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EXPERIMENTAL STUDIES OF SUCCESSION AND STABILITY IN ROCKY INTERTIDAL COMMUNITIES SUBJECT TO ARTISANAL SHELLFISH GATHERING

A.H. DYE
Department of Zoology, University of Transkei, P/Bag X1, UNITRA, Umtata, Transkei, 5100, Southern Africa

ABSTRACT

Rocky-shore communities on the east coast of southern Africa are subject to intense shellfish exploitation by coastal people. Large-scale removal of sessile species, such as the mussel *Perna perna*, creates areas of bare rock, providing space for colonization. Rates of recolonization of experimentally-cleared areas in both protected and exploited sites were found to be variable. There was as much as a two-year delay before sessile macro-organisms reappeared, and the course of subsequent succession depended on the nature of the initial colonists. Large spatial and temporal variations in species diversity and richness were observed where it appeared that emergent communities were less stable than adjacent controls. After eight to nine years, few of the cleared areas have developed communities similar to the original or to controls.

These results are compared with those of a controlled exploitation experiment conducted in a nature reserve. Similar results were obtained despite the fact that exploitation was more selective for target species and did not involve total clearance. The long-term effects of human exploitation involve shifts in community structure towards earlier successional stages which may persist for long periods of time. Consequently, management options such as rotational cropping may be inappropriate in such a system.

1. INTRODUCTION

The role of disturbance in structuring natural communities is well documented (PAYNE, 1966; DAYTON, 1971; CONNELL, 1978; MENGE & SUTHERLAND, 1987). In space-limited environments, such as a rocky intertidal zone, disturbance may increase species diversity by removing competitive dominants and exposing bare rock which is then recolonized. The successional process which follows disturbance is influenced by such factors as the intensity and season of the disturbance (EMMERSON & ZEDLER, 1978; SOUSA, 1980a; HAWKINS, 1981), the position within the disturbed patch (FARRELL, 1989), life history strategies (SOUSA, 1980b, 1984; SUCHANEK, 1981) and biological interactions such as competition, grazing and predation (MENGE & SUTHERLAND, 1987; FARRELL, 1991).

Disturbance takes many forms and there has been some debate over the definition of the term (McGUINNESS; 1987, PICKETT & WHITE, 1985; PICKETT *et al.*,1989; LAKE, 1990). In an intertidal zone, physical disturbance is caused mainly by wave action which can directly remove organisms, or indirectly transport either sediment, which in turn may cause smothering, or larger objects such as logs, which may scrape or crush organisms (DAYTON, 1971; SEAPY & LITTLER, 1982; DIETHER, 1984; DENNY *et al.*, 1985). The formation of sea ice may also cause large-scale removal of organisms by scouring (BERGERON & BOURGET, 1986). Biological interactions, such as predation, are intrinsic forces within communities which usually act at the individual level. Therefore, it is debatable whether predation can be considered a disturbance. Perhaps the term should be applied only in cases where predator abundance is great enough to cause high mortality of prey (CHESHER, 1969) or where the predator causes incidental damage to the community (BRANCH, 1975; DAYTON, 1971; CHOAT, 1977; UNDERWOOD *et al.*, 1983). A good example of the latter occurs in areas subject to human exploitation. In this case, disturbance results from the direct effects of collecting intertidal organisms either as bait for angling (CRYER *et al.*, 1987), for commercial gain (PAINE, 1989) or as food on a subsistence basis (MORENO *et al.*, 1984; HOCKEY & BOSMAN, 1986; CATTERALL & POINER, 1987a, 1987b; LASIAK & DYE, 1989; LASIAK, 1992). Disturbance may also result from digging or trampling (BEAUCHAMP & GOWING, 1982).

On the east coast of southern Africa, evidence indicates that collection of shellfish for food on a subsistence basis is common and that this practice dates back to prehistoric times (VOIGT, 1975; DERRICOURT, 1977; LASIAK, 1992). Although a wide range of organisms is collected, the brown mussel *Perna perna* and various patellid limpets are preferred (LASIAK, 1991). Despite a number of earlier studies (BIGALKE, 1973; BRANCH, 1975; SIEGFRIED *et al.*, 1985; HOCKEY & BOSMAN, 1986; HOCKEY *et al.*, 1988), an assessment of the effects of this exploitation has been hampered by a lack of continuous long-term data on natural fluctuations in the structure of communities and populations within protected and exploited sites. Such information which is essential for determining the degree of ecological stability of the system (CONNELL & SOUSA, 1983) is now emerging (CASTILLA & DURAN, 1985; OLIVA & CASTILLA,1986; ORTEGA, 1987; DYE, 1988, 1989, 1990, 1992).

The present paper describes the long-term effects of disturbance in the infralittoral zone on the east coast of southern Africa. Disturbance resulting from total clearance as well as controlled human exploitation is investigated.

2. METHODS

2.1. STUDY SITES

Two of the study sites, Dwesa (28°50'E; 32°18'S) and Mkambati (29°58'E; 31°20'S) are within nature reserves which have been protected from human activity for 13 years (Fig. 1). Although the third site, Port St Johns (29°30'E; 31°39'S), was incorporated into a nature reserve in 1986, low-level exploitation has continued at this site. The substrata at Dwesa and Port St Johns consist of shale platforms while metamorphosed sandstone characterizes the Mkambati site. All sites experience moderate to heavy wave action from a southwesterly direction. The infralittoral fringe at Mkambati and Dwesa (up to 30 cm above the spring low-tide level) consists of large clumps or beds of the mussel *Perna perna* interspersed by patches of coralline algae and bare rock. The latter is maintained by a variety of grazers, primarily patellid limpets. Although the community is similar at Port St Johns, mussels and limpets are less abundant and generally smaller.

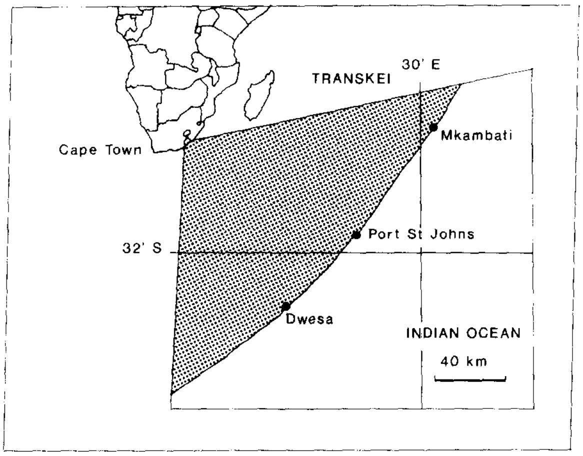

Fig. 1. Map showing the position of Transkei on the southern African coast and the study sites.

2.2. LONG-TERM EXPERIMENTS

At each site in the infralittoral zone, eight replicate 1-m^2 quadrats (4 controls and 4 cleared) were randomly positioned within an area of approximately 100 m^2. Macro-organisms were removed from the clearance areas using a paint scraper but byssus threads and the remains of encrusting algae were left *in situ* to simulate the effect of harvesting methods used by local people (LASIAK & DYE, 1989; LASIAK, 1991). The experiments commenced in July 1982 at Dwesa and Port St Johns and in July 1983 at Mkambati. Before clearance, the cover of dominant organisms was assessed and initial estimates of macro-invertebrate diversity (Shannon index) (ZAR, 1974) and richness (MAGURRAN, 1988) were made based on the numbers of organisms removed from these areas. Shannon indices were calculated from the following expression:

$$H = \frac{n \log n - \sum_{i=1}^{k} f_i \log f_i}{n},$$

where n is the total number of individuals and f_i the total number of species.

Richness was determined from the expression:

$$D_{Mn} = \frac{S}{\sqrt{N}}$$

where S is the number of species and N is the total number of individuals summed over all species.

Since continued destructive sampling was undesirable, the scraped quadrats and nearby undisturbed controls were subsequently monitored photographically using 35-mm colour slide film at yearly intervals up to July 1991. Photographs were taken through a 0.25-m^2 quadrat divided into hundred 25-cm^2 squares with yellow nylon line. The cover percentage of sessile organisms was estimated by counting the number of intersections of the lines which fell on a particular species. Because this procedure probably underestimated diversity and richness in the controls, cover percentage was used instead as the major parameter for comparison between treatments.

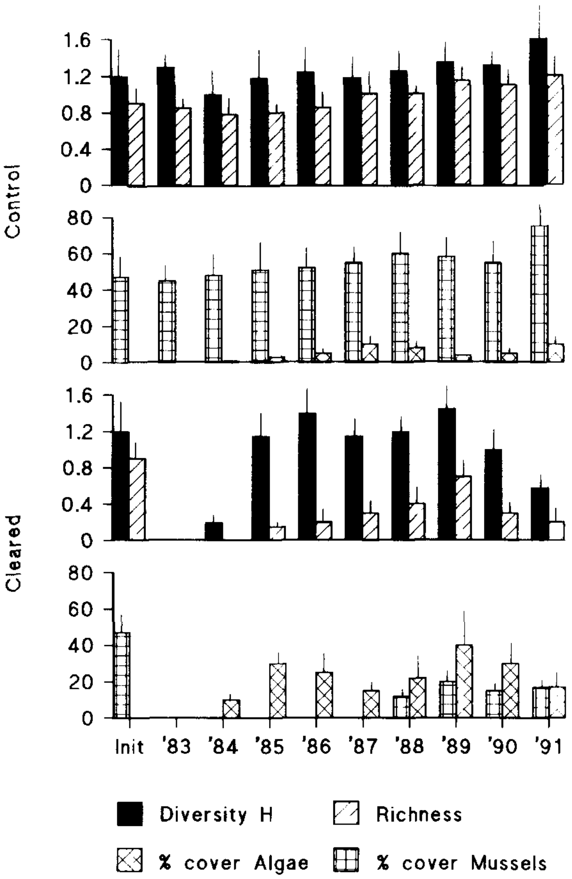

Fig. 2. Response of the infralittoral community at Dwesa (protected) to total clearance. Vertical lines indicate standard deviations (N=4).

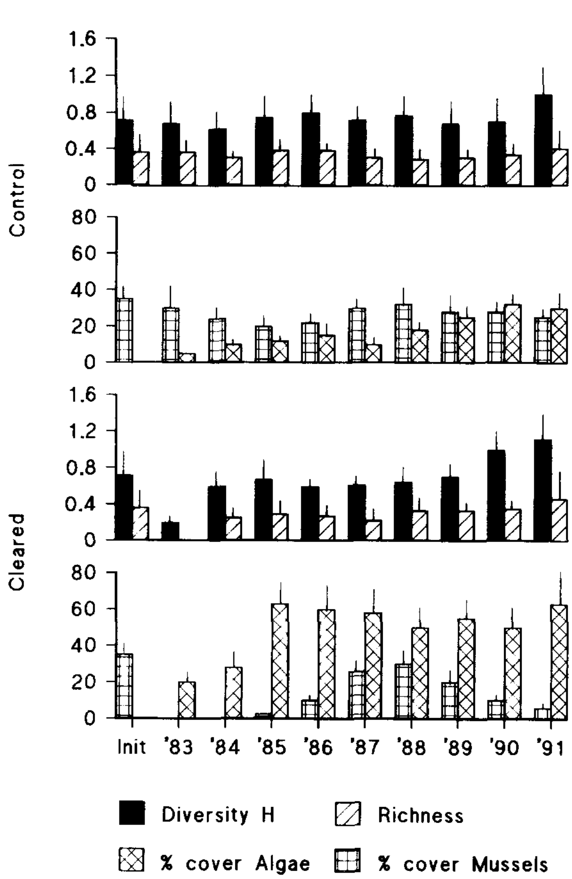

Fig. 3. Response of the infralittoral community at Port St Johns (exploited) to total clearance. Vertical lines indicate standard deviations (N=4).

2.3. CONTROLLED EXPLOITATION EXPERIMENT

In this experiment, which began in 1986, a 150-m horizontal strip of shore was harvested in the Dwesa Nature Reserve by subsistence gatherers at a rate of 16 to 20 man-days per month for two years. Harvesting shellfish is normally prohibited in this area and permission for controlled harvesting for a two-year period was obtained from local conservation authorities. Baseline information on the intertidal community of this shore was available from prior studies (DYE, 1988). Over 2000 kg of shellfish comprising several species were removed, of which brown mussels were the most prevailing (LASIAK, 1991). The status of the infralittoral communities in the exploited area and an adjacent control site was monitored at yearly intervals by photographing eight fixed 1-m^2 quadrats in each area. Cover, species diversity and species richness were recorded before, during and after disturbance. Logistical constraints, related to controlling the activities of the harvesters, meant that only one area could be exploited. Because of the limitations inherent in such pseudo-replicated designs, no inferential statistical analyses have been attempted (HURLBERT, 1984).

3. RESULTS

The low shore community at the protected sites (Dwesa and Mkambati) was dominated by the brown mussel *Perna perna*, both numerically and in terms of cover. Even so, cover rarely exceeded 50%. Although coralline algae were abundant, they grew mainly on the mussel shells and occupied less than 10% of the primary space. Significant areas of bare rock (Table 1) were maintained by a variety of grazing gastropods, such as the periwinkle *Oxystele tabularis* as well as the limpets *Patella longicosta* at Dwesa and *P. granularis* at Mkambati. The cover of sessile organisms in the controls was fairly constant throughout the study period; only minor fluctuations were recorded. However, there was a gradual increase in mussel cover at Dwesa. There was relatively little spatial or temporal variability in species diversity and richness in the control areas of the protected sites. At the

TABLE 1

Species composition and abundance (number per m^2) of macro-invertebrates prior to (I) and 8 or 9 years after clearing 1-m^2 quadrats in the infralittoral.

species	*Dwesa*		*Port St Johns*		*Mkambati*	
	I	+9 y	I	+9 y	I	+8 y
Mollusca						
Acanthochiton garnoti	1	0	0	0	0	0
Burnupena cincta	6	0	0	0	0	0
B. lagenaria	40	0	10	0	5	0
B. pubescens	2	0	0	0	4	0
Cellana capensis	0	0	11	2	1	3
Fissurella mutabilis	22	0	27	0	12	0
F. natalensis	12	0	49	4	8	1
Gibbula acer	4	0	0	0	0	0
Helcion dunkeri	3	0	1	0	1	0
H. prunosus	15	0	0	0	4	0
Nucella squamosa	2	0	0	0	0	0
Oxystele littoralis	1	0	2	0	0	0
O. sinensis	2	0	0	0	0	0
O. tabularis	125	20	48	55	117	12
O. variegata	2	0	0	0	0	0
Patella barbara	2	0	1	0	0	0
P. cochlear	1	1	0	0	2	0
P. concolor	0	0	0	1	0	
P granularis	22	0	83	33	88	13
P longicosta	40	27	9	3	20	2
P miniata	12	0	2	0	0	0
P. oculus	7	3	0	0	21	0
Patelloida profunda	2	0	3	0	1	0
Perna perna	1200	412	945	123	1906	189
Siphonaria aspera	26	0	6	0	5	0
S. concinna	1	0	0	0	0	0
Thais capensis	17	0	2	0	1	1
T. dubia	0	0	0	0	1	0
Turbo sarmaticus	1	0	0	0	0	0
Tricolia capensis	34	0	2	0	0	0
Echinodermata						
Patiriella exigua		270	0	0	1	0
Parechinus angulosus	16	0	0	0	0	0
Coelenterata						
Actinia equina	18	0	12	0	8	0
Crustacea						
Chthamalus dentatus	0	0	0	0	5	1
Octomeris angulosus	0	0	0	0	40	46
Tetraclita serrata	0	0	0	0	77	1
Algae						
Corallines (% cover)	0	16	0	63	0	36
bare rock (% cover)	54	68	64	31	64	46
number of animal species	31	5	17	6	23	10

exploited site (Port St Johns), the shore supported only 50 to 60% of the cover of mussels characteristic of the protected sites. Coralline algae were generally more abundant at this site and often equalled or exceeded the cover of mussels, particularly in the latter part. Patches of bare rock, maintained by patellid limpets, were a prominent feature of the site. Diversity and richness, although less than in the protected sites, exhibited little variability. Data on species abundance and composition at these sites are given in Table 1.

The responses of the infralittoral community to total

TABLE 2

Species composition and abundance (number per m²) of macro-invertebrates in the infralittoral at Dwesa prior to controlled exploitation (I), after two years of exploitation (+2 y) and after a subsequent three-year recovery period (+5 y).

species	*I*	*+2 y*	*+5 y*
Mollusca			
Acanthochiton garnoti	3	1	0
B. lagenaria	21	1	1
B. pubescens	1	1	0
Fissurella natalensis	5	0	0
Helcion dunkeri	1	0	0
H. prunosus	5	0	0
Oxystele tabularis	70	4	8
O. variegata	5	0	0
Patella barbara	1	0	0
P. cochlear	1	0	0
P. concolor	1	0	0
P. granularis	12	0	1
P. longicosta	30	6	3
P. miniata	1	0	1
P. oculus	3	0	1
Perna perna	1281	28	207
Siphonaria aspera	8	0	0
S. concinna	2	0	0
Thais capensis	3	0	0
Turbo sarmaticus	2	0	0
Tricolia capensis	10	0	0
Echinodermata			
Patiriella exigua	10	1	1
Parechinus angulosus	5	0	1
Coelenterata			
Actinia equina	5	0	4
Crustacea			
Octomeris angulosus	2	0	0
Tetraclita serrata	45	0	0
Algae			
Corallines (% cover)	44	63	58
bare rock (% cover)	18	36	42
number of animal species	26	7	10

clearance at Dwesa, Port St Johns and Mkambati are shown in Figs 2, 3 and 4, respectively. Total denudation had profound long-term effects on the nature and stability of the infralittoral community at all three sites. Patterns of recovery were variable, and in all cases the initial mussel-dominated communities were replaced by other species assemblages. Grazing by patellid limpets appeared to have a significant effect on recolonization, resulting in a delay of one to two years in the establishment of sessile species. At both Dwesa and Port St Johns, mussels were replaced by a coralline algal turf. The process was most rapid and extensive at the latter site. Recovery at Mkambati was totally different; the macrobenthos which recolonized those quadrats was dominated by the barnacles *Tetraclita serrata* and *Octomeris angulosus*. Only towards the end of the study did coralline algae become a significant feature.

At each site the recovery of mussels was not only poor but also variable. Even after eight or nine years, mussel cover at protected sites accounted for no more than 25% of the control values. The exploited site (Port St Johns) showed the greatest recovery; by 1988, the cover of mussels in cleared areas was similar to that of the controls (Fig. 3). However, these had largely disappeared by the end of the study. Species richness was variable following disturbance and remained consistently below control levels throughout the study. Diversity was also variable but approximated the controls in many cases. Neither of these indices adequately reflected the changes in the nature of the community that occurred subsequent to disturbance. The removal of mussels results in the

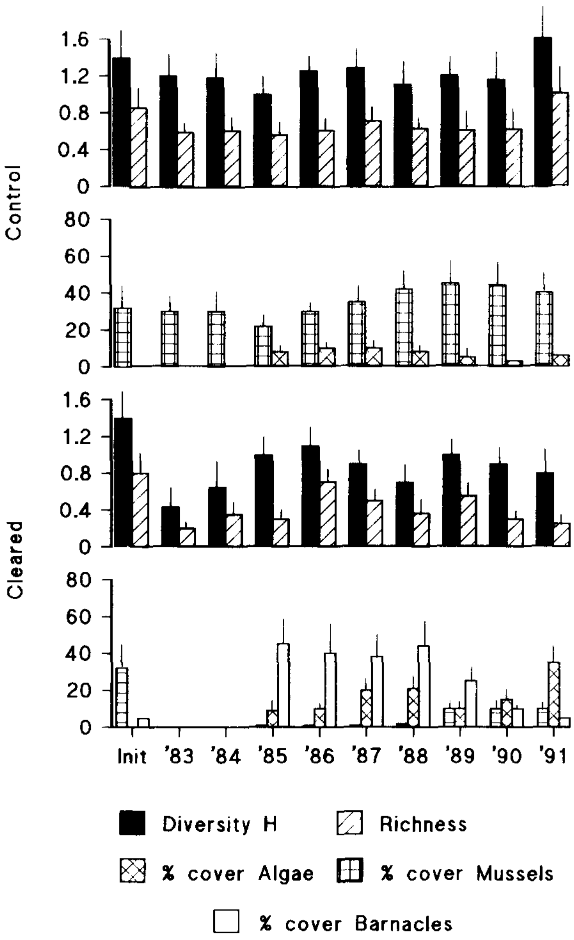

Fig. 4. Response of the infralittoral community at Mkambati (protected) to total clearance. Vertical lines indicate standard deviations (N=4).

loss of many cryptic species which comprise a significant proportion of the infralittoral community (Table 1). By the end of the study, only 16 to 48% of the original number of species had been re-established; most of these were limpets grazing on primary space.

Fig. 5 shows the effect of controlled exploitation at Dwesa. Despite the shorter time scale involved and the fact that exploitation was selective for size and species, patterns of recovery were similar to those found after total clearance. During the exploitation period, community structure in the exploited area changed markedly. Within two years, mussels were virtually eliminated and replaced by coralline algae. Limpets were reduced to 25% of their initial abundance during this period. Since 1988, when exploitation was stopped, the exploited area remained dominated by coralline algae and little recovery by animal species had occurred. Diversity and richness remained relatively high in undisturbed areas and even tended to increase towards the end of the study. Coralline algae and mussels occupied similar amounts of space with the exception of two periods (1988 and 1991) when recruitment led to increased mussel cover. Species diversity and richness declined in the exploited area and exhibited considerable variability throughout the study period. There was a substantial decrease in the number of species (Table 2), with only ten remaining after two years. By 1991 only nine of the original 26 species had returned and the majority of these were limpets.

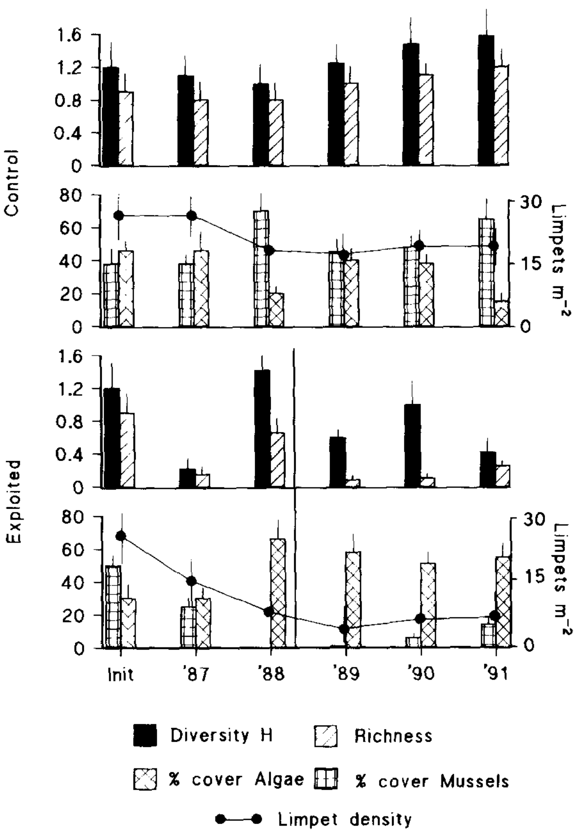

Fig. 5. Effect of controlled harvesting on the infralittoral community at Dwesa. Vertical line indicates the point at which harvesting was stopped. Vertical lines on bars indicate standard deviations (N=8).

4. DISCUSSION

Quantitative assessment of the long-term effects of disturbance relies on the implicit assumption that one or more stable points exist with which the effects can be compared and to which the system eventually returns (HOLLING, 1973; SUTHERLAND, 1974). Efforts to test this assumption are confounded by difficulties related to the choice of appropriate temporal and spatial scales of study (FRANK, 1968; CONNELL & SOUSA, 1983). Time scales should include at least one turnover of all species, and it therefore follows that when long-lived species are involved, lengthly study periods are required. Marine intertidal communities, however, have a high proportion of relatively short-lived species with rapid turnover, allowing for the completion of several life cycles within a reasonable time period. The time span of eight to nine years used in the present study encompasses the ecological life span of the majority of the species. Therefore, it should be possible to demonstrate stability if it exists (CONNELL & SOUSA, 1983).

In the present study, in the absence of disturbance, infralittoral community structure did not change appreciably with time. Mussels dominated and occupied approximately the same amount of primary space throughout the study. Coefficients of variation between replicate quadrats and successive samples rarely exceeded 20%. However, community structure at the exploited site did change during the study. While mussel cover remained fairly constant, coralline algae became more prevalent, eventually exceeding the mussel cover. This change was not reflected in the indices of richness and diversity.

An ecosystem may be considered stable if it returns to its original state or domain of attraction following disturbance (HOLLING, 1973). The present study indicates that *Perna perna* was unable to fully recolonize cleared areas after eight years. Disturbance shifted the infralittoral community away from its original state to one in which mussels were rare. The new community consisted of a mosaic of open grazed rock with patches of coralline algae or barnacles. Similar findings have been reported from Natal by LAMBERT & STEINKE (1986), who also found that *Perna* did not reappear in cleared areas even after eight years. Since there is little evidence that disturbed mussel patches return to their original state, even after relatively long periods of time, it must be concluded that these mussel-dominated communities are unstable when faced with a disturbance of the magnitude of total clearance. It may therefore be that, unlike other mytilids (SUCHANEK, 1981; JANKE, 1990; VAN ERKOM SCHURINK & GRIFFITHS, 1990), *Perna perna* is not a competitive dominant and is easily replaced by other occupants of primary space. This is supported by LASIAK (1991), who found that *Perna perna* has low resilience to exploitation and is therefore susceptible to stock depletion.

Moderate levels of disturbance are often associated with increases in diversity and richness (CONNELL, 1978; SOUSA, 1980b). This was not apparent in the present study because the structural complexity of mussel patches was replaced by a relatively simple community in which grazers played a dominant role. In a study of succession on central Oregon shores, FARRELL (1991) found grazers delayed the establishment of sessile organisms and continued to exert a controlling influence on space occupancy throughout the study. Only when grazer abundance was low, as at Port St Johns, was there extensive algal colonization.

The fact that the response of the infralittoral community to controlled exploitation is similar to that of total clearance can be understood in terms of the low resilience of *Perna perna*. All but the mildest forms of disturbance will result in loss of mussel cover and a decrease in structural heterogeneity and species richness. If disturbance takes the form of human exploitation, in which both mussels and limpets are removed, the resulting primary space will be colonized by competitive dominants such as algae or barnacles. A mosaic of grazed areas and algae results where limpets are not totally removed. Such communities are common along most areas of the Transkei coast where exploitation is practiced.

PICKETT & WHITE (1985) make the point that the components of diversity, *i.e.* species richness, evenness, community structure and genetic diversity, may not be equally affected by disturbance. The relative insensitivity of the diversity index to all but the most extreme effects of clearance is apparent in the present study. Apart from the initial delay, diversity usually returned to pre-disturbance levels in spite of the altered state of the community. This may be related to the numerical dominance of *Perna* in the initial communities (see Table 1). If diversity and richness are recalculated excluding mussels, the indices increase twofold and, when compared with subsequent data, give a better indication of the changes which follow disturbance.

Since *Perna perna* is preferred among shellfish gatherers in this region, what are the implications of the above findings for management of this resource? The low resilience of this species and poor recovery following disturbance severely restrict the range of management options that can be applied. Two approaches have been suggested: 1. harvesting should be regulated so that the takings are in line with production; and 2. encouraging rotational cropping (SIEGFRIED *et al.*, 1985; HOCKEY & BOSMAN, 1986). Unfortunately, neither of these suggestions provides a viable managerial strategy. The former requires changes in traditional harvesting practices which would be difficult to effect and police. The latter would, on its own, be impractical due to prolonged recovery times.

Another possibility which deserves attention is to reduce the dependence of local people on shellfish as a protein source by providing alternative or supplementary, land-based resources. This depends on socio-economic development and requires government subsidies and/or external aid for the region. Another possibility which is being investigated in Transkei is the restocking of denuded shores. This could significantly reduce recovery times and when combined with rotational cropping may be a viable management option.

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