Journal of Theoretical Biology 339 (2013) 70–83

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

When can a single-species, density-dependent model capture the dynamics of a consumer-resource system?

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ARTICLE INFO

Available online 5 September 2013

Keywords:
Continuous-time
Functional response
Handling time
Logistic model
Smith model

ABSTRACT

Single-species population models often include density-dependence phenomenologically in order to approximate higher order mechanisms. Here we consider the common scenario in which density-dependence acts via depletion of a renewed resource. When the response of the resource is very quick relative to that of the consumer, the consumer dynamics can be captured by a single-species, density-dependent model. Time scale separation is used to show analytically how the shape of the density-dependent relationship depends on the type of resource and the form of the functional response. Resource types of abiotic, biotic, and biotic with migration are considered, in combination with linear and saturating functional responses. In some cases, we derive familiar forms of single-species models, adding to the justification for their use. In other scenarios novel forms of density-dependence are derived, for example an abiotic resource and a saturating functional response can result in a nonlinear density-dependent relationship in the associated single-species model of the consumer. In this case, the per capita relationship has both concave-up and concave-down sections.

1. Introduction

Single-species models have a long tradition in ecology. They have been used to make predictions about empirical populations, informing management decisions such as those concerning sustainable harvesting (Guthery and Shaw, 2012). Additionally, they serve as fundamental components of more complex models, such as food web models or models of species interactions. Single-species models are, however, simplifications of a complex reality. In the field, the species being modeled is just one member of a large, interacting ecosystem, which consists of many other species and nutrients that are not explicitly referenced in the model. Even in a laboratory setting, where the researcher can limit the number of species and types of interactions, a single-species model does not explicitly take into account the dynamics of the nutrients which the organism must consume in order to survive. Instead, single-species models, such as the logistic model, attempt to capture direct and indirect interactions with other species by incorporating their effects into an abstract concept such as a carrying capacity.

A diverse set of single-species models, both continuous-time and discrete-time models have been proposed (Brannstrom and Sumpter, 2005; Sakanoue, 2007; Wu et al., 2009). Arguably, the most widely used model is the Verhulst–Pearl logistic (Verhulst, 1838; Pearl and Reed, 1920), which assumes a linear decrease in the per capita growth rate with increasing density. Various justifications for the logistic model have been made (Thornley et al., 2007); however, they are not without controversy (Ginzburg, 1992; Berryman, 1992). Typical textbook derivations simply posit a linear relationship between per capita growth rate and density as an approximation (Begon et al., 2007; Gotelli, 2008). In general, phenomenological single-species models lack mechanistic explanations for their functional form. However, there have been periodic efforts to derive single-species models on first principles. A more explicit spatial derivation of the logistic equation considers individuals as competing, overlapping circles on a surface (Royama, 1992), although the derivation is vague as to the identity and dynamics of that for which individuals are competing. The discrete-time Ricker model has found mechanistic justification through several derivations, including one in which adult fish cannibalize juveniles (Gurney and Nisbet, 1998) and another in which it approximates a stochastic individual-based model for a mite (Sumpter and Broomhead, 2001). A series of discrete-time models have been derived based on a spatially implicit framework of safe sites (Brännström and Sumpter, 2005). Additionally, several well-known discrete-time models have been derived through the

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0022-5193/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2013.08.025

time scale analysis of underlying within year consumer-resource dynamics (Geritz and Kisdi, 2004). The continuous-time within year dynamics provide a mechanistic explanation for the cyclic and chaotic dynamics that can be expressed in single-species discrete-time models.

Density-dependence is a central feature of many single-species models, and indeed even an increasingly important feature of age-structured models (Neubert and Caswell, 2000). Nonetheless, there is a large and sometimes inconsistent lexicon associated with the concept of density-dependence (Herrando-Perez et al., 2012). Here we define density-dependence as the effects of population density upon population per capita growth rate. Density-dependence can be described by the shape of a per capita growth rate (PCGR) curve which is a plot of population per capita growth rate, $dN/(N\,dt)$, versus population density, N, a relationship that can be examined empirically and modeled mathematically. For example, the PCGR curve of the logistic model is linear. Since per capita growth rate can be thought of as a function of density, $dN/(N\,dt)=f(N)$, a single-species PCGR curve implies the single-species model, $dN/dt=f(N)N$. Density-dependence can arise for various reasons, including changes in the availability of nesting sites, nutrients, or suitable mates with density. As in Abrams (2009a), we limit the consideration of density-dependence to that due to the availability of consumable, renewable resources, such as prey items or nutrients.

In a single-species, density-dependent model a real-world ecosystem, which may consist of n interacting species, has been reduced from an n-dimensional system to a one-dimensional equation. In essence, a reduction in system dimensionality is occurring. Schaffer (1981) refers to the reduction of a real-world ecosystem with n interacting species to a mathematical model with $m<n$ interacting species as “ecological abstraction”. In this sense, single-species models are the limiting case of ecological abstraction. This perspective raises a few questions: (1) What methods can be used to abstract a single-species model from a multi-dimensional system? (2) What functional forms of single-species models are constructed from these methods of abstraction? (3) Are there ecological situations in which these methods are better at capturing the actual dynamics of the organism of study? We consider these questions in the framework of continuous-time, deterministic, unstructured models; in other words those lacking age-structure or size-structure. Such models are a natural first consideration, as methods of incorporating density-dependence in single-species models often become the basis of how density-dependence is incorporated into more complex models.

Ideas about how a consumer-resource system can be translated into consumer single-species dynamics have been explored by making substitutions determined from equilibrium relationships (Mac Arthur, 1970; Schoener, 1973). While these approaches were not discussed as time scale separation problems, for the best accuracy they inherently assume that the resource dynamics take place on a much shorter time scale than the consumer dynamics (Mac Arthur, 1970). Schaffer (1981) develops a general method of abstraction that determines growth equations for $m<n$ species from a known n-dimensional ecosystem. The abstracted growth equations most accurately describe the growth seen in the full system when the dynamics of the omitted species occur on relatively fast time scales (Schaffer, 1981) and the species of focus are near their equilibrium values. Using Schaffer's method, a single-species model abstracted from an n-dimensional ecosystem is always of logistic form. Despite the wide use of the logistic model, the existence of several data sets with non-logistic behavior has spurred the development of various alternative single-species models (Wu et al., 2009; Tsoularis and Wallace, 2002). While Schaffer was able to make many insightful remarks on the topic of ecological abstraction, his method is not flexible enough to capture the nonlinear PCGR relationships observed in some empirical systems (for example Forrester et al., 2011). However, not all past single-species model abstraction methods have resulted in the logistic model; in Thieme (2003) a single-species model with a convex PCGR curve is abstracted from a consumer-resource system via time scale separation. Furthermore, recent work by Abrams (2009a,b) suggests a method of abstraction that can produce nonlinear PCGR curves.

Abrams' approach differs from those mentioned above. Instead of using the equilibrium values of an original two-dimensional consumer-resource system, he uses the equilibrium values that result from applying a constant per capita harvest rate to the consumer. By relating the harvest rate to the consumer growth rate, Abrams abstracts a single-species density-dependence curve. Since Abrams' density-dependence curves are displayed in a nonstandard format, which has hindered their interpretation, it is worthwhile to discuss the implications of Abrams' work and the format in which it is presented. Abrams (2009a) shows there are types of consumer-resource systems that lead to the consumer having nonlinear, i.e. non-logistic, density-dependence curves. Furthermore, he demonstrates that there are cases where the nonlinear density-dependence curves of the consumer cannot even be accurately described by the curves of the theta-logistic model (Gilpin and Ayala, 1973). While these results are clear from Abrams' figures, unfortunately, the curves Abrams finds, $N=g(dN/(N\,dt))$, are the inverse functions of the PCGR curves described above, $dN/(N\,dt)=f(N)$. In some cases g is not invertible. Moreover, it is unclear under which ecological situations the method Abrams applies will be the most accurate in describing actual per capita growth rate curves.

As in Thieme (2003), we formally consider the abstraction of a single-species model from a consumer-resource system as a separation of time scales problem. Time scale separation is a tool used in many adaptive dynamics approaches (Abrams, 2001, 2005; Dieckmann and Law, 1996; Geritz et al., 1996), which typically assume that ecological processes occur on a much faster time scale than evolutionary changes. For a few consumer-resource systems, we explicitly identify a small parameter ε, which justifies a separation of time scales approach under the assumption that resource dynamics occur rapidly compared with those of the consumer. The time scale problems considered here can be addressed more rigorously using the technique of matched asymptotics (Edelstein-Keshet, 2005; Logan, 2006; Lakin and Van Den Driessche, 1977) from singular perturbation theory (O'Malley, 1991; Schaffer, 1981; Thieme, 2003), which has also been used in describing Michaelis–Menten kinetics (Heineken et al., 1967). As desired, the solutions from matched asymptotics converge to the equations presented here as $\varepsilon \to 0$. By using time scale separation to abstract single-species models from consumer-resource systems, we ground the abstraction methods of Abrams in a more formal mathematical approach. In doing so, the ecological situations under which Abrams' approach best represents consumer dynamics can be described. Furthermore, we calculate explicit functional forms of single-species models abstracted from a few particular consumer-resource systems. The models, including their density-dependence curves and their relation to previous literature, are discussed.

2. Models and results

2.1. General approach

A consumer with population density, N, interacting with a single resource population of density, R, is represented by the