Studies on the ecology of *Saccostrea cucullata* (Born, 1778) (Mollusca: Bivalvia) on the east coast of southern Africa

A.H. Dye
Department of Zoology, University of Transkei, Private Bag X1, Unitra, Umtata, 5100 Transkei

Received 27 May 1988; accepted 24 October 1988

Aspects of the population ecology of the rock oyster *Saccostrea cucullata* were studied in Transkei and southern Natal. Population size structure was determined from a survey of 12 sites in Transkei and five in Natal, while data on recruitment, growth and mortality were obtained from photographic monitoring of fixed quadrats at selected sites in Transkei. Most populations had a unimodal size distribution in which small individuals were poorly represented. Truncated size spectra were evident in both nature reserves and exploited areas, suggesting that size distribution was unrelated to human exploitation. Recruitment at all sites was poor at approximately 2 – 4 individuals m^{-2} y^{-1}. After three years, recovery of experimentally denuded areas was minimal both in nature reserves and exploited sites. Annual mortality varied considerably, being highest in exploited areas, (9 – 11,5 individuals m^{-2} y^{-1}), compared with 1,5 – 1,8 m^{-2} y^{-1} in reserves. Newly settled animals reached a total length of 19 mm in their first year. Thereafter growth increments decreased rapidly to 11 mm and 5 mm in the second and third years respectively. It is estimated that the largest animals found (90 mm) were approximately 20 years old. *S. cucullata* exhibits characteristics typical of a species close to its geographical limit of distribution. Poor recruitment and slow growth rate decrease the resistance of the species to disturbance and reduce the potential of denuded populations for recovery.

Aspekte van die bevolkingsekologie van die oester *Saccostrea cucullata* is in Transkei en suid-Natal bestudeer. Die bevolkingsgroottestruktuur is by 12 gebiede in Transkei en vyf in Natal bepaal, terwyl data oor aanwerwing, groei en mortaliteit deur middel van fotografiese studies van vaste kwadrate by geselekteerde gebide in Transkei verkry is. Die meeste van die bevolkings het 'n eenmodale grootteverspreiding waarin klein indiwidue swak verteenwoordig was. Afgeknotte groottespektra is in beide natuurreservate en ontginde gebiede gevind, wat daarop dui dat daar nie 'n eenvoudige verwantskap tussen grootteverspreiding en ontginning is nie. Aanwerwing was swak by alle gebiede met net 2 – 4 nuwe indiwidue m^{-2} y^{-1}. Herstel van gebiede wat eksperimenteel ontvolk was, was minimaal na drie jaar in beide natuurreservate en ontginde gebiede. Jaarlikse mortaliteit het baie gevarieer met die hoogste syfers in ontginde areas (9 – 11,5 m^{-2} y^{-1}), in vergelyking met natuurreservate (1,5 – 1,8 m^{-2} y^{-1}). Pasgevestigde diere het 'n totale lengte van 19 mm in die eerste jaar bereik, maar daarna het die groeitempo progressief afgeneem tot 11 mm en 5 mm in die tweede en derde jare respektiewelik. Daar is beraam dat die grootste oesters wat gevind is (90 mm) ongeveer 20 jaar oud is. *S. cucullata* toon kenmerke wat tipies is van 'n spesie wat naby die goegrafiese limiet van sy verspreiding is. Swak aanwerwing en lae groeitempo verminder die spesie se weerstand teen versteuring en die potensiaal vir herstel van ontvolkte gebiede is beperk.

The rock oyster *Saccostrea cucullata* (Born, 1778) is abundant on the east coast of southern Africa, where it often forms a distinct band in the mid to upper balanoid zone. Although not of commercial importance in Transkei it is heavily exploited by coastal people who eat the oysters while gathering other intertidal organisms for food. Although *S. cucullata* is not a major component of the diet of these people when compared to other intertidal species (Mills 1985), the effect of exploitation on the rock oyster populations may be severe in some areas.

Little is known of the biology of *S. cucullata* in Africa. The east coast of southern Africa marks the southern limit of its distribution, but it is abundant around the Indian Ocean (Kilburn & Rippey 1985). In Kenya it is commercially exploited and Van Someren & Whitehead (1961) have studied reproduction, spatfall and growth of spat in this area. More recently Lasiak (1986) studied the reproductive cycle in Transkei. The present paper gives data on recruitment and mortality, growth, population size structure and the effect of human exploitation.

Methods

Demographic parameters were studied at 12 sites on the Transkei coast separated by distances varying from 0,5 to 20 km (Figure 1). The sites were chosen to facilitate a comparison of populations in exploited and protected areas, as well as to investigate spatial variability within a protected area (Dwesa Nature Reserve).

The abundance of *S. cucullata* was determined by counting all the animals in 30 quadrats, of 0,25 m^2, placed at random within the rock oyster zone. Population size structure was obtained by measuring the maximum length (equivalent to dorso-ventral height (Kilburn & Rippey 1985)) of 100 to 300 individuals to the nearest 0,5 mm. Additional data on size and abundance were obtained from five sites in Natal (Figure 1).

Recruitment and mortality were determined by counting the number of animals appearing and disappearing with time in sets of photographs of fixed 0,25 m^2 quadrats taken at three monthly intervals over a period of three years (1982–1985). The photographs were taken through a 0,25 m^2 quadrat divided into 100 5 × 5 cm squares for scaling purposes. Data are presented for the Dwesa and Mkambati reserves and for two exploited sites, Ndumbi and Mbotyi.

Growth was determined by measuring the maximum length of 80 individuals in sets of photographs of fixed quadrats taken in the Dwesa and Mkambati Nature

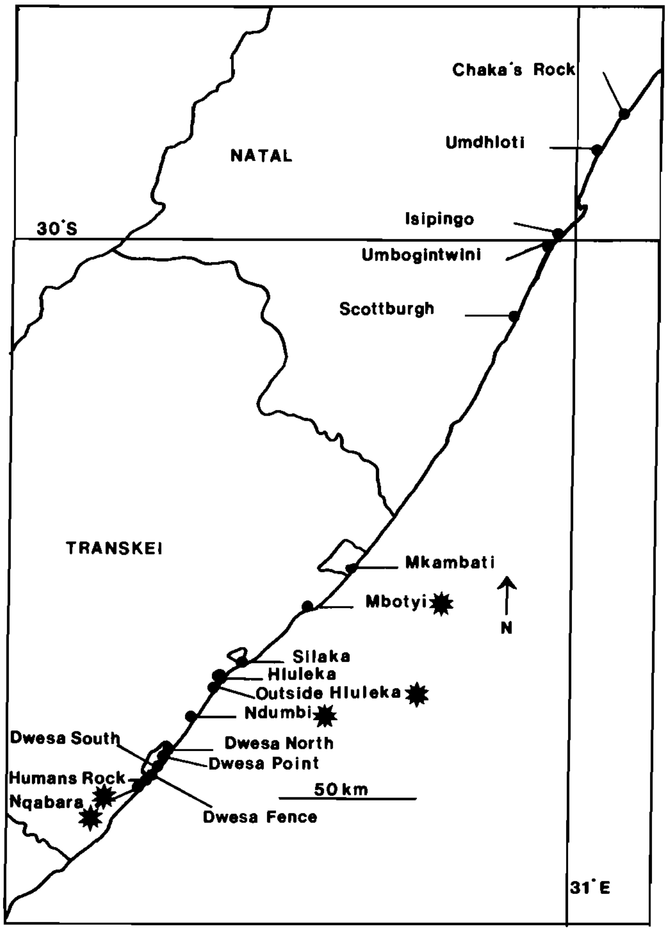


Figure 1 Map of the Transkei and southern Natal coasts showing the positions of the sampling sites. Asterisks indicate exploited sites in Transkei.

Reserves over a period of five years (1982–1987). Measurements were made from the most recent photographs back to the start of the study or until the individual in question first appeared, the same axis of measurement being used throughout. The animals were divided into seven size classes from < 10 mm to 70 mm and annual growth rates determined for each class. Composite growth curves were calculated from the mean, maximum and minimum growth observed in each size class over the five-year period. Corrections were made against *in situ* measurements of the same animals. These photographs form part of an archive resulting from an ongoing long-term surveillance programme on rocky shores in Transkei (Dye 1988).

The potential recovery of denuded populations of *S. cucullata* was investigated by removing all oysters in four 1-m^2 quadrats at each site and monitoring these areas for three years.

Results

Population size structure and abundance for each site are shown in Figures 2a, b, and c. Statistical analysis revealed significant differences in median size between individual sites, irrespective of whether they were exploited or protected (Median Test, $p < 0{,}0001$, Conover 1980). The test also showed that, with the exception of Scottburgh, the median size of the Natal populations (40,5 mm) was significantly lower than those in protected sites Transkei (48,6 mm) ($p < 0{,}001$), but there was no difference between the median size of rock oysters in Natal and those at exploited sites in Transkei (37,8 mm). Size frequency tended to appear unimodal with most of the sites skewed to the left of the median, but animals smaller than 20 mm were rare at all sites.

Although population density tended to increase in a northerly direction there was considerable variability over short distances (Figures 2a, b, c). In addition to the differences between exploited and protected sites, there was, for example, a three-fold difference in population density between sites within the Dwesa Reserve (30 – 85 m^{-2}). No relationship was found between median size and abundance ($r = 0{,}04$; $p > 0{,}25$) at Dwesa.

Figure 3 shows annual recruitment and mortality rates for two unexploited and two exploited sites in Transkei. Recruitment was poor at all sites and rarely exceeded three individuals m^{-2} y^{-1}. Annual mortality was less than recruitment at Dwesa North but the opposite was found at Mkambati where the mortality rate was more than double that of recruitment. Mortality accounted for 1,7 to 2,9% of standing stock at Dwesa and Mkambati respectively. As would be expected mortality was very high at the exploited sites (8,5 and 11,5 m^{-2} y^{-1} at Mbotyi and Ndumbi respectively) and constituted an annual loss of between 27 and 37% of standing stock.

Figure 4 shows the recovery of experimentally denuded areas at protected and exploited sites in Transkei. Recruitment was low at all sites and after three years new animals represented only 3,6 to 14,5% of the initial standing stocks (1 – 12 animals m^{-2}). There were no significant differences in recovery between the sites. Ongoing work at Dwesa (Dye 1988) and Mkambati indicates that this condition is stable and has persisted for nearly six years. The denuded quadrats now have less than 5% cover of oysters, from an initial 50%, and the areas are dominated by grazers such as *Cellana capensis, Patella granularis, Siphonaria concinna* and *Littorina africana*. Considerable variation in recruitment was evident on a year to year basis. At Dwesa North, for example, all the recruitment shown in Figure 3 occurred in the first year of the study. At Ndumbi recruitment varied from 0 to 2 individuals m^{-2} y^{-1}, while at Mkambati recruitment was constant throughout the study.

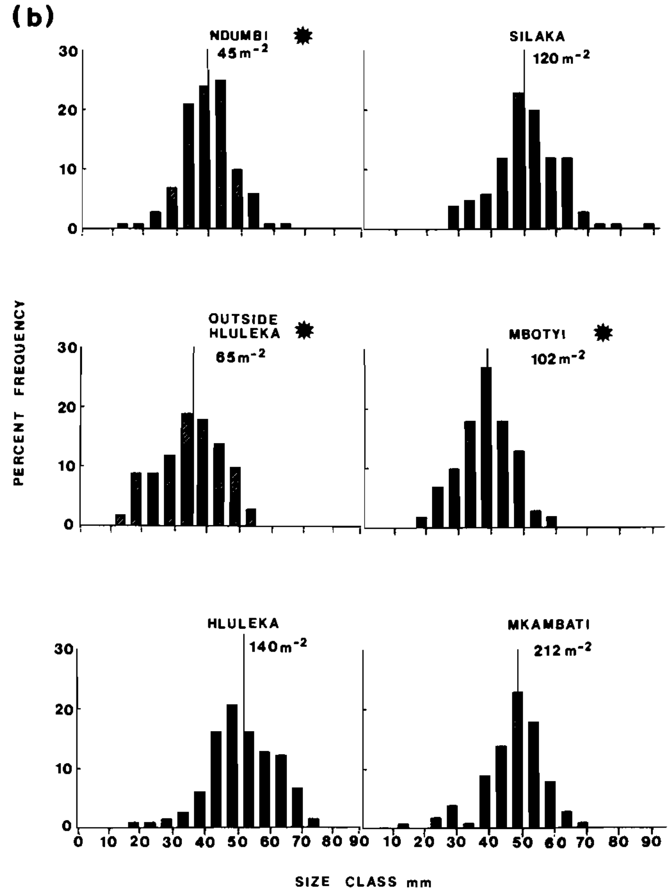
Composite curves for mean, maximum and minimum growth of *S. cucullata* are shown in Figure 5. As no difference could be found between growth at Dwesa North and Mkambati, the data were combined in the derivation of the curves. Growth is rapid in the newly settled individuals which attain a length of 19 mm in the first year. Thereafter growth increments decline progressively to 11 mm and 5 mm in the second and third years respectively. In the 60–70 mm size class growth is only 1,4 mm y^{-1}. *S. cucullata* appears to be particularly long-lived and the largest specimens found (90 mm) are estimated to be between 15 and 20 years old.

Discussion

Populations of rock oysters on the southern African coast are characterized by what appears to be a unimodal size distribution in which small individuals are scarce and adults dominate. This characteristic is common in species at or near their geographical limits of distribution and can be traced to repopulation failure. Recruitment is erratic with one or two good years separated by several bad years in which larvae fail to establish themselves (Lewis 1986).

Recruitment is the result of a sequence of steps; reproduction, larval dispersal, settlement and post-settlement survival of spat. Repopulation failure may result from problems arising at any of these steps. It seems unlikely that lack of gonadal output is the primary cause of poor recruitment. Studies by Lasiak (1986) on the reproduction of this species in Transkei indicate a well defined spawning period from February to March during which over 40% of animals examined were in spawning condition. The answer must therefore be sought in the vagaries of larval dispersal and/or post-settlement survival.

There is no direct information on larval dispersal along the Transkei coast, but ongoing studies implicate wind as an important factor. Settlement patterns of the barnacle *Tetraclita serrata* appear to be strongly influenced by offshore winds (Dye 1988), and wind has been



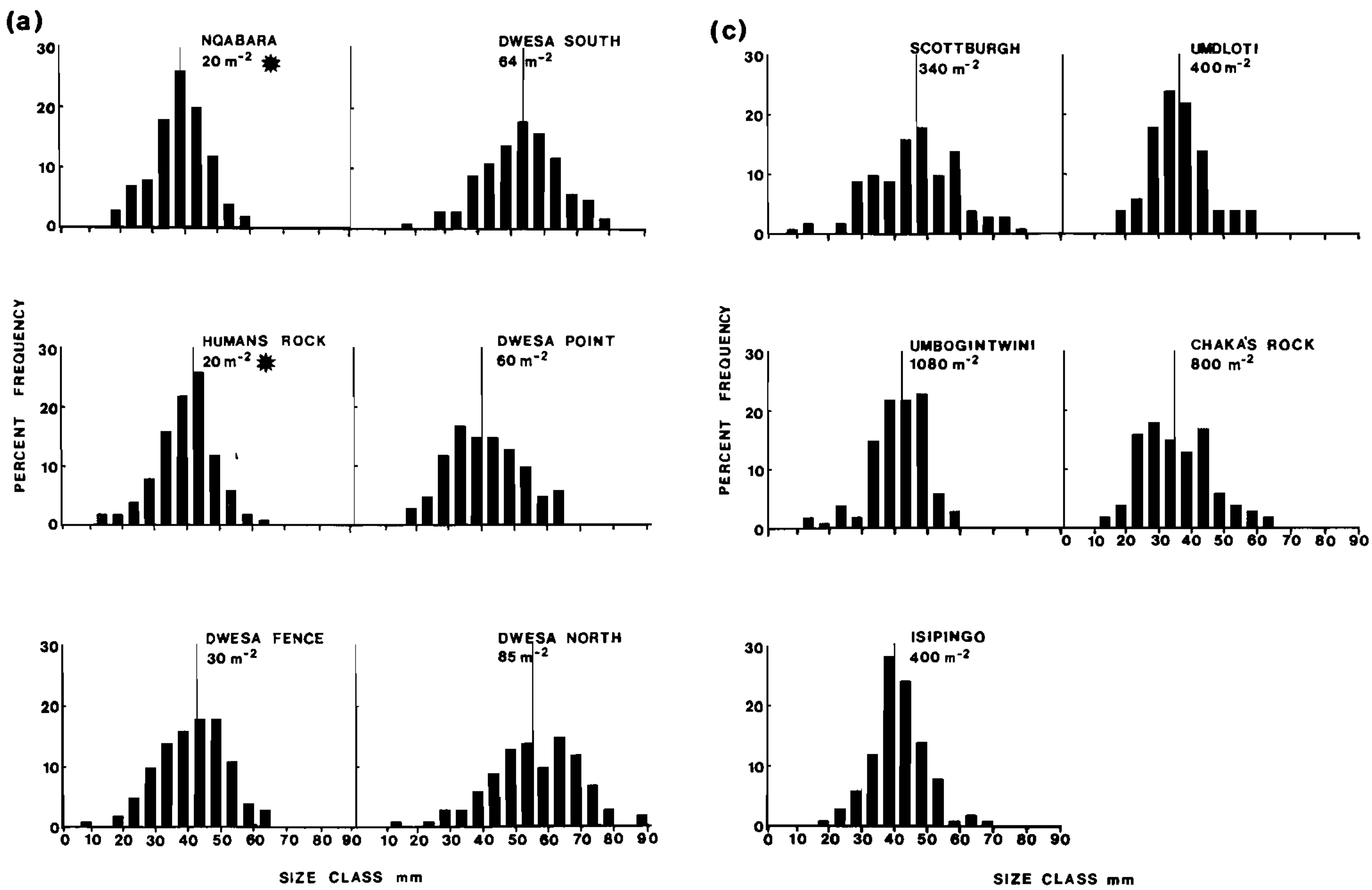


Figure 2a, b & c Size frequency histograms for populations of *Saccostrea cucullata* at 17 sites along the Transkei and Natal coasts. Vertical lines indicate the median, the asterisk indicates exploitated areas in Transkei. Numbers below the site names give the abundance.

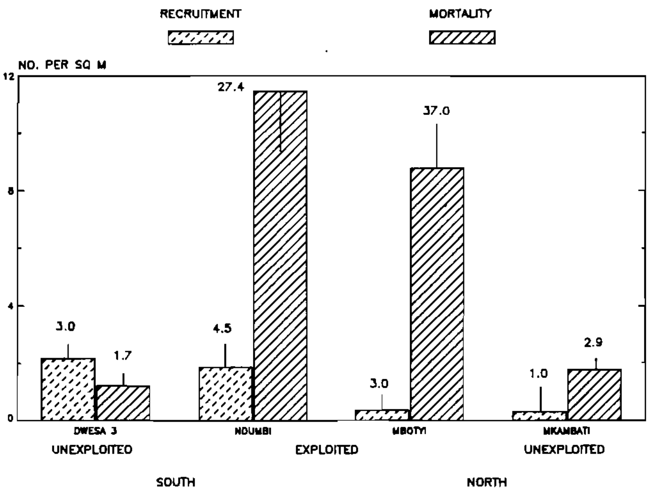


Figure 3 Mean annual recruitment and mortality at two exploited and two protected sites in Transkei. Vertical lines indicate standard deviations (based on three years' data). Numbers indicate recruitment and mortality as percentages of the initial standing stock.

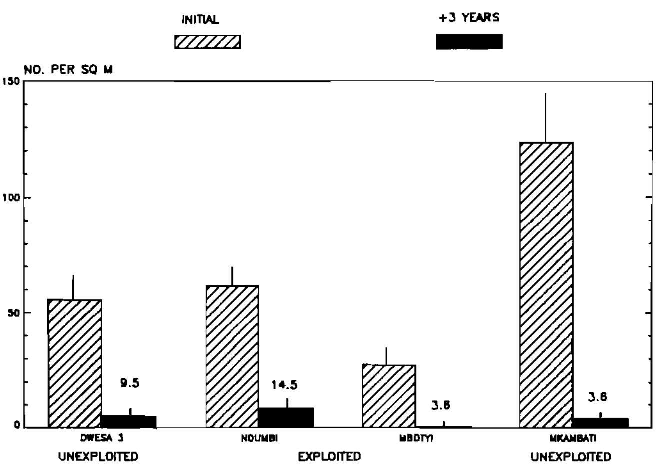


Figure 4 Recovery of experimentally denuded areas in the rock oyster zone in two exploited and two unexploited sites in Transkei. Vertical lines indicate standard deviations (based on 4×1 m^2 areas at each site). Numbers indicate recovery as percentages of the initial standing stock.

shown to be important in this regard on British shores (Barnes 1956; Hawkins & Hartnoll 1982; Kendall, Bowman, Williamson & Lewis 1982). The prevailing wind at the time of settlement of *S. cucullata* (April/May), being longshore from the south and south-west, would be expected to retain larvae inshore and thereby enhance the chances of successful settlement.

There appears to be no shortage of suitable settlement sites for *S. cucullata* on the Transkei coast. Rarely do rock oysters cover more than 50% of available rock surface in the upper balanoid zone. This area is characterized by a mosaic of sessile organisms and open space grazed by a variety of limpets and other gastropods. This is in contrast to the situation described by Van Someren & Whitehead (1961) in Kenya where *S.*

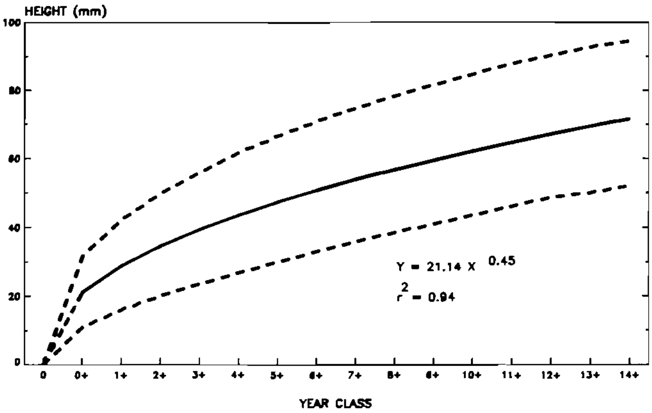


Figure 5 Composite growth curves for *Saccostrea cucullata* showing maximum, mean and minimum growth with the mean growth equation. The curves are extrapolated beyond five years to show the estimated age of the largest individuals found (± 90 mm).

cucullata settles on mangrove prop roots and the odd rocky outcrop. Suitable settlement sites are scarce and this results in poor recruitment. They surmised that the existing standing stock was the result of the slow accumulation of long-lived individuals into the population. Unless there is an intrinsically high planktonic mortality of *S. cucullata* off the Transkei coast it would seem that poor post-settlement survival is the primary cause of low recruitment in this area. The situation may be somewhat different in Natal where the density of rock oysters can approach 1000 m^{-2} (> 80% cover). Here intraspecific competition for space may be a significant factor affecting recruitment.

Numerous factors affect post-settlement survival. The most important physical factors are high rock surface temperature during hot days and associated desiccation stresses. Temperature extremes have been shown to play an important role in the survival of barnacle cyprids (Lewis 1986). The grazing activity of limpets and other molluscs is probably one of the most important biological factors affecting survival of spat (Branch 1981). Limpets are important grazers in the upper balanoid zone and reach densities of 28–105 m^{-2} (Dye 1988). They constitute a source of 'indirect predation' by bulldozing newly settled larvae (Branch 1981; Denley & Underwood 1979; Underwood, Denley & Moran 1983). Only those individuals which settle in crevices or small depressions in the rock surface, or which grow rapidly to a size which exceeds the range over which bulldozing is effective, will survive and recruit into the adult population. This number appears to be very small. The major molluscan predators are *Thais dubia* and *Morula granulata* and although no accurate estimates of their abundance in this region have been made, the low 'natural' mortality found in nature reserves suggests that their effect is minimal.

Comparable data on growth are scarce since growth studies are usually made under culture conditions and refer to increments in tissue weight or volume rather than length (Potter 1983; Ramos, Nascimento Silva

1986; Nell & Holliday 1988). However, Van Someren & Whitehead (1961) measured size increments of *S. cucullata* spat on artificial substrata and obtained rates equivalent to 80 mm y^{-1}. This is approximately four times the rate for the first year of growth in Transkei populations and may be ascribed to the consistently higher water temperature off the Kenyan coast. Unfortunately their study did not extend beyond the first year of growth. The present study indicates that *S. cucullata* is particularly long-lived and may reach 20 years. Based on median size, however, the average age of rock oysters along the Transkei coast is only six years.

Low recruitment and slow growth results in an apparently unimodal size structure with few small individuals. The idea of a slow accumulation of long-lived individuals is attractive and would certainly explain the observed population size structure at most of the sites studied. Strictly speaking the populations are multi-modal but the number of new recruits is too low and growth rates too slow for the modes to be discrete.

It is difficult to explain the differences in population size distribution between protected and exploited sites since variations of an equal magnitude occur within protected areas. It could be argued that in exploited areas the larger animals are preferentially selected leaving 'young' populations with median sizes considerably smaller than those in nature reserves. The lower limit for selection appears to be 35 mm, at which size the animals are approximately three years old. Presumably animals smaller than this yield insufficient flesh to make collection worthwhile. Since individuals as small as 17 mm have been found with developed gonads (Dye pers. obs.), it is likely that the animals are reproductively active well below the size at which they are first exploited. Some recruitment can therefore be expected even in heavily exploited areas but reproductive output as a whole will be lower than in unexploited populations.

Human exploitation cannot be invoked to explain the differences in size distribution of rock oysters in the Dwesa Nature Reserve. At sites such as Dwesa Fence and Dwesa Point, the size structure is characteristic of heavy exploitation. There are two possible explanations for this. On one hand growth rate may vary between sites, possibly as a result of slight differences in elevation which affect the duration of submergence and food intake, or because of differences in food quality between sites. The populations would thus be approximately the same age but the median and maximum size would be variable. Growth was mesaured only at Dwesa North and Mkambati and although they did not differ the possibility of differential growth within Dwesa cannot be ruled out. On the other hand, if growth does not vary significantly, there must be differences in the age of these populations. In that case the largest individuals at Dwesa Fence and Dwesa Point may have settled 8 to 10 years ago, while the majority will be only 4 to 5 years old. This is compared with a median age of 7 to 8 years and a maximum of 20 years at the other site in the reserve. Given the poor recruitment of this species it is possible that localized extinctions may have occurred in the past. If such areas subsequently experience relatively good recruitment, then the populations will be smaller and younger than juxtaposed populations. Unfortunately no long-term data are available for such sites and it is not known whether periods of unusually successful recruitment have occurred in the recent past. No such events have been noted in the other sites which have been monitored since 1982.

Most of the rock oyster populations surveyed in Natal resemble those at exploited sites in Transkei. One important difference between the two areas is the much higher density of oysters in Natal. This may result in competition for space and place an upper limit on size which in turn may offset the enhanced growth expected in warmer waters (Van Someren & Whitehead 1961; Ramos *et al.* 1986). There may be a greater turnover of *S. cucullata* in Natal, with individuals having a higher growth rate but a shorter life span than in Transkei. In the absence of long-term demographic data, however, this must remain speculative.

Whatever the reason for variations in size between areas, the results suggest that no simple relationship exists between population size structure and the degree of exploitation. While exploited sites will always exhibit a truncated size spectrum, the converse, namely that protected sites will always have a wide size range including very large individuals, is not true. In recent years there have been several attempts to assess the effect of human exploitation on rocky shores by comparing population and community structure on exploited and unexploited sites (Moreno, Sutherland & Jara 1984; Castilla & Duran 1985; Siegfried, Hockey & Crowe 1985; Hockey & Bosman 1986; Oliva & Castilla 1986). This assumes that human interference is the major difference between such sites. The foregoing discussion, however, indicates that significant intrinsic differences between populations exist. Hockey & Bosman (1986) used *inter alia* the population size structure of *S. cucullata* on protected and exploited shores to illustrate the effect of human exploitation in Transkei. Although it may be logical to expect that exploitation will reduce the abundance and maximum size of individuals, interpretation of the results of such surveys is difficult without a knowledge of past recruitment patterns.

Acknowledgements

This research was supported by a grant from the University of Transkei. Dr A.J. De Freitas and Ms L. Martin of the Oceanographic Research Institute are thanked for their assistance and transport during the Natal phase of the work. Dr T.A. Lasiak is thanked for assistance during the course of the work and, along with Dr W. Emmerson, provided constructive criticism of the manuscript.

References

BARNES, H. 1956. *Balanus balanoides* in the Firth of Clyde, the development and annual variations of the larval population and causitive factors. *J. anim. Ecol.* 25: 72–84.

BRANCH, G.M. 1981. The biology of limpets: physical factors, energy-flow and ecological interactions. *Oceanogr. Mar. Biol. Ann. Rev.* 19: 235–379.

CASTILLA, J.C. & DURAN, L.R. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Choncholepas choncholepas* (Gastropoda). *Oikos* 45: 391–399.

CONOVER, W.J. 1980. Practical Non-parametric Statistics. (2nd Ed.) John Wiley, New York.

DENLEY, E.J. & UNDERWOOD, A.J. 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. *J. Exp. Mar. Biol. Ecol.* 36: 269–293.

DYE, A.H. 1988. Rocky shore surveillance on the Transkei coast southern Africa: Temporal and spatial variability in the balanoid zone at Dwesa. *S. Afr. J. mar. Sci.* 7: 87–99.

HAWKINS, S.J. & HARTNOLL, R.G. 1982. Settlement patterns of *Semibalanus balanoides* in the Isle of Man. *J. Exp. Mar. Biol. Ecol.* 62: 271–283.

HOCKEY, P.A.R. & BOSMAN, A.L. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* 46: 3–14.

KENDALL, M.A., BOWMAN, R.S., WILLIAMSON, P. & LEWIS, J.R. 1982. Settlement patterns, density and stability in the barnacle *Balanus balanoides*. *Neth. J. Sea Res.* 16: 119–126.

KILBURN, R. & RIPPEY, E. 1982. Sea Shells of Southern Africa. Macmillan, South Africa.

LASIAK, T.A. 1986. The reproductive cycles of the intertidal bivalves *Crassostrea cucullata* (Born, 1778) and *Perna perna* (Linnaeus, 1758) from the Transkei coast, southern Africa. *Veliger* 29: 226–230.

LEWIS, J.R. 1986. Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiologia* 142: 1–13.

MILLS, C.G. 1985. Shellfish utilization and its effect on rocky shore biota in Transkei. M.Sc thesis, University of Cape Town.

MORENO, C.A., SUTHERLAND, J.P. & JARA, H.F. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* 42: 155–160.

NELL, J.A. & HOLLIDAY, J.E. 1988. Effects of salinity on the growth and survival of the Sydney rock oyster (*Saccostrea commercialis*) and Pacific oyster (*Crassostrea gigas*) larvae and spat. *Aquaculture* 68: 39–44.

OLIVA, D. & CASTILLA, J.C. 1986. The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *P.S.Z.N.I. Mar. Ecol.* 7: 201–217.

POTTER, M.A. 1983. Growth rates of cultivated Sydney rock oysters, *Saccostrea (Crassostrea) commercialis*, in two estuaries in subtropical southern Queensland. *Qld. J. Agric. Anim. Sci.* 40: 137–140.

RAMOS, M.I.S., NASCIEMENTO, I.A. & SILVA, J. 1986. The comparative growth survival of Pacific oyster (*Crassostrea gigas* Thunberg, *C. gigas* var. *kumamoto*) and mangrove oyster (*C. rhizophorae*) in Todos os Santos Bay, Brazil. *Cientia e Cultura* 38: 1604–1615.

SIEGFRIED, W.R., HOCKEY, P.A.R. & CROWE, A.A. 1985. Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Env. Cons.* 12: 303–307.

UNDERWOOD, A.J., DENLEY, E.J. & MORAN, M.J. 1983. Experimental analysis of the structure and dynamics of rocky intertidal communities in New South Wales. *Oecologia* 56: 202–219.

VAN SOMEREN, W.R. & WHITEHEAD, B.A. 1961. An investigation of the biology and culture of an East African oyster *Crassostrea cucullata*. *Fish. Publ. Lond.* 14: 1–41.