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Note

A discrete-time logistic model of frond dynamics for *Mazzaella parksii* (Rhodophyta, Gigartinales)

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Abstract

Mathematical modelling is useful in population ecology and resource management. Logistic models have traditionally been applied to unitary organisms, but it is unclear whether they could be used at the frond (ramet) level for clonal seaweeds. This study shows that frond dynamics for the clonal seaweed *Mazzaella parksii* (= *M. cornucopiae*) can be described by a discrete-time logistic model. The model is realistic in that it includes density-dependence, which was previously demonstrated experimentally for this species, and only necessitates data on frond density measured at discrete time intervals. This may constitute a useful tool for the management of clonal seaweeds of economic importance that occur in dense stands.

The proper management of a seaweed resource must be based on knowledge on its population dynamics, which can be furthered through the use of mathematical models. Many seaweed species of economic importance are clonal and occur in dense stands in nature. The term clonal refers to the fact that the holdfast of such algae produces many fronds (ramets) that have the potential for independent life if they are physically separated from the parent thallus. In dense stands of these algae, the visual identification of genets (defined as the thallus that develops from a single spore; Scrosati, 2002) is usually very difficult, if not impossible. Reasons for such a limitation include coalescence of neighboring sporelings (as in Gigartinales; Santelices et al., 1999), stolon interminglement (as in Gelidiales), rupture of one original genet into two or more clonal fragments (sensu Eriksson & Jerling, 1990), and high frond densities per se. Therefore, population models are most easily developed for these algae when focused on fronds rather than genets.

Logistic models describe the dynamics of populations that are affected by density-dependence (Gurney & Nisbet, 1998); they have been used for a variety of unitary (nonclonal) species of plants and animals (Gotelli, 1995; Silvertown & Charlesworth, 2001). It is unclear whether such models would describe adequately the dynamics of fronds of clonal seaweeds. This contribution investigates this question using *Mazzaella parksii* (Setchell & Gardner) Hughey, P. C. Silva & Hommersand (formerly *M. cornucopiae*, according to Hughey et al., 2001) as a model species. The thallus of *M. parksii* is composed of a crustose holdfast and many foliose fronds; natural stands can cover extensive areas of the substrate (Figure 1). This species occurs in rocky intertidal areas in the NE Pacific coast (Hughey et al., 2001). In Barkley Sound, southwestern Canada, frond density and stand biomass increase between winter and summer, and decrease during the rest of the year. New fronds are mostly produced by perennating holdfasts; recruitment from spores is relatively marginal (Scrosati, 1998). The per capita rate of production ('natality') of new fronds during the growth season was experimentally shown to be density-dependent (Scrosati & DeWreede, 1997), meaning that less fronds are produced per existing

Figure 1. Stand of *Mazzaella parksii*, photographed in August 1994 at Prasiola Point. Lens cap is 5 cm in diameter.

frond as density increases. A density-dependent natality rate promotes logistic growth in a population, regardless of whether mortality is density-dependent or not (Gotelli, 1995). Therefore, the density of *M. parksii* fronds might increase following the logistic growth model. This study tests this hypothesis using an existing data set that was collected during the 1995 growth season.

Between the winter and summer seasons of 1995, frond density was measured for *Mazzaella parksii* in five permanent, 100-cm^2 quadrats randomly established at the high intertidal zone of Prasiola Point (48° 49' N, 125° 10' W), located on southern Barkley Sound, Vancouver Island, British Columbia, Canada (see map and site description in Scrosati, 1998). Sampling dates were 30 January 1995, 30 March 1995, 14 May 1995 and 13 July 1995.

The logistic growth model is (Gotelli, 1995):

$$dN_t/dt \ = rN_t(1 - N_t/K),$$

where dN_t/dt is the instantaneous rate of population change, t is time, N_t is population density at time t, r is intrinsic growth rate, and K is carrying capacity. This equation is of a continuous nature, but the available data on *Mazzaella parksii* were collected at discrete time intervals. Therefore, a discrete-time version of the logistic equation that gives a highly accurate approximation to the continuous model was used (Gurney & Nisbet, 1998):

$$N_{t+\Delta t} \ = (KN_t)/[N_t + \gamma(K - N_t)],$$

where N_t is population density at a given sampling date, $N_{t+\Delta t}$ is population density at the following sampling date, K is carrying capacity, and γ is defined as: $e^{-r\Delta t}$ (r being intrinsic growth rate). For practical purposes, the average time interval between consecutive sampling dates (Δt) was considered to be two months.

Model parameters (K and γ) were calculated through nonlinear least-squares estimation, using SYSTAT 5.2 for Macintosh (Wilkinson et al., 1992). To assess the degree of fit of the data to the model, the Pearson correlation coefficient (Howell, 1992) was calculated between model-predicted values and observed values of $N_{t+\Delta t}$. When a given model is appropriate for the data, all predicted-observed data pairs are expected to fall on a straight line (StatSoft, 1994). To test for the significance of a correlation coefficient using standard parametric tables, data must be collected at random (Howell, 1992). Since there was some dependency among data for consecutive sampling dates, significance was assessed through a randomization test. Randomization tests can compare any observed statistic with a distribution that is generated each time a significance test is done, by randomly reshuffling the sample data and recalculating the statistic many times (Edgington, 1987). In this way, there are no assumptions to meet on any parametric distribution for the statistic. The randomization test was done with Resampling Stats 5.0 for Macintosh (Bruce et al., 1999), making 1000 random permutations.

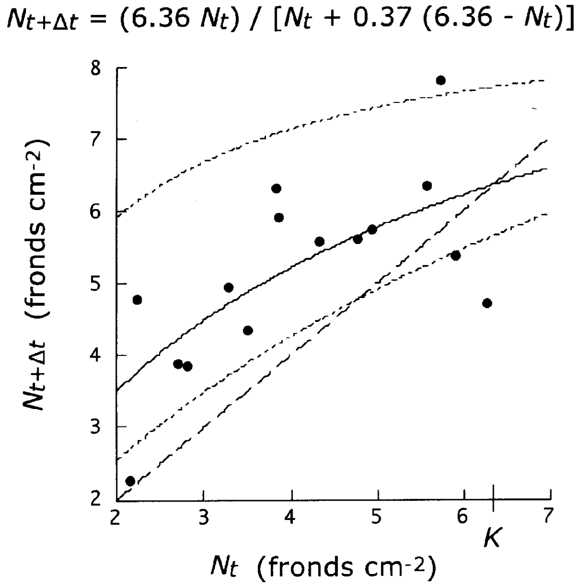

Figure 2. Mazzaella parksii frond density for successive sampling dates during the 1995 growth season at Prasiola Point (n = 15). The discrete-time logistic model for these data is stated at the top. The functional relationship is indicated by the continuous line, whereas its 95% confidence limits are indicated by the two dotted lines (see their respective parameter values in the text). Points above the equality function ($N_t = N_{t+\Delta t}$; indicated by the dashed line) represent density increases, whereas those below it represent density decreases. The logistic and equality functions intersect at $N_t = K =$ 6.36 fronds cm^{-2}.

Data on N_t and $N_{t+\Delta t}$ were significantly related through the discrete-time logistic model stated above (Figure 2). The Pearson correlation coefficient between predicted and observed values of $N_{t+\Delta t}$ was 0.70 ($p = 0.003$, n = 15). Parameter values (with 95% confidence intervals stated between parentheses) were: $K = 6.36$ fronds cm^{-2} (4.79–7.94) and $\gamma = 0.37$ (0.11–0.63). Once both γ and Δt were known, r (intrinsic growth rate) was estimated to be 0.50 month^{-1} (0.24–1.09). Therefore, frond dynamics during the growth season can be described by a logistic model for *Mazzaella parksii*.

The similarity between the carrying capacity estimated by the model (6.4 fronds cm^{-2}) and the average frond density measured in July (6.0 ± 0.5 fronds cm^{-2}, mean ± S.E., n = 5) indicates that *Mazzaella parksii* reaches its carrying capacity in early summer. High abiotic stress, particularly high desiccation and irradiance during low tides (Scrosati & DeWreede, 1998), and herbivory by *Littorina* snails (Kim & DeWreede, 1996; Heaven & Scrosati, 2003) contribute together to the decline in density that normally occurs between summer and autumn. Therefore, logistic modelling should be restricted to the growth season (winter to summer) for this species.

A useful feature of this discrete-time logistic model is that the data needed for its parameterization are simply frond density changes over time. Another useful feature is that the data can be collected not continuously, but at discrete time intervals, which is what field studies can only do. If desired, this discrete-time version of the logistic equation will give a highly accurate approximation to the continuous-time version (Gurney & Nisbet, 1998). Another positive feature of this model is its built-in density-dependence, which is a recognized characteristic affecting the dynamics of many algal populations (Reed, 1990; Ang & DeWreede, 1992; Scrosati & DeWreede, 1997; Creed et al., 1998; Arenas et al., 2002; Steen, 2003).

In conclusion, a discrete-time logistic model has been shown here to describe frond dynamics for *Mazzaella parksii*. Therefore, this modelling approach might be useful to study and manage the population dynamics of other clonal seaweeds that grow in dense stands and are subjected to density-dependence. By manipulating frond density (such as with periodic harvests), the population growth rate (dN_t/dt) could be kept at higher levels than at naturally high frond densities, theoretically increasing the rate of production of new fronds (Gotelli, 1995). It must be stressed, though, that the model presented here is a simplified version of reality, as implied in any modelling approach. Future research along this line should refine the current demographic knowledge on these algae. For example, future work should investigate the spatial, seasonal, and interannual dependence of frond natality and mortality rates on frond density, and the exact form of the corresponding functions. This will allow production of models applicable to different spatial and temporal scales.

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