

## Recruitment Dynamics and Growth of the Barnacle *Tetraclita Serrata* on the East Coast of Southern Africa

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Recruitment of *Tetraclita serrata* was determined from archival photographs of permanent 0.25 m<sup>2</sup> quadrats at several sites along the Transkei coast. Periodogram analyses revealed regular annual recruitment although both spatial and interannual variation in recruitment intensity was high. Differences in long-term abundance between sites showed no geographic pattern nor were they related to human disturbance. Recruitment intensity, however, was found to be related to mean abundance indicating limited larval dispersal. Barnacles increased in basal diameter by 7.6 mm in the first year, declining to 4 mm by the third year. Individual growth was variable with bursts of rapid growth interspersed with periods of little or no growth. Barnacles larger than 20 mm comprised only 6% of the population and an analysis of individual longevity indicated a mean lifespan of  $2.7 \pm 1$  year (SD). The important role of this species in structuring intertidal communities is discussed in relation to the effects of human exploitation.

### Introduction

Temporal and spatial variations in recruitment of benthic invertebrates often have a significant influence on the structure of intertidal rocky shore communities (Caffey, 1985; Gaines *et al.*, 1985). Large scale studies on barnacles have attributed these variations to reproductive periodicity, availability of larvae, nearshore current patterns and coastal topography (Kendall *et al.*, 1982; Gaines *et al.*, 1985).

On a local scale, recruitment of barnacles has been related to predation during the planktonic larval phase (Gaines & Roughgarden, 1987), the abundance of adults (Sutherland, 1987; Chabout & Bourget, 1988), substratum heterogeneity (Raimondi, 1988; Chabout & Bourget, 1988), resistance to desiccation (Kendall *et al.*, 1985) and biological interactions resulting in high post-settlement mortality (Denley & Underwood, 1979; Branch, 1981; Hawkins, 1983). Recent studies have indicated that variations in settlement may have a modulating effect on community interactions such as predation (Connell, 1985; Fairweather, 1988).

Apart from a paucity of data on nearshore hydrology, there is also a lack of long-term data which could establish correlations between oceanic and intertidal processes. This in

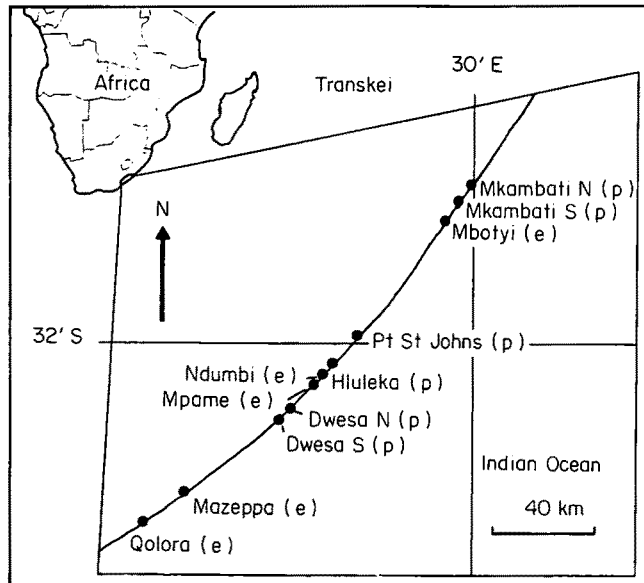


Figure 1. Map of the Transkei coast showing the positions of the monitoring sites. e = exploited area; p = protected reserve.

turn precludes accurate prediction of the intensity of larval settlement and subsequent recruitment. Such predictions, however, would be of considerable importance in the management of exploited intertidal communities.

Shellfish resources along the eastern coastline of southern Africa, for example, have long been important in the diet of coastal people (Lasiak & Dye, 1989). Several species of patellid limpets are exploited in addition to the low-shore mussel *Perna perna* (Linnaeus, 1758), the removal of which creates patches of bare rock. The numerically dominant barnacle *Tetraclita serrata* (Darwin), which normally occupies the mid-shore zone, is able to colonize these bare areas and it has been suggested that removal of mussels and other molluscs may result in their replacement by barnacles (Hockey & Bosman, 1986). This suggestion may be tested by comparing long-term patterns in abundance and recruitment of barnacles in areas subjected to and protected from human exploitation.

The present paper provides such data for populations of *T. serrata* on the Transkei coast of Southern Africa. The data are derived from an ongoing long-term rocky shore monitoring programme being conducted in this region (Dye, 1988).

### Methods

Figure 1 shows the positions of 11 monitoring sites on the Transkei coast which represents a transition zone between the warm temperate south coast region of Southern Africa and the sub-tropical east coast. Mazeppa, Dwesa North (N) and Mkambati South (S) are the sites of ongoing monitoring programmes initiated in 1982 (1983 at Mkambati) while the others were monitored for a period of 3 years from 1982–85. The symbols 'e' and 'p' denote whether a site is subject to human exploitation or protected within reserves. The Transkei coast is irregular with numerous small bays and headlands separated by several river mouths. The intertidal at eight of the sites consists of shale platforms while at Qolora and the Mkambati sites the rock is composed of sandstone and quartzitic sandstone

respectively. The prevailing winds are south-westerly and mean sea temperature is 18 °C. The shore experiences moderate to heavy wave action and semi-diurnal tides with an amplitude of approximately 2 m.

The major occupiers of primary space on the mid and lower shore are the barnacles *T. serrata*, *Chthamalus dentatus* and *Octomeris angulosus*, the rock oyster *Saccostrea cucullata* and the encrusting polychaete *Pomatoleios kraussii*. Most of the benthic mobile animals are grazers, the most abundant of these being the limpets *Cellana capensis* and *Patella granularis* and the whelks *Oxystele tabularis* and *Littorina africana*. Predatory molluscs such as *Burnupaena lagenaria* and *Thais dubia* are present in low numbers (Dye, 1988).

The abundance of *T. serrata* in the lower balanoid zone was determined from photographs of fixed 0.25 m<sup>2</sup> quadrats taken at 3-monthly intervals. These measurements yielded continuous data sets covering a period of 8 years at Mazeppa and Dwesa N, 7 years at Mkambati S and 3 years elsewhere. After differencing to remove autocorrelations (lag=1) the detrended data series were compared using cross-correlation analyses. Shannon-Wiener species diversity ( $H; \log_{10}$ ) and Pielou's evenness (J) (Zar, 1974) within each quadrat were also calculated for the three long-term data sets. Cross-correlation and periodogram analyses were performed on the resulting time series (Chatfield, 1989). The average densities over the whole period of observation at each site were compared using Tukey's highest significant difference (HSD) multiple comparisons test which is robust against Type I errors (Wilkinson, 1989).

Growth estimates of *T. serrata* were based on 3-monthly measurements of the basal diameter of 120 individuals in photographs from Mazeppa taken between November 1988 and November 1989. This site was chosen since the individual barnacles were easy to identify and measure precisely owing to their uniform spacing. The barnacles were divided into 10 × 2 mm size classes ranging from 2 mm to 22 mm and the mean, maximum and minimum growth rates were used to construct composite growth curves. Population size structure was determined at the beginning and end of the growth period. Longevity was estimated by following 50 individual barnacles back from the time of death (determined to within 6 weeks) to the time at which they first appeared on the photographs at a size of approximately 1.5 mm. All size data were calibrated against *in situ* measurements of live barnacles.

## Results

Temporal fluctuations in the abundance of *T. serrata* at the 11 sites are shown in Figures 2 and 3. No significant temporal relationships were evident, even at sites that were relatively close together such as the sites at Dwesa and Mkambati, indicating that recruitment and mortality patterns are independent of site. No consistent differences could be detected between areas subjected to human exploitation and those within reserves. Periodogram analyses revealed a well defined annual cycle at Mkambati corresponding to annual winter recruitment. At Mazeppa there was a 6 month interannual variation in the timing of peak recruitment ( $f: 0.75-1.25 y$ ) while at Dwesa the recruitment frequency was 1.25  $y$  with evidence of a 2.25  $y$  cycle as well.

Table 1 gives the results of a Tukey HSD test applied to the abundance data in Figures 2 and 3. Although many of the sites differed significantly from each other there was no clear pattern to these differences. As with the time series analyses there were no consistent differences (or similarities) either between juxtaposed sites or in relation to their status as an exploited or protected area.

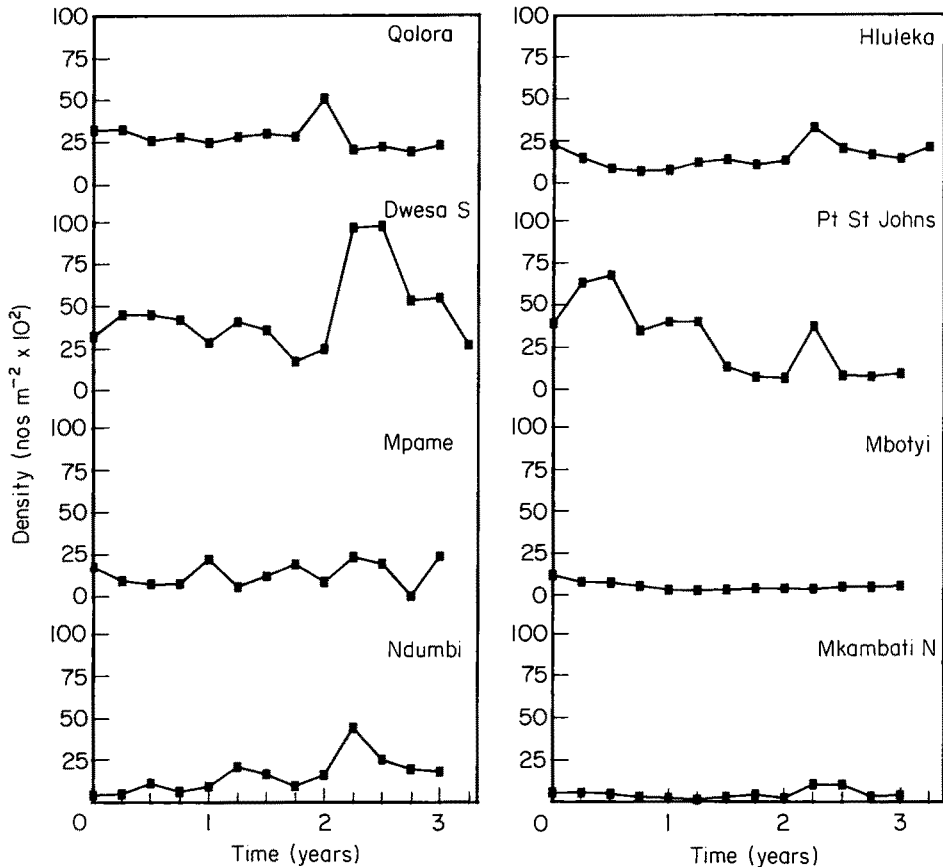


Figure 2. Temporal fluctuations in the abundance of *T. serrata* at 8 sites monitored over a 3 year period (1982-1985).

Cross-correlation analyses of barnacle abundance against diversity ( $H$ ) (Figure 3) and evenness ( $J$ ) indicated that temporal fluctuations in the abundance of *T. serrata* accounted for 40% of the variation in diversity at Mazeppa but only for 30% at Dwesa and Mkambati. Similarly, 50% of the variation in evenness at Mazeppa could be ascribed to *T. serrata* whereas at Dwesa and Mkambati this species accounted for 30% and 40% of the variation in evenness respectively.

Figure 5 shows the relationship between long-term mean abundance and maximum recruitment calculated as the mean of all points greater than 2 SD above the long-term mean. The relationship is highly significant and suggests that recruitment is a function of standing stock. Sites at which barnacles were more abundant tended to experience heavy recruitment while the converse is true of sites with low abundance. Cluster analysis revealed that the 11 sites could be divided into three distinct groups indicated by dashed lines. The groupings are not related to human activity but may suggest a geographic influence on abundance and recruitment.

The population size structure of *T. serrata* at Mazeppa is shown in Figure 6. The annual winter recruitment is evident in the 4-8 mm cohort prominent in 1989. The remainder of the population increased in modal size from 12 to 14 mm during the growth period. In

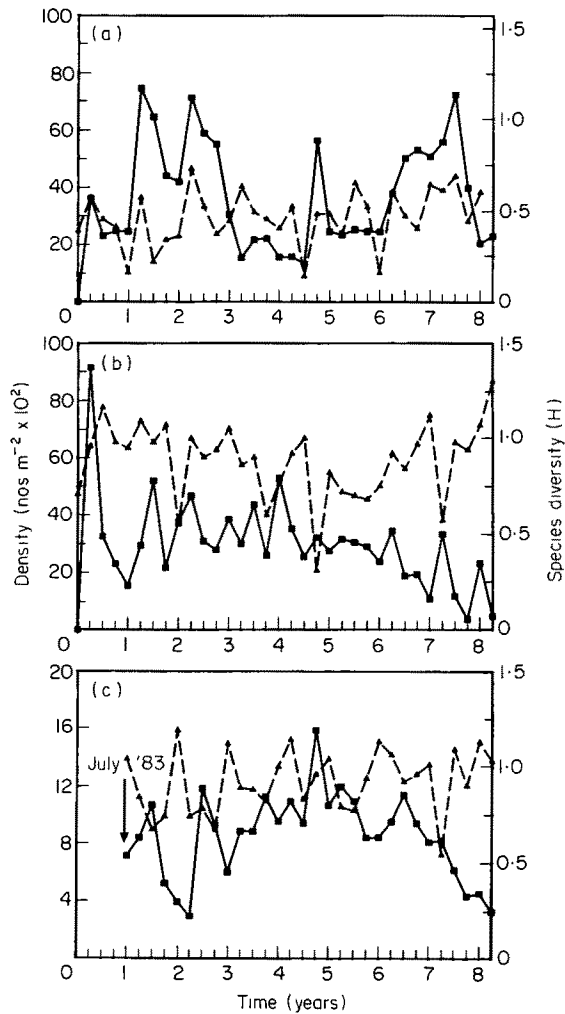


Figure 3. Temporal fluctuations in the abundance of *T. serrata* monitored over 8 years (July 1982–July 1990) at (a) Mazeppa S and (b) Dwesa N and over 7 years (July 1983–July 1990) at (c) Mkamabti. Also shown are the corresponding fluctuations in species diversity (H) represented by dashed lines.

both cases less than 6% of the population was larger than 20 mm. There was considerable variation in individual growth with some animals growing at twice the mean rate part of the time then exhibiting little or no measurable growth at other times. Figure 7 shows the mean, maximum and minimum growth curves derived from individual measurements. The mean curve gives a growth rate of 7.6 mm in the first year declining to approximately 4 mm after 3 years and indicates that the largest individuals recorded (34 mm) may be about 8 years old. Periods of very slow growth were more common among the older individuals leading to a divergence of the minimum curve from the mean. Calculations based on a modal size of 14 mm for the adult population (Figure 6; 1989) indicate that the average age is about 2.3 years. This estimate is close to that of  $2.7 \pm 1$  (SD) years obtained by direct observation of individual lifespan.

TABLE 1. Multiple comparison analysis (Tukey HSD) of long-term mean abundance of *T. serrata* at 11 sites on the Transkei coast. Values of  $P < 0.05$  are considered significant

Site	DWS	Hluleka	PSJ	Mkb N	Qolora	Mpame	Ndumbi	Mbotyi	Mkb S	Mazeppa
DWS (p)	0.001									
Hluleka (p)	0.016	0.438								
PSJ (p)	0.001	0.508	0.000							
Mkb N (p)	0.019	0.399	1.000	0.001						
Qolora	0.000	1.000	0.482	0.463	0.443					
Mpame	0.000	1.000	0.488	0.457	0.448	1.000				
Ndumbi	0.000	1.000	0.001	1.000	0.001	0.610	0.604			
Mbotyi	0.000	0.654	0.001	1.000	0.000	0.805	0.800	1.000		
Mkb S (p)	0.012	0.844	0.000	1.000	0.772	0.012	0.013	0.000	0.000	
Mazeppa	0.012	0.013	0.000	0.000	0.772	0.012	0.013	0.000	0.000	
DWN (p)	0.846	0.000	0.313	0.000	0.354	0.000	0.000	0.000	0.000	0.772

DWS = Dwesa S; DWN = Dwesa N; PSJ = Pt St. Johns; Mkb S = Mkambati S; Mkb N = Mkambati N; (p) = protected within reserve.

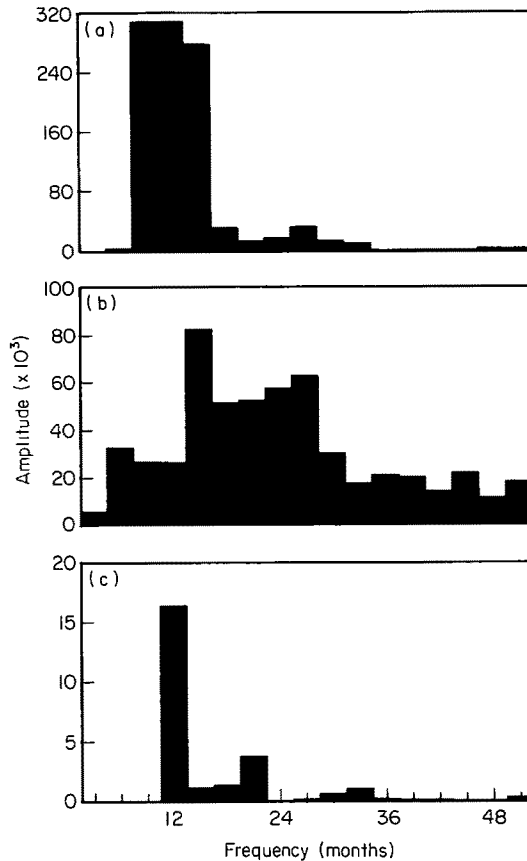


Figure 4. Smoothed periodograms (3 point MA) of the detrended data from Figure 3. (a) Mazeppa, (b) Dwesa N, (c) Mkambati S.

## Discussion

Despite the relatively short extent of the Transkei coastline large temporal and spatial differences in populations of *T. serrata* were evident. Although there are regular cycles of recruitment the timing of these is not consistent and their amplitude varies spatially by more than an order of magnitude. Such spatial variability appears to be a characteristic of barnacle populations. Kendall *et al.* (1982) found large differences in the abundance and recruitment of *Semibalanus balanoides* between the rugged west coast of Scotland and the relatively straight north-east coast of England. They concluded that the orientation and configuration of the coastline were major factors determining larval dispersal and settlement intensity. Spatial variability is also a characteristic of *S. balanoides* in this region (Kendall *et al.*, 1985), and of *Balanus glandula* on the Californian coast (Judge *et al.*, 1988). Variations covering several orders of magnitude in the abundance and recruitment of *Tesseropora rosea* have also been reported from New South Wales, Australia (Caffey, 1985).

It has become apparent that much of the spatial variation in abundance of benthic organisms results from variability in the supply of larvae (Gaines & Roughgarden, 1985; Sutherland, 1987) and significant correlations have been found between settlement and

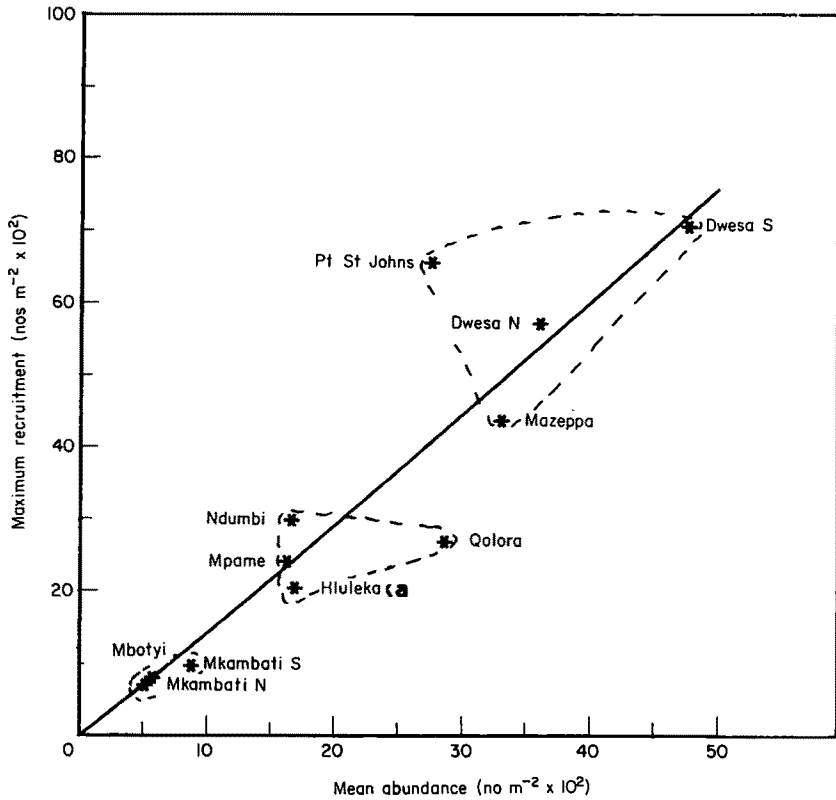


Figure 5. Relationship between long-term mean abundance and maximum observed recruitment at 11 sites on the Transkei coast. Calculations are based on the detrended abundance data in Figures 2 and 3.

recruitment (Caffey, 1985; Gaines *et al.*, 1985). Although settlement *per se* was not determined in the present study a significant relationship was found between maximum recruitment and mean abundance over periods of several years, which implies that the dispersal of cyprids may be limited, possibly because larvae are retained close inshore by eddy currents resulting from the interaction of the prevailing winds and the broken coastline. Unfortunately no small-scale nearshore hydrological data are available to test this idea. The separation of the sites into the groups indicated in Figure 5 may at first sight indicate some geographic influence on recruitment and abundance. However, while the northern sites are clearly segregated from the rest, the other sites are not grouped according to their position on the coast. In view of this it seems more likely that the groupings simply reflect the general relationship between abundance and recruitment.

It is important to distinguish between persistent differences in abundance resulting from the above and small scale fluctuations which arise as a result of predation (planktonic and benthic), selectivity of settlement site by cyprids and abiotic factors such as temperature extremes and desiccation. Much of the 'background noise' in recruitment and abundance can be attributed to the interaction of these factors leading to the observed lack of correlation (or patterns of correlation) between sites.

*T. serrata* is the numerically dominant sessile species in the mid intertidal in Transkei and it is therefore not surprising that fluctuations in its abundance have a noticeable



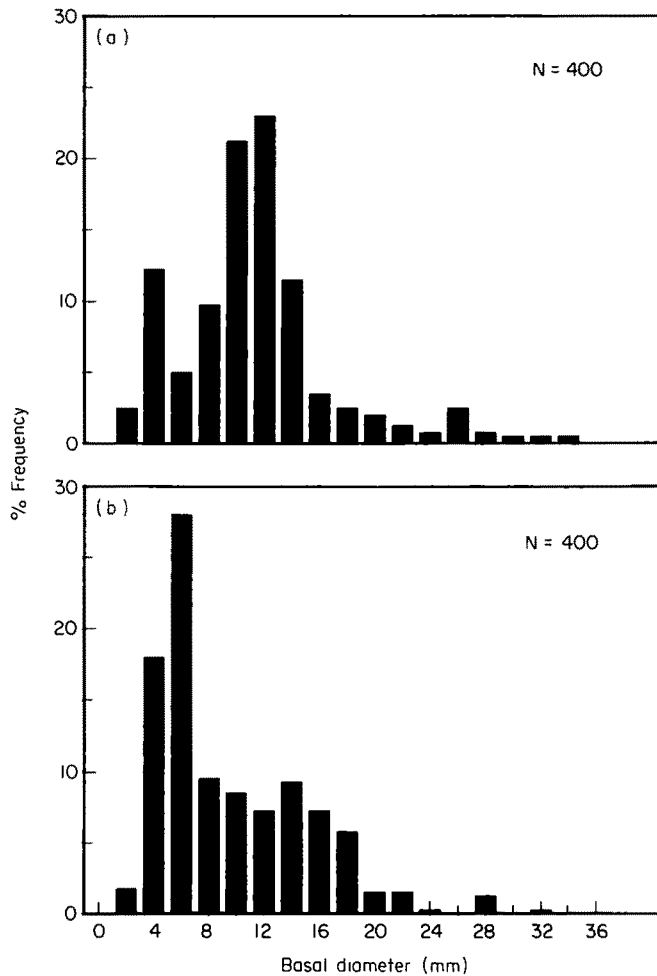


Figure 6. Size frequency histograms of the *T. serrata* population at Mazeppa in (a) November 1988 and (b) November 1989.

influence on species diversity. The general relationship is such that diversity is reduced after periods of recruitment and it follows that any measure of community structure based on relative abundance will be strongly influenced by past recruitment of *T. serrata*.

Crisp (1960) and more recently Wethey (1983) have shown growth in individual barnacles to be highly variable. This was also the case in the present study where the variability was such that some individuals were overtaken by smaller conspecifics during the growth period. As a result calculated growth rates have a range of 3–4 fold between minimum and maximum. An interesting feature of the curve is that growth does not slow down rapidly with time and therefore very large specimens are theoretically possible. In practice, however, large specimens (> 30 mm) are rare and the largest recorded at Mazeppa was 34 mm (approx. 8 years old). Based on a modal size of 14 mm the average age of the population is 2.3 years which is close to the lifespan of  $2.7 \pm 1$  (SD) years determined by direct observation. This implies a turnover time of about 3 years and compares well with age estimates made by Sutherland (1987) for *Tetraclita panamensis* in Costa Rica and

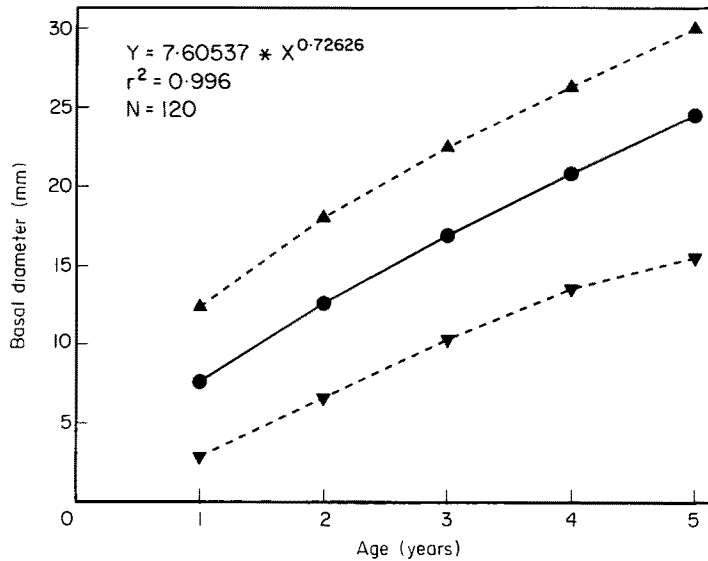


Figure 7. Mean, ●—●, maximum, --▲--, and minimum, ▼--▼, growth curves for *T. serrata* at Mazeppa.

by Caffey (1985) for *T. rosea* in Australia. The persistence of *T. serrata* is thus not so much a function of longevity as of the continual supply of recruits to a fairly rapidly cycling population.

The implications of the above are important in several respects. Firstly, if the dispersal of cyprids of *T. serrata* on the Transkei coast is constrained by localized hydrographic conditions, then the same may be true of other species with similar dispersal mechanisms. If this applies to exploited species such as mussels (*Perna perna*), oysters and limpets then it raises questions about the efficiency of management strategies involving coastal reserves, if these are intended as sources of larvae which are presumed to disperse to adjacent coastal areas. Indeed this would be an important consideration in any area where the dispersal of planktonic larvae is constrained in some way.

A second implication of the above concerns the use of apparently stable populations of benthic organisms as 'indicators' of the intensity of human disturbance. In a recent study of the effects of human exploitation on community structure on the Transkei coast Hockey and Bosman (1986) reported significant 'community convergence' towards a state of dominance by barnacles at exploited sites as compared with protected sites situated in reserves. Much of the data for this work was obtained during the latter half of 1984 which coincided with a period of heavy recruitment of *T. serrata* (Dye, 1988). The intensity of this event was related to the initial abundance of barnacles and was not constant along the coast (see Figures 2 and 3). However, as can be seen from the present study, the abundance of barnacles may have more to do with coastal topography than with the degree of human disturbance and the demonstration of spatial heterogeneity at one instant in time does not shed light on its cause. Studies such as those by Kendall *et al.* (1982), Caffey (1985) and Judge *et al.* (1988) illustrates the importance of information on the recruitment dynamics of benthic populations covering sufficiently large spatial and temporal scales for the interpretation of structural differences between intertidal communities.

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