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TEMPORAL AND SPATIAL VARIATIONS IN EXPLOITED AND NON- EXPLOITED POPULATIONS OF THE INTERTIDAL LIMPET *CELLANA CAPENSIS*

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ABSTRACT

Temporal and spatial variations in the density, size composition and growth of exploited and non-exploited populations of the intertidal limpet *Cellana capensis* from the Transkei coast of southern Africa, between 1989 and 1991, are described. The timing and intensity of recruitment varied between shores and amongst sites within shores. Recruitment success was relatively poor and, in fact, at some of the protected sites no recruitment was recorded until July 1991. Juvenile and adult limpets were both significantly more abundant at the exploited than at the protected sites. The gradual decline in density of limpets observed at the latter sites reflected poor recruitment as well as senescence of older individuals. The extent of variations in density amongst shores was also found to vary from census to census. Limpets at the exploited sites tended to be much smaller than those found at the protected sites. Although there were initially no differences in the size of limpets amongst sites within shores marked differences became apparent during the course of the study. This finding, together with the observation of marked annual differences in population size composition at several of the study sites highlighted the temporal instability of these populations. Such results have profound implications for comparative studies of population size composition.

The absence of significant differences in growth rate amongst shores suggests that differences in the intensity of competitive interactions may have been offset by the higher microalgal production at the exploited shore. It is also suggested that upshore migration of larger individuals may counter the intense competition experienced at mid-tidal levels on the exploited shore. Differences in the rate of recruitment could also account for some of the observed differences in population characteristics. Both of these explanations are viable alternatives to an earlier proposal which attributed differences solely to the effects of size-selective predation by man.

INTRODUCTION

The life history characteristics and population dynamics of intertidal limpets have been extensively documented. Marked intraspecific variations have been noted in a number of species (Sutherland, 1970; Lewis & Bowman, 1975; Bowman & Lewis, 1977; Branch, 1976; Choat, 1977; Creese, 1980; Thompson, 1980; Workman, 1983; Fletcher, 1984a & b, 1987; Bosman & Hockey, 1988a & b). These studies revealed considerable differences in life history characteristics amidst populations at different tidal heights and in different habitats. Although such phenotypic variation is known to be the result of genotypic, environmental and interactive forces most workers have assumed that the populations they are comparing are genotypically similar and have consequently attributed differences solely to environmental parameters. This assumption is based on the premise that isolation of different genotypes among localized habitats is extremely unlikely in marine invertebrates with dispersive larval stages (Jablonski, 1986).

Environmental factors known to influence the population characteristics of limpets include: (1) intraspecific competition, (2) interspecific competition, (3) physical conditions (e.g. height on the shore and exposure to wave action), and (4) differences in food availability (Branch, 1981). The fact that each intertidal population is subject to a unique combination of abiotic and biotic influences, due to the heterogeneous nature of the intertidal environment, has profound implications when attempting to evaluate the role of individual environmental factors. These relate to problems in separating the influence of different environmental factors in field studies. It is difficult to establish whether intraspecific differences observed between habitats are due to the effects of a specific environmental factor, or a combination of factors. Despite these limitations, studies of the potential flexibility of life history patterns of a species are important, especially with reference to the role and interactions of that species in the structure of natural communities (Fletcher, 1987).

Most of the afore-mentioned studies on intraspecific variations are also subject to criticism because they were based on unreplicated or pseudo-replicated designs. In many cases only one population/sub-population was examined at each site and/or in each habitat (Fletcher, 1984a & b, 1987; Bosman & Hockey, 1988a & b). The lack of within-habitat and/or within-shore replication has meant that the variations observed can not be compared statistically and their significance assessed. The purpose of the present study was to obtain information on temporal and spatial variations in density, population size structure and growth of the intertidal limpet *Cellana capensis* (Gmelin, 1791) at three shores on the Transkei coast of southern Africa. The investigation was designed to assess variations within-shores (i.e. between-sites) and between-shores and to examine differences between exploited and non-exploited shores. This limpet is one of the many species of intertidal invertebrates used by the indigenous coastal population to supplement their maize-based diet (Bigalke, 1973; Voigt, 1975; Hockey & Bosman, 1986; Lasiak, 1991, 1992). Relatively little is known of the biology of this species. Branch (1975a) has given a brief description of the geographic distribution, zonation and feeding habits of *C. capensis* and Lasiak (1987, 1990) has outlined the reproductive cycle. Further knowledge of the life history characteristics of various populations of this species is needed to assess the effects of perturbations, such as exploitation, on population dynamics.

METHODS

Three study areas were established between the Nqabara and Kabole rivers on the Transkei coast of southern Africa. Two of these shores, referred to subsequently as I and II, were located within the Dwesa Nature Reserve (32°18′S, 28°50′E) and are therefore protected from the intensive exploitation of shellfish which takes place at the third shore, Nqabara (Fig. 1). On each of these shores three mid-tidal populations of *Cellana capensis*, each separated by a distance of at least 10 m and in most instances >50 m, were selected for study. The terms north, mid and south site will be used to differentiate between the locations of the three populations on each shore. Migration between these populations was limited by topographic features such as cracks in the substratum and gulleys. No interchange of marked individuals between sites within shores was recorded during the present investigation.

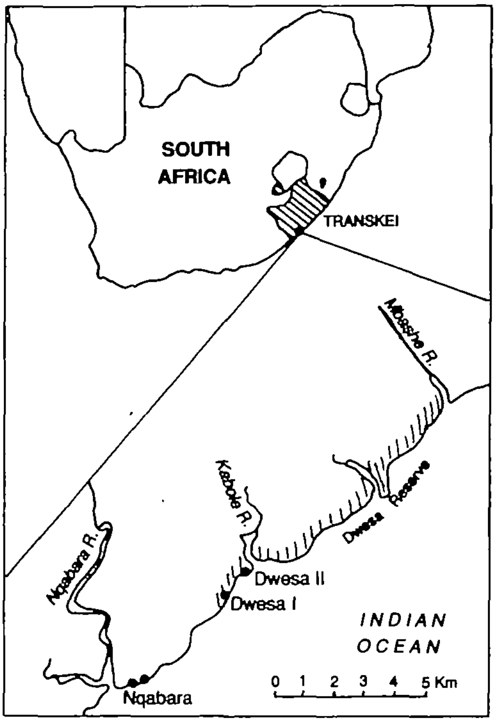


Figure 1. Map showing the position of the three study sites, located between the Nqabara and Kabole rivers, on the Transkei coast of southern Africa.

At quarterly intervals from September 1989 to October 1991 the density of limpets in each of these populations was estimated by counting the number of animals found in 16 randomly placed 50 × 50 cm quadrats. The numbers of recruits (<7.5 mm), juveniles (>7.5 mm and 20 mm) and adults (>20 mm) present in each quadrat were counted. The maximum shell lengths of all individuals found within these quadrats were also recorded, measurements being made to the nearest 0.5 mm with Vernier calipers. These data were used in the compilation of size frequency histograms. Some indication of the growth rate of *C. capensis* was obtained by following the progression of well-defined cohorts in consecutive size frequency histograms. No data were collected between December 1989 and July 1990.

The rate of growth of limpets in each population was determined by monitoring the increment in shell length of individually labelled animals. Initially 50–60 limpets, encompassing the size range available within each population, were marked *in situ* with dymo tags embedded in rapid-setting epoxy glue (Pratleys Quickset White). To maintain the number of tagged individuals in each population above 40, additional limpets were labelled whenever necessary. Every six weeks, from September 1989 to October 1991, the maximum shell lengths of these tagged individuals were measured to the nearest 0.5 mm. On two occasions growth increments could only be assessed after an interval of eight weeks because heavy seas during the previous spring tide had precluded access to the limpet populations. Every 6 to 8 weeks the growth rate of each population of limpets was estimated by means of Ford-Walford plots, in which length of limpet at time *t* is regressed against length at time *t* + *1* according to the equation $L_{t+1} = mL_t + I$, where m = the rate of increase in shell length and I = the vertical intercept (Rao, 1976; Branch, 1981). From these data the mean asymptotic length L_∞, the predicted growth increments and composite growth of 'standard' 30 mm limpets were estimated (Rao, 1976). The investigation of temporal differences in growth rate was based on the predicted daily growth increment because the interval between observations was not consistent.

Temporal and spatial variations in density, size composition and growth of *C. capensis* were examined by means of analyses of variance. The partitioning of spatial variation in density of *C. capensis* on the three shores was examined by means of two-level nested analyses of variance computed for each census date. From the expected mean squares generated in these anovas the variance components were estimated, thus enabling the variation at each spatial scale to be expressed as a percentage of the total variation (Sokal & Rohlf, 1969). As the raw data rarely met the assumptions of normality and/or homogeneity of variances transformation of data was necessary. Details of these transformations are given in the text. As standard transformations of most data sets based on the size of limpet failed to meet the assumptions of analysis of variance the non-parametric Kruskal-Wallis one-way anova by ranks was used to examine temporal and spatial variability in this parameter (Sokal & Rohlf, 1969). Two-level analyses of variance using size of limpet as the covariate could only be computed for the September 1989 and June 1991 data sets.

RESULTS

Density

Although a precise estimate of the recruitment period was not feasible, because of the 3 month interval between censuses, newly-recruited (<7.5 mm) limpets were found to be more abundant during the winter/spring (July–October) period (Fig. 2a). Recruitment success appeared to be relatively poor; the density of recruits never exceeded 3 limpets per m^2 at any of the study sites. The timing and intensity of recruitment varied both among and within shores. Although two major recruitment periods, one per year, were apparent at Dwesa I and Nqabara no significant recruitment was observed at Dwesa II until July 1991. Significant ($p < 0.05$) variations in the density of recruits amongst shores were evident during four of the eight census periods (Table 1). Three of the exceptions, December 1989, January and April 1991, coincided with periods of negligible recruitment. The lack of variation in July 1991 reflects the fact that no data were obtained from Nqabara due to rough seas and that the densities of newly-recruited limpets were similar at the six sites within the reserve.

Table 1. Results of two-level nested analyses of variance based on estimates of the density (log x + 1) of newly-recruited, juvenile and adult *Cellana capensis* recorded at each site during each census (Symbols: F, F-ratio; P, Probability; * denotes significance at $p < 0.05$).

Month	Source of variation	Recruits F	Recruits P	Juveniles F	Juveniles P	Adults F	Adults P
September 1989	Shore	5.95	0.003*	17.80	<0.001*	3.35	0.038*
	Site {shore}	0.20	0.977	2.49	0.026*	2.12	0.055
December 1989	Shore	1.00	0.371	14.49	<0.001*	1.77	0.174
	Site {shore}	1.00	0.428	1.94	0.079	1.21	0.306
July 1990	Shore	5.00	0.008*	49.83	<0.001*	2.00	0.140
	Site {shore}	3.64	0.002*	1.11	0.363	2.68	0.018*
October 1990	Shore	5.97	0.003*	29.95	<0.001*	29.24	<0.001*
	Site {shore}	2.49	0.026*	0.29	0.941	1.69	0.127
January 1991	Shore	—	—	11.99	<0.001*	9.95	<0.001*
	Site {shore}	—	—	3.68	0.002*	1.84	0.096
April 1991	Shore	1.00	0.371	7.71	0.001*	21.49	<0.001*
	Site {shore}	1.00	0.428	1.24	0.290	3.37	0.004*
July 1991	Shore	0.11	0.744	0.77	0.384	2.08	0.152
	Site {shore}	0.66	0.620	1.22	0.309	3.57	0.009*
October 1991	Shore	5.05	0.008*	53.95	<0.001*	83.04	<0.001*
	Site {shore}	1.85	0.094	4.08	0.001*	4.24	0.001*

Significant variations in the density of recruits amongst sites within shores were recorded on only two occasions (July and October 1990) (Table 1). The absence of recruits at Dwesa I north and Nqabara north in July 1990 suggests that recruitment is not concomitant at all sites. No consistent trends in recruitment amongst sites within particular shores were evident other than a tendency for recruitment to be more intense at Nqabara mid than at the two adjacent sites.

Variations in the density of recruits attributable to differences amongst shores and amongst sites within shores were relatively low, ranging from 0–10.1% and from 0–16.2% respectively. The marked variation (80.9–100%) observed amongst replicate quadrats reflects the patchy distribution of recruits in the field (Table 2). Recruitment as a function of time and space was examined by means of two-way analysis of variance using estimates of the mean density of recruits at each site as replicates per shore ($n = 3$) (Table 3). Although this showed that the density of recruits varied both with time and shore the interaction between these factors was fairly weak ($0.05 < p < 0.10$). The latter result does, however, indicate that differences amongst shores in the density of recruits changed from census to census.

The Nqabara sites supported the highest densities of juvenile (7.5–20 mm) limpets, numbers found ranged between 1 and 20 per m^2 at the northern site, from 2–38 per m^2 at the mid site and from 2–24 per m^2 at the southern site. At Dwesa II, where the lowest densities (0–5 per m^2) of juvenile *C. capensis* were recorded, there was little variation amongst sites. Intermediate densities of juveniles were present at Dwesa I, numbers ranged between 1 and 7 per m^2 at the southern site, from 0–9 per m^2 at the mid site and from 1–11 per m^2 at the northernmost site (Fig. 2b). The peaks in density of juveniles observed around July–October generally corresponded with or followed periods of peak recruitment. The increase in density of juveniles at two of the Nqabara sites in July 1990, which apparently preceded the peak of recruitment, suggests that an earlier recruitment event may have been overlooked due to the three month interval between censuses.

Two-level nested analyses of variance indicated that variations in the density of juvenile *C. capensis* amongst shores were significant on all census dates except for July 1991 when comparisons were based only on the shores within the reserve. Significant variations in the density of juvenile limpets amongst sites within shores were observed only in September 1989, January and October 1991 (Table 1). The variation in the density of juveniles amongst shores (1.4–53.5%) was generally greater than that amongst sites within shores (0.3–12.5%) (Table 2). As in the case of recruits differences amongst replicates accounted for most (44.8–97.3%) of the spatial variation. A two-way anova showed that the variations in density of juvenile limpets associated with the factors time and shore were significant and that the interaction term was also significant (Table 3). The latter finding indicates that the differences amongst shores in the mean density of juveniles changed from census to census.

The Nqabara shore also supported the highest densities of adult (>20 mm) limpets. Densities varied considerably amongst sites, ranging from 4–21 per m^2 at the northern site, between 6 and 30 per m^2 at the mid site and from 15–37 per m^2 at the southern site. The numbers of adult *C. capensis* recorded at the six Dwesa sites were similar. Densities varied between 1 and 24 per m^2 at Dwesa I and from 2–18 per m^2 at Dwesa II (Fig. 2c). Little within-shore variation was evident at the latter. Adult densities increased during the winter/spring period, reached a peak in summer and then declined. As the increase in density of adults coincided with the decline in density of juveniles it is assumed that these trends reflect juvenile limpets attaining adult size. During the course of the study the density of adult limpets at Dwesa I and II showed a gradual decline, such trends were not evident at the exploited shore.

Two-level nested analyses of variance indicated that variations in the density of adult *C. capensis* amongst shores were significant on all occasions except for December 1989, July 1990 and 1991. Significant variations in the density of adults between sites within shores were found in September 1989, July 1990, April, July and October 1991 (Table 1). Differences amongst shores accounted for between 1.2 and 57.7% of the spatial variation in density of adult limpets. This marked variation reflects differences in the number of adults present at the various census times. Although spatial variation attributed to sites within shores was relatively low (1.3–13.4%) on some census dates (September and December 1989, July 1990 and 1991) it exceeded that attributed to differences amongst shores. Most of the spatial variation in density of adult limpets was associated with differences amongst replicate quadrats (Table 2). Two-way anova revealed that density of adult limpets varied with time and shore and that the

Table 2. The percentage variation in density of recruit, juvenile and adult *Cellana capensis* at each of the spatial scales examined.

Density of recruits

Source of variation	Percentage variation							
	Sep 89	Dec 89	Jul 90	Oct 90	Jan 91	Apr 91	Jul 91	Oct 91
Shores	10.1	0.0	2.9	5.9	—	0.0	1.6	7.1
Sites	4.4	0.0	16.2	8.2	—	0.0	2.1	3.6
Replicates	85.5	100.0	80.9	85.9	—	100.0	96.3	89.3

Density of juveniles

Source of variation	Percentage variation							
	Sep 89	Dec 89	Jul 90	Oct 90	Jan 91	Apr 91	Jul 91	Oct 91
Shores	22.6	19.8	53.5	37.1	12.8	11.4	1.4	46.5
Sites	6.6	4.4	0.3	2.7	12.5	1.6	1.4	8.6
Replicates	70.8	75.8	46.2	60.2	74.7	87.0	97.2	44.8

Density of adults

Source of variation	Percentage variation							
	Sep 89	Dec 89	Jul 90	Oct 90	Jan 91	Apr 91	Jul 91	Oct 91
Shores	2.4	1.2	1.5	35.6	13.8	24.8	3.7	57.7
Sites	6.4	1.3	10.7	2.7	4.3	9.6	13.4	7.2
Replicates	91.2	97.6	87.8	61.7	81.9	65.6	82.9	35.1

Table 3. Summary of two-factor analyses of variance based on estimates of density (log x + 1) of recruit, juvenile and adult *Cellana capensis* with factors time (census dates) and shore (Symbols: SS, sum of squares; DF, degrees of freedom; MS, mean squares; P, probability).

Density of recruits

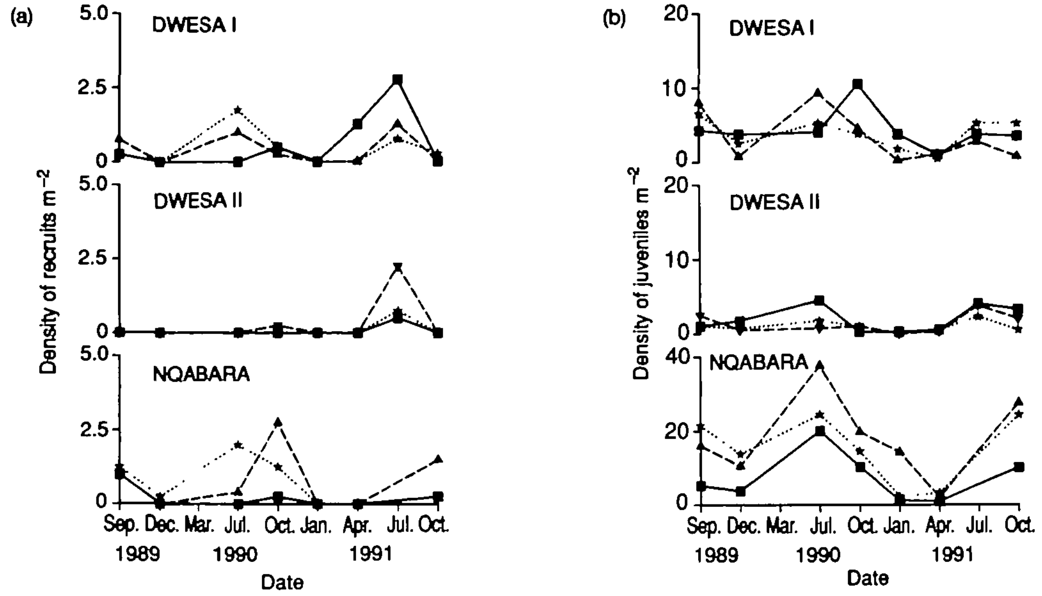
Source of variation	SS	DF	MS	F-ratio	P
Time	1.534	6	0.256	3.920	0.003
Shore	1.311	2	0.656	10.055	<0.001
Time* Shore	1.341	12	0.112	1.714	0.098
Error	2.738	42	0.065		

Density of juveniles

Source of variation	SS	DF	MS	F-ratio	P
Time	12.222	6	2.037	8.385	<0.001
Shore	27.295	2	13.647	56.173	<0.001
Time* Shore	6.878	12	0.573	2.359	0.020
Error	10.204	42	0.243		

Density of adults

Source of variation	SS	DF	MS	F-ratio	P
Time	6.716	6	1.119	7.988	<0.001
Shore	7.783	2	3.892	27.771	<0.001
Time* Shore	5.145	12	0.429	3.059	0.004
Error	5.886	42	0.140		



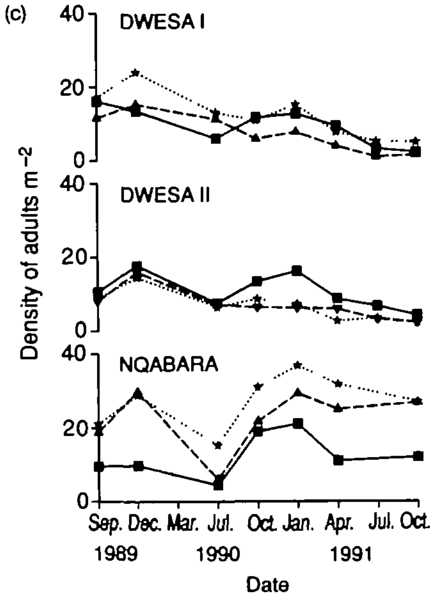


Figure 2. Fluctuations in the density of (a) newly-recruited, (b) juvenile and (c) adult *Cellana capensis* per m^2 observed at each of the study sites (The symbols, square, triangle and star represent trends at the northern, mid and southern sites on each shore respectively.)

interaction term was also significant (Table 3). The latter finding indicates that differences amongst shores in the mean density of adult limpets also changed from census to census.

Size

There were marked differences in the size of *C. capensis* found at the nine study sites (Table 4). Limpets from Nqabara were generally smaller than those from Dwesa. The greatest minimum, maximum and mean sizes recorded at Nqabara were 15.0, 39.5 and 28.3 mm respectively; whereas at Dwesa I and II the corresponding sizes were 17.5, 51.5 and 32.2 mm and 24.5, 50.0 and 33.4 mm respectively.

The two-level nested anovas based on size of limpets measured in September 1989 and June 1991 (Table 5) indicate there were significant variations in size of *C. capensis* amongst shores as well as among sites within shores. This implies that observations made at one site cannot be used to predict the size of limpets found at either nearby sites or on adjacent shores. A similar argument also applies to the prediction of densities. The Kruskal-Wallis tests revealed significant variation in the size of limpets among sites on all sampling dates but the last (October 1991). Subsequent pairwise multiple comparisons indicated that initially there were no significant differences among sites within each of the shores (Table 6). However, marked differences in size became apparent later in the study, particularly at Nqabara and Dwesa I. Differences in the size of *C. capensis* found at Dwesa II remained non-significant until June 1991. Kruskal-Wallis one-way anovas based on the size of limpets recorded in censuses separated by intervals of a year (i.e. September 1989, October 1990 and 1991) revealed significant differences in population size composition at five of the nine study sites (Table 7). Visual inspection of the pertinent size frequency distributions for the four sites within the Dwesa nature reserve (Fig. 3a–d) reveal a shift in the predominant size classes with smaller limpets becoming more important as a result of senescence of the larger, older limpets. At Nqabara south, however, significant differences reflect the fact that the proportion of juvenile and adult limpets fluctuated markedly from one year to the next (Fig. 3e).

Table 4. Minimum, maximum and mean size of *Cellana capensis* found at each of the nine study sites. Data presented are the range of values observed during the study period.

	Size range (mm		
Site	Minimum	Maximum	Mean
Nqabara N	6.5–14.5	31.0–39.5	16.6–28.3
Nqabara M	4.5–15.0	32.5–37.5	15.1–26.2
Nqabara S	5.0–13.5	32.0–36.0	18.6–26.5
Dwesa I N	5.5–12.5	35.0–50.5	17.6–27.7
Dwesa I M	5.5–17.5	41.0–51.5	14.2–32.2
Dwesa I S	6.0–15.5	38.0–40.5	20.2–30.2
Dwesa II N	5.0–17.0	34.5–50.0	22.6–33.0
Dwesa II M	5.5–22.5	37.5–46.0	17.6–33.0
Dwesa II S	5.5–24.5	36.5–41.5	23.1–33.4

Table 5. Results of two-level nested analyses of variance based on size of *Cellana capensis* found at each site (Symbols: as in Table 3).

			September 1989		
Source of variation	SS	DF	MS	F-ratio	P
Shore	7183.86	2	3591.93	68.89	<0.001
Site {shore}	1736.47	6	289.41	5.55	<0.001
Error	39471.20	757	52.14		
			June 1991		
Source of variation	SS	DF	MS	F-ratio	P
Shore	1166.90	1	1166.90	7.83	0.006
Site {shore}	1905.24	4	476.31	3.20	0.014
Error	30843.51	207	149.00		

Table 6. Results of Kruskal-Wallis one-way analyses of variance and subsequent multiple comparisons based on the variate size of *Cellana capensis* (Symbols: H, Kruskal-Wallis Test statistic; P, probability, DF, degrees of freedom; n.s., non significant at $p > 0.05$; and * denotes significance at $p < 0.05$).

Date	H	P	DF	Differences: sites within shores		
				Nqb	DI	DII
Sep 89	39.79	<0.0001	8	n.s.	n.s.	n.s.
Dec 89	214.27	<0.0001	8	n.s.	*	n.s.
Jul 90	115.19	<0.0001	8	*	n.s.	n.s.
Oct 90	130.69	<0.0001	8	*	*	n.s.
Jan 91	196.22	<0.0001	8	*	*	n.s.
Apr 91	105.05	<0.0001	8	*	n.s.	n.s.
Jun 91	21.14	0.0008	5	—	*	*
Oct 91	10.82	0.2100	8	not applicable		

Table 7. Results of Kruskal-Wallis one-way analyses of variance based on the size of *Cellana capensis* recorded at each site during censuses taken approximately 12 months apart. (Symbols as in Table 6.)

Site	H	DF	P
Dwesa I north	13.78	2	0.001*
Dwesa I mid	0.54	2	0.762
Dwesa I south	15.75	2	<0.001*
Dwesa II north	24.12	2	<0.001*
Dwesa II mid	11.75	2	0.003*
Dwesa II south	1.14	2	0.565
Nqabara north	0.86	2	0.652
Nqabara mid	1.59	2	0.453
Nqabara south	21.12	2	<0.001*

Growth

The methodology of following cohorts through the quarterly size frequency distributions to obtain estimates of annual growth rate was of limited application. This was due partly to the relatively low density of *C. capensis* and rapid merging of cohorts, particularly at the Dwesa sites, and also to the time interval (>3 months) between censuses. The absence of a cohort common to all sites precluded comparisons of the growth of a particular size class across shores. From July 1990 until April 1991 it was possible to follow the progression of a distinct cohort at each of the three Nqabara sites. During this period the modal length of the cohort increased from 12.5–15 mm to 27.5–30 mm at two of the sites and from 15–17.5 mm to 27.5–30 mm at the third site.

Growth estimates obtained by monitoring the growth of marked limpets and calculation of Ford-Walford plots, indicate relatively little difference between years in the predicted increment of a 'standard' 30 mm limpet (Table 8). The major exception being Nqabara north, where the predicted annual increment decreased from 8.95 mm in 1989/1990 to 5.84 mm in 1990/1991. Marked differences in predicted increments, however, were evident amongst sites within shores, particularly at Dwesa I and Nqabara. The estimated mean asymptotic length (L_∞) was in close accordance with the maximum size of *C. capensis* observed at all sites except for Dwesa II north and Nqabara south.

Despite some variability similar temporal trends in rate of growth were apparent at all study sites (Fig. 4). From October/December 1989 until June 1990 the daily growth increment declined gradually, from June 1990 until the following February/March the rate of growth generally increased. A second period of decline was evident between February/March and June/July 1991, thereafter to the end of the study the rate of growth tended to increase. One-way analysis of variance, based on m, the rate of increase in length, revealed no significant differences in the rate of growth of *Cellana capensis* amongst sites within shores. Two-way analysis of variance, using time and shore as factors and estimates of rate of increment (m) from each site as replicates, indicated significant temporal differences but no significant variation amongst shores and no significant interaction between time and shore (Table 9). Subsequent Tukey HSD multiple comparisons suggested that the temporal differences in growth rate were fairly weak (p >0.15).

DISCUSSION

Hockey & Bosman (1986) attributed differences in the population size structure of *C. capensis* on exploited and protected shores in Transkei to the effects of size-selective predation by the indigenous coastal people. Their conclusion was based on the observation that the specimens of *C. capensis* discarded in shell middens were, on average, significantly larger than those found on an adjacent rocky shore. The fact that a concomitant reduction in the density of this limpet on exploited shores has not been demonstrated (Hockey & Bosman, 1986; Lasiak, 1991; Lasiak, this study), however, suggests that this species may not be subject to as intense exploitation as some of the other organisms taken. Detailed analyses of trends in midden composition suggest that *C. capensis* is certainly not a major component of the diet of the indigenous people. This conclusion was based on the facts that the frequency of occurrence of this species in middens never exceeded 50% and that significant numbers (>100) have been recorded on only a few occasions. Lasiak (1992) has suggested that the presence of these limpets in middens probably represents part of an opportunistic rather than a targeted foraging strategy. Several informants in the present study area have confirmed that *C. capensis* are taken only when mussels, the preferred food, are unavailable due to heavy seas. Such observations prompt the question: Is the intensity of exploitation of *C. capensis* sufficient to cause the observed differences in population size composition?

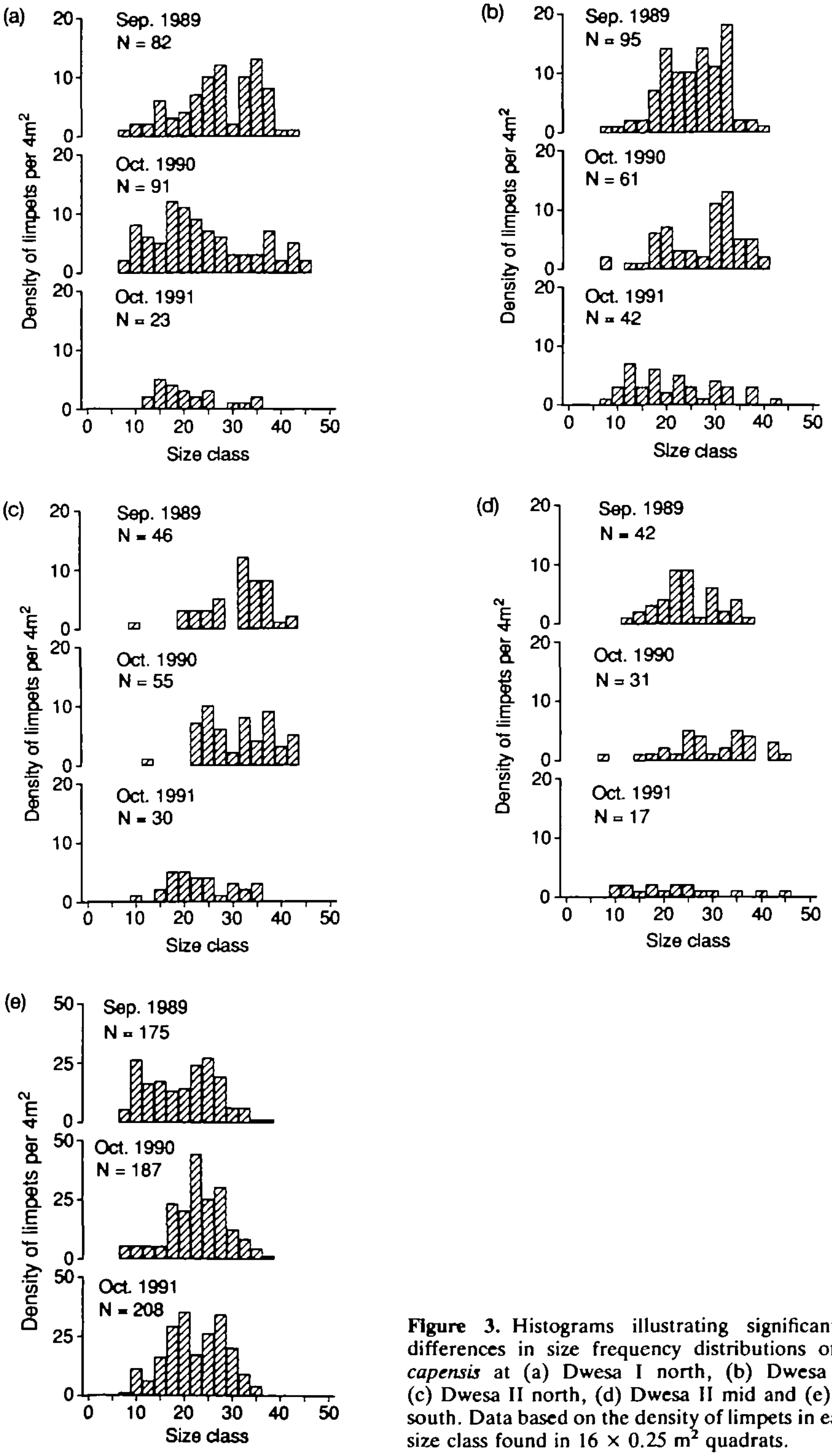


Figure 3. Histograms illustrating significant annual differences in size frequency distributions of *Cellana capensis* at (a) Dwesa I north, (b) Dwesa I south, (c) Dwesa II north, (d) Dwesa II mid and (e) Nqabara south. Data based on the density of limpets in each 5 mm size class found in 16 × 0.25 m^2 quadrats.

Table 8. Predicted mean L∝ for each site and the predicted increments of a 30 mm *Cellana capensis* at each site after a period of eight months in each of the two years of observations. This time period was chosen as it was common to all sites. Annual estimates shown in brackets were not available for all sites.

Site	Mean L∝	Predicted increment (mm)	
		1989/1990	1990/1991
Dwesa I north	48.9	9.35 (12.04)	9.92 (12.06)
Dwesa I mid	53.5	9.13 (11.64)	8.69
Dwesa I south	40.0	4.90 (6.70)	6.14 (7.56)
Dwesa II north	43.8	5.94 (7.93)	6.63 (9.44)
Dwesa II mid	45.3	7.69 (9.23)	6.58 (9.18)
Dwesa II south	39.6	5.55 (6.79)	6.62 (7.79)
Nqabara north	40.9	10.19 (8.95)	5.41 (5.84)
Nqabara mid	39.0	4.75	6.54 (7.98)
Nqabara south	41.1	6.36	4.77

Lasiak & Dye (1989) have also questioned the recent tendency to assign differences in the population size composition and/or community structure of protected and exploited shores solely to the effects of human intervention. They have pointed out that a number of other, potentially confounding factors, need to be taken into consideration. These include differences in the intensity of settlement/recruitment, intra- and interspecific interactions, food availability as well as sources of mortality other than human predation. An appreciation of temporal and spatial variability in various aspects of population dynamics is undoubtedly of paramount importance. The present study is the first to examine (a) whether the differences between exploited and protected populations of *C. capensis* in Transkei are consistent amongst sites within shores and (b) whether these differences are consistent on a temporal scale.

Marked spatial and temporal differences in several population parameters were recorded. Significant variations in the density of recruit, juvenile and adult *C. capensis* amongst shores were evident throughout most of the study period. On some occasions significant variations in density amongst sites within shores were also observed, these were recorded more frequently in adult limpets than in either

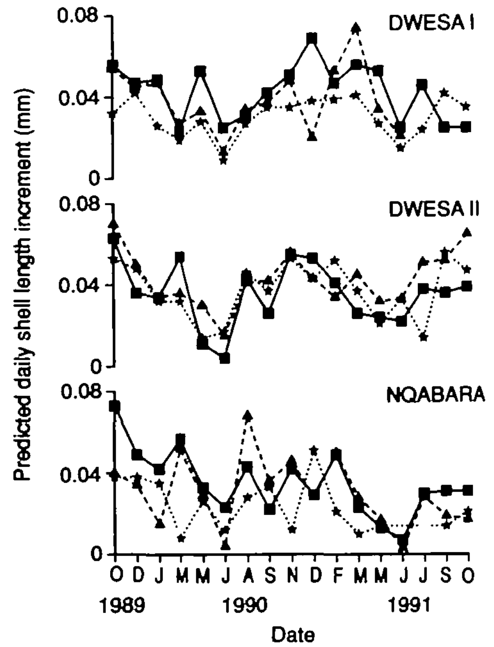


Figure 4. Temporal fluctuations in the growth of *Cellana capensis* at (a) Dwesa I, (b) Dwesa II and (c) Nqabara. Data are expressed as mean daily increment (mm) of a 'standard' 30 mm limpet (symbols as in Figure 2).

Table 9. Two-way analysis of variance based on growth rate estimates at each site and factors time and shore. Only the sampling dates that were common to all sites were used in these analyses. (Symbols: as in Table 3.)

Source of variation	SS	DF	MS	F	P
Time	0.144	10	0.014	2.004	0.047
Shore	0.020	2	0.010	1.394	0.255
Time*Shore	0.211	20	0.011	1.468	0.124
Error	0.474	66	0.007		

recruits or juveniles. The extent of the variations in density amongst shores varied from census to census. Such temporal fluctuations in density probably reflect changes in very local conditions as well as general fluctuations in annual recruitment (Lewis & Bowman, 1975). One of the most surprising observations was the fact that there was no evidence of a decline in the density of *C. capensis* populations at Nqabara as might have been expected from their exploited status. A steady decline in the density of limpet populations on the non-exploited shores, however, was noted. The latter was apparently due to poor recruitment coupled with senescence of older limpets.

Further evidence of the instability of the *C. capensis* populations comes from the examination of trends in size composition. Although significant differences in size of limpets amongst sites within shores were not detected initially marked differences became apparent during the course of the study, particularly at Nqabara and Dwesa I. This finding, together with the observation of marked annual differences in the length frequency distributions of several populations has serious implications for comparative studies of population size composition. Comparisons based on a single period of observation, such as those of Hockey & Bosman (1986) should clearly be treated with caution as the reliability of observed differences can not be established. An appreciation of the effects of temporal fluctuations in the various parameters (recruitment, age structure, growth rate and longevity) which influence the form of length frequency distributions is clearly a prerequisite for determining the diagnostic value of any particular size frequency histogram.

Variations in the size of individuals of different populations of the same species have been correlated previously with both intra- and interspecific competition (Sutherland, 1970; Lewis & Bowman, 1975; Underwood, 1976; Creese, 1980). Recent studies (Lasiak & White, in press) have demonstrated that strong intraspecific effects amongst enhanced densities of *C. capensis* lead to increased mortality and reductions in the rate of growth and tissue weight. The fact that *C. capensis* and other intertidal grazers (Dye & White, 1991) are far more abundant at Nqabara suggests that competitive interactions generally may be more intense on this shore than at Dwesa. The smaller size attained by limpets at Nqabara may therefore simply be a consequence of the intensity of competitive interactions on this shore. The fact that no significant difference in the growth rate of *C. capensis* amongst shores was found, however, suggests that the competitive effects associated with the enhanced densities of grazers may have been offset by the higher microalgal production at Nqabara (Dye & White, 1991). Likewise, the potential increase in intraspecific effects brought about by the increase in density during the winter/spring recruitment may be ameliorated by the higher microalgal production at that time of year. In some species of limpets the effects of competition may be countered by upshore migrations (Breen, 1972; Branch, 1975b; Mackay & Underwood, 1977). As these limpets generally migrate upshore as they age such behaviour leads to the establishment of vertical size gradients with the largest animals found highest on the shore. A similar migration mechanism may explain the smaller limpets found at mid-tidal levels at Nqabara. Although direct proof of such behaviour is currently lacking *C. capensis* certainly does extend further upshore at Nqabara than at Dwesa, the animals found at the higher levels also tend to be larger than those found at the mid-tidal level (Lasiak & Dye, pers. obs.).

Differences in the rate of recruitment have been found to influence various population characteristics of limpets (Sutherland, 1970; Lewis & Bowman, 1975; Creese, 1980; Thompson, 1980; Workman, 1983; Fletcher, 1984a and 1987). The apparent lack of recruitment and low density of juvenile limpets recorded at Dwesa II relative to that on the other shores, and the fact that concomitant recruitment pulses were not recorded at all sites, suggests that differential rates of recruitment may be an important factor. Whether this is the result of spatial differences in the intensity of settlement or post-settlement mortality has, however, yet to be resolved. One of the most likely factors responsible for differences in the rate of post-settlement mortality on these shores is the difference in availability of microhabitats. As the mid-tidal levels of the shore at Nqabara are more rugged and broken than the flat rock platforms found at Dwesa I and II crevice and pool microhabitats tend to be more common on this shore. The survivorship of recruit and juvenile limpets may well be enhanced by the presence of such refugia (Lewis and Bowman, 1975). Differences in the number of juveniles recorded at these study sites might also reflect the varying extent to which recruitment to the open rock face is the result of direct settlement or immigration, or both.

The results of this study suggest that the marked differences in population characteristics of *C. capensis* observed in exploited and non-exploited stocks may in fact have relatively little to do with exploitation. The avoidance of intense competition by upshore migration is a plausible alternative explanation for the observed differences in size composition. The temporal and spatial variation observed in these populations also suggest that fluctuations in recruitment success may be a major determinant of several population characteristics. Results such as these emphasize the need for studies of human impacts to be set against a knowledge of the natural fluctuations in distribution and abundance of populations, and aspects of ecology, such as recruitment and growth rates, that are of direct relevance to harvesting (Fairweather, 1991).

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