Recovery and recruitment of the brown mussel, *Perna perna* (L.), in Transkei: implications for management

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Received 14 April 1997; accepted 8 September 1997

The brown mussel *Perna perna*, has been an important food resource for indigenous inhabitants of the Transkei coast for centuries. The impoverished state of mussel stocks in this region and major differences in low-shore community structure between exploited and protected areas, have been ascribed to the ever-increasing exploitation of this species. In spite of this there has been no effective management of this resource owing to political and logistical problems related to law-enforcement, and misconceptions concerning the resilience of *P. perna* and the interspecific interactions which govern its recovery. Our present understanding of the ecological impacts of exploitation, and of the potential for recovery, is based on a series of studies and observations made over the last 15 years. These studies have shown that algae usually replace mussels following disturbance and that recovery may take more than eight years. As mussels tend to recruit preferentially into existing mussel beds, exploitation not only affects reproductive output but also reduces the preferred habitat. Recruitment onto both natural and artificial substrata is extremely low, even in marine reserves where standing stock is considerably higher than in exploited areas. Under these conditions stock enhancement in conjunction with rotational cropping may be the best management strategy.

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Evidence from shell middens indicates that rocky shores in Transkei have provided a rich variety of shellfish to the indigenous coastal inhabitants for centuries (Derricourt 1977). In Transkei shellfish gathering is done mainly by women and children who utilise low spring tides for this purpose (Bigalke 1973). Mussels and limpets are removed from the rocks with a flat steel bar approximately 50 mm wide, usually obtained from discarded vehicle leaf springs (Lasiak & Dye 1989). Whole clumps of mussels are removed leaving gaps of bare rock ranging in size from a few square centimetres to more than a quarter square metre. Small mussels and other inedible species are discarded on the high-shore. Where mussels are scarce individuals are removed from surrounding barnacles or algal turf, leaving no visible gaps (Lasiak & Dye 1989).

As in prehistoric times, the brown mussel, *Perna perna*, remains one of the preferred species along much of the coast, accounting for more than 90% of the takings at some sites (Siegfried, Hockey & Crowe 1985; Lasiak & Dye 1989; Lasiak 1993). While mussels may contribute to the nutrition of the coastal people (Siegfried *et al.* 1985), Bigalke (1973) and Mqakama & Lasiak (1996) have shown that shellfish gathering in general has a social dimension which goes beyond mere food gathering. With the increase in the coastal population, current pressure on shellfish resources is probably higher than at any earlier time. The overall effect has been a reduction in standing stock to almost negligible levels in unprotected areas (Fielding, Robertson, Dye, Tomalin, van der Elst, Beckley, Mann, Birnie, Schleyer & Lasiak 1994), nearly two orders of magnitude less than that found in the Dwesa Nature Reserve.

Studies of the ecological effects of this exploitation have shown that, in areas where mussels and patellid limpets are removed on a regular basis, the low-shore community becomes dominated by macroalgae, which forms a dense turf to the exclusion of sessile organisms (Dye 1992). These changes are accompanied by shifts in dominance structure and species composition (Lasiak & Field 1995).

Although various suggestions for the management of mussel stocks have been made, these have been based on superficial comparisons between exploited and protected areas, and on assumptions about the resilience of brown mussels, based on extrapolations of life history characteristics from KwaZulu-Natal (Siegfried *et al.* 1985). More recent studies have, however, shown that *P. perna* has low resilience and relatively poor recovery potential (Lasiak 1991a; Dye 1992; Lasiak & Barnard 1995).

As this review will show, the recovery of exploited mussel beds is a far more complex process than was initially thought, involving as it does the interaction of a number of different plant and animal species. While this does place some constraints on what can be done, an appreciation of the recovery process has also created new possibilities for management of both exploited and protected stocks.

Long-term studies

The idea that rotational cropping might be an effective form of management was based on the opinion that exploited shores would recover within a short period of time if left undisturbed (Siegfried *et al.* 1985). Work by Berry (1978) in Natal indicated that *P. perna* was a relatively short-lived species (2–3 y), with a rapid growth rate (55 mm y^{-1}), and high reproductive output. Given these characteristics, and the belief that there were substantial subtidal stocks which could replenish intertidal populations, there seemed no reason to believe that recovery would be anything but rapid. In 1982 a total clearance experiment was initiated in which 16 0.25-m^2

areas were cleared of mussels at three sites in Transkei, namely Isilaka, near Port St Johns, Dwesa and Mkambati (Figure 1), in order to obtain empirical data on the rate of recovery of mussels in protected areas (Dye 1992). Data from this study are shown in Figure 2. Apart from a brief period during 1988–89, when mussel cover reached 69% of the original cover at Isilaka and 39% at Dwesa in 1991, no significant recovery has been recorded. This is in spite of the fact that adjacent areas continue to support a similar cover of mussels to that which was recorded initially.

These results were corroborated by two subsequent studies. In the first, local people were allowed to exploit shellfish along a pre-defined (150 m) section of shore in the Dwesa Reserve, where collecting effort was maintained at approximately 16 person-days per month for two years from 1986 to 1988 (Dye 1992). The results of this study (which did not involve total clearance) and more recent data, are shown in Figure 3. Within the two year exploitation period mussels were virtually eliminated from the exploited area, the density of patellid limpets was reduced by 80%, and the cover of coralline turf doubled to 65%. After seven years limpet abundance and algal cover returned to their original levels, but only 50% of the original cover of mussels returned, the remaining area being largely occupied by corraline algae. In the adjacent control area, mussel cover actually doubled between 1986 and 1993, although there has subsequently been a decrease. The reasons for this are unknown but the discovery of fresh shell middens in the foredunes suggests the possibility of poaching.

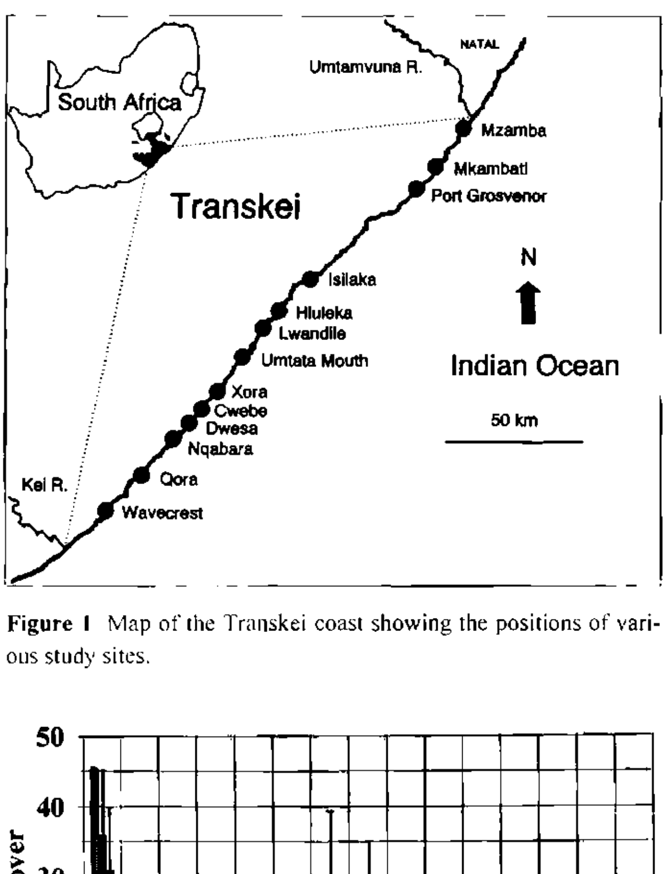

Figure 1 Map of the Transkei coast showing the positions of various study sites.

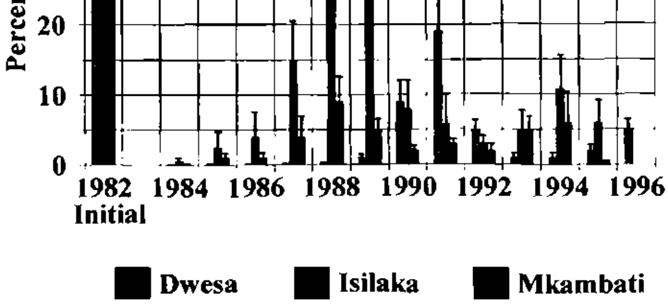

Figure 2 Long-term recovery of experimentally cleared mussel areas. $n = 4$ (± *SD*).

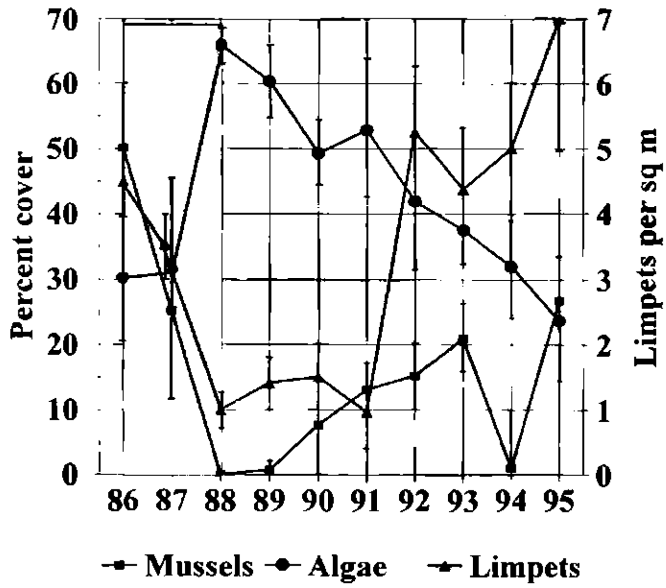

Figure 3 Recovery of mussel areas after controlled exploitation within the Dwesa Reserve. Shaded area indicates period of exploitation. $n = 8$ (± *SD*).

In the second experiment mussels were removed at various rates over a year (1992) from a series of 1-m² quadrats within the Dwesa Nature Reserve. The treatments ($n = 8$) were total removal of mussels, 25% removal at quarterly intervals, and 12% removal at eight random intervals. A set of undisturbed quadrats served as controls. The results of this experiment are shown in Figure 4. After 46 months less than 30% of the initial mussel cover had returned, irrespective of the treatment. The substratum instead became covered with upright or encrusting coralline algae. In contrast, the control areas remained fairly stable with no significant change in mussel cover.

Contrary to expectations, natural recovery is clearly a slow process. Some indication of why initial expectations of recovery were optimistic can be obtained by re-examining the work of Berry (1978). Not only was that work done in an area where the average sea temperature is several degrees higher than in Transkei, but it also involved subtidal mussel populations. Under these conditions growth and reproductive output are both enhanced, relative to intertidal populations, which cannot feed continuously. It is consequently unrealistic to assume that such parameters apply to intertidal populations, a fact which has been borne out by subsequent studies (Lasiak, unpubl.; Dye & Gabula 1996), which have shown that growth rates in Transkei are barely 60% of that reported by Berry (1978). In addition, a recent survey of subtidal shellfish

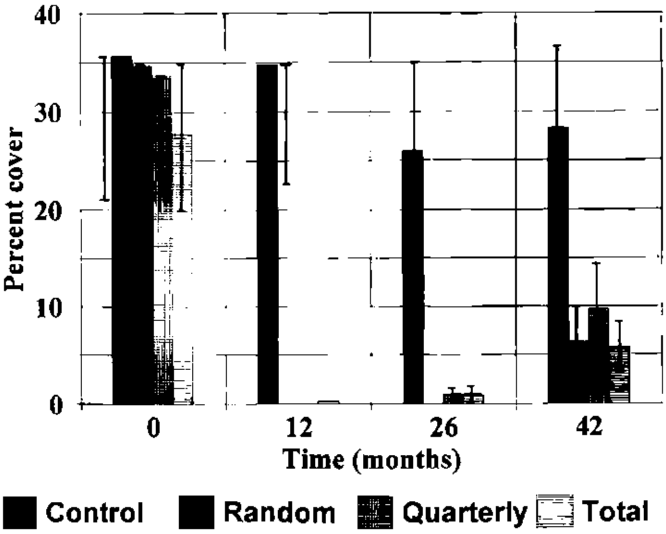

Figure 4 Recovery of mussel areas subjected to different levels of clearance within the Dwesa Reserve. $n = 8$ (± *SD*).

stocks in Transkei (Fielding *et al.* 1994) has indicated that subtidal stocks are scarce and here unlikely to act as reservoirs for intertidal recruitment.

Effects of exploitation

1. Standing stock

A number of studies have shown that both the abundance and size of mussels at exploited sites are greatly reduced compared with those at protected sites (Siegfried *et al.* 1985; Hockey & Bosman 1986; Lasiak & Dye 1989; Lasiak 1991a, b; Lasiak & Field 1995). The recent survey of shellfish stocks along the Transkei coast by Fielding *et al.* (1994) revealed the extent of impoverishment of mussel stocks in this area (Table 1). The average mass of mussels at Nqabara, a typical exploited site in Southern Transkei, for example, was shown to be two orders of magnitude lower (7.3 g.m^{-2} dry) than that in the adjacent Dwesa Nature Reserve (636 g.m^{-2} dry) (Lasiak & Field 1995). The effect of exploitation is even more striking when standing stock is compared with areas in KwaZulu-Natal, for instance, where mussel biomass may range between 2 100 and 7 900 g.m^{-2} (de Freitas, unpubl. data).

It is important to note that the existence of a reserve does not mean that there will be a high mussel biomass. Other factors, such as topography, grazer abundance and the size of the reserve all play a role in determining the size of mussel populations. At Hluleka, for instance, biomass is only 11.2 g.m^{-2} dry. One reason for this, apart from poaching, may be the small extent of this reserve, only 4 km, much of which is precipitous or sandy. Being surrounded by heavily exploited areas, it may simply be too small to act as a refuge of any significance. Mkambati, on the other hand, consists of steep shores of quartzitic sandstone supporting large numbers of patellid limpets which effectively keep the substratum clear.

2. Settlement and recruitment

While reduced growth rates, lower reproductive output and the absence of subtidal reservoir stocks (Fielding *et al.* 1994) undoubtedly helps to explain the slow recovery of this mussel, other factors, such as variable recruitment and competition for primary space, also play a role. Evidence for low and temporally variable rates of recruitment has been obtained from a recent study at Dwesa involving the use of polyethylene ropes as collectors. Using angle iron frames bolted to the substratum, sets of 15 ropes were deployed and replaced every two weeks during the peak recruitment period (May–September) in 1995 and 1996 and the number of plantigrades attached to the ropes counted. Figure 5 indicates that peak settlement in 1995 was almost an order of magnitude lower than in 1996. Overall recruitment, however, was two to three orders of magnitude lower than that reported for sites elsewhere in the Eastern Cape (McQuaid, pers. comm.), and in KwaZulu-Natal (Harris, pers. comm.). Data obtained during the period of peak settlement at five sites between Cwebe and Nqabara (Figure 1) also indicated considerable spatial variability (Figure 6), particularly in 1996. Despite Cwebe's status as a reserve, recruitment at this site was among the lowest recorded, possibly reflecting its proximity to exploited areas, and the fact that the northern area of Dwesa and Cwebe itself were heavily impacted by poachers in late 1994.

Early work on mytilids showed that post-larvae attach and detach themselves several times from the substratum (Verwey 1952; De Blok & Geelen 1958), and then enter a secondary bysso-pelagic migration phase (Bayne 1964), before settling onto a permanent attachment site. As filamentous algae were thought to play an important part in the primary settlement process, it might be expected that primary settlement may be enhanced in areas where algae have become dominant as a result of the exploitation of mussels. Recent studies on mytilids, however, have provided evidence of

Table 1 Abundance and biomass of mussels along the Eastern Cape coast and selected sites in KwaZulu-Natal. Transkei sites are shown in bold

Locality	Mean abundance m^{-2}	Mean dry mass g.m^{-2}	Source
Kwaaihoek	4400	–	Doubell & Lindsay (pers. comm.)
Diaz Cross	5060	–	,,
Fish River	6420	–	,,
Mgwalana	5180	–	,,
Riet River	5600	–	,,
Rufanes	6320	–	,,
Wavecrest	52	15.1	Fielding *et al.* 1994
Qora	0.6	1.6	,,
Nqabara	76	29.2	Lasiak & Field 1995
Dwesa Reserve	529	636	,,
Xora	2	0.1	Fielding *et al.* 1994
Umtata Mouth	1	0.6	,,
Lwandile	6	0.4	Lasiak (unpubl. data)
Hluleka Reserve	85	11.2	,,
Port Grosvenor	32	3.8	,,
Mkambati Reserve	233	68.8	,,
Mzamba	19	3.9	Fielding *et al.* 1994
Umdloti	–	2100	de Freitas (unpubl. data)
Cape Rock	–	7900	,,

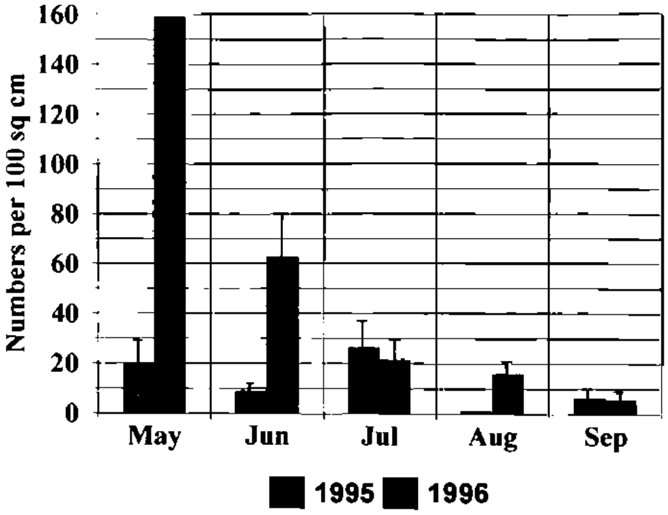

Figure 5 Temporal variability in settlement of plantigrades onto artificial collectors at one site within the Dwesa Reserve. n = 15 (± *SD*).

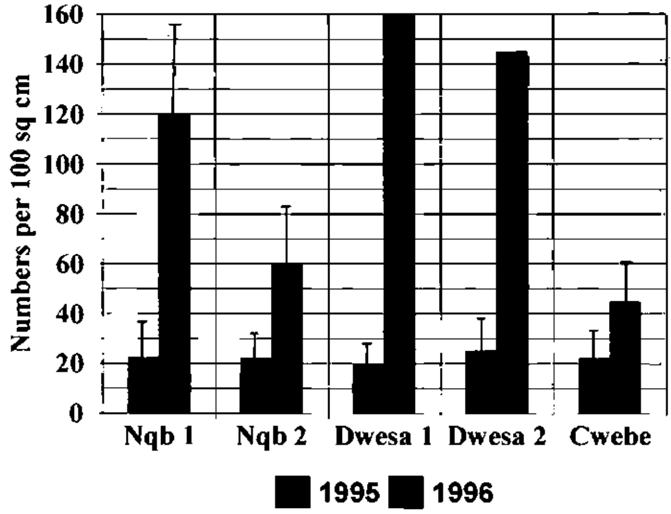

Figure 6 Spatial variability in settlement of plantigrades onto artificial collectors at five sites in and around the Dwesa Reserve. n = 5 (± *SD*).

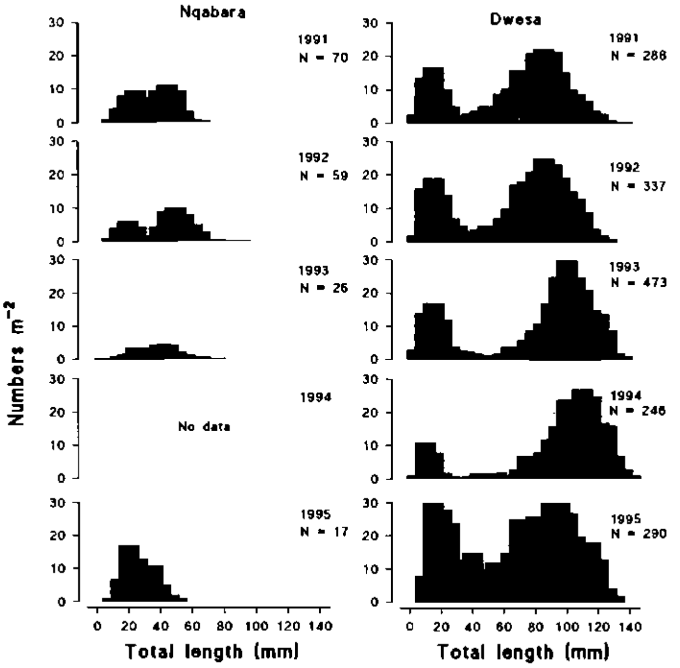

Figure 7 Size distribution and abundance of mussels between 1991 and 1995 during February at an exploited site (Nqabara) and during March in the Dwesa Reserve.

direct settlement onto established mussel beds (McGrath, King & Gosling 1988; Cáceres-Martinez, Robledo & Figueras 1993), and a study of *Perna* in Transkei also found higher numbers of plantigrades among mussels than on algae (Lasiak & Barnard 1995).

The effect of exploitation on recruitment and size distribution of *Perna* can be seen in Figure 7, which shows the results of annual surveys of mussel population size structure made during peak recruitment periods at Nqabara (exploited) and Dwesa (protected) respectively. Mean total mussel abundance at Nqabara varied between 17–70 m^{-2}, compared with 290–473 m^{-2} at Dwesa. Mussels larger than 60 mm were rare at Nqabara, where the majority of the population were between 10 and 50 mm. At Dwesa most mussels were 70–130 mm in length. New recruits (≤ 20 mm) were rare at Nqabara, accounting for only 3–25 individuals m^{-2}, as compared to 22–68 m^{-2} at Dwesa.

A disturbing trend, evident in Figure 7, is the 75% decrease in abundance of mussels at Nqabara over the four year study period. Another cause for concern is that, even in protected areas, abundance (see Table 1) and rates of recruitment are low (Figure 6) when compared with sites in KwaZulu-Natal, where recruitment is measured in hundreds, if not thousands per square metre (Harris, pers. comm.). The limited stocks and low recruitment of mussels within reserve areas raises the alarming possibility that stock depletion along the Transkei coast has reached a point where protected populations are now threatened because they are too small to be viable.

3. Community structure

The fact that *Perna* appears to require adult mussels for successful recruitment (Lasiak & Barnard 1995) may provide the final part of the explanation for poor recovery. In regions where exploitation is extensive and intense, mussel gathering may induce a negative feedback in which a reduction in adult standing stock causes a decrease in reproductive output, leading to low and variable settlement and recruitment, which further reduces standing stock. Concomitant removal of limpets, even on relatively modest spatial and temporal scales, alters the low-shore habitat by allowing a luxuriant growth of upright algae, which prevent mussels from attaching directly to the primary substratum (Dye 1993) thus intensifying the negative feedback process. Figure 8 presents a conceptual model of these interactions which suggests a mechanism for the establishment and maintenance of multiple stable states in low-shore communities. Two types of low-shore communities are commonly found within reserves in the Transkei: mussel-dominated communities (A), consisting of extensive beds of *Perna* interspersed with small open areas of rock maintained by patellid limpets, which undercut encroaching coralline algae (Dye 1993), and limpet-dominated communities (B), consisting of numerous patches of open rock, maintained by limpets, interspersed with clumps of *Perna* and ribbons of coralline algae. While these two states are generally stable (Dye 1993), variations in the abundance of lim-

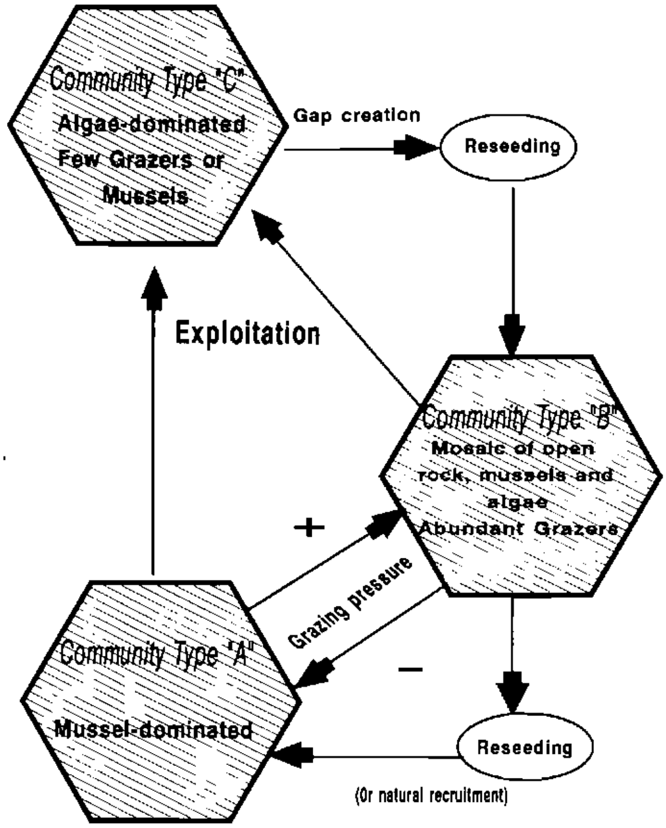

Figure 8 Conceptual model of the effect of exploitation on low-shore community structure.

pets, and hence grazing pressure, can induce the community to oscillate between them. In exploited areas, on the other hand, both mussels and limpets are removed, leading to domination by coralline algae (C). This state is particularly stable and persistent and spontaneous recovery to either of the other states has never been reported (Dye 1993). To a large extent successful recruitment of *Perna* depends on finely balanced grazing pressure; too little and primary substratum is dominated by algal turf, too much and the rock is kept clear of both algal turf and mussels.

Biological management options

Sensitivity to disturbance, low rates of recruitment and an inability to compete with encroaching algae in the absence of limpets, means that natural recovery of denuded mussels in the Transkei is generally a slow process, requiring at least 8–10 years (Dye 1992). Prohibition of exploitation along sections of the coast may eventually result in some recovery but, apart from the time involved, this would be unpopular and impossible to enforce. Such a strategy would also place increasing pressure on mussel stocks within remaining open sections of coast. Selective harvesting, in which the wholesale removal of mussel clumps would be prohibited in favour of removal of individuals, would also be difficult, if not impossible, to enforce. Rotational cropping, while ineffective on its own, for the same reasons as above, may become a workable solution if some way could be found to enhance recovery, thus reducing periods of closure to a minimum. Figure 8 indicates that, in principle, it should be possible to induce a shift from a C- to a B-type community by creating gaps in the algal turf and transplanting mussels into these gaps. If the transplanted mussel clumps survive and are not disturbed, natural recruitment of both mussels and limpets will ensure that a B-type community develops. Further re-seeding or natural mussel recruitment may even complete the transformation to an A-type community. The important point is that intervention would be required to start this process.

In 1995 a project involving the development of a technique for re-seeding of *Perna* in the intertidal zone was initiated. The requirement was for a cost-effective, yet simple, method for assisting juvenile mussels to attach to the substratum and thereafter be self-sufficient and self-perpetuating. The most effective technique which was developed was to place a number of small mussels (25–35 mm) under quarter sections of perforated PVC drainage pipe bolted to substratum that had been cleared of algae. It was found that after a month the pipe could be removed and the mussel clump, now firmly attached to the rock, left to its own devices (Dye & Gabula 1996). In a preliminary study from February to December 1995, which included a particularly stormy winter, 20 clumps of *Perna* were established in the Dwesa Nature Reserve. Eighty per cent of the clumps survived and there was a 78% survival of individuals within clumps at the end of the trial. Growth rates of individual mussels (35.8 ± 5.2 mm) and recruitment into the clumps (5.1%) were of the same order as measured in natural populations. Figure 9 shows the change in size distribution over the 10-month period. Trials were also conducted at three sites south of Dwesa and, while survival also appeared to be good (based on photographic records), the mussels were presumably exploited when they reached approximately 50 mm. Comparable data on survival and growth are consequently not available from these trials.

Conclusion

Through a series of experiments and observations made over the past 15 years, it has become clear that *Perna* in Transkei is far less resilient to exploitation than previously thought. High rates of recovery are rare, even in protected areas, and the species is easily displaced, particularly by coralline algae. Mussel stocks in reserves are not extensive and even these may be threatened by low recruitment rates and the virtual absence of subtidal refuge stocks. The degradation of mussel resources has placed increasing pressure on protected areas and demands for access are increasing. When one considers

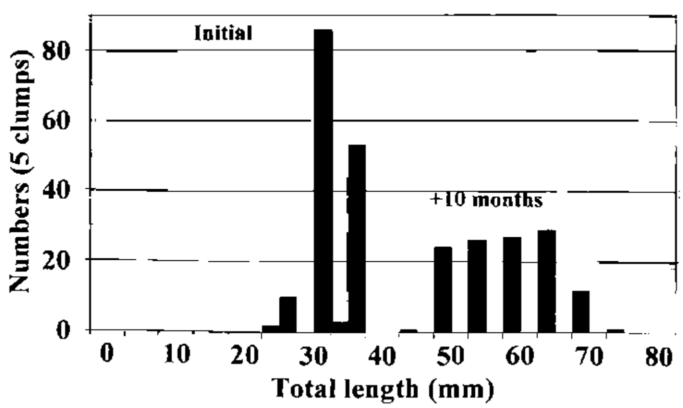

Figure 9 Growth and survival over a 10-month period of mussels transplanted within the Dwesa Reserve.

that the mean standing stock in Dwesa is more than ten times that of the Transkei coast in general, and is itself a tenth of that which can be found elsewhere, it becomes clear that such demands must be resisted in favour of rehabilitation. The development of techniques which allow for the successful transplanting of juveniles may provide the basis for a management strategy which involves re-seeding within reserves and rotational cropping elsewhere. This could be done relatively easily within reserves by nature conservation authorities and elsewhere by local user communities. Notwithstanding increasing social pressures, in the final analysis, the success of future management strategies will depend on how well they embody ecological realities.

Acknowledgements

The authors are indebted to colleagues and postgraduate students who assisted with field and laboratory work over the years. The financial and logistical assistance of the University of Transkei, as well as financial support from SANCOR, the FRD and the Department of Environmental Affairs and Tourism, are gratefully acknowledged. Much of the work would have been impossible without the support of the former Transkei Division of Nature Conservation and latterly, the Ministry of Economic Affairs, Environment and Tourism of the Eastern Cape Government.

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