Population dynamics and growth of the gastropod *Oxystele variegata* (Anton) on an exposed rocky shore

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Oxystele variegata (Anton) was found to exhibit a gradient of increasing size up the shore with settlement of veliger larvae occurring primarily in the lower balanoid zone. This has a marked effect on biomass in different regions of the beach and, in combination with zone-dependent density, may be expected to affect the impact of the species as a grazer in different zones. Settlement was continuous during the sampling period but with a marked peak of recruitment in summer. Juvenile cohorts appear at 2 – 4 mm and grow to approximately 14 mm in their first year, after which growth declines, a mean size of 18 mm being reached after the second year. Growth of all size classes in the mid balanoid zone was markedly slower than in the lower balanoid zone because of greater snail densities and lower microphyte productivity. Low primary productivity in the upper balanoid, where large animals occur, may also be partially responsible for the slow growth rates recorded for these animals. Mean monthly mortality of adults was found to be 4,04% and that of juveniles 12,44%. Total population showed a decline of 30,80% over a period of 13 months. Decrease in numbers, however, occurred only on the lower shore and was related to high juvenile mortality rates.

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Oxystele variegata (Anton) toon 'n gradiënt van toenemende grootte met toenemende hoogte teen die strand op en die afsak van die veiliger larwes vind hoofsaaklik in die laer balanoïedgebied plaas. Hierdie verskynsel het 'n belangrike invloed op die biomassa in die verskillende gebiede van die strand en kan waarskynlik saam met gebiedsafhanklike digtheid, die uitwerking van hierdie spesie as weidende diere beïnvloed. Die afsak van larwes was deurlopend gedurende die periode van monsterneming met 'n duidelike piek gedurende die somer. Onvolwasse tydgenote kom te voorskyn as hulle 2 – 4 mm groot is en groei tot ongeveer 14 mm gedurende hulle eerste jaar; daarna neem die groeitempo af. 'n Gemiddelde grootte van 18 mm word na die tweede jaar bereik. Groeitempo van alle grootteklasse in die middel balanoïedgebied is merkbaar stadiger as in die laer balanoïed as gevolg van groter slakdigthede en laer mikrofiet-produktiwiteit. Lae primêre produktiwiteit in die boonste balanoïed, waar groot diere voorkom, mag ook 'n rede wees vir die stadiger groei van hierdie diere. Gemiddelde maandelikse mortaliteit van volwassenes was 4,04% en dié van onvolwassenes 12,44%. Die totale bevolking het met 30,80% oor 'n periode van 13 maande afgeneem. Afname in getalle het egter slegs in die laer strandgebied plaasgevind en is met hoë onvolwasse mortalitiet geassosieer.

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Conflicting evidence exists in recent ecological literature as to whether the regulation of rocky intertidal communities occurs through the effects of key predator species or of intra- and interspecific competition. Experimental manipulation of predator densities has indicated the importance of predation in controlling community structure and maintaining species diversity (eg. Paine 1971, 1974; Menge 1976). However, there is abundant evidence of the effects of competition on growth rates, body size, survival etc. (Connell 1961a,b; Menge 1972; Branch 1975, 1976; Underwood 1976, 1978; Branch & Branch 1980).

The present paper and that of McQuaid (1982), while not attempting to resolve this issue, provide evidence of the effects of predation on the structure of populations of the gastropod *Oxystele variegata* (Anton) and indicate that food availability and intraspecific competition may have an important influence on growth rates.

Four species of *Oxystele* occur on the east coast of South Africa, of which only three extend as far west as the Cape Peninsula. Of these *O. sinensis* reaches the limits of its distribution in False Bay while *O. tigrina* and *O. variagata* occur along the west coast as far as Namibia. *O. sinensis* and *O. tigrina* are lower and mid balanoid species respectively while *O. variegata* (the smallest of the three) is common throughout the balanoid zone.

At Dalebrook (34°07′S/18°27′E) on the Cape Peninsula, *O. variegata* is extremely abundant, forming the bulk of mid and upper balanoid herbivore biomass, and may be expected to constitute an important element in community energetics. Because of this, data are needed on the population structure and dynamics of this species. These include details of seasonal and long-term changes in the population as well as estimates of life expectancy, mortality and growth rates.

Methods

Study site

The balanoid zone at Dalebrook forms a wide, gentle slope of hard sandstone. In this paper, the lower, middle and upper balanoid zones are referred to as Zones 1 – 3 respectively. The dominant algae are mainly rhodophytes. Zone 1 is dominated by *Gigartina radula* while Zone 2 is more sparsely colonized by *Gelidium pristoides, Ulva* sp. (Chlorophyta) and the barnacle *Tetraclita serrata*. The only macrophyte present in Zone 3 is *Porphyra capensis*, which is a transient colonizer.

Population structure and size

The *Oxystele variegata* occupying each of the three balanoid zones were considered separately and are referred to as 'sub-populations' for convenience. Each sub-population was examined during low spring tide at six-weekly intervals, for 15 months (Sept. 1976 – Dec. 1977) in Zone 1 and for 13 months (Nov. 1976 – Dec. 1977) in Zones 2 and 3. Estimates of size frequencies were derived from collections of 250 – 400 animals in each zone which were measured and then returned to the beach during each sampling session. The measure of body size used was maximum shell mouth diameter which is highly correlated with acidized body weight:

$$\log y = \log 0{,}00001445 + 3{,}5980 \log x \; (r^2 = 0{,}98).$$

The total area sampled was 420 m^2, comprising 182 m^2 in Zone 1, 149 m^2 in Zone 2 and 89 m^2 in Zone 3. Local conditions necessitated different methods of quantifying the population in each zone. Zones 1 and 2 were sampled by counting all animals inside three fixed quadrats of 1 m × 4 m (Zone 1) and three of 2,5 m × 2,5 m (Zone 2). Distribution in Zone 3 was so clumped that population size could only be determined by counting all snails in the zone.

Growth rates

Growth rates were derived by cohort analysis of the size-frequency data using the computer program NORMSEP (Hasselblad 1966). NORMSEP separates size-frequency distributions into component normal distributions (cohorts) under the assumption that animal sizes are normally distributed within age groups. Growth rates were then derived from changes in the mean sizes of animals in each cohort. Normally distributed curves were superimposed on the cohorts that had been recognized, by using the program NHIST, written by M. Ripp of the School of Environmental Studies, University of Cape Town.

Results

Size distribution and settlement

Each zone contained a bi- or trimodal sub-population dominated by a particular size class. In Zone 1 rapidly growing juveniles were predominant after February 1977 (Figure 1). In Zone 2 the 13 – 14 mm size classes were most abundant throughout the sampling period and there was only limited settlement. Zone 3 was clearly dominated by animals of 15 – 18 mm with very few juveniles appearing even during heavy settlement in Zone 1 (Figure 1).

There was virtually no settlement at the top of the shore and, as the overall population was physically isolated from neighbouring populations, recruitment into Zones 2 and 3 can only be explained by upshore migration of larger animals from the lower balanoid. Progressively larger size classes predominated higher up the beach and Zone 3, the highest zone, was dominated by the size classes missing from the lower zones. Animals of up to 22 mm also occurred in Zone 3 but animals larger than 18 mm never occurred in Zones 1 and 2.

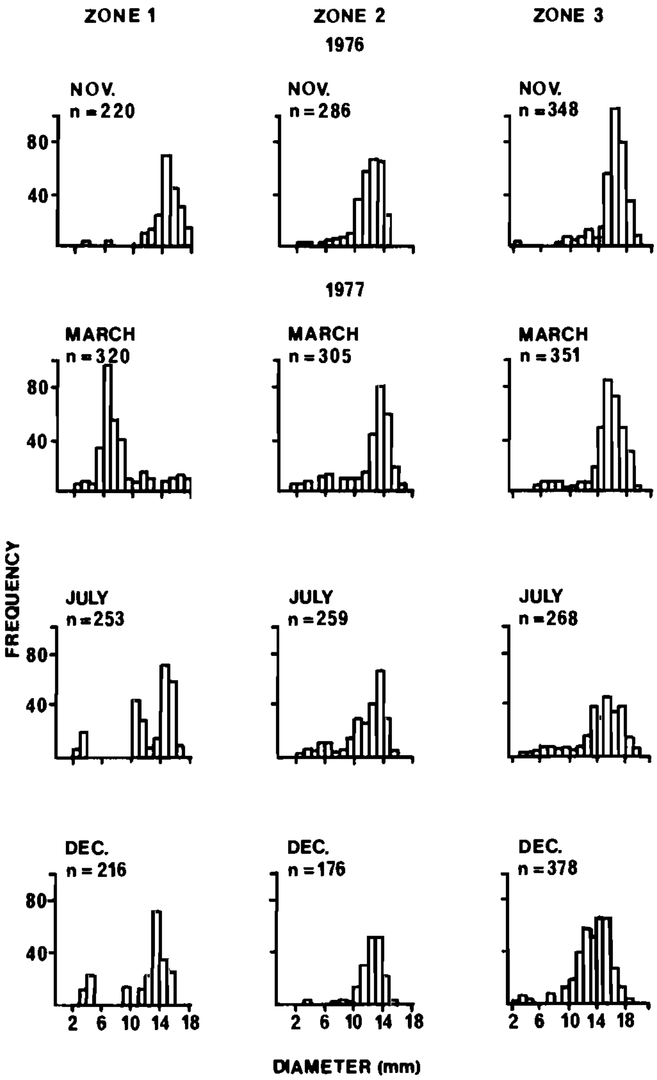

Figure 1 Size-frequency distribution of *Oxystele variegata* in Zones 1 – 3 at intervals of four months where *n* indicates sample size and size is given as the maximum diameter of the shell.

Pooled size-frequencies for the entire population are given in Figure 2. There was a modal peak at about 14 – 16 mm, probably representing the fusion of several older cohorts. Reproduction was continuous, juveniles being present throughout the year, but there was a marked peak of settlement in February 1977 (cohort B on Figure 2).

The mean size for this cohort increased as a result of growth and by September 1977 it had merged completely with the older cohort A already present which probably comprised several previously fused cohorts. Smaller settlements yielded two small juvenile cohorts (C and D) which appeared in March 1977 and October 1977.

Population size

The total population reached peak numbers in February when there was heavy settlement in Zone 1 and then declined for the remainder of the sampling period (Figure 3). Total population in December 1977 was 30,80% lower than in December 1976. This was owing to limited recruitment after February 1977 and high rates of juvenile mortality.

Mortality

Mortality may be estimated from the data on population

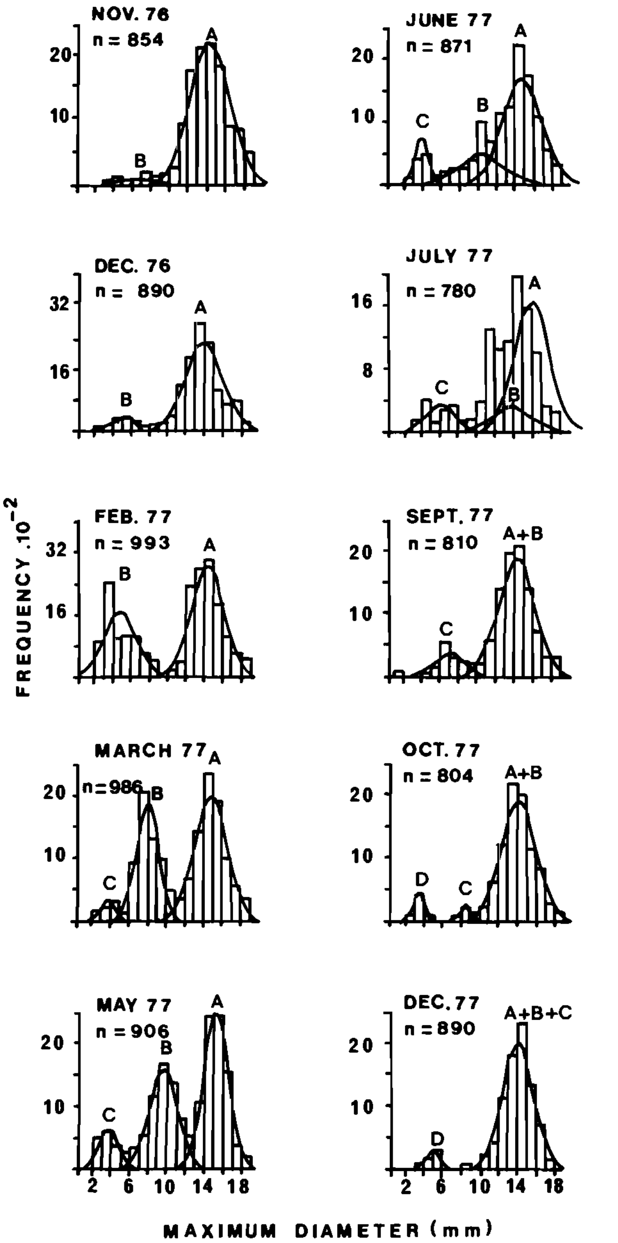

Figure 2 Size-frequency distribution at six-week intervals for the entire population of *Oxystele variegata* at Dalebrook. The histograms are based on data pooled from Zones 1 – 3 and weighted for the numbers in each zone. Pooled sample size is given as *n*, and normal distribution curves are superimposed on each identified cohort.

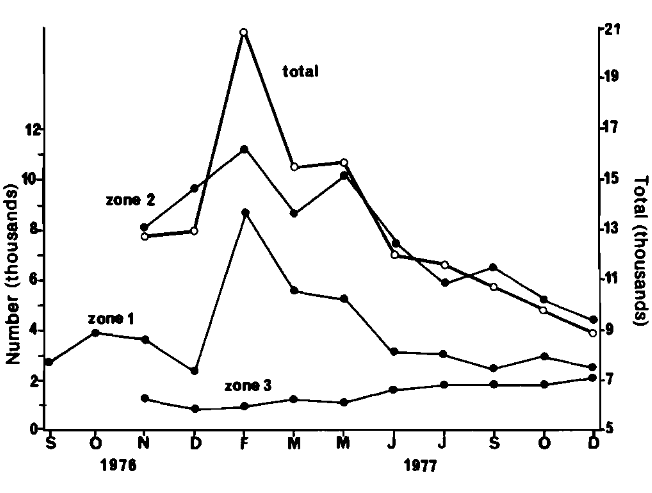

Figure 3 Numbers of *Oxystele variegata* in Zones 1 – 3 and total population at Dalebrook, derived at six-weekly intervals.

size and structure on the assumption that migration occurs up the shore only and not horizontally into or out of the overall population, which was physically isolated from neighbouring populations. Because of vertical migration between zones mortality may be derived only for the total population but not for each separate sub-population. The absolute size for each of the cohorts derived from Figure 2 is plotted against time in Figure 4.

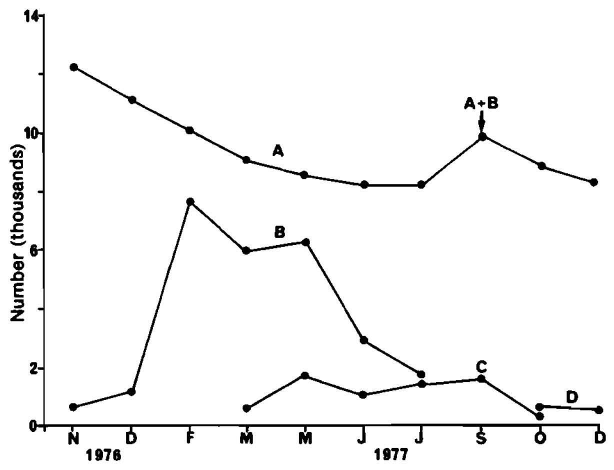

Figure 4 Total numbers of *Oxystele variegata* in cohorts A – D and the combined cohort A + B identified in Figure 2.

Cohort D was sampled only twice at the end of the sampling period and data for cohort C showed irregular fluctuations owing to extended recruitment into this cohort. However, data for cohorts A and B may be used to derive mortality rates for adult and juvenile animals respectively. These two cohorts are separable using NORMSEP even in the region of overlap where they begin to converge owing to a decrease in the growth rate of the larger animals. Each cohort could therefore be treated as a separate unit experiencing no recruitment after the initial settlement, and declining slowly owing to mortality until they fused to form a single cohort in September 1977. The mean monthly mortality for cohort A (calculated for Nov. – July) was 4,08%, which was much lower than for the juveniles of cohort B (12,44%, calculated for Feb. – July).

Numerical distribution

Although the total population and the sub-populations in Zones 1 and 2 decreased after February 1977, numbers in Zone 3 increased over the same period (Figure 3). This was most obvious after May when the sub-populations in Zones 1 and 2 decreased rapidly; an effect that may be explained by vertical migration into Zone 3. Mean density values are of limited usefulness for Zone 3 where distribution was extremely clumped, but nevertheless may be calculated for all three zones from data on numbers and the area of each zone given above. There was no correlation between density and mean size in the different zones.

Biomass

The mean biomass in each zone was calculated as acidized dry mass m^{-2} (Figure 5) from the size frequencies, densities and the diameter/weight equation given above. Mean biomass was greatest in Zone 2 owing to much greater densities than in Zone 3 and the predominance of larger animals than in Zone 1. There was a decline in biomass in Zones 1 and 2 owing to migration and mortality. Although density in Zone 1 increased greatly with the appearance of cohort B in February the newly settled juveniles made a negligible contribution to biomass because of their small size. Because of the exponential relationship between size and weight, decline of biomass primarily reflects a decline in the number of larger animals present. Biomass in Zone 3 rose as biomass in the lower zones dropped, owing to upshore migration, the effect being marked because medium and large-sized animals were involved. A gradual drop in biomass in Zone 3 after May/June may be attributed to mortality of the largest animals which were replaced by smaller animals from below.

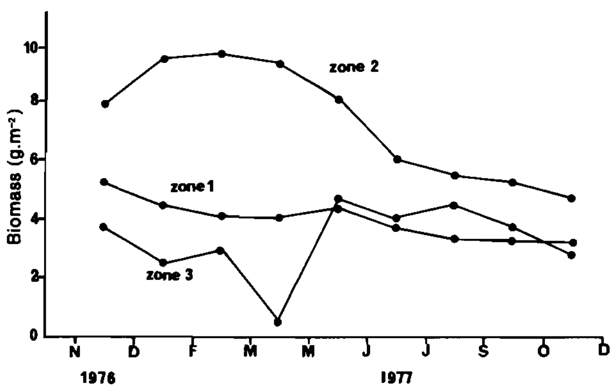

Figure 5 Biomass (expressed as shell-free dry mass m^{-2}) of *Oxystele variegata* in Zones 1 – 3.

Growth rates

Growth rates of the identified cohorts are shown as mean shell diameter versus time in Figure 6. The merging of cohorts in Figure 2 is clearly brought out here. Where there was no merging of cohorts the growth curves were roughly sigmoidal with most rapid growth between 5 and 14 mm. No animals of less than 2 mm were found during the study, suggesting very rapid growth up to 2 mm. Animals reached

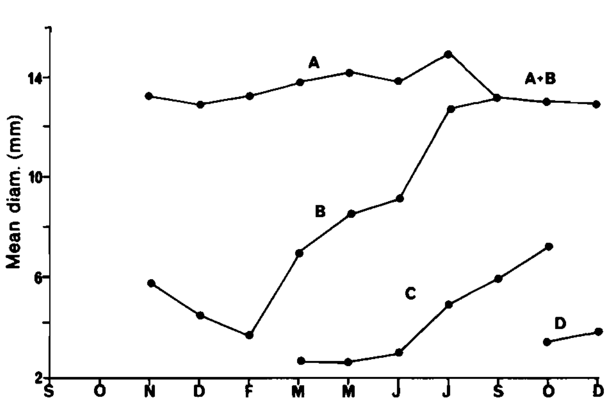

Figure 6 Composite growth curves for cohorts A – D, derived for the total population of *Oxystele variegata*, based on Figure 2.

approximately 14 mm in their first year. Growth after that was slow, and extrapolation from the oldest animals (cohort A) indicates that they reach 18 mm after 2 years. Animals of over 20 mm are probably 3 – 4 years old although they may simply be individuals showing particularly rapid growth.

The sub-populations in each zone may be defined as follows:

Zone 1 dominated by juveniles during settlement along with a small, residual, presumably breeding population of about 1 year old.

Zone 2 mainly 1 year old or over. Only a few juveniles appear here and very few animals remain here after reaching 1,5 years (i.e. 16 mm).

Zone 3 animals of 1,5 to 2 or 3 years old.

Monthly growth rates are plotted against initial shell diameter for the cohorts in each zone in Figure 7. As may be expected, growth was strongly size-dependent, but in addition to this growth rates were lowest in Zone 2 and highest in Zone 1.

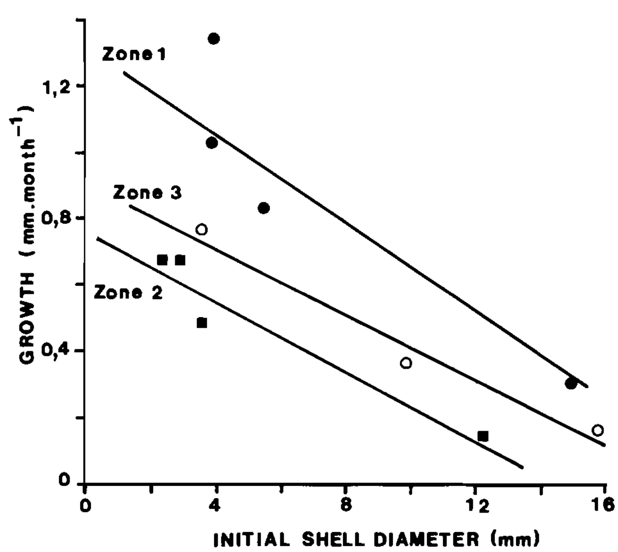

Figure 7 The relationship between mean monthly growth rates of *Oxystele variegata* and initial shell diameter for Zones 1 – 3.

Discussion

Recruitment of *Oxystele variegata* was continuous with juvenile animals occurring throughout the year but, as with other trochids (Williams 1964; Desai 1966; Paine 1969; Regis 1969), there was a marked seasonal peak of settlement. This occurred in late summer (February 1977) with other smaller peaks occurring in May/June and October 1977. The February peak in particular led to a large increase in population but high juvenile mortality rates and limited recruitment after this period led to a gradual decline of population over the following 10 months. Over the entire sampling period of 13 months the population fell by 30,80%.

Settlement decreased markedly from Zone 1 to Zone 3 and the great majority of juveniles appeared in Zone 1, a reflection of increasing environmental stress (especially desiccation) further upshore (McQuaid 1980, 1982). This was in part responsible for the occurrence of a marked size gradient of increasing shell diameter further up the shore so that the zones were dominated by different size classes of snails. There was no correlation between density and size when comparing these zones. The establishment and maintenance of this size gradient is dealt with separately (McQuaid 1980, 1982) but it has an important influence on the population dynamics of the species. The total population, and the sub-population in Zones 1 and 2 declined after February 1977 owing to high mortality rates of juveniles and to migration up the shore by animals which had grown large enough to tolerate the harsher conditions. In Zone 3, however, there were extremely few juveniles present and numbers increased over the same period owing to the much lower mortality rates of adults and recruitment by upshore migration. These numerical changes were mirrored by changes in biomass in each zone, the biomass falling in Zones 1 and 2 while rising in Zone 3.

A second effect of this size gradient was that, because of the exponential relationship between shell size and body weight, the biomass in the different zones was strongly influenced by the size of animals in each zone. This in turn may influence grazing impact in the different zones and the degree of intraspecific competition for food. Examination of the gut contents and faeces indicated that *O. variegata* is a generalized herbivore which feeds by rasping the rock substratum. Faeces contain large numbers of diatoms which are assimilated (confirmed by staining with Rose Bengal) as well as odd particles such as sponge spicules which remain undigested. Some of the unidentifiable organic matter present may be macrophytic in origin but large algae are unlikely to be important in the diet as the animals at the top of the shore live in a zone where macroalgae are never more than temporarily present. The productivity of microphytes at Dalebrook, including that of macroalgal sporelings which would also be grazed, decreases rapidly in an upshore direction (McQuaid 1980).

There is no direct evidence that food availability limits growth of *O. variegata* but observed growth rates were most rapid in Zone 1 where primary productivity was highest and snail biomass low, and slowest in Zone 2 where the productivity was lower but biomass higher (Figure 7). In Zone 3 growth was slightly faster than in Zone 2, for although algal productivity is lowest in Zone 3, the biomass of *O. variegata* is also low, and the animals are mostly large, slow-growing winkles requiring relatively little food. The situation resembles that of low and high-level populations of the limpet *Acmaea scabra*, described by Sutherland (1970). High-level populations of *A. scabra* exhibited low densities (owing to limited recruitment) but higher growth rates and maximum size, despite greater seasonality of food supplies and reduced feeding time at the top of the beach.

Growth was strongly size-dependent and decreased after the first year (about 14 mm), most animals attaining 18 mm by the end of their second year. A small number of animals grow to 20 mm or more (maximum size recorded was 22 mm) and these may be either much older animals (cf. Comfort 1959; Darby 1964; Paine 1969) or individuals exhibiting particularly rapid growth. Low growth rates of the larger animals may be partly owing to the fact that they occur in Zones 2 and 3 where the growth of all size classes was reduced.

While there is little doubt that predation has a critical influence on community structure (McQuaid 1980) it is also evident from previous work (Underwood 1976; Branch & Branch 1980 etc.) that herbivore densities may become great enough to lead to intraspecific competition. Experimentation is required to confirm this in the case of *O. variegata*, but there is clearly a close relationship between zone-dependent food availability, growth rates and mean snail sizes.

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