CHAPTER IV

POPULATION STUDIES
4.1 POPULATION STRUCTURE

Mean monthly densities of the limpet, *C. radiata* at Anjuna are presented in Fig. 38. It can be seen that the densities varied from month to month, with maximum densities recorded during the pre-monsoon and post-monsoon seasons: in October '93 (14.7/m²) and September '94 (13.4/m²) and in February '94 (10.0/m²). Density of limpets in October '94 was however very low. Low densities were recorded during the monsoon period.

In order to determine the population structure, frequency histograms of shell lengths of *C. radiata* recorded in the field were constructed for each month and the shifts in modal peaks of statistically fitted Gaussian curves analysed. Figure 39 to Fig. 41 illustrates the size frequency distribution of the natural population of limpets at Anjuna from September '93 to October '94. It can be seen that limpets of shell length less than 14mm are not well represented in the frequency histograms. Smaller sized individuals were recorded in September, December and March. Only one modal group could be observed in August '94.

The resulting frequency histograms exhibited modal peaks which were not very well defined. Attempts were made to
Fig. 38 The monthly variations in the density of *C. radiata*.
Fig. 39. Normal curves superimposed on the size frequency histograms of the limpet population from September '93 to October '94. (N = number of limpets).
**Fig. 40.** Normal curves superimposed on the size frequency histograms of the limpet population from September '93 to October '94. (N = number of limpets).
Fig. 41. Normal curves superimposed on the size frequency histograms of the limpet population from September '93 to October '94. (N = number of limpets)
statistically separate the polymodal frequency distribution into their component Gaussian curves representing various age groups, but only two normal curves. Sometimes one could be reasonably fitted to the data (Fig. 39 to Fig. 41).

Shifts in the peaks of modal shell length could be observed. Taking into account the frequency size distribution of all limpets during the study and the statistical fit of normal curves, four population groups of limpets could be distinguished and their growth pattern followed. One population group could be observed from September '93 to February '94. The growth of the second group could be followed up to July '94. The third population group was observed from March '94 up to October '94 while the fourth group made its appearance in September '94.

For the sake of clarity, the mean shell length and their 95% confidence limits, extracted from Fig. 39 to 41, are plotted in Fig. 42. It can be seen that group A shows a clear shift in modal shell length from September '93 up to February '94. The mean size of this group increased from 21.52mm in September '93 to 28.38mm in February '94. The growth of group B limpets could be traced from September '93 up to July '94, after which it could not be traced. During this period, the mean shell size increased from 17.31mm to 29.5mm. During September and December '93 smaller size classes of limpets were recorded, which apparently masked the mean size of group B. The growth of group C, apparent in March '94 could be followed up to the end of the sampling period. These limpets grew from a mean shell length
Fig. 42. Monthly variations in the mean shell length (± S.E.) of the different groups of the limpet population from September '93 to October '94.
of 20.70mm up to 24.95mm. A new group D, as evidenced by the presence of smaller sized limpets, appeared in September '94. This population group increased in shell length from 17.78mm in September '94 to 20.08mm in October '94. In group B and C, there was sometimes an apparent decrease in mean shell length as indicated by the broken lines.

Small limpets grew faster than larger limpets. It can be seen that the growth rate, inferred from monthly increase in shell length, was relatively high from December '93 to March '94. No other particular trend could be observed. The approximate mean growth rate during the pre-monsoon, monsoon and post-monsoon seasons was 1.32mm/month, 1.22mm/month and 1.60mm/month respectively. The mean shell length as well as the number of individuals comprising each group of the population are given in Table 7. It can be seen that the population size of the groups, which ought to decrease or remain constant, at times increased. These problems highlight the practical difficulties faced in separating polymodal frequency distribution data into component curves.

4.2 ESTIMATION OF GROWTH BY TAGGING

Information required to understand the population dynamics can also be obtained by tagging individual organisms. A considerable amount of time was spent experimenting with different glues to select a suitable adhesive which would
**TABLE 7**

Mean shell length of different groups of the population of *C. radiata* from Sept. '93 - Oct. '94 (*n*=number of limpets).

<table>
<thead>
<tr>
<th>GROUPS</th>
<th>MONTHS</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>September'93</td>
<td>21.52</td>
<td>17.81</td>
<td>(n=38)</td>
<td>(n=46)</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>21.55</td>
<td>18.00</td>
<td>(n=71)</td>
<td>(n=76)</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>23.69</td>
<td>20.84</td>
<td>(n=27)</td>
<td>(n=34)</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>26.19</td>
<td>20.94</td>
<td>(n=51)</td>
<td>(n=46)</td>
</tr>
<tr>
<td></td>
<td>February '94</td>
<td>28.38</td>
<td>22.85</td>
<td>(n=49)</td>
<td>(n=51)</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>26.40</td>
<td>20.70</td>
<td>(n=34)</td>
<td>(n=33)</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>26.18</td>
<td>21.73</td>
<td>(n=20)</td>
<td>(n=18)</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>27.40</td>
<td>22.96</td>
<td>(n=31)</td>
<td>(n=32)</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>26.69</td>
<td>19.93</td>
<td>(n=17)</td>
<td>(n=16)</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>29.50</td>
<td>23.59</td>
<td>(n=07)</td>
<td>(n=10)</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>22.54</td>
<td></td>
<td>(n=17)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>23.60</td>
<td>17.78</td>
<td>(n=70)</td>
<td>(n=64)</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>24.95</td>
<td>20.08</td>
<td>(n=08)</td>
<td>(n=13)</td>
</tr>
</tbody>
</table>
withstand the rigours of the nature. The difficulty was compounded because it was intended to track individual limpets. Out of 447 limpets marked, only 190 (20%) of them could be observed on subsequent field visits. Of these 190 limpets, only 112 (59%) could be observed subsequently. One of the individual limpets marked on 2-10-1993 could be recovered on 20-4-94, i.e. after 200 days. Marked limpets sometimes migrated out of the study area and some, not all, returned subsequently, after a period of 41-200 days. Some marked limpets were found amidst boulders, adjacent to the study area. During the monsoon season, when wave action is intense, most limpets were restricted to protected areas or perhaps migrated out of the study area to safer areas among the rocky boulders.

Data on the shell length of marked limpets was used to study its growth. In the von Bertalanffy growth model, three parameters need to be estimated: $L_\infty$, the asymptotic shell length, $K$, the growth constant and $t_0$, the theoretical age of limpets at zero shell length. Since growth is rapid in the early stages, it was reasonable to assume that the value of $t_0$ was negligible. Similar assumption was made by Rao (1976) in his study on $C. radiata$ and by Ward (1967) in his study on $Fissurella barbadensis$. The coefficient of variation of trial values of $L_\infty$ obtained from the Munro plot is shown in Fig. 43. The optimal value of $L_\infty$ was 39.41mm with a $K$ value of 0.089. The estimated value of $L_\infty$ lies close to the actual size of the largest limpet (36.75mm) recorded in the field.
Fig. 43. The coefficient of variation of trial values of $L_\infty$. 
The von Bertlanffy growth curve obtained using the estimated parameters is shown in Fig. 44. The age of marked limpets was estimated using the estimated parameters and are superimposed with the curve. Data obtained in the laboratory on the age and growth of juvenile limpets are also plotted. It can be seen that observed growth of the limpet follows the von Bertlanffy growth model.

The growth curve of *C. radiata* is asymptotic. The limpet attains a shell length of 25mm after the first year and subsequently a shell length of 34.72mm, 37.79mm, 38.85mm and 39.41mm in the second, third, fourth and fifth year respectively. The size when the limpet attains sexual maturity would correspond to age between 3 to 5 months. The theoretical estimated longevity is around 5 years.

Data obtained from tagged limpets was also used to estimate seasonal growth rates using the 'forced' Gulland and Holt plot (Fig. 45). \( L_\infty \) value was obtained earlier using the Munro plot. The growth constant, \( K \), during October to January (post-monsoon) was 0.11; 0.09 during February to May (pre-monsoon) and 0.07 during June to September (monsoon). The seasonal growth rates were 1.32mm/month, 1.05mm/month and 1.94mm/month for the pre-monsoon, monsoon and post-monsoon seasons respectively. The mean growth rate estimated by pooling the data obtained during the entire study period was 1.34mm/month.
Fig. 44. The von Bertalanffy curve showing the size attained at specific ages.
Fig. 45. The seasonal variations in the growth rates of *C. radiata*. Post-monsoon (a) Pre-monsoon (b) Monsoon (c).
4.3 DISCUSSION

4.3.1 POPULATION STRUCTURE

One of the pre-requisites for the study of the population dynamics or population structure of any organism is the age of the organism. As the size of organisms is related to its age, many ecologists have been analysing the polymodal frequency distribution of sizes of the population of organisms with time in order to follow the dynamics of the population. Harding (1949) and later, Cassie (1954) used probability paper to analyse the component Gaussian curves. Taylor (1965) also suggested a technique for analysing such data. These methods have been widely employed wherever the age groups of the organism had to be delineated.

In the present study, the statistical fitting of Gaussian curves was employed to separate age groups and its goodness of fit tested. The results obtained confirmed some of the practical problems encountered, such as the separation of distinct size classes representing age groups. As the limpet, *C. radiata*, breeds and grows throughout the year, well defined size groups were not formed. Similar observations were made by Ward (1967) while studying the distribution of the keyhole limpet, *Fissurella barbadensis* in the West Indies and by Rao (1976) in his study of *C. radiata* at Waltair, on the east coast of India. Rao (1976) observed about 2 modal groups but could trace the fate of only
one of them. Older limpets could not be successfully statistically separated into separate age groups because of their asymptotic growth, resulting in the merger of their size groups.

Analysis of the frequency distribution revealed the presence of at least four groups and their shift in modal peak as well as growth could be reasonably followed. The goodness of fit of the Gaussian curves were in some cases not significant, highlighting the difficulties in analysing the data. The number of individuals in each group varied from month to month and in some cases increased, indicating that the population was complex and could possibly further comprise of a number of sub groups. Attempts to statistically separate these sub groups were futile. Further, the density of limpets varied from month to month. Observations on marked limpets suggested that limpets migrated out and into the study area. Thus the low densities recorded during the monsoon period could perhaps be ascribed to migration. During this period only a few limpets of the different size groups remained in the study area.

The non observation of limpets less than 10mm in shell length during this study implies that either they were missed or they were inaccessibly located in the narrow fissures and crevices of the study area.

The largest number of small sized limpets were recorded in September '94. From the von Bertalanffy growth curve, these limpets can be assumed to have been born in March-April '95.
Similarly, the juvenile limpets recorded in December '93 and March '94 could be assumed to have been born in July '93 and October '93 respectively. These observations reaffirm that C. radiata is a continuous breeder.

4.3.2 GROWTH

Tagging has been used to follow the growth of limpets by several investigators. Marking methods employed ranged from marking the shell using enamel paint (Rao, 1976), filing marks on shells (Magruder & Kay, 1983; Fletcher, 1984a) to the elaborate sticking of numbered tags (Branch, 1974b; Phillips, 1981). The last two methods enables monitoring of individual limpets. In a study carried out at Waltair, Rao (1976) marked 60 limpets using common enamel paint marks for a number of limpets of similar shell size and monitored their growth for four months, remarking them whenever necessary. The percentage recovery of marked limpets (20%) was similar to that obtained in the present study. The low recovery percentage necessitates marking of a large number of limpets, a laborious process. Nevertheless, results obtained from tagged individuals are much more accurate.

The growth of C. radiata measured as changes in the shell length varied with the limpets age. Smaller limpets grew faster than larger ones. There were slight variations in the seasonal growth rates. Both methods of estimating growth (analysis of size frequency histograms and tagging) yielded roughly the same
results. Growth is rapid in the early stages, sharply declining after the first year. The decline in growth rate could possibly indicate increased allocation of energy for reproduction. The curve attains the asymptote after the third year.

Though the theoretical life span of the limpet, when the limpet attains the asymptotic shell length, was estimated to be 5 years, the maximum size of limpets in the field was not more than 34mm suggesting that they survive in the field for about two years. The cause of mortality could be due to the presence of predators. Besides crows, crabs (Grapsus sp.) and molluscs (Euplica versicolor, Gyraneum natator, Conus planorbis) are the likely predators of limpets. These molluscs were however not abundant and no observations were recorded in the field. During field visits, it was also observed that some of the limpets were being collected for human consumption.

The growth curve of C. radiata inhabiting the rocky shores of Waltair, along the eastern coast of India, was different. Seasonal variations in growth rates were not observed, probably because marking was carried out for a few months only, and ascribed to the absence of marked climatic variations (Rao, 1976). Further, they attained a length of 20mm at the end of the first year, 30mm at the end of the second year, 36mm at the end of the third year and 39mm at the end of the fourth year. Their asymptotic shell length, $L_\infty$, was 42.55mm, growth constant, $K$, 0.05434, mean monthly growth rate 1.16mm, theoretical life span, 8 years and they were presumed to survive for 3 years. Thus,
when compared to *C. radiata* at Anjuna, they exhibit a slower growth rate, a longer theoretical life span but a longer survival period in the field and a larger asymptotic shell length.

Limpets have variable growth rates depending upon a multitude of factors. Several investigators have related growth rates with food availability (Blackmore, 1969; Sutherland, 1970; Phillips, 1981; Parry, 1982a). *Patella cochlear, P. granatina, P. granulata, and P. oculus* attain a first year length of 22mm, 35mm, 18mm and 56mm respectively (Branch, 1974b). These differences in growth rates have been partly attributed to the nutritive value of different food sources. In *Siphonaria diemenensis*, growth rates vary and food availability has been reported to be the major determinant of variation of not only of its growth but also of its survival (Quinn, 1988a).

At Anjuna, analysis of the gut contents of *C. radiata* revealed that its diet could be related to the abundance of algae in the study area. The limpet could be considered as a generalist grazer and not a species specific grazer. The presence of other grazers is likely to increase interspecific competition thereby restricting the area available for feeding. The dominant grazers at Anjuna are prosobranch such as littorinids (*Littorina* spp., *Nodilittorina* spp.), neritids (*Nerita chamaeleon, Nerita albicilla*), *Trochus stellatus, Turbo intercostalis, Euchelus quadricarinata, Planaxis sulcatus* and *Ochetocllava sinensis* (Coutinho, 1993). There are however no studies on the competition amongst these grazers at Anjuna.
Observations revealed that the limpet wandered for longer distances, as indicated by the mean daily displacements, and homed during the hot season. Wandering would enable the limpets to explore larger areas for grazing. At Aniuna, algal growth begins in September with peak growth in February-March and minimal growth during the monsoon season (Dhargalkar, 1981). Limpets being grazers might also be affected by this seasonal trend in food availability. Thus, this would imply that the growth rate would be higher during the pre-monsoon season. This was however not the case. On the other hand, consideration of physical factors prevailing during the seasons could perhaps explain this apparent anomaly. During the pre-monsoon season, the overall mean environmental temperature rises resulting in a higher metabolic activity. Further, during this season, the low tide periods occur in the middle of the day, when temperatures are high resulting in increased metabolic activities. Such increased energy utilization might therefore reduce energy apportionment for growth. Field observations revealed that C. radiata homed during this season. Homing, as an adaptation to withstand desiccation stress, enables the limpets to conserve energy.

Quinn and Brown (1988) have related growth rates to wave action. Increased wave action reduces foraging time. Increased wave action would force the animals to adhere firmly to the substratum to prevent dislodgement. Thus energy that could be utilized for growth would then be expended on countering physical
stress. Thompson (1980) observed that with intensification of wave action, the ratios of \textit{P. vulgata} to \textit{P. aspera} numbers and growth declines. Branch (1981) attributes these differences to the increased oxygen consumption in the animals that are forced to adhere tightly to the substratum resulting in increased energy losses. Lower growth rates observed in the study area during the monsoon season could thus be not only because of shortage of food but also because of increased metabolic activity.

4.3.3 LIFE HISTORY TRAITS

Shorter life span, faster growth and precocious maturity are some of the life history traits generally associated with the tropical species (Naylor, 1965). The limpet, \textit{C. radiata}, in this study conforms with these traits. The life span of the limpet at Anjuna was estimated to be about 2 years. Along the east coast of India, this limpet is reported to live for approximately 3 years (Rao, 1976). The life span of \textit{Cellana exarata} and \textit{C. sandwicensis} along the Hawaiian coast is reported to be around 1.5 years (Magruder & Kay, 1983). In sharp contrast, \textit{Patella vulgata} survives for about 3 to 15 years along the temperate British coasts (Fretter & Graham, 1962).

Growth of limpets is also faster in tropical regions. At Anjuna, \textit{C. radiata} attains a shell length of 25mm in the first year. At Waltair, it grows to 20mm during the same period. \textit{Fissurella barbadensis} from the West Indies is 26.5mm in length.
at the end of one year (Ward, 1967). The two species of Hawaiian patellid limpets viz. Cellana exarata and C. sandwicensis attain a shell length of 40mm after the first year (Magruder & Kay, 1983). Most temperate limpets, however, grow at a comparatively slower rate. *Patella vulgata* grows to a length of 9mm in one year (Lewis & Bowman, 1975). *Acmaea scabra* is only 2mm-6mm at the end of one year (Sutherland, 1970). There are however exceptions. *Patella oculus* attains a shell length of 55mm in one year (Branch, 1974b). Orton (1928) reported a maximum size of 35mm for one year old *Patella vulgata*.

Early sexual maturity and intensive breeding has been reported in limpets of tropical regions. At Waltair, *C. radiata* attains sexual maturity when 6-8 months old and measures 10-15mm in shell length and breeds continuously (Rao, 1973, 1976). At Anjuna too, observations suggest that the limpet attains sexual maturity when 10-15mm in size (3 to 5 months old). The Hawaiian patellid limpets attain sexual maturity when 4-5 months old (Magruder & Kay, 1983). The temperate limpet, *Patella vulgata*, however attains sexual maturity only when one year old, when they are about 20mm in length.

Many investigators have obtained a striking inverse correlation between the growth coefficient, *K*, and longevity. This has been particularly true in the case of *Patella vulgata* inhabiting different localities (Choque, 1968; Lewis & Bowman, 1975; Thompson, 1979, 1980; Branch, 1981). In contrast to the fast growing species discussed earlier, there are also slow
growing species like the Antarctic limpet, *Nacella concinna*, which has a low K value (0.07), a low metabolic rate. sexually matures after 7-8 years, and has a prolonged longevity (30 years) probably as an adaptation to the low availability of food (Picken, 1980). In South Africa, *P. longicosta* and *P. cochlear* too are slow growing species having a longevity of approximately 12-17 and 15-25 years respectively (Branch, 1974b).

An exception to this hypothesis is the observations by Sutherland (1970) that though high shore *Collisella scabra* grew faster than low shore individuals, they suffered a lower mortality and lived longer. Creese (1981), in his studies on some species of limpets in New South Wales reported the growth pattern of two patellid species *Patelloida latistrigata* and *P. alticostata*: the former grew slowly, attained a size of 15.1mm but had a longevity of only 3 years while the latter grew faster, attained a size of 22.3mm and had a longevity of 5-6 years. He explained that *P. latistrigata* lives in close association with barnacles which may limit the maximum size to which it can grow.

Branch (1981), reviewing this relationship, suggests that the life expectancy would shorten with rapid growth and early sexual maturity as these traits would exhaust energy reserves. In addition, these may also reduce energy available for defensive structures thus enhancing mortality risks. He concluded that although growth pattern may be flexible, different species display different patterns as adaptations to particular circumstances.