

Subsistence and recreational mussel (*Perna perna*) collecting in KwaZulu-Natal, South Africa: fishing mortality and precautionary management

Bruce J. Tomalin*

Oceanographic Research Institute, P.O. Box 10712, Marine Parade, Durban, 4056 South Africa
E-mail: seaworld@neptune.lia.co.za

Robert Kyle

KwaZulu Department of Nature Conservation, P.O. Box 43, KwaNgwanase, 3973 South Africa.

Both recreational and subsistence collectors utilise *Perna perna* in KwaZulu-Natal. The former collect 200–250 t of mussels annually from about 110 km of rocky shore and the latter 12–50 t from 3 km of rocky shore. Recreational collectors are subject to a daily bag limit of 50 mussels and so select larger mussels than subsistence collectors. In central KwaZulu-Natal, there were 700–800 mussels of the size range selected by recreational collectors per running metre of rocky shore and, at Kosi Bay, 1400–1500 mussels in the subsistence size range per running metre. This excludes stretches of rocky shore in both areas where mussels are virtually absent. Parametric bootstrapping was used to estimate variance in fishing mortality from variances in input parameters (including catch). Fishing mortality at two recreational zones was 0.6 (95% confidence interval: 0.58–0.62) and 0.46 (0.45–0.47) and at two rocky points at Kosi Bay where subsistence collectors target mussels, 0.42 (0.41–0.44) and 0.27 (0.26–0.28). Decision tables are provided of target fishing mortalities for three levels of risk of exceeding fishing mortality at maximum sustainable yield for each fishery vs three assumptions about the variability in catch estimates. One recreational zone requires a substantial reduction in effort to reduce fishing mortality to the target. No change in subsistence collecting at Kosi Bay is required, but the limited access policy should be maintained.

* To whom correspondence should be addressed

Subsistence intertidal fisheries have been discussed by Avery & Siegfried (1980); Dye, Schleyer, Lambert & Lasiak (1994); Eekhout, Raubenheimer, Branch, Bosman, & Bergh (1992); Kyle, Pearson, Fielding & Robertson (1997a); Kyle, Robertson & Birnie (1997b); Mathews & Oiterong (1995); Siegfried, Hockey, & Branch (1994). Many previously artisanal intertidal fisheries for molluscs have developed into commercial fisheries and mariculture operations (Appukuttan, Prabhakaran & Thomas 1989; MacKenzie, Burrell, Rosenfield & Hobart 1997; Mason 1976; Siegfried *et al.* 1994), or recreational fisheries with cultural significance to specific groups of people (Underwood 1993). Commercial mussel fisheries are generally based on subtidal stocks of species which can survive on soft substrates and so are easily harvested (e.g. *Mytilus edulis*). One exception is the commercial fishery for intertidal *Mytilus californianus* in Oregon, USA (Yamada & Peters 1988). Recreational intertidal fisheries are poorly documented in the primary literature except in Australia, where mussels are not collected (Underwood 1993), and in South Africa (Dye *et al.* 1994). The FAO (Anonymous 1996) documented a world-wide mussel catch of 1.2 million metric tons (t) in 1994 with 415 000 t from China (unspecified species), 560 000 t from Europe (*M. edulis* and *M. galloprovincialis*) and 366 t from Venezuela (*Perna perna*). Modern day subsistence/artisanal fisheries on *Perna* spp. (Vakily 1989) occur in India (*P. viridis* and *P. indica*), Indonesia (*P. viridis*) and South Africa (*P. perna*).

Brown mussels, *P. perna*, in KwaZulu-Natal (KZN), South Africa, are utilised by three groups of users: licensed recreational collectors (Tomalin 1995a), unlicensed illegal poachers, and licensed subsistence harvesters. The latter group consists of 300 permit holders north of Richards Bay (Ander-

son & Griffiths 1997; J. Harris pers. comm. 1997) and about 200 collectors at Kosi Bay (Kyle *et al.* 1997a) who harvest inside the Maputaland Marine Reserve. Their activities are sanctioned by the park custodians (Natal Parks Board - NPB), and managed by the KwaZulu Department of Nature Conservation (KDNC). The current management regime at Kosi Bay is one of restricting access to local residents who harvest several intertidal species, including 12–50 t of mussels per annum (p.a.), from about 3 km of rocky shore (Kyle *et al.* 1997b). Poachers are active along some areas of the KZN coastline, but no attempt has been made to quantify their catch. Their overall impact is likely to be low because most of the KZN coast is intensively patrolled by the NPB (over 5000 patrols during 1995 — Tomalin, Tomalin & Kruger 1997). Approximately 11 000 recreational collectors harvest 200–250 t of mussels p.a. from about 110 km of rocky shore (Tomalin & Tomalin 1997) and are currently managed by the Natal Fisheries Licensing Board using a permit system and limited entry (Tomalin 1995a). The entire management system for coastal harvesting in South Africa will probably be reviewed in the near future (Anderson & Griffiths 1997).

The biology of the brown mussel in South Africa is relatively well known (Berry 1978; Dye *et al.* 1994; Lasiak & Dye 1989; Tomalin 1995b). Its population dynamics and ecology are quite different to those of the exceptionally well-studied *Mytilus edulis* (Seed 1976), but similar to those of *Mytilus californianus* from the west coast of North America (Suchanek 1981). Similar concerns have been raised about extensive intertidal harvesting of both *P. perna* and *M. californianus*, particularly if harvesting is unselective and removes whole clumps of mussels (Dye 1992), or creates large gaps in mussel beds (Paine 1989). Such cleared areas

may take several years to recover because most settlement occurs onto existing adult mussels (Dye 1992; Lambert & Steinke 1986; Paine & Levin 1981 — but see Dye *et al.* 1994 for an example of faster recovery). However, small gaps $< 10 \times 10$ cm recover much faster (Paine 1989; pers. obs.) and, in KZN in some years, settlement occurs on all rocky intertidal surfaces with a subsequent dramatic increase in mussel cover (during 1976 — Berry 1978 and during 1994 — pers. obs.). Therefore more active management of the recreational mussel fishery in KZN has not been considered necessary (A. De Freitas pers. comm. 1997). Blanket spatfall does not appear to occur in the Transkei (A. Dye pers. comm. 1997) possibly because mussel beds outside reserves have been decimated by unregulated subsistence users (Dye 1992).

Conservationists (e.g. Heydorn & Hughes 1969) have expressed the view that the impact of subsistence collectors at Kosi Bay was very high and implied that substantial mussel stocks would occur there in the absence of mussel harvesting. A marine reserve was established in 1985, but subsistence harvesting was still allowed under condition that the situation was monitored. Close to 100% of the subsistence fishery offtake has been monitored by a community-based observer programme since 1988 (Kyle *et al.* 1997b). Kyle *et al.* (1997a) used catch per collector-day and mean size collected as an index of stock size and concluded that the current levels of offtake were sustainable. Similar concerns have been expressed about the effect of recreational collectors just north of Durban and their catch has been monitored since 1974 (Tomalin & Tomalin 1997). Dye *et al.* (1994) documented an increase in time required to collect 50 mussels and a decline in mean size collected from 1986 to 1991 for that fishery. However, mussel 'catch' per unit effort (CPUE) may not be a reliable index of stock size until stocks have almost disappeared because, in central KZN, mussels usually occur in highly visible clumps and handling time is longer than search time. Consequently the CPUE time series will display hyperstability (Hilborn & Walters 1992). On the other hand, at Kosi Bay, mussels appear to occur lower on the shore and thus part of the stock is protected from harvesting. This would result in a rapid initial decline in CPUE as more accessible stocks are removed, followed by sustained low CPUE which would not necessarily be indicative of a low stock size, i.e. the CPUE time-series will display hyperdepletion (Hilborn & Walters 1992). For the same reasons, mean size in the catch is also unlikely to be a sensitive indicator of exploitation pressure. Hence there are problems with fishery-dependent indices of mussel stock sizes and it would be preferable to conduct surveys of stock size. Only one survey of the mussel stocks at Kosi Bay has been carried out (Fielding, Robertson & Lambert 1991), but was hampered by high seas (P. Fielding pers. comm. 1996). Van Erkom Schurink & Griffiths (1990) estimated standing stocks of mussels in KZN, but this was based on only two transects at sites chosen specifically for the presence of mussels.

Intertidal fisheries have not, in general, been subjected to standard fisheries analyses. Management recommendations have been made from qualitative predictions based on biological and ecological knowledge and experiments at a small spatial scale (e.g. Dye *et al.* 1994; Lasiak & Dye 1989; Paine 1989; Underwood 1993 — but see Castilla & Duran 1985;

Dye 1992 for intermediate scale experiments). There is a need for quantitative stock assessment (*sensu* Hilborn & Walters 1992) of intertidal fisheries at the spatial scales at which fisheries operate. For example, Eekhout *et al.* (1992) assessed an experimental limpet fishery at three spatial scales. In this paper, we attempt to place intertidal mussel fisheries within the current standard fisheries stock assessment framework. Our objectives were to estimate standing stock sizes of mussels from dedicated surveys and to estimate fishing mortality rates (F) caused by two contrasting fisheries. We used parametric bootstrapping (Punt & Butterworth 1993) to determine the variance in the estimation of F from the variance of all input parameters including the catch (Ludwig, Hilborn & Walters 1993). In line with the precautionary approach to fisheries management (FAO 1993), the management consequences of the results are presented as decision tables (Hilborn, Pikitch & Francis 1993) after setting target reference points based on the probability of exceeding a limit reference point (Caddy & McGarvey 1996). The latter authors suggested that F at maximum sustainable yield (F_{msy}) was a suitable (conservative) limit reference point. This approach should satisfy the requirements for sustainable harvesting decided upon by participants at a 'Mussel research and Management' workshop held in South Africa (Anderson & Griffiths 1997).

Methods

Surveys

Two regions of KZN (Figure 1) were surveyed: central KZN from Isipingo to Chaka's Rock (during 1993 and 1994) and the Kosi Bay area in northern KZN from Black Rock to about 10 km south of Kosi mouth (during October 1996). In central KZN, sampling was only undertaken when tide tables predicted a low tide less than 0.2 m above chart datum and swell was relatively low. A stratified approach was taken to guide sampling effort and reduce variance (Table 1). In central KZN, the whole length of each stratum was covered and survey sites were selected every 200–400 m on the nearest low shore rock available. At Kosi Bay, each rocky point was divided into strata.

Different survey methods were used in each region because harvesting practices differ. In central KZN, recreational collectors usually take mussels from within well-defined mussel beds at low water springs (LWS) level. In order to randomize observation, 20-m transects were laid at each site within the mussel zone parallel to the shore at LWS and the percent cover of mussel beds within a 0.25-m² quadrat was scored by eye every 1 m along the transect. This method resulted in some quadrats being close to the lower edge of the bed and others being at the upper edge. Therefore it was considered that a reasonable estimate of mean per cent cover over the width of the bed was obtained. The width of the dense mussel zone was estimated at each quadrat. The product of these two measures gave an estimate of the area of mussel bed per 0.5 m (the width of the sampling quadrat) length of rocky shore. Three samples of mussels from a 10 × 10 cm area within a dense mussel bed (i.e. 100% cover) were taken close to each transect. At Kosi Bay, subsistence collectors not only collect from within mussel beds at LWS, but also pick scattered individual mussels from mid-water level (MW) to LWS. There-

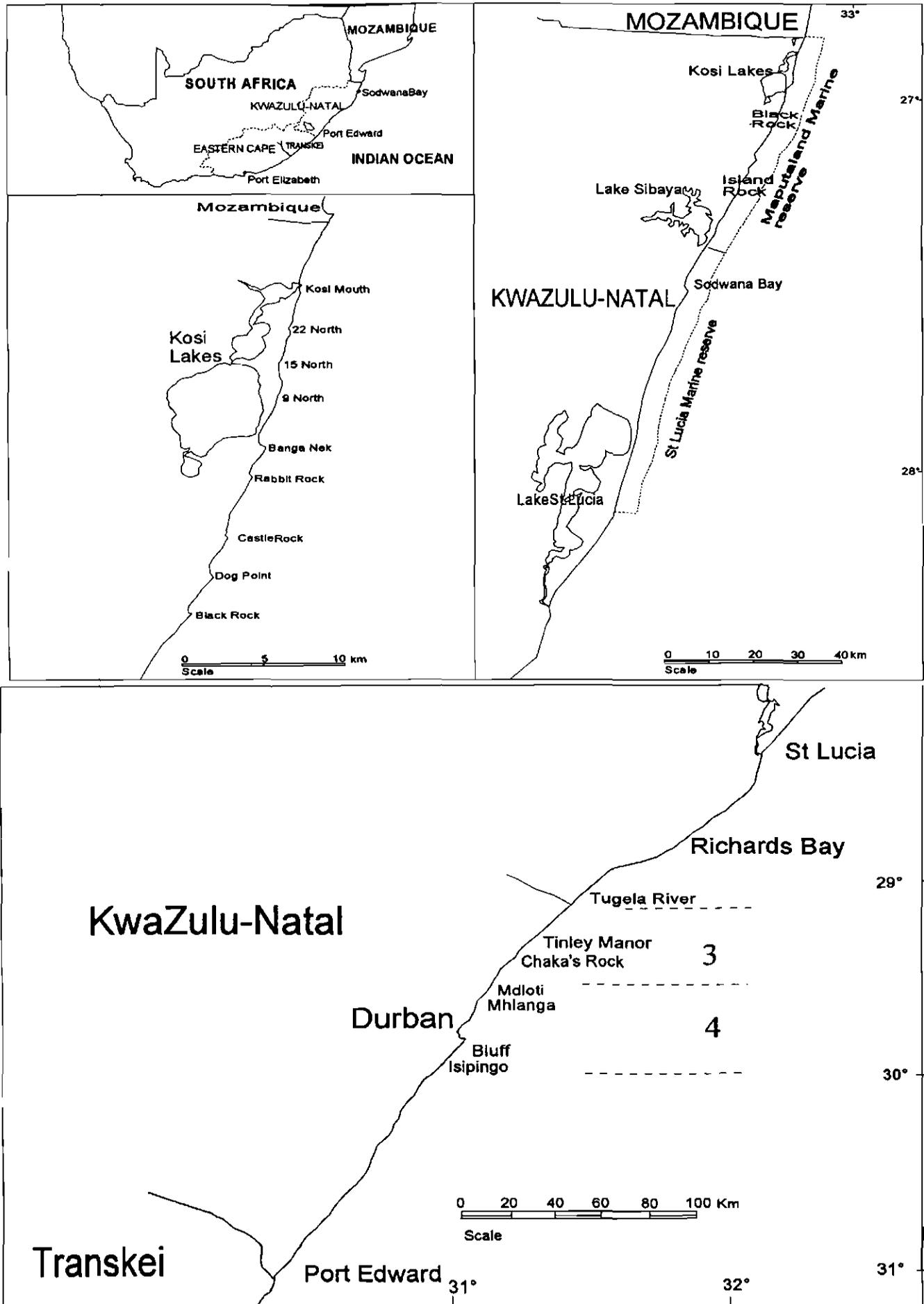


Figure 1 Map of the survey area and sites mentioned in the text. Zones 3 and 4 refer to zonation used for analysis of recreational catches.

fore, in that area, 0.25-m² quadrats were rolled down the shore from above the mussel zone to LWS (i.e. transects were at right angles to the shore) and the number of mussels greater than 20 mm length in each quadrat was counted, or per cent cover was estimated. Per cent cover was converted to numbers using data from quadrats where both per cent cover and numbers were obtained. The sum of all the quadrats for a transect estimated the number of mussels per 0.5 m length of rocky shore. At least one random sample of mussels was taken from each stratum.

The size distribution of mussels collected by recreational harvesters during 1993/94 in central KZN was obtained from a 'volunteer collector' programme and, at Kosi Bay, from three large samples of subsistence catches during 1996. A selectivity function was estimated from these samples using the method in Sparre, Ursin & Venema (1989). This was applied to the size distributions sampled during the surveys to obtain the fraction of total numbers available to collectors.

Data analysis

In central KZN, the mean of each transect parallel to the shore was used as input data (because mussel cover data from adjacent quadrats within transects were highly autocorrelated and using data from each quadrat would have constituted pseudo-replication). At Kosi Bay the sum of mussel counts for each transect at right angles to the shore was used as input data. Raw data were $\ln(N + 1)$ transformed in both areas and, by ignoring the strata with very few or no mussels, the resultant transformed data were approximately normally distributed and the variance was not correlated to the mean. Overall means and variances (weighted by the length of rock in each stratum) were determined using equations for stratified sampling in Seber (1982). Results are reported as back-transformed means and confidence intervals (Sokal & Rohlf 1995).

In central KZN, density of mussels within mussel beds was obtained from a regression of $\ln(\text{numbers}/\text{m}^2)$ vs mean size. Total numbers of mussels present were obtained by multiplying mussel area/m rocky shore by density by total length of rocky shore in the zone. Numbers available to collectors using the relevant selectivity function were obtained by multiplying the above by the fraction available. It was assumed that survey estimates represented the average number of mussels available during the year. This assumption is not entirely justified because mussels in KZN have a fairly well defined settlement season and natural mortality is high (Tomalin 1995b). However, as we used the number of large mussels (selected by collectors) for the calculation of fishing mortality, the error should be small.

Catch and fishing mortality

Catch at Kosi Bay was obtained from a community-based monitoring program (catch in mass — Kyle *et al.* 1997a) and, for recreational catches in central KZN, from a voluntary catch-return system (catch in numbers — Tomalin & Tomalin 1997). The latter were reported on a zonal basis (Figure 1). Independent data have been used to validate the recreational catch estimates (Kruger & Tomalin 1996; Tomalin *et al.* 1997) and these results guided the choice of potential variance and bias in catch estimates (catch assumption column in

Table 3). At Kosi, it was necessary to convert total catch in mass to numbers using the mean length from the samples and the following length-mass equation (Tomalin unpubl. data):

$$\text{Total wet mass (g)} = 0.000291 \times \text{length (mm)}^{2.6498}$$

The annual fishing mortality rate was calculated as follows:

$$F = \text{annual catch} / \text{average number available}$$

A parametric bootstrapping procedure (Punt & Butterworth 1993) was implemented using a spreadsheet to estimate the variance and confidence limits of estimates of F . For central KZN, each bootstrap replicate was drawn from a uniform distribution for area occupied by mussel beds (mean \pm 95% CI), a normal distribution for density, no error in the fraction available and three uniform distributions for catch in numbers. After 100 replicates, the mean, 95% CI and the coefficient of variance of F were determined for each of the three catch assumptions. A similar approach was used for Kosi Bay, but each replicate was drawn from a uniform distribution for population size, a normal distribution for mean mass of collected mussels (to calculate catch in numbers) and three uniform distributions for catch by mass. The range of catches considered (catch assumption column in Table 3) was much smaller than in central KZN because close to 100% of the catch is monitored.

Target fishing mortality rates

Target fishing mortalities were calculated using the coefficient of variance of estimates of current F from the above, a limit reference point of F_{msy} and three probabilities of exceeding the limit reference point (Caddy & McGarvey 1996). F_{msy} was obtained for each selectivity pattern from a model linking a size-based yield-per-recruit table to a deterministic stock-recruit function so giving total yield (Tomalin in prep.). The equation for F_{target} from Caddy & McGarvey (1996) is:

$$F_{target} = \frac{F_{msy}}{1 + CV_F \left(t - \frac{a_0 + a_1 t}{1 + b_1 t + b_2 t^2} \right)}$$

where

$$t = \sqrt{\log_e \left(\frac{1}{[P(F > F_{msy})]^2} \right)}$$

and $a_0 = 2.3075$, $a_1 = 0.27061$, $b_1 = 0.99229$, $b_2 = 0.04481$ and CV_F = coefficient of variation of F .

Results

Surveys

During the survey period at Kosi Bay, tides were exceptionally low and swell was moderate. Table 1 indicates that there were several strata in central KZN with no sites containing mussel beds on rocky shores (there may well have been isolated individual mussels which were not surveyed). These

Table 1 Design of stratified random surveys in central KZN and at Kosi Bay. Strata with no mussels were excluded from further analysis

Zone/Site	Number of strata	Number of transects	Number of strata with no mussel beds	Length of rock with mussels (m)
Central KZN				
Bluff-Isipingo	5	16	2	1400
Mhlanga-Mdloti	12	34	3	2700
La Mercy-Tinley Manor	10	26	1	5910
Kosi Bay				
22N	4	18	0	215
15N	3	6	0	90
9N	4	9	0	180
Dog Pt.	4	13	0	478
Rabbit Rock	5	18	2	858
Black Rock	4	16	0	403

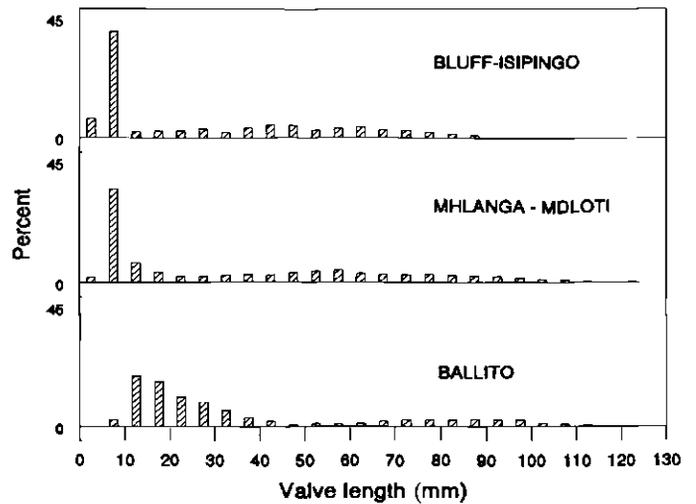


Figure 3 Size distributions of mussels sampled at low water spring tide level in central KZN during 1993-94.

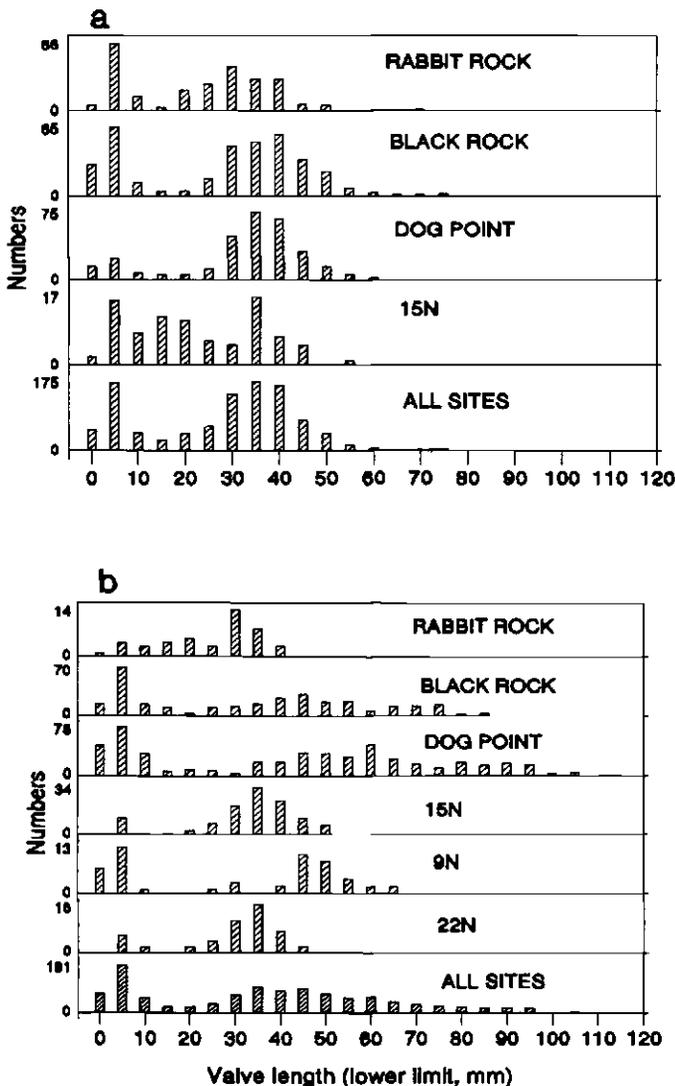


Figure 2 Size frequencies of mussels sampled at Kosi Bay during October 1996. (a) At mid-tide level and (b) at low water spring tide level. 'All sites' refers to all sampled sites (there were no mid-tide samples from 9N and 22N).

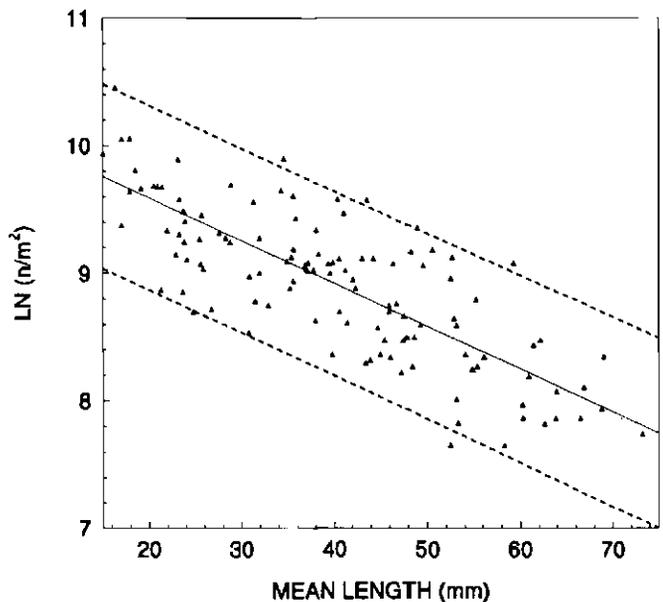


Figure 4 Relationship between Ln(density) and mean length of mussels sampled from 10 × 10 cm quadrats within dense mussel beds in central KZN (dotted lines = 95% confidence interval).

strata were on the Bluff, between Mhlanga and Mdloti, and at La Mercy. There were only two strata at Kosi Bay which had no mussels at all (Table 1). However, out of six rocky points surveyed, only Black Rock and Dog Point had significant beds of mussels. Size frequencies of mussels at Kosi Bay are shown in Figure 2 and for central KZN in Figure 3. Figure 4 shows the relationship between Ln (density) and mean size for mussel samples from within 100% mussel cover in central KZN. The line of best fit to these data was:

$$\text{Ln}(\text{density}, n/m^2) = 10.26 - 0.0335 * \text{mean size (mm)}$$

$$r^2 = 0.63, n = 121$$

This equation was used to convert areal cover to numbers in central KZN.

The relationship between area covered and number of mus-

sels greater than 20 mm at Kosi Bay was:

$$\text{Number mussels (> 20 mm)} = 1264.6 * \text{area (m}^2\text{)}$$

$$r^2 = 0.61, n = 21$$

This equation was used to convert percentage cover to numbers within a 0.25-m² quadrat at Kosi Bay.

Table 2 lists survey results: area of mussel beds, density, available population and estimated catch (in numbers) for two zones immediately north of Durban and total population > 20 mm, available population and catch (in mass) at Kosi Bay. There were very few mussels in the Bluff-Isipingo section of zone four (Figure 1) and it was therefore assumed that all catches in zone four came from the Mhlanga-Mdloti stretch of coast. It was also assumed that very little of the catch in zone three came from the section north of Tinley Manor (pers. obs.). The survey only extended to Chaka's Rock and the zone three average was used for mussel density per running metre of rocky shore from Chaka's Rock to Tinley Manor.

Table 2 Population size and catches of mussels in two zones in central KZN during 1993/94 and at six rock points at Kosi Bay during 1996 (± 95% confidence intervals). Estimates are back-transformed from ln(N+1) therefore the confidence intervals are not symmetrical. Survey methods were different in the two areas (see text). Catch was estimated in numbers for central KZ and mass at Kosi Bay

	Central Kwazulu-Natal	
	Mhlanga-Mdloti	La Mercy-Tinley
Area of mussels (m ²)	2919 (2394–3560)	4672 (4162–5246)
Mean size (mm)	36.0	36.9
Number/m ²	8553 (4188–17536)	8298 (4053–16984)
Fraction available	0.094	0.103
Available population (10 ⁶)	2.33 (1.91–2.85)	3.99 (3.56–4.48)
Estimated catch (10 ⁶)	1.42	1.85

Site	Kosi Bay		Catch (kg)
	Total population > 20 mm (10 ³)	Available population (10 ³)	
22N	1.7 (1.6–1.9)	0.9 (0.8–1.0)	162
15N	10.7 (8.0–1.4)	5.7 (4.2–7.6)	499
9N	11.8 (10.6–13.0)	6.2 (5.6–6.9)	92
Rabbit Rock	10.9 (9.4–12.6)	5.8 (5.0–6.7)	49
Dog Pt.	1374.1 (1272.5–1483.7)	727.7 (673.9–785.8)	3980
Black Rock	1066.8 (949.3–1199.0)	565.0 (502.7–635.0)	4758

Catch and fishing mortality

The size distribution of the catches and selectivity function for each fishery are shown in Figure 5. The average whole mass of a collected mussel at Kosi Bay in 1996 was 20.9 g (SD = 3.69, 3 samples) and 53% of mussels > 20 mm long were selected by collectors. In central KZN, during 1993/94, the average mass of a collected mussel was 48.7 g and 22% of mussels > 20 mm long (10% of all sizes) were selected by collectors.

Table 3 shows the estimated fishing mortalities and their

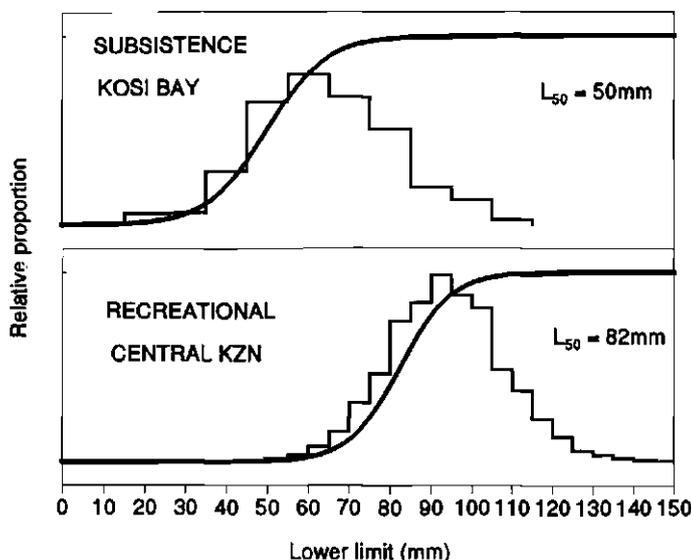


Figure 5 Size distribution and corresponding selectivity function for mussels collected by recreational collectors in central KZN (1993–1994) and subsistence collectors at Kosi Bay (1996).

Table 3 Estimated current fishing mortality rates (± 95% CI) in central KZN and at Kosi Bay under different assumptions about the uncertainty in catch estimates. For example, –50%, +100% means the true value could vary from half to twice the current estimate. Confidence intervals were calculated using a parametric bootstrap method. Input parameters were different for the two areas and estimates of catch were assumed to be more uncertain in central KZN than at Kosi Bay (see text). CV = coefficient of variance

Catch assumption	Central KZN		
	Mhlanga-Mdloti	La Mercy-Tinley	Mean CV
± 20%	0.60 (0.58–0.62)	0.46 (0.45–0.47)	0.19
± 50%	0.60 (0.56–0.64)	0.46 (0.43–0.49)	0.31
–50%, +100%	0.77 (0.71–0.82)	0.60 (0.56–0.64)	0.40

Catch assumption	Kosi Bay		Mean CV
	Black Rock	Dog Pt.	
± 5%	0.42 (0.41–0.44)	0.27 (0.26–0.28)	0.205
± 10%	0.42 (0.40–0.44)	0.27 (0.26–0.28)	0.223
± 20%	0.43 (0.41–0.45)	0.28 (0.26–0.29)	0.255

coefficient of variance for the two areas when different assumptions were made about variance in the estimation of catch. Note that the estimate of F when catch is assumed to range from twice to half the estimate (–50% + 100%) is increased over the other assumptions because, under a uniform distribution, the expected catch would be increased by 25%. The range of variance at Kosi Bay is much lower than in central KZN because close to 100% of the catch is monitored at Kosi Bay (Kyle *et al.* 1997a) versus 10% in central KZN (Tomalin & Tomalin 1997). Note that the central catch assumption (± 50% for central KZN and ± 10% for Kosi Bay) is, in our opinion, the most likely variance.

Target fishing mortality

Table 4 shows calculated target fishing mortalities under 12

combinations of catch assumption and level of risk of exceeding the limit reference point ($F_{msy} = 0.7$ for the recreational fishery and 0.56 for the subsistence fishery — Tomalin in prep.). Table 5 shows the management consequences for central KZN of these target fishing mortalities. Given the central assumption about the variability in catch estimates, catches in

Table 4 Target fishing mortalities in central KZN and at Kosi Bay given a limit reference point, three assumptions about uncertainty in catch estimates and four levels of probability of exceeding the limit F . The limit reference point is $F = 0.7$ (recreational F_{msy}) in central KZN and $F = 0.56$ (subsistence F_{msy}) at Kosi Bay. CV = coefficient of variance of current estimate of F

Central KZN			
Catch assumption			
	$\pm 20\%$	$\pm 50\%$	+100%, -50%
P($F > 0.7$)	CV of F : 0.19	CV of F : 0.31	CV of F : 0.40
5%	0.54	0.46	0.42
10%	0.57	0.50	0.47
20%	0.61	0.56	0.53
30%	0.64	0.60	0.58
Kosi Bay			
Catch assumption			
	$\pm 5\%$	$\pm 10\%$	$\pm 20\%$
P($F > 0.56$)	CV OF F : 0.205	CV OF F : 0.223	CV OF F : 0.255
5%	0.42	0.41	0.40
10%	0.44	0.44	0.42
20%	0.48	0.47	0.46
30%	0.51	0.50	0.49

Table 5 Percentage increase or decrease in annual catch compared to that in 1993/94 required to meet F_{target} (Table 4) for recreational mussel harvesting in central KZN. CV = coefficient of variance of current estimate of F

Mhlanga-Mdloti			
Catch assumption			
	$\pm 20\%$	$\pm 50\%$	+100%, -50%
P($F > 0.7$)	$F_{curr} = 0.6$	$F_{curr} = 0.6$	$F_{curr} = 0.77$
	CV: 0.19	CV: 0.31	CV: 0.40
5%	-10.5	-22.7	-45.6
10%	-5.7	-16.5	-40.4
20%	+1.0	-7.3	-32.6
30%	+6.3	-0.5	-25.6
La Mercy-Tinley Manor			
Catch assumption			
	$\pm 20\%$	$\pm 50\%$	+100%, -50%
P($F > 0.7$)	$F_{curr} = 0.46$	$F_{curr} = 0.46$	$F_{curr} = 0.6$
	CV: 0.19	CV: 0.31	CV: 0.40
5%	+16.7	+0.9	-31.6
10%	+23.0	+8.9	-25.0
20%	+31.7	+20.9	-15.2
30%	+38.7	+31.1	-6.5

the Mhlanga-Mdloti zone should be reduced by up to 23% depending on the risk management is willing to take. Catches need only be reduced in the La Mercy-Tinley Manor zone under the most pessimistic catch scenario. At Kosi Bay, catches need only be reduced at Black Rock under the most risk averse management strategy and even then, by less than 10% (Table 6).

Discussion

Surveys

Table 7 summarises and compares survey data between regions and zones. The number of mussels (> 20 mm) m^{-1} of rocky shore are very similar within regions in areas where

Table 6 Percentage increase or decrease in annual catch required to meet F_{target} (Table 4) for subsistence mussel harvesting at Kosi Bay. CV = coefficient of variance of current estimate of F

Black Rock $F_{curr} = 0.42$			
Catch assumption			
	$\pm 5\%$	$\pm 10\%$	$\pm 20\%$
P($F > 0.56$)	CV OF F : 0.21	CV OF F : 0.23	CV OF F : 0.26
5%	-0.7	-2.9	-6.7
10%	+5.2	+3.3	0.0
20%	+13.3	+12.1	+9.5
30%	+20.2	+19.3	+17.4
Dog Point $F_{curr} = 0.27$			
Catch assumption			
	$\pm 5\%$	$\pm 10\%$	$\pm 20\%$
P($F > 0.56$)	CV OF F : 0.20	CV OF F : 0.22	CV OF F : 0.25
5%	+55.9	+52.2	+47.0
10%	+65.2	+61.9	+57.0
20%	+77.8	+75.2	+71.5
30%	+87.8	+85.9	+83.3

Table 7 Comparison between zones and sites in terms of mussel numbers and biomass per running m of rocky shore - numbers of mussels > 20 mm, number of mussels available to collectors (using the selectivity function for each zone), catch in mass and numbers. Figures in brackets are the percentage of total biomass caught and F = fraction of available numbers collected

Site / zone	Mass (kg)	Number (>20 mm)	Numbers available	Catch (kg) (% present)	Catch (n) (F)
Mhlanga-Mdloti	65	4 323	865	25.6 (39)	525 (0.6)
La Mercy-Tinley Manor	61	4 055	676	15.2 (25)	312 (0.46)
Black Rock	40	2 647	1 402	11.8 (30)	565 (0.42)
Dog Pt.	43	2 875	1 522	8.3 (19)	398 (0.27)
Rabbit Rock	0.2	13	7	0.1	3 (0.43)
9 N	1	65	35	0.5	24 (0.37)
15 N	1.8	119	63	5.5	265 (2.2)
22 N	0.1	8	4	0.8	36 (4.5)

mussels occur. However, when comparing between regions, areas with mussels in central KZN have 1.5 times more mussels (> 20 mm) m^{-1} than similar areas at Kosi Bay. Biomass m^{-1} of rocky shore at Kosi Bay is about 60% that in the central region. However, there were fewer mussels available to collectors in central KZN because recreational collectors chose larger mussels than subsistence collectors at Kosi Bay. Note that we have used the current selectivity function and collectors may change their selectivity pattern as the relative abundance of different sizes of mussels changes.

Emanuel, Bustamente, Branch, Eekhout & Odendaal (1992) place both central KZN and the Kosi Bay area in the subtropical east coast province, whereas Jackson (1976) considered that there was an ecological break at around Cape Vidal. Berry (1980) postulated that this ecological change was due to an increase in temperature and the lack of river-borne silt in the coastal zone northwards of Cape Vidal. Certainly the fact that the large volcano barnacle, *Tetraclita squamosa rufotincta*, occurs at Kosi Bay but not in central KZN is striking. There are virtually no *P. perna* south of Kosi Bay on the extensive intertidal rocks at Sodwana Bay (pers. obs.) and few mussels were found in a survey of southern Mozambique (Robertson, Schleyer, Fielding, Tomalin, Beckley, Fennessy, Van der Elst, Bandeira, Macia & Gove 1996) or in central and northern Mozambique (Kalk 1958 and 1959). Siddal (1980), using published literature, thought that *P. perna* would occur in western Madagascar and central East Africa, but Hartnoll (1976) did not record *P. perna* at Dar Es Salaam. Therefore, we were surprised to record substantial mussel stocks at two rocky points in the Kosi Bay area.

In both central KZN and Kosi Bay there are stretches of rocky shore where mussels are virtually absent (Table 1). In addition to those areas where exploitation takes place, mussels are also virtually absent in some areas where exploitation is not possible (e.g. Island Rock — pers. obs.), presumably as a result of natural causes. If subsistence collectors at Kosi Bay could be persuaded not to collect mussels at the points where mussels are rare (e.g. Rabbit Rock) for several years, the assertion that mussels are absent owing to natural causes could be evaluated by observing the recovery or lack thereof of mussel beds at those sites. Alternatively, if a sanctuary area at each point was possible, this would serve the same purpose.

Distribution in relation to absolute tidal height was not measured, but we gained the impression that mussel beds at Kosi Bay occur somewhat lower on the shore than in central KZN (corroborated by K. Sink, pers. comm. 1997). Together with the frequency of large swells at Kosi Bay and the subsistence collectors' lack of footwear (reducing their ability to dodge waves), this makes access to the lower limit of the mussel beds only possible on rare occasions. In contrast, in central KZN, the lower limits of mussel beds are accessible on several low tides per year.

There are virtually no truly subtidal stocks of mussels in KZN, including the Kosi Bay area. An exception is the Vetch's Pier – Limestone reef area, north of Durban harbour, where about 4.7 million mussels occur (100 t), 2.6 million of which are subtidal down to about 5m (Tomalin unpubl. data 1997). However, in southern Mozambique, large mussels

were commonly observed among red-bait pods down to about 5 m (Robertson *et al.* 1996). Therefore, in KZN, there are no large adjacent stocks to form a reservoir and, as mussel larvae probably do not travel long distances alongshore (Phillips 1995), mussel collecting should be conservatively managed as if each area held an independent mussel stock.

Fishing mortality

Offtake rates in terms of mass removed compared to mass available are similar in central KZN and at Kosi Bay (20–40%), but when the selectivity pattern is taken into account and fishing mortality is calculated, rates are higher in central KZN than at the two exploited sites at Kosi Bay (Table 7). Even though mussels are not targeted at the other Kosi Bay sites (Kyle *et al.* 1997a), the offtake rates are high owing to the very small numbers present during the survey. The coefficient of variance around these estimates is low, although we have attempted to be explicit about all potential sources of uncertainty (Table 3). In both fisheries, the highest contribution to uncertainty lies in the estimate of total catch. This is in contrast to commercial fisheries where it is usually assumed that catch is known exactly. In this study survey results are relatively precise and we have assumed them to be unbiased — i.e. they estimate absolute stock size. In commercial fisheries, surveys are usually assumed to give a relative index of current stock size, which is estimated using a fisheries model and time series of such relative indices. In other words, the estimate of current stock size (and hence F) is usually confounded with estimates of the dynamics of the response of the stock to exploitation. In this study, the estimates of F are independent of any fisheries model or population dynamic parameter (e.g. natural mortality).

On the other hand, in order to assess the status of the stocks (i.e. the 'wisdom' of allowing the current F), we used a standard fisheries model which links a size-based yield-per-recruit model to a stock-recruit function (Tomalin in prep.), and assumed that F_{msy} for each fishery is estimated without error and is unbiased. However, even if the estimates of F_{msy} prove to be in error, the fact remains that fishing mortality in central KZN resulting from recreational mussel collecting is significantly higher than that at Kosi Bay from subsistence mussel collecting. Also note that the values of current F estimated here are substantially less than annual total mortality rates estimated from catch-curves for *Perna perna* populations in central KZN (1.0–1.5 — Tomalin 1995b). The stock-recruit function in the model was fitted ignoring the occasional blanket settlement of mussel spat (Berry 1978) which would restore mussel populations even after very heavy exploitation. In this respect, the model is conservative and treats blanket spatfall as a bonus.

The model and the mortality rates used here refer to a population of mussels. This is justified in KZN, because recreational collectors target individual mussels and subsistence collectors create small gaps in mussel beds (Kyle *et al.* 1997a). However, in Transkei, subsistence collectors remove whole clumps of mussels. Therefore, in that area, the dynamics of interest will be that of clumps of mussels. As these clumps are likely to have much slower rates of recruitment, growth and natural mortality than individual mussels (Dye 1992; Paine & Levin 1981), this may explain the apparent dif-

ference in productivity between the two areas (Kyle *et al.* 1997a). It is also important to realise that harvesting will always reduce stock size below the unexploited state and that the model (Tomalin in prep.) predicts that maximum sustainable yield is obtained when current stock size is around half the unexploited stock size. Using the precautionary approach, as implemented here, the aim is to keep stock size somewhat above that level.

We must emphasise that these results apply only to one year and that interannual changes in recruitment to the available stock, levels of offtake and/or harvesting practises (e.g. changes in implement and selectivity) will result in changes in fishing mortality. For example, offtake at Kosi Bay was much higher in the recent past (Kyle *et al.* 1997a) and F may have been correspondingly higher. We recommend that, in addition to the ongoing catch-monitoring programs, regular surveys of stock size and structure be carried out on an appropriate spatial scale.

Management consequences

There are profound differences between the fisheries in the two regions examined (Table 8 and Figure 5) and it is to be expected that they would have different effects on the respective mussel stocks. In view of the social differences between the harvesting communities, they should be managed with different objectives. For example, at Kosi Bay, mussel protein contributes 6% of the adult protein RDA per person fed (Table 8). This may well be an underestimate because many children eat mussels and their total protein intake is probably less than the adult RDA. The incidence of kwashiorkor is lower among children living close to the coast than inland

Table 8 Comparison between recreational and subsistence mussel fisheries in KZN. Data from ¹ Tomalin 1995a, ² Tomalin & Tomalin 1997 and ³ Kyle *et al.* 1997a. RDA = recommended daily allowance of protein for adults

	Recreational	Subsistence
Licence	individual, R35.00 ¹	group, free
Issuing authority	NFLB (policed by NPB)	NPB (managed by KDNC)
Licence number limits	11 000 ¹	none (about 200 collectors) ³
Daily bag limit	50 mussels (\pm 2.4 kg) ¹	none (carry about 11 kg) ³
Annual catch	200–250 t (5–6 million) ²	12–20 t (0.6–1 million) ³
Access to shore	vehicles, 300 km shore (110 km rocky)	foot, 30 km shore (3 km rocky)
Mobility	wear shoes, frequent access to lowest mussels	no shoes, rare access to lowest mussels
Efficiency	wear gloves, implement < 100 mm \times 12 mm ¹	no gloves, implement 1 m \times 45 mm ³
Gender	both sexes	women only
Trips / year	8 ²	18.5 ³
Catch / year	20 kg ²	200 kg ³
Other people fed	? 1	6 ³
Flesh mass / year / person	3.8 kg	10 kg
% protein RDA / person	2.3	6.1

(Avery & Siegfried 1980). Therefore, at Kosi Bay, the social costs of banning the collection of mussels are likely to be high. In contrast, the contribution of mussel flesh to the nutritional status of recreational collectors is likely to be extremely small.

The method used here is an implementation of the precautionary principle (Caddy & McGarvey 1996; FAO 1993) and the results are laid out so that managers can clearly see the trade-off between risk and uncertainty (Tables 5 and 6). The decisions to be taken are what level of risk (of exceeding the limit reference point — F_{msy} in this case) is acceptable for each fishery, and which assumption about the variability in the catch estimate is most likely. Our personal opinion is that risk levels should be set much lower in the recreational fishery ($p = 5–10\%$), where social costs of reduced catch are low, than in the subsistence fishery ($p = 10–30\%$), where the social costs of reduced catches are likely to be high. However, objectives and risk levels should be set in consultation with the users (Anderson & Griffiths 1997).

The main management result for central KZN is that effort should be reduced in the zone immediately north of Durban and possibly re-directed to the area north of the Mdloti river (Table 5). There seems little justification in continuing to allow mussel collecting in the Bluff–Isipingo zone, where very few mussels were present during the survey. Note that if the assumption about the catch estimate in the fourth column of Table 5 is true (i.e. true catch is 25% higher than currently estimated), then both zones in central KZN are seriously over-exploited.

No dramatic action is required at Kosi Bay (Table 6) where intertidal harvesting appears to be declining (Kyle *et al.* 1997a). The reasons for the decline in effort are controversial — one view is that it is due to changing economic circumstances in the area (Kyle *et al.* 1997a), the other is that it is a response to declining stocks (J. Harris pers. comm. 1997). If the latter is true, then, assuming a reasonable recovery rate, the system as a whole is self-regulating and there is still no need for management intervention apart from not allowing new entrants to the fishery. However, care should be taken that increases in efficiency (e.g. use of long-handled rakes or shoes — both would enable easier access to stocks lower on the shore) or incentive (e.g. sale to resorts) do not occur. Collectors should be discouraged from collecting mussels at points where mussels are rare and encouraged to focus on species common in those areas, such as red bait. The new Sea Fisheries Act will require individual subsistence harvesters to obtain permits.

We are of the opinion that mussels in the marine reserve at Kosi Bay should remain a protein source of last resort for the very poor in the adjacent community. Besides, the ama-Thonga living at Kosi Bay have a centuries long history of utilisation of the area's natural resources (Avery & Siegfried 1980; Bruton, Smith & Taylor 1980) and thus have historical access rights to resources within the marine reserve. In fact, they could be considered to be an integral part of the ecosystem and their culture and dependence on natural resources may well be an attraction for eco-tourists to the area. In contrast, the Nguni linguistic group, who form the majority of the inhabitants of KwaZulu-Natal south of Kosi Bay, do not have a long tradition of eating seafoods (Avery & Siegfried 1980).

Conclusion

Exploitation rates at Kosi Bay are substantially lower than in central KZN. This result is independent of any fisheries model or population dynamic parameter. We think the difference is due to the more seaward distribution of mussels and the restricted mobility of a small number of subsistence collectors, which prevents them from accessing the lowest tidal level. In contrast, high numbers of recreational collectors at popular spots in central KZN can often access the lowest mussel beds.

Given the range of assumptions and observed variability in survey estimates, there is a low probability that current fishing mortality at Kosi Bay exceeds subsistence F_{msy} . In contrast, in central KZN, there is a substantial probability that current fishing mortality exceeds recreational F_{msy} in one zone. However, the latter conclusions are dependent upon the conservative fisheries model used.

We recommend a reduction in mussel harvesting in the zone north of Durban and that the status quo is maintained at Kosi Bay. Surveys similar to those discussed here should be undertaken on a regular basis and the results fed back into a formal management plan.

Acknowledgements

Wendy Robertson, Peter Fielding, Shelly Birnie and Kirsten Bond assisted on field surveys and Diane Kyle and Mariana Tomalin with data analysis. Jean Harris organised the workshops at Cape Vidal and Kosi Bay. Comments, criticisms and ideas of all who took part in those workshops have been freely drawn upon. Michael Schleyer initiated the surveys. Kerry Sink shared impressions from her surveys. Many of the above made useful comments on the text as did Arthur Dye and Charles Griffiths. Funding was provided by the SANCOR (FRD Sea and Coast programme), the HSRC (Human needs, Resources and the Environment programme), the Natal Parks Board, the KZN Department of Nature Conservation and the South African Association for Marine Biological Research.

References

- ANDERSON, R.J. & GRIFFITHS, C.I. 1997. Community co-management of intertidal mussel resources: progress and problems. *S. Afr. J. Sci.* 93: 151–152.
- ANONYMOUS. 1996. FAO Yearbook, Fishery statistics: Catches and landings 78 (1994): 1–700. Food and Agricultural Organisation of the United Nations, Rome.
- APPUKUTTAN, K.K., PRABHAKARAN NAIR, T., & THOMAS, K.T. 1989. Spat settlement of brown mussel *Perna indica* Kuriakose and Nair in the southwest coast of India. *J. mar. Biol. Ass. India* 31(1&2): 266–275.
- EVERY, G. & SIEGFRIED, W.R. 1980. 150,000 year Tradition: Food Gatherers along South Africa's seashore. *Oceans* 13(4): 32–37.
- BERRY, P.F. 1978. Reproduction, growth and production in the mussel, *Perna perna*, on the east coast of South Africa. *Invest. Rep., Oceanographic Research Institute* 48: 1–28.
- BERRY, P.F. 1980. The inter- and subtidal invertebrate fauna of Maputaland. In: Studies on the Ecology of Maputaland, (eds) Bruton, M.N. and Cooper, K.H. Rhodes University and S. Afr. Wildlife Soc., Grahamstown. pp. 102–110.
- BRUTON, M.N., SMITH, M., & TAYLOR, R. 1980. A brief history of human involvement in Maputaland. In: Studies on the Ecology of Maputaland, (eds) Bruton, M. and Cooper, K.H. Rhodes University and S. Afr. Wildlife Soc., Grahamstown. pp. 432–459.
- CADDY, J.F. & MCGARVEY, R. 1996. Targets or limits for management of fisheries? *J. Fish. Manage.* 16: 479–487.
- CASTILLA, J.C. & DURAN, L.R. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas*. *Oikos* 45: 391–399.
- DYE, A.H. 1992. Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish gathering. *Neth. J. Sea Res.* 30: 209–217.
- DYE, A.H., SCHLEYER, M.H., LAMBERT, G. & LASIAK, T. 1994. Intertidal and subtidal filter feeders in southern Africa. In: Rocky shores: exploitation in Chile and South Africa, (ed.) Siegfried, W. *Ecological Studies* 103. Springer-Verlag, Berlin. pp. 57–74.
- EEKHOUT, S., RAUBENHEIMER, C.M., BRANCH, G.M., BOSMAN, A. L. & BERGH, M.O. 1992. A holistic approach to the exploitation of intertidal stocks: limpets as a case study. *S. Afr. J. mar. Sci.* 12: 1017–1030.
- EMANUEL, B.P., BUSTAMANTE, R.H., BRANCH, G.M., EEKHOUT, S. & ODENDAAL, F.J. 1992. A zoogeographic approach to the selection of marine reserves on the west coast of South Africa. *S. Afr. J. mar. Sci.* 12: 341–354.
- FAO (Food and Agriculture Organisation of the United Nations). 1993. The precautionary approach to fisheries with reference to straddling fish stocks and highly migratory fish stocks. FAO Fisheries circular 871.
- FIELDING, P.J., ROBERTSON, W.D. & LAMBERT, G. 1991. Stock assessment of some intertidal organisms in the Kosi Bay area. *Unpubl. Rep., Oceanographic Research Institute* 75: 1–26.
- HARTNOLL, R.G. 1976. The ecology of some rocky shores in tropical east Africa. *Est. Coast Mar. Sci.* 4: 1–21.
- HEYDORN, A.E.F. & HUGHES, G.R. 1969. Urgent need for more marine reserves. *Afr. Wildl.* 23: 270–278.
- HILBORN, R. & WALTERS, C.J. 1992. Quantitative Fisheries Stock Assessment: Choice, dynamics and uncertainty. Chapman and Hall, New York. pp. 570.
- HILBORN, R., PIKITCH, E.K. & FRANCIS, R.C. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. *Can. J. Fish. Aquat. Sci.* 50: 874–880.
- JACKSON, L.F. 1976. Aspects of the intertidal ecology of the east coast of South Africa. *Invest. Rep., Oceanogr. Res. Inst.* 46: 1–72.
- KALK, M. 1958. Ecological studies on the shores on Mozambique. 1. The fauna of intertidal rocks at Inhaca Island, Delagoa Bay. *Ann. Natal Mus.* 14(2): 189–242.
- KALK, M. 1959. A general ecological survey of some shores in northern Mozambique. *Revta Biol., Lisb.* 2(1): 1–22.
- KRUGER, A. & TOMALIN, B.J. 1996. Usage of mussel and crayfish licences and the attitudes of licence holders in KwaZulu-Natal: Results from a telephone survey for 1994 and 1995. *Data Rep., Oceanogr. Res. Inst.* 96.4: 1–13.
- KYLE, R., PEARSON, B., FIELDING, P.J., & ROBERTSON, W.D. 1997a. Subsistence shellfish harvesting in the Maputaland marine reserve in northern KwaZulu-Natal, South Africa: rocky shore organisms. *Biol. Cons.* 82: 183–192.
- KYLE, R., ROBERTSON, W.D. & BIRNIE, S.L. 1997b. Subsistence shellfish harvesting in northern KwaZulu-Natal, South Africa: sandy beach organisms. *Biol. Cons.* 82: 173–182.
- LAMBERT, G. & STEINKE, T.D. 1986. Effects of destroying juxtaposed mussel-dominated and coralline algal communities at Umdoni Park, Natal coast, South Africa. *S. Afr. J. mar. Sci.* 4: 203–217.
- LASIAK, T. & DYE, A.H. 1989. The ecology of the brown mussel *Perna perna* in Transkei: implications for the management of a traditional food source. *Biol. Cons.* 47: 245–257.

- LUDWIG, D., HILBORN, R. & WALTERS, C. 1993. Uncertainty, resource exploitation and conservation: lessons from history. *Science* 260: 17,36.
- MACKENZIE, C.L.Jr., BURREL, V.G., ROSENFELD, A. & HOBART, W.L. (eds) 1997. The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Volume 3, Europe. US Dep. Commer. *NOAA Tech. Rep.* 129: 1–240.
- MASON, J. 1976. Cultivation. In: Marine mussels: their ecology and physiology, (ed.) Bayne, B.L. Cambridge University Press, Cambridge. pp. 385–410.
- MATHEWS, E. & OITERONG, E. 1995. Marine species collected by women in Palau, Micronesia. *Micronesica* 28(1): 77–90.
- PAINE, R.T. 1989. On commercial exploitation of the sea mussel, *Mytilus californianus*. *NW Environm. J.* 5: 89–97.
- PAINE, R.T. & LEVIN, S.A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51(2): 145–178.
- PHILLIPS, T.E. 1995. Dispersal, settlement and recruitment: their influence on the dynamics of intertidal mussels. Ph.D. Thesis, Rhodes University. pp. 246.
- PUNT, A.E. & BUTTERWORTH, D.S. 1993. Variance estimates for fisheries assessment: their importance and how best to evaluate them. In: Risk evaluation and biological reference points for fisheries management, (eds) Smith, S.J., Hunt, J.J. & Rivard, D. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 145–162.
- ROBERTSON, W.D., SCHLEYER, M.H., FIELDING, P.J., TOMALIN, B.J., BECKLEY, L.E., FENNESSY, S.T., VANDER ELST, R.P., BANDEIRA, S., MACIA, A. & GOVE, D. 1996. Inshore marine resources and associated opportunities for development of the coast of southern Mozambique: Ponta de Ouro to Cabo de Santa Maria. *Unpubl. Rep., Oceanogr. Res. Inst.* 130: 1–51.
- SEBER, G.A.F. 1982. The estimation of animal abundance. 2nd ed. Griffin and Co. Ltd. London. pp. 654.
- SEED, R. 1976. Ecology. In: Marine mussels: their ecology and physiology, (ed.) Bayne, B.L. Cambridge University Press, Cambridge. pp. 13–65.
- SIDDALL, S.E. 1980. A clarification of the genus *Perna* (Mytilidae). *Bull. Mar. Sci.* 30(4): 858–870.
- SIEGFRIED, W.R., HOCKEY, P.A.R. & BRANCH, G.M. 1994. The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa — an overview. In: Rocky shores: exploitation in Chile and South Africa, (ed.) Siegfried, W.R. *Ecological Studies* 103. Springer-Verlag, Berlin. pp. 1–15.
- SOKAL, R.R. & ROHLF, F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edn. Freeman and Co. USA. pp. 887.
- SPARRE, P., URSIN, E. & VENEMA, S.C. 1989. Introduction to tropical fish stock assessment. 1. Manual. *FAO Fish tech. pap.* 306/1: xii + 337 pp.
- SUCHANEK, T.H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. *Oecologia* 50: 143–152.
- TOMALIN, B.J. 1995a. Invertebrates harvested in KwaZulu-Natal: Their ecology, fishery and management. *Information Booklet, Oceanogr. Res. Inst.* 1: 1–22.
- TOMALIN, B.J. 1995b. Growth and mortality rates of brown mussels *Perna perna* in KwaZulu-Natal: a comparison between sites and methods using non-parametric length-based analysis. *S. Afr. J. Mar. Sci.* 16: 241–254.
- TOMALIN, B.J. & TOMALIN, M. 1997. Estimated landings of coastal invertebrates by recreational collectors in KwaZulu-Natal, 1963–1995. Part 1: Annual totals. *Data Rep., Oceanogr. Res. Inst.* 96.2: 1–29.
- TOMALIN, B.J., TOMALIN, M. & KRUGER, A. 1997. Natal Parks Board recreational marine data collection: 1995 annual data report. *Data Rep., Oceanogr. Res. Inst.* 96.2: 1–29.
- UNDERWOOD, A.J. 1993. Exploitation of species on the rocky coast of New South Wales (Australia) and options for its management. *Ocean Coast. Manage.* 20: 41–62.
- VAKILY, J.M. 1989. The biology and culture of mussels of the genus *Perna*. *ICLARM Studies and Reviews* 17. ICLARM, Manila, Philippines. pp. 63.
- VAN ERKOM SCHURINK, C. & GRIFFITHS, C.L. 1990. Marine mussels of southern Africa — their distribution patterns, standing stocks and culture. *J. Shellfish Res.* 9(1): 75–85.
- YAMADA, S.B. & PETERS, E.E. 1988. Harvest management and the growth and condition of submarket-size sea mussels, *Mytilus californianus*. *Aquaculture* 74: 293–299.