map showing the position of the five sampling sites, located between the Nqabara and Kabole rivers, on the Transkei coast of South Africa. The shaded area on the detailed map shows the location of the Dwesa Nature Reserve.

within a zoogeographic transition zone (Kilburn & Rippey, 1982) the present comparison was restricted to sites situated along a relatively short (10 km) stretch of coastline. The nested-sampling design employed permits the assessment of variations within-localities (i.e. amongst-sites), and between-localities (i.e. exploited versus non-exploited sites). Comparisons are based on a variety of univariate, graphical and multivariate techniques which are commonly used to contrast impacted and non-impacted sites (Warwick & Clarke, 1991; Clarke, 1993).

## 2. Materials and methods

### 2.1. Study area

Five study sites were selected between the Nqabara and Kabole rivers on the Transkei coast of South Africa (Fig. 1). Two of these sites, referred to subsequently as D1 and D2, are situated ≈ 1 km apart towards the southern end of the Dwesa Nature Reserve (32° 18′ S, 28° 50′ E) and are therefore protected from the exploitation which takes place at the three sites (N1, N2 and N3) situated along a 4-km stretch of shore between Nqabara Point and Nqabara river. The presence of a gulley, which funnels waves onto the shore at N2, restricts exploitation to calm conditions, this site is consequently less disturbed than its adjacent counterparts. All study sites were situated on gently sloping rock platforms. In the case of D1, D2 and N3 the underlying substratum consisted of shale whereas at N1 and N2 the platforms were composed of mudstone.

### 2.2. Field and laboratory procedures

During equinoctial spring low tides, hammers and paint scrapers were used to remove ten 0.5 $m^2$ quadrat samples of infratidal biota from each of the study sites. Sample locations within-sites were selected to represent similar aspects and elevations on the shore. The 50 quadrat samples were preserved in 10% formalin for subsequent analysis. In the laboratory the individual samples were sorted, and, whenever possible, the macrofauna and macroalgae were then identified to species level. The macrofaunal components were also 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. Owing to the highly-intertwined nature of the algal mat, separation of macroalgae into individual species was not feasible, comparisons are therefore limited to overall algal biomass.

### 2.3. Data analysis

Various descriptive univariate statistics were computed. The number of macrofaunal species present, as well as their overall abundance and biomass, were determined for each quadrat sample. Estimates of total abundance and biomass were derived by summation of values for individual macrofaunal species. An index of disturbance, based on the macrofaunal biomass:abundance ratio, B/A = mean biomass in g. per 0.5 $m^2$/

mean abundance per 0.5 $m^2$, was also estimated (Pearson et al., 1982). Cumulative ranked macrofaunal abundance and biomass data were plotted against log species rank for each site. These so-called k-dominance curves for abundance and biomass were then juxtaposed to form the Abundance/Biomass Comparison (ABC) curves proposed by Warwick (1986). Following the recommendations of Ludwig & Reynolds (1988), Hill's diversity numbers N1 ($N1 = e^{H'}$ where H′ is Shannon's diversity index) and N2 ($N2 = 1/\lambda$ where $\lambda$ is Simpson's diversity index) were used as measures of macrofaunal species diversity, and the modified Hill's ratio E5 ($E5 = (N2\text{-}1)/(N1\text{-}1)$) was used as a measure of evenness. Two-way nested analyses of variance of these measures permitted the partitioning of spatial variance into a treatment component, reflecting the presence or absence of exploitation, as well as a sites-within-treatments component. The expected mean squares generated in these analyses were used to estimate the percentage of total variation attributable to differences among replicates, sites and treatments (Sokal & Rohlf, 1981).

Multivariate analyses were based on two data matrices, one containing estimates of the number of individuals of each macrofaunal species found in each of the 50 quadrat samples, and the other comprising the corresponding biomass estimates. Following the recommendation of Field et al. (1982), these data matrices were subject to root-root transformations prior to the computation of triangular matrices of similarities between each pair of samples, based on the Bray-Curtis similarity measure $S_{jk} = 1 - \delta_{jk}$: where

$$\delta_{jk} = \frac{\sum_{i=1}^{s} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}$$

and $Y_{ij}$ = score for the $i$th species in the $j$th sample; $Y_{ik}$ = score for the $i$th species in the $k$th sample; $\delta_{jk}$ = dissimilarity between the $j$th and $k$th samples summed over all $s$ species. Before dendrograms and ordination analyses were initiated, a multivariate analogue of analysis of variance, the two-way nested ANOSIM randomization test, was used to test for differences between treatments and among sites (Clarke, 1993).

In separate analyses, a hierarchical classification technique based on group-average sorting was used to generate dendrograms from the similarity matrices. The latter were also summarized diagrammatically in the form of 2-dimensional ordinations derived from non-metric multidimensional scaling (MDS) (Kruskal & Wish, 1978). The extent to which the 2-D maps represented the relationships between samples was assessed by means of Shephard diagrams (not shown) and "stress coefficients". The major species responsible for the division of samples into clusters as well as those species responsible for discriminating between clusters were determined using the similarity percentages (SIMPER) routine (Clarke, 1993). The software package "PRIMER", developed by the Plymouth Marine Laboratory, was used for the multivariate analyses (Warwick & Clarke, 1991; Clarke, 1993).

## 3. Results

### 3.1. Discrimination among sites

Fig. 2 shows that the overall algal biomass was generally higher at the exploited sites whereas D1 supported the highest mean macrofaunal abundance and biomass. The macrofaunal biomass at D2 was also significantly higher than that at the three exploited sites. The undisturbed nature of these sites is confirmed by the relatively high macrofaunal biomass:abundance ratios (D1 = 0.33 and D2 = 0.28). Sites N1 and N3 on the other hand, appeared to be the most disturbed, as indicated by macrofaunal biomass: abundance ratios of 0.08 and 0.09, respectively. Site N2, with a biomass:abundance ratio of 0.21, exhibited an intermediate condition. Among-sites differences in the other univariate parameters were not consistently linked with the presence/absence of ex-

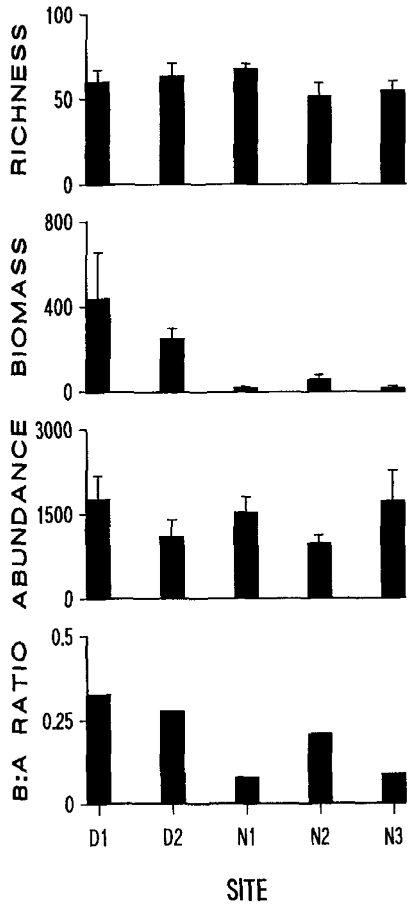


Fig. 2. Mean (± SD) algal biomass, density and biomass of macrofaunal species and biomass:abundance ratio recorded in infratidal quadrat samples ($n = 10$) from the five study sites.

ploitation. For example, N1 had the highest mean number of macrofaunal species per quadrat and N2 the lowest; N2 had the highest mean evenness and N3 the lowest; D2 had the highest mean diversity whereas N3 had the lowest values followed closely by D1 (Fig 3).

The results of the two-way nested analyses of variance revealed significant treatment (i.e. exploited versus non-exploited localities) effects on only one parameter, macrofaunal biomass (Table 1). All parameters, however, showed highly significant variations amongst sites within treatments. Variations attributable to differences amongst treatments were generally lower than those attributed to differences amongst sites within treatments, the exceptions being variations in macrofaunal and algal biomass (Table 2). Variations in these univariate parameters attributable to differences amongst replicates were relatively high, ranging from 26.7 to 57.5%, except for macrofaunal biomass, where this accounted for only 8.5% of the variation.

The ABC curves for each site are shown in Fig. 4. According to the designations of Warwick (1986) sites D1, D2 and N2 would be categorized as undisturbed as their

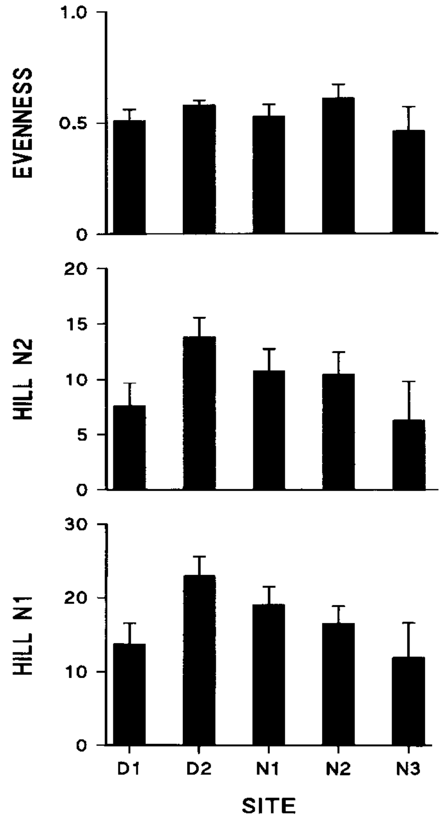


Fig. 3. Mean (± SD) richness, diversity (Hill's N1 and N2) and evenness (Hill's modified ratio E5) estimates of infratidal macrofaunal assemblages at the five study sites.

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

| Univariate measure | Source of variation | *F*-ratio | *p* |
|---|---|---|---|
| Macrofaunal abundance | Treatment | $<0.01$ | $>0.25$ |
| | Site {treatment} | 12.69 | $<0.001$* |
| Algal biomass | Treatment | 4.88 | $>0.10$ |
| | Site {treatment} | 3.26 | 0.03* |
| Macrofaunal biomass | Treatment | 21.05 | $<0.025$* |
| | Site {treatment} | 22.94 | $<0.001$* |
| Species richness | Treatment | 0.33 | $>0.25$ |
| | Site {treatment} | 11.98 | $<0.001$* |
| Evenness | Treatment | 0.07 | $>0.25$ |
| | Site {treatment} | 9.50 | $<0.001$* |
| Diversity (N1) | Treatment | 0.32 | $>0.25$ |
| | Site {treatment} | 21.82 | $<0.001$* |
| Diversity (N2) | Treatment | 0.27 | $>0.25$ |
| | Site {treatment} | 17.63 | $<0.001$* |

* Denotes significance at $p<0.05$.

biomass curves are located well above the abundance curves. Site N1, where the abundance and biomass curves are closely coincident, would be classed as moderately disturbed and site N3, where the abundance curve lies in close proximity to, but also distinctly above, the biomass curve would be categorized as moderately/severely disturbed.

Two-way nested ANOSIM tests revealed highly significant differences among sites within localities (Table 3). The null hypothesis of no difference between exploited and non-exploited localities, however, could only be rejected at the $p<0.10$ significance level in the case of similarities based on abundance and at the $p<0.20$ significance level for those based on biomass. As the total number of distinct permutations was relatively small (10), owing to paucity of sites within each treatment locality, strong

Table 2
The percentage variation, calculated as MS/total MS, in macrofaunal abundance, biomass, species richness, evenness and diversity (Hill's N1 and N2) attributable to each of the spatial scales examined (Sokal & Rohlf 1981)

| Source of variation | Macrofaunal abundance | Macrofaunal biomass | Algal biomass | Percentage variation | | | |
|---|---|---|---|---|---|---|---|
| | | | | Richness | Evenness | Hill's N1 | Hill's N2 |
| Treatment | 18.9 | 84.6 | 29.4 | 13.2 | 18.2 | 17.7 | 16.1 |
| Sites | 43.7 | 14.2 | 13.1 | 45.4 | 36.4 | 55.6 | 52.4 |
| Replicates | 37.4 | 8.5 | 57.5 | 41.4 | 45.4 | 26.7 | 31.5 |

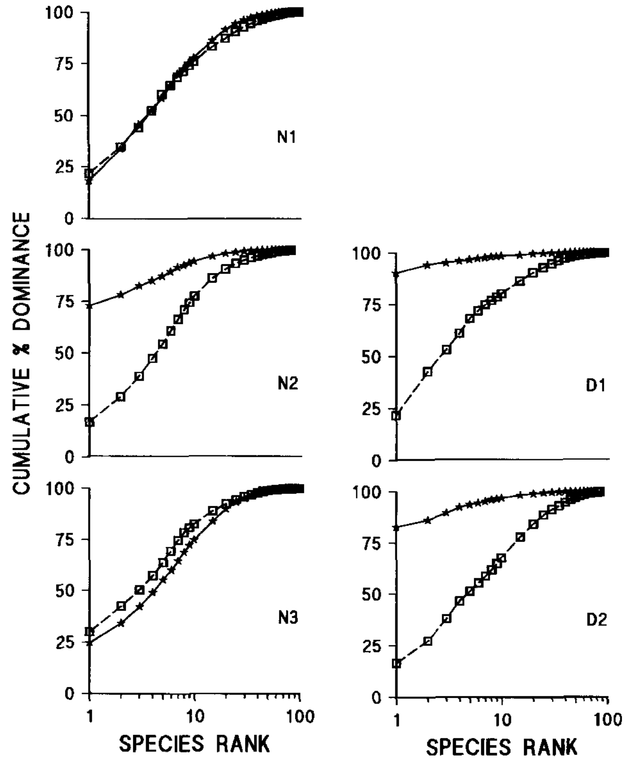


Fig. 4. Abundance/biomass curves based on macrofaunal species data for each of the five study sites (symbols □, ★ represent the abundance and biomass curves, respectively).

inferences about differences between exploited and non-exploited localities could not be drawn.

The dendrograms depicted in Fig. 5 show the affinities between quadrat samples defined in terms of (a) abundance and (b) biomass. In both cases two major divisions are evident, Cluster I representing samples from the two non-exploited sites and Cluster

Table 3
Results of two-way nested ANOSIM randomization tests based on macrofaunal abundance and biomass

| Grouping | Source of variation | | | |
|---|---|---|---|---|
| | Treatments | | Sites | |
| | *R* | Probability | *R* | Probability |
| Abundance | 1.000 | 0.10 | 0.724 | <0.001* |
| Biomass | 0.750 | 0.20 | 0.631 | <0.001* |

* Denotes significance at $p < 0.05$.

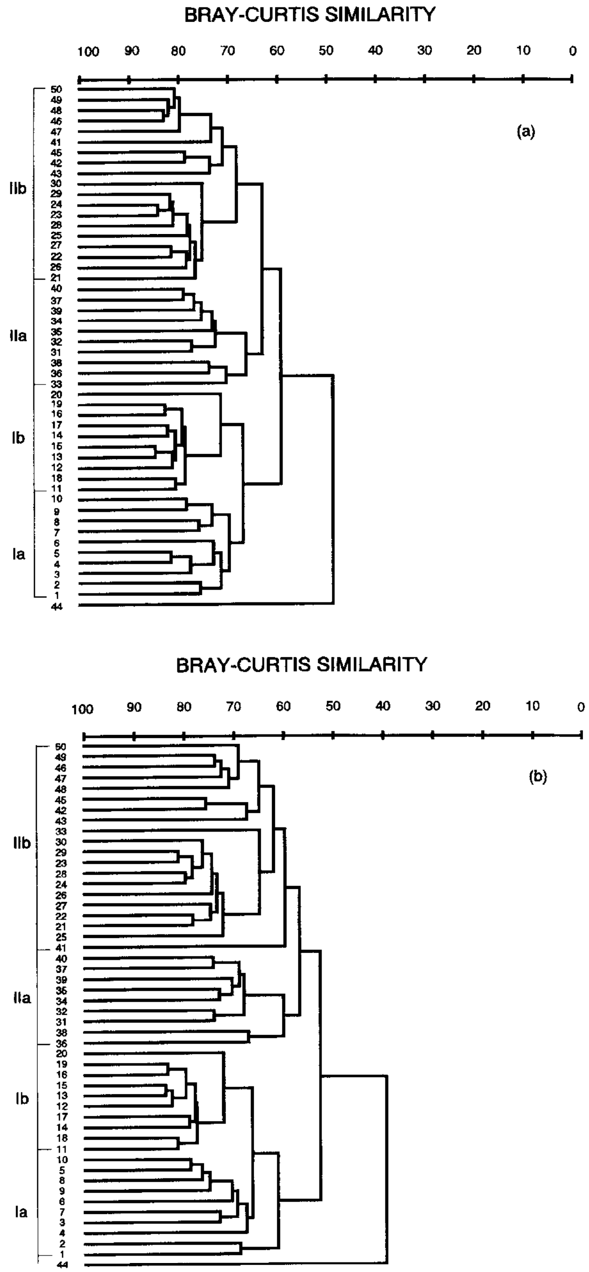


Fig. 5. Dendrograms showing group average clustering of Bray-Curtis indices of similarity based on root-root transformed macrofaunal abundance (a) and macrofaunal biomass (b) at the five study sites. Numbers refer to replicate quadrat samples 1–10, 11–20, 21–30, 31–40 and 41–50 representing sites D1, D2, N1, N2 and N3, respectively; letters indicate clustering of quadrat samples.

II comprising samples from the three exploited sites. Cluster I splits into two major sub-groupings, designated Ia and Ib, representing the replicates from Dwesa 1 and 2, respectively. A smaller sub-grouping comprising replicates 1 and 2 is also evident in the dendrogram based on the biomass data. Cluster II consists of three major sub-groupings, Group IIa comprising the samples from Nqabara 2 and Groups IIb and IIc representing replicates from Nqabara 1 and 3, respectively. Quadrat 44 is an obvious outlier.

The grouping of samples resulting from MDS of the similarity matrices also indicated that replicate samples within sites were more similar than samples from different sites. As the stress coefficients for both ordinations were relatively low (0.14) and the groupings evident in the ordinations (Fig. 6a,b) were similar to those in the corresponding dendrograms these 2-D plots were deemed adequate representations of the relationships between samples. In both cases two major clusters were apparent, one representing replicates from the two non-exploited sites and the other comprising replicates from the three exploited sites. Considerable overlap was, however, evident between the sub-Groups IIb and IIc. Note the major outlier, quadrat 44, as in the dendrograms.

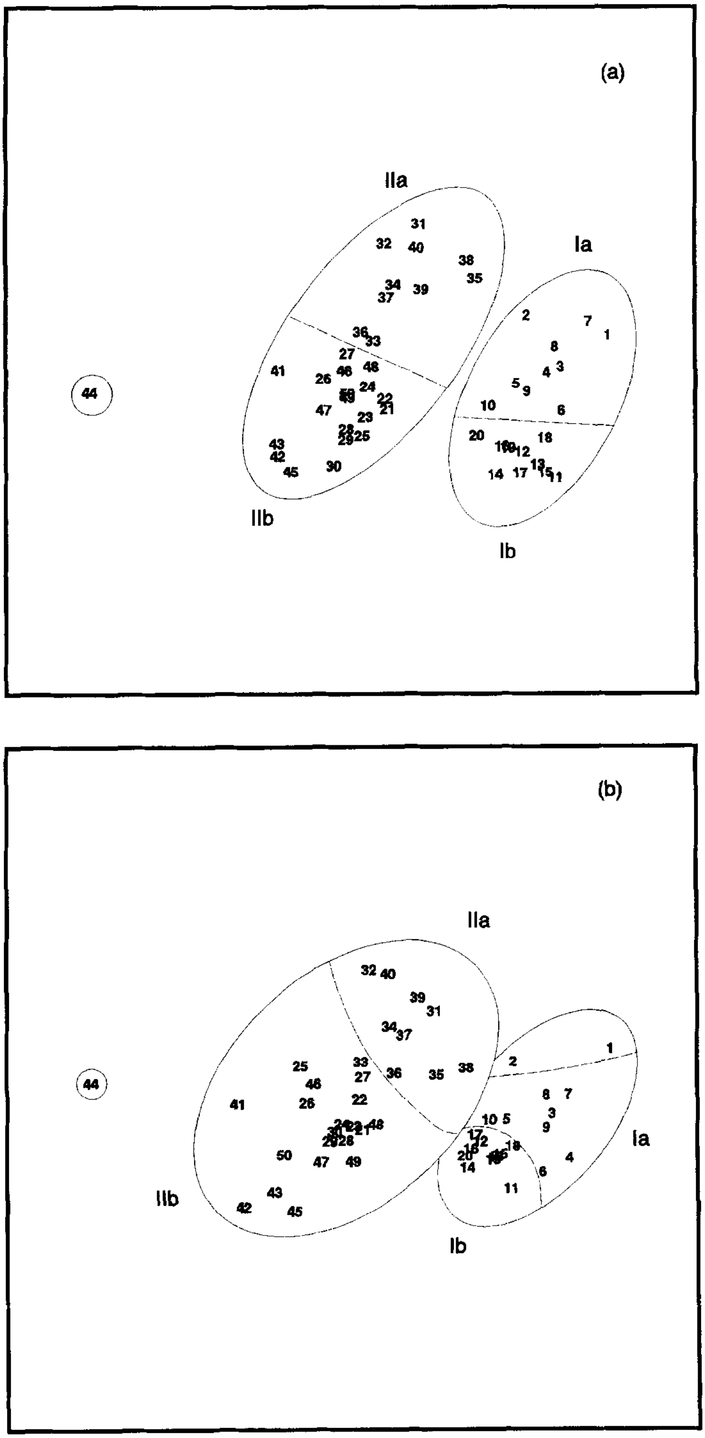
### 3.2. *Typicality of species within groups*

Table 4 and Fig. 5a show that the average similarity within Group I was generally higher than that within Group II. SIMPER analyses of within-group similarities based on abundance data indicate that 16 species account for 50% of the similarity within Group I as compared with 13 species in Group II. Since nine of these species are common to both groups it is evident that typicality within a group does not signify that a particular species is likely to be a good discriminator between groups. The principal species contributing to similarity within Group I which did not feature prominently in Group II were the anemones *Pseudactinia flabellifera* and *Anthothoe stimpsoni*, the molluscs *Patella longicosta*, *Anachis kraussi* and *Perna perna*, and the echinoderms *Patiriella exigua* and *Parechinus angulosus*. The major species which featured prominently in Group II but not Group I were the amphipod *Lysianassa ceratina*, the brittle star *Ophionereis porrecta*, and the nemerteans *Lineus* spp. and *Cerebratulus* spp.

SIMPER analyses based on biomass data indicate that 11 species accounted for 50% of the similarity within Group I as compared with 13 species in Group II (Table 4). Eight of these species were common to both groups. The principal species contributing to similarity within Group I which did not feature prominently in Group II were the anemone *Pseudactinia flabellifera* and the gastropods *Haliotis spadicea* and *Patella barbara*. Species typical of Group II but not Group I were the polychaetes *Marphysa corallina* and *Syllis variegata*, and the gastropods *Burnupena lagenaria*, *Fissurella mutabilis* and *Tricolia capensis*.

### 3.3. *Discrimination between groups*

Although many species played a role in determining the dissimilarities between Groups I and II, for the sake of brevity, only the 20 major contributors are listed in


(a)
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Ia
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Ia
IIb
Ib
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45

Table 5. Eleven of the 20 highest-ranked species accounting for differences between groups were more abundant in Group I than II. Seven of these, namely *Perna perna, Pomatoleois kraussi, Balanus amphitrite, Chthamalus dentatus, Tetraclita serrata, Balanus venustus* and *Gunnarea capensis* are sessile filter feeders which are found permanently attached to hard substrata. Three of the other species, the anemone *Pseudactinia flabellifera*, the cushion star *Patiriella exigua* and the limpet *Patella oculus* are sedentary species dependent on primary substrata. The principal species which were more abundant in Group II than I were generally found in association with the dense algal mats characteristic of exploited sites. The major species within this grouping were the brittle star *Ophionereis porrecta* and the amphipods *Elasmopus japonicus, Lysianassa ceratina, Paragrubia vorax* and *Paramoera capensis*. These 20 species accounted for 29.9% of the average between-group dissimilarity ($\delta = 41.3\%$). This analysis also revealed that 32 of the species represented in Group I were absent from Group II and vice versa 33 of the species represented in Group II were absent from Group I (not tabulated).

Similar analyses based on biomass data showed that the 20 major contributors accounted for 47.2% of the average dissimilarity ($\delta = 47.9\%$) between Groups I and II (Table 5). The majority of these attained higher biomass in Group I than in Group II. Five of the species, *Perna perna, Haliotis spadicea, Patella barbara, Patella miniata* and *Patella oculus* featured regularly in the shell middens accumulated by people living in the vicinity of Nqabara (Lasiak, 1992). Three of the others, *Pentacta doliolum, Parechinus angulosus* and *Pseudactinia flabellifera* are normally found in association with clumps of the mussel *Perna perna.*

The 10 principal species discriminating between groups Ia and Ib are listed in Table 6. The molluscs, *Perna perna, Patella aphanes* and the crustaceans, *Elasmopus japonicus* and *Dynamanella taurus* were more abundant in Group Ia. The other six species, namely the polychaetes *Pomatoleois kraussi* and *Syllis* sp., and the molluscs *Oxystele tabularis, Burnupena lagenaria, Tricolia insignis* and *Patella oculus* were more abundant in Group Ib. These 10 species accounted for 18.1% of the average dissimilarity ($\delta = 33.1\%$) between the groups. Thirty-four species of macrofauna present in Group Ia were absent from Group Ib and vice versa 18 species present in Group Ib were absent from Group Ia (not tabulated). Similar analyses based on biomass data indicated that five of the principal species responsible for between-group differences attained higher biomass in Group Ia (Table 6). These were the molluscs *Perna perna, Patella barbara, Patella granularis* and *Thais capensis* and the sponge *Haliclona sp.*. The molluscs, *Oxystele tabularis, Burnupena cincta, Burnupena lagenaria, Patella oculus*, and *Haliotis spadicea*, were the principal discriminators which attained higher biomass in Group Ib. These 10 species accounted for 25.8% of the average dissimilarity between Groups Ia and Ib.

The principal species discriminating between Groups IIa and IIb are listed in Table 7. Six of the most highly-ranked species were more abundant in Group IIa. These were the polychaete *Thelepus* sp., the molluscs *Turbo sarmaticus, Ischnochiton oniscus,*

Fig. 6. Multi-dimensional scaling ordinations based on (a) macrofaunal abundance and (b) macrofaunal biomass data for the five study sites. Designations as in Fig. 5.

Table 4
Major species contributing to the average similarity within Groups I (non-exploited) and II (exploited) as determined by SIMPER analyses based on root-root transformed data and the Bray-Curtis measure of similarity

| Species | Group I | | Group II | |
|---|---|---|---|---|
| | Av. Ab. | $S_i$ | Av. Ab. | $S_i$ |
| (a) Abundance (number of individuals per 0.5 $m^2$) | | | | |
| *Pentacta doliolum* | 277.3 | 3.6 | 306.7 | 3.3 |
| *Perna perna* | 264.4 | 3.4 | | |
| *Pseudonereis variegata* | 135.3 | 3.1 | 138.4 | 3.2 |
| *Tricolia capensis* | 120.4 | 2.9 | 116.0 | 3.0 |
| *Pseudactinia flabellifera* | 57.4 | 2.5 | | |
| *Fissurella mutabilis* | 37.5 | 2.1 | 34.5 | 2.1 |
| *Lepidonotus durbanensis* | 33.0 | 2.1 | 39.0 | 2.1 |
| *Elasmopus japonicus* | 76.0 | 2.0 | 139.9 | 2.9 |
| *Parechinus angulosus* | 31.8 | 2.0 | | |
| *Syllis variegata* | 25.8 | 1.9 | 88.2 | 2.9 |
| *Patella longicosta* | 18.4 | 1.9 | | |
| *Anthothoe stimpsoni* | 32.3 | 1.9 | | |
| *Dynamanella huttoni* | 18.3 | 1.8 | 30.3 | 2.1 |
| *Hyale grandicornis* | 18.9 | 1.6 | 76.5 | 2.3 |
| *Anachis kraussi* | 25.7 | 1.6 | | |
| *Patiriella exigua* | 10.2 | 1.5 | | |
| *Lysianassa ceratina* | | | 52.6 | 2.0 |
| *Ophionereis porrecta* | | | 63.4 | 2.0 |
| *Lineus* sp. | | | 17.1 | 1.8 |
| *Cerebratulus* sp. | | | 29.4 | 1.7 |
| Average similarity | | 70.7 | | 66.5 |
| (b) Biomass (g per 0.5 $m^2$) | | | | |
| *Perna perna* | 318.0 | 10.5 | 14.6 | 3.9 |
| *Pentacta doliolum* | 13.6 | 3.8 | 2.3 | 3.4 |
| *Pseudactinia flabellifera* | 3.1 | 3.2 | | |
| *Parechinus angulosus* | 5.3 | 3.1 | 0.8 | 1.8 |
| *Haliotis spadicea* | 6.4 | 2.8 | | |
| *Pseudonereis variegata* | 1.4 | 2.6 | 0.9 | 3.2 |
| *Patella longicosta* | 1.3 | 2.3 | 1.2 | 2.0 |
| *Patella miniata* | 1.6 | 2.1 | 1.3 | 1.6 |
| *Lepidonotus durbanensis* | 0.4 | 1.9 | 0.3 | 2.4 |
| *Anthotoe stimpsoni* | 0.4 | 1.8 | 0.2 | 1.7 |
| *Patella barbara* | 1.7 | 1.7 | | |
| *Tricolia capensis* | | | 0.4 | 2.5 |
| *Marphysa corallina* | | | 0.7 | 2.2 |
| *Fissurella mutabilis* | | | 0.3 | 2.2 |
| *Burnupena lagenaria* | | | 0.4 | 1.9 |
| *Syllis variegata* | | | 0.1 | 1.8 |
| Average similarity | | 68.7 | | 60.7 |

The average abundances (Av. Ab.) and biomasses (Av. B.) of these species across sites within each group and their individual contributions ($S_i$) to the average similarity within each group are presented.

Table 5
Major species, ranked in order of importance, contributing to the average dissimilarities between Groups I (non-exploited) and II (exploited) as determined by SIMPER analyses based on root-root transformed data and the Bray-Curtis measure of dissimilarity

| Species | Abundance | | | | Species | Biomass | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Av. Ab. | | $\delta_i$ | $\Sigma\delta_i$ | | Av. B. | | $\delta_i$ | $\Sigma\delta_i$ |
| | I | II | II:I | | | I | II | II:I | |
| *Pseudactinia flabellifera* | 57.4 | 0.5 | 3.0 | 3.0 | *Perna perna* | 318.0 | 14.6 | 8.8 | 8.8 |
| *Perna perna* | 264.4 | 38.0 | 2.3 | 5.3 | *Haliotis spadicea* | 6.4 | 0.5 | 3.9 | 12.7 |
| *Pomatoleios kraussi* | 17.3 | 0.2 | 1.7 | 7.0 | *Pseudactinia flabellifera* | 3.1 | <0.1 | 3.9 | 16.6 |
| *Ophionereis porrecta* | 8.7 | 63.4# | 1.7 | 8.7 | *Pentacta doliolum* | 13.6 | 2.3 | 2.7 | 19.3 |
| *Balanus amphitrite* | 10.6 | 0.6 | 1.7 | 10.3 | *Parechinus angulosus* | 5.3 | 0.8 | 2.6 | 21.9 |
| *Chthamalus dentatus* | 5.2 | 0.0 | 1.6 | 12.0 | *Patella barbara* | 1.7 | 1.6 | 2.1 | 24.0 |
| *Tetraclita serrata* | 5.1 | 0.3 | 1.5 | 13.5 | *Tetraclita serrata* | 0.3 | <0.1 | 1.9 | 25.9 |
| *Balanus venustus* | 24.6 | 5.8 | 1.5 | 15.0 | *Patella miniata* | 1.6 | 1.3 | 1.9 | 27.9 |
| *Paragrubia vorax* | 0.2 | 6.7# | 1.5 | 16.4 | *Thais capensis* | 0.6 | <0.1 | 1.9 | 29.8 |
| *Patiriella exigua* | 10.2 | 1.0 | 1.4 | 17.9 | *Patella oculus* | 0.6 | <0.1 | 1.9 | 31.6 |
| *Lysianassa ceratina* | 7.7 | 52.6# | 1.3 | 19.2 | *Oxystele tabularis* | 0.9 | 0.2 | 1.8 | 33.4 |
| *Patella oculus* | 4.5 | 0.0 | 1.3 | 20.4 | *Burnupena lagenaria* | 1.0 | 0.4 | 1.7 | 35.2 |
| *Elasmopus japonicus* | 76.0 | 139.9# | 1.3 | 21.7 | *Patiriella exigua* | 0.3 | <0.1 | 1.7 | 36.9 |
| *Planocera* spp. | 0.3 | 4.9# | 1.2 | 22.9 | *Haliclona* spp. | 0.3 | 0.1 | 1.6 | 38.5 |
| *Pentacta doliolum* | 277.3 | 306.7# | 1.2 | 24.1 | *Chiton tulipa* | 0.5 | 0.1 | 1.6 | 40.1 |
| *Paramoera capensis* | 0.7 | 3.5# | 1.2 | 25.3 | *Burnupena cincta* | 0.6 | 0.2 | 1.6 | 41.7 |
| *Anachis kraussi* | 25.7 | 8.8 | 1.2 | 26.5 | *Patella longicosta* | 1.3 | 1.2 | 1.5 | 43.2 |
| *Gunnarea capensis* | 9.9 | 2.3 | 1.2 | 27.7 | *Fissurella natalensis* | 0.2 | 0.1 | 1.5 | 44.7 |
| *Lumbrinereis tetraura* | 0.1 | 3.7# | 1.1 | 28.8 | *Marphysa corallina* | 0.2 | 0.7 | 1.4 | 46.1 |
| *Lumbrinereis coccinea* | 0.4 | 4.4# | 1.1 | 29.9 | *Patella cochlear* | <0.1 | 0.2 | 1.2 | 47.2 |
| Average dissimilarity | | | | 41.3 | | | | | 47.9 |

The average abundances (Av. Ab.) and biomasses (Av. B.) of these species across sites within each group, and both their individual ($\delta_i$) and cumulative contributions ($\Sigma\delta_i$) to the average dissimilarity between groups are presented (# indicates species which were more abundant at the exploited sites).

and *Anachis kraussi* and the echinoderms *Pentacta doliolum* and *Ophionereis porrecta*. These 10 species accounted for 17.1% of the average dissimilarity ($\delta = 37.0\%$) between Groups IIa and IIb. Seventeen of the macrofaunal species present in Group IIa were absent from Group IIb and vice versa 37 of the species present in Group IIb were absent from IIa (not tabulated). Discrimination between Groups IIa and IIb on the basis of biomass indicated that five of the six species which attained higher biomass in Group IIa are classified as exploited molluscs. These were *Perna perna, Patella barbara, Patella cochlear, Patella longicosta* and *Fissurella natalensis*. The sixth species was the sea urchin *Parechinus angulosus*. The polychaete *Marphysa corallina*, the molluscs *Patella miniata* and *Oxystele tabularis*, and the echinoderm, *Pentacta doliolum* all attained higher biomass in Group IIb. These 10 species accounted for 28.0% of the average dissimilarity ($\delta = 43.1\%$) between Groups IIa and IIb.

Table 6

Major species, ranked in order of importance, contributing to the average dissimilarities between Groups Ia and Ib as determined by SIMPER analyses based on root-root transformed abundance and biomass data and the Bray-Curtis measure of dissimilarity

| Species | Abundance | | | | Species | Biomass | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Av. Ab. | | $\delta_i$ | $\Sigma\delta_i$ | | Av. B. | | $\delta_i$ | $\Sigma\delta_i$ |
| | Ia | Ib | Ia:Ib | | | Ia | Ib | Ia:Ib | |
| *Pomatoleois kraussi* | 1.6 | 32.9 | 2.3 | 2.3 | *Oxystele tabularis* | <0.1 | 1.8 | 3.7 | 3.7 |
| *Oxystele tabularis* | 0.8 | 12.5 | 2.3 | 4.6 | *Burnupena lagenaria* | 0.2 | 1.9 | 3.3 | 7.0 |
| *Elasmopus japonicus* | 136.3 | 15.6 | 2.0 | 6.6 | *Perna perna* | 453.1 | 205.1 | 3.2 | 10.2 |
| *Perna perna* | 410.0 | 118.7 | 1.8 | 8.4 | *Patella oculus* | 0.1 | 1.1 | 2.8 | 13.0 |
| *Burnupena lagenaria* | 5.0 | 12.9 | 1.7 | 10.1 | *Haliotis spadicea* | 4.9 | 8.5 | 2.5 | 15.5 |
| *Tricolia capensis* | 0.7 | 3.5 | 1.7 | 11.8 | *Burnupena cincta* | 0.6 | 0.7 | 2.3 | 17.8 |
| *Syllis* spp. | 0.0 | 3.1 | 1.6 | 13.4 | *Patella barbara* | 1.6 | 0.9 | 2.1 | 19.9 |
| *Dynamanella taurus* | 5.8 | 0.3 | 1.6 | 15.0 | *Patella granularis* | 0.4 | 0.0 | 2.0 | 21.9 |
| *Patella oculus* | 1.6 | 7.3 | 1.6 | 16.6 | *Thais capensis* | 1.0 | 0.3 | 2.0 | 23.9 |
| *Patella aphanes* | 7.0 | 0.5 | 1.6 | 18.2 | *Haliclona* spp. | 0.5 | 0.1 | 1.9 | 25.8 |
| Average dissimilarity | | | | 33.1 | | | | | 33.6 |

The average abundances (Av. Ab.) and biomasses (Av. B.) of these species across samples within each group, and both their individual ($\delta_i$) and cumulative contributions ($\Sigma\delta_i$) to the average dissimilarity between groups are presented.

Table 7

Major species, ranked in order of importance, contributing to the average dissimilarities between Groups IIa and IIb as determined by SIMPER analyses based on root-root transformed abundance and biomass data and the Bray-Curtis measure of dissimilarity

| Species | Abundance | | | | Species | Biomass | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Av. Ab. | | $\delta_i$ | $\Sigma\delta_i$ | | Av. B. | | $\delta_i$ | $\Sigma\delta_i$ |
| | IIa | IIb | IIa:IIb | | | IIa | IIb | IIa:IIb | |
| *Pentacta doliolum* | 446.7 | 67.1 | 2.7 | 2.7 | *Perna perna* | 39.6 | 4.1 | 5.9 | 5.9 |
| *Perna perna* | 8.2 | 98.5 | 2.2 | 4.9 | *Patella barbara* | 3.3 | 1.0 | 3.4 | 9.3 |
| *Ophionereis porrecta* | 82.6 | 32.8 | 1.8 | 6.7 | *Patella cochlear* | 0.6 | <0.1 | 2.9 | 12.2 |
| *Patella cochlear* | 1.0 | 8.1 | 1.7 | 8.4 | *Patella longicosta* | 2.5 | 0.7 | 2.7 | 14.9 |
| *Turbo sarmaticus* | 2.8 | 0.0 | 1.6 | 10.0 | *Patella miniata* | 0.9 | 1.6 | 2.7 | 17.6 |
| *Stenothoe valida* | 1.6 | 7.9 | 1.5 | 11.5 | *Pentacta doliolum* | 1.0 | 3.0 | 2.4 | 20.0 |
| *Thelepus* sp. | 3.6 | 0.0 | 1.5 | 13.0 | *Parechinus angulosus* | 1.4 | 0.6 | 2.2 | 22.2 |
| *Ischnochiton oniscus* | 10.3 | 3.8 | 1.4 | 14.4 | *Fissurella natalensis* | 0.4 | <0.1 | 2.0 | 24.2 |
| *Balanus venustus* | 4.1 | 21.5 | 1.4 | 15.8 | *Osystele tabularis* | 0.2 | 0.2 | 1.9 | 26.1 |
| *Anachis kraussi* | 12.5 | 4.5 | 1.4 | 17.2 | *Marphysa corallina* | 0.5 | 0.8 | 1.8 | 27.9 |
| Average dissimilarity | | | | 37.0 | | | | | 43.1 |

## 4. Discussion

Shellfish-gathering takes place primarily during spring low tides (Bigalke, 1973; Lasiak, 1993). The regularity of collecting varies not only with the demand for this resource but also according to sea and weather conditions, exploitation effort is consequently somewhat variable. There is also considerable spatial variation in effort owing to the fact that the shellfish-gatherers go, at irregular intervals, to several different areas of shore during their search for food (Lasiak, 1993). Rocky littoral assemblages in Transkei are, in effect, subject to a series of disturbances of variable intensity. The fact that such disturbances are neither temporally nor spatially sustained suggests that exploitation should be viewed as a repeated pulse disturbance rather than as a press disturbance, more commonly associated with anthropogenic impacts. As exploitation results in the removal of the larger individuals of several species of invertebrates the immediate response of the assemblage will be a decrease in the abundance of these species. While other species may be unaffected by such disturbances, those species, previously constrained by competition etc., may actually increase in abundance. Comparisons between perturbed and unperturbed assemblages should therefore reveal marked differences in various community attributes. As press and pulse phenomena are likely to have different effects on assemblages (Underwood, 1989), the impact of exploitation should also differ from anthropogenic disturbances which take the form of sustained, long-term, chronic perturbations.

Early studies of anthropogenic impacts tended to focus on univariate community parameters such as species richness and diversity (Gray, 1992). Reductions in such indices have, in the past, been cited as a universal response to environmental degradation (Rapport et al., 1985). Warwick & Clarke (1993), however, have recently pointed out that diversity behaves neither consistently nor predictably in response to environmental stress. The fact that diversity indices confound a number of variables characterizing community structure also makes the interpretation of trends in species diversity somewhat problematic (Ludwig & Reynolds, 1988). The results of the present study suggest that exploitation has no significant effect on neither species richness nor diversity. This finding conflicts with the observations of Hockey & Bosman (1986) who reported an increase in the species richness of balanoid zone assemblages in response to exploitation. Our results are also somewhat contrary to expectations based on Connell's (1978) intermediate disturbance hypothesis. This predicts that disturbances of intermediate severity and frequency should give rise to a mosaic of patches at differing successional stages, and should, therefore, have a positive effect on species richness. However, cognizance also needs to be taken of the fact that the relationship between species richness and frequency of disturbance, underlying this hypothesis, varies from community to community. The shape of this relationship is also dependent on the competitive abilities of the various successional stages (Connell & Keough, 1985). Differences in the competitive abilities of "early" and "late" successional species may well account for the apparent discrepancies. Experimental studies indicate that, unlike most mussel species, *Perna perna* is not a competitive dominant. If clumps of *Perna perna* are removed, they are replaced rapidly by either coralline algae or barnacles which not only persist but also dominate the community for several years thereafter (Lambert & Steinke, 1986; Dye, 1992). Exploited infratidal areas are, in fact, characterized by a marked homogeneity due to the extensive mats of algae which occupy most of the available primary space (Dye, 1993). In Transkei it is actually the non-exploited shores which exhibit a well-defined mosaic structure comprising clumps of mussels, and tufts of coralline algae, interspersed by patches of crustose algae and large patellid limpets (Dye, 1992).

While sustained anthropogenic disturbances, such as pollution, may lead to the eradication of species, there is no evidence to suggest that exploitation results in localized extinctions. The results of the present study do, however, indicate that a considerable number (32) of the species represented in the non-exploited grouping were absent from the exploited sites and vice versa (33 species). As inspection of the raw data matrix indicates that 12 of these "lost" species were singletons their absence may simply be a sampling artefact. A further possibility that requires consideration is the fact that some species may have been absent naturally from the exploited shore. Whilst our knowledge of the distribution patterns of many of the smaller species is poor, the fact that several temperate species reach their limits of distribution just north of Dwesa (Kilburn & Rippey, 1982), suggests that longshore trends cannot be discounted. However, the fact that some of the "lost" species are fairly common higher up the shore suggests that their absence from the infratidal may be related to the absence of suitable habitats. Two of these "lost" species, *Patella oculus* and *Octopus vulgaris*, are known to feature regularly in the collections of the indigenous people (Lasiak, 1992 & 1993). The fact that the apparent "loss" of species from the non-exploited sites was compensated by the gain of an equivalent number of new species may well have countered any change in univariate community parameters.

The biomass:abundance ratios and the abundance/biomass curves were generally more consistent in their abilities to discriminate between exploited and non-exploited sites. Both methods led to the categorization of Dwesa 1 and 2 as undisturbed, Nqabara 1 and 3 as disturbed with Nqabara 2 being of intermediate status. Despite the marked differences in disturbance regime these ABC curves showed similar trends to those associated with pollution-impacted comunities (Warwick, 1986). This implies that repeated pulse & chronic press disturbances have the same fundamental effects on the distribution of individuals and biomass among species. Undisturbed communities tend to be dominated by conservative species, characterized by large body size and long life-span, which are usually dominant in terms of biomass but not numbers. In polluted situations the conservative species are often disadvantaged and it is the opportunistic species which usually become both the numerical and the biomass dominants (Warwick, 1993). At Dwesa I and II, the community dominant, *Perna perna*, which comprised more than 75% of the overall biomass was ranked second in terms of abundance. As this is the major species harvested by the indigenous people exploitation was expected to result in a reduction in the importance of this species. Although the numerical importance of *Perna perna* was less at the exploited sites, on the basis of biomass, this species still remained a community dominant, being the first ranked species at Nqabara 1 and 2 and the third most important species at Nqabara 3. The importance of *Perna perna* relative to other species at the exploited sites was, however, certainly reduced.

Multivariate analyses of abundance and biomass data resulted in very similar groupings. The hierarchical cluster analyses and the MDS ordinations both demonstrated a clear-cut separation of exploited and non-exploited sites, thereby indicating substantial differences in community structure. The SIMPER analyses indicated that the major reasons for this division were (1) the decreased abundance of sessile filter feeders, (2) increased abundance of seaweed-associated species such as the brittlestar *Ophionereis porrecta* and various species of amphipods, (3) decreased biomass of five exploited species, namely *Perna perna, Haliotis spadicea, Patella barbara, Patella miniata* and *Patella oculus*, and (4) decreased biomass of species normally found in association with clumps of *Perna perna* at the exploited sites. These responses are all inter-related; the reduction in the biomass of large grazing gastropods (patellids and abalone) promotes the domination of primary space by algae. This either precludes the settlement of sessile fauna or leads to their elimination as a result of over-growth and smothering. This, in turn affects any associated fauna. The seaweed-associated species appear to benefit from increased algal cover at exploited sites (Dye, 1993).

These multivariate techniques also revealed differences in community structure amongst sites within treatments. The differences in community structure between Dwesa 1 and 2 may reflect marked differences in the overall biomass and general pattern of space occupancy (Lasiak & Dye, unpubl. obs). The distinct separation of Nqabara 2 from Nqabara 1 and 3 undoubtedly reflects the relatively undisturbed nature of this site, as indicated by the B:A ratio and ABC curves. The SIMPER analyses confirmed that several of the major species responsible for discriminating between these two groups were, in fact, exploited species which were more abundant at Nqabara 2.

Previous studies employing multivariate analyses to discriminate between impacted and non-impacted sites have, for the most part, been concerned with detecting press disturbances associated with chronic sustained pollution (Gray et al., 1988, 1990; Heip et al., 1988; Warwick et al., 1990; Agard et al., 1993; Nicolaidou et al., 1993). The present study appears to be one of the few to have used such techniques to distinguish between undisturbed sites and those exposed to repeated pulse disturbances. Whilst we acknowledge the shortcomings of multivariate analyses based on surveys from the point of view of demonstrating causal relationships (Warwick & Clarke, 1991) our results indicated that such techniques were far more informative, and hence, more readily interpretable, than the commonly-used univariate community attributes. This reflects the fact that, unlike multivariate analyses, univariate measures do not conserve species identity. Whilst it is evident that shellfish-gathering is not a temporally sustained activity the fact that the interval between successive bouts of exploitation is probably insufficient for recovery of the affected populations suggests it may be more appropriate to regard exploitation as a press disturbance. This may well explain why many of our results paralleled those associated with chronic sustained disturbances.

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