Life-history patterns of populations of the limpet *Patella granularis*: the dominant roles of food supply and mortality rate

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Summary. Rates of algal production were measured at 6 rocky intertidal sites on the southwestern Cape coast, South Africa, where populations of the limpet *Patella granularis* occur. Rates of algal production and limpet mortality were recorded at each site and both factors affected limpet reproductive fitness. Limpet growth rates and biomass at different sites were significantly correlated with rates of algal production, and limpet mortality was related to the density of African Black Oystercatchers, important predators of *P. granularis*. Life-time gametic output of a hypothetical cohort of limpets at each site was modelled using the measurements of growth, reproduction and mortality made at each site. Limpet cohorts at sites with rapid rates of algal production were predicted to have a longer life-time production of gametic material than cohorts at sites with slow algal production rates, except in instances of acute predatory pressure. In the light of the overriding influence of food supply on the expression of limpet life-history parameters, it is imperative that researchers consider food availability before assuming that local, population-specific differences in life-history patterns are due to genetic differences.

Key words: Primary production - Limpets - Oystercatchers - Predation - Life-histories

The 'fitness' of an individual organism generally is considered in terms of the number of its offspring which themselves survive to reproduce (Horn 1978; Grahame and Branch 1985). When applying this term to marine or intertidal invertebrates with external fertilization of gametes, the success of the individual is equated with the biomass of gametic material released during the organism's life-time (Fletcher 1984b). The expressions of life-history parameters of an organism - such as growth rate, age and size at maturity, reproductive effort and longevity - represent a combination of solutions to particular ecological problems (Stearns 1980), each solution being the optimal outcome of conflicting demands placed on the organism by its environment. Life-history patterns combine to maximize the individual's life-time reproductive success, given the constraints placed on the organism by the abiotic and biotic conditions prevailing (Grahame and Branch 1985), and are therefore adaptive.

Methods and materials

Study sites

In December 1982, 5 study sites were established on the shores of Marcus Island (33°02'S, 17°58'E), a granitic seabird-breeding island in Saldanha Bay on the southwestern coast of South Africa. The sites were on smooth, rocky slopes inclined at 80°, 60°, 45°, 20° and 0° to the horizontal, respectively, and were positioned at intervals along a 100 m stretch of coastline. All sites were at approximately the same height above the mean spring low-tide level. An additional 0° (level) site was established at Cape Columbine (32°49'S, 17°51'E), on the mainland approximately 40 km north of Saldanha Bay (Fig. 1). Both study areas are in the Benguela
Algal production

A herbivore exclusion plot was established at each site, by enclosing a 0.1 m² rectangular area with a strip of copper-based marine anti-fouling paint. The paint was renewed whenever it became worn. Each month for 15 months, after the rock had been scraped clean and burned with a blow-torch to kill existing algal spores, 4 high-intensity polystyrene settlement strips (each 30 x 50 x 2 mm) were glued to the rock inside the exclusion plot, using rapidly setting epoxy. After a month in position the strips were lifted, wrapped in aluminium foil to exclude light, and frozen for subsequent analysis.

Chlorophylls a, b and c were extracted from the algae that had grown on each strip, using the method of Strickland and Parsons (1972), and were quantified using a Beckman model 25 spectrophotometer and the equations of Jeffrey and Humphrey (1975) (see also Underwood 1984a for details of method). The values obtained were corrected for the exact area of each strip, and the number of days in position, so that the final index of algal production was expressed in ug chlorophyll cm⁻² month⁻¹. The mean of the 4 monthly samples was used in analysis.

Limpet growth and mortality

Adjacent to each limpet exclusion plot, between 30 and 50 P. granularis were labelled individually with punched plastic labels and rapidly setting epoxy. Each month for 15 months, maximum shell length of recovered individuals was recorded. Predation and other factors caused the mortality of limpents, and supplementary individuals were labelled when numbers fell below 10. For each site, in each month, a linear regression of limpet length in the current month (Lt+1) on limpet length in the previous month (Lt) (Ford-Walford plot) was calculated using the measured values. If the parameters were not significantly linearly related the data for that month were considered of no predictive value and were discarded. The regression line was described by the equation:

\[ L_{t+1} = m L_t + i \]

where \( m \) = rate of increase in length and \( i \) = growth in the first month (Balaparameswara Rao 1976; Branch 1981).

The predicted monthly growth of a ‘standard’ 30 mm limpet was calculated from each regression. Limpets of ca. 30 mm in length were common at all sites, and the monthly increment of a limpet this size was deemed a useful index of overall rate of limpet growth, considering that absolute growth rate is dependent on limpet size (Branch 1981). No true replication of study sites was obtained using this experimental design, and thus the statistical testing of mean predicted limpet growth is inappropriate (Hurlbert 1984). Multiple linear regression analysis (Sokal and Rohlf 1981) was employed to regress the dependent variable (predicted monthly increment in shell length of a 30 mm limpet) on the independent variables algal production rate, month and site. In addition, the predicted increment of a limpet this size was deemed a useful index of overall rate of limpet growth, considering that absolute growth rate is dependent on limpet size (Branch 1981). No true replication of study sites was obtained using this experimental design, and thus the statistical testing of mean predicted limpet growth is inappropriate (Hurlbert 1984). Multiple linear regression analysis (Sokal and Rohlf 1981) was employed to regress the dependent variable (predicted monthly increment in shell length of a 30 mm limpet) on the independent variables algal production rate, month and site. In addition, the predicted increment of a limpet which measured 30 mm in January 1983 and which grew, according to the predictions of monthly Ford-Walford plots, until December 1983, was calculated for each site. When the line described by the equation \( L_{t+1} = L_t \) (i.e. no growth) is superimposed on each Ford-Walford plot, the intercept of the 2 lines indicates the predicted maximum length of a limpet growing at that site \( (L_m) \) (Balaparames-