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

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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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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

differential equations model

$$\frac{dN}{dt} = bf(R)N - mN$$

$$\frac{dR}{dt} = g(R) - f(R)N. \qquad (1)$$

Consumer-resource systems of this form are considered by Abrams (2009a). The function g represents the rate of change of the resource density in the absence of the consumer, and the function f is the consumer's functional response. The per capita growth rate (PCGR) of the consumer, at any point in time, is given by the difference between the per capita gain in population size due to resource consumption and the per capita loss of population size due to natural causes, m. Consumer growth is always assumed linearly dependent upon resource uptake (linear numerical response), where b is a conversion efficiency parameter.

We examine three types of resource and two types of consumer functional responses (Table 1) in combination to form six particular examples of consumer-resource models of form (1). In the absence of the consumer, each resource type undergoes different dynamics. The abiotic resource increases at a constant rate and naturally declines at a rate proportional to its concentration, as in a chemostat. The biotic resource is assumed to have logistic dynamics with intrinsic growth rate r and equilibrium density K. Any factor contributing to the logistic dynamics of the resource behave independently of predation by the consumer. The biotic resource with migration exhibits logistic dynamics, however, the growth of the population is supplemented by a constant immigration rate into the population. Emigration is also possible and occurs at a rate proportional to the density of resource already present.

For both functional responses the consumer encounters resources with attack rate c. In situations where the consumer exhibits a linear functional response to the resource, an average consumer depletes cR units of resource per unit time. In situations where the consumer exhibits a saturating, Holling Type II functional response, a non-negligible handling time h accounts for the time it takes to secure and process food before resource encounters can again occur.

Each model will be non-dimensionalized in a way that focuses on consumer dynamics. Assuming time to death is exponentially distributed, $1/m$ represents the consumer's average lifespan, and therefore, is a good choice for a time scale. For the purposes of looking at a consumer-resource system with a stable steady-state equilibrium, how large or small a population is relative to its equilibrium is of interest. Hence, the coexistence equilibrium values of $R^\star$ and $N^\star$ will serve as good reference values for the resource and consumer densities, respectively. Using these reference values, (1) is transformed into a non-dimensionalized consumer-resource system of the form

$$\frac{d\tilde{N}}{d\tilde{t}} = G(\tilde{R}, \tilde{N}),$$

$$\varepsilon \frac{d\tilde{R}}{d\tilde{t}} = F(\tilde{R}, \tilde{N}),$$

where $\tilde{t}$, $\tilde{N}$, and $\tilde{R}$ represent the scaled values for time, consumer density, and resource density, respectively.

Assuming the response of the resource is fast compared to that of the consumer, i.e. $\varepsilon \ll 1$, a first order approximation is found for the consumer via time scale separation. By separating the time scales, the problem can be thought of as two pieces. The fast process involves the resource rapidly adjusting to consumer density while the consumer population remains constant up to first order. This results in the system quickly reaching quasi-equilibrium. During the slow process the resource remains near its quasi-equilibrium value as the consumer density evolves towards its equilibrium density. It is only the slow process of consumer growth that is of interest, and setting $\varepsilon = 0$ finds a first order approximation for this growth. Using $F(\tilde{R}, \tilde{N}) = 0$, $\tilde{R}$ can be solved for in terms of $\tilde{N}$ and substituted into the consumer equation to obtain a single-species model. The smaller the value of ε, the better the order one approximation will be to the consumer's dynamics as projected by the consumer-resource system. For large values of ε, the consumer-resource system can exhibit non-monotonic behavior, such as damped oscillations, which cannot be captured by a single-species model of the form considered (see Fig. 1).

2.2. Biotic resource and linear functional response

The order one consumer results of the biotic resource and linear functional response model are logistic (Schaffer, 1981). Before moving on to novel results, we use this section to illustrate the described process and expand upon previous work by discussing model robustness in reference to an explicit small parameter ε. Here, the interactions and growth of a biotic resource and a consumer with a linear functional response is given by

$$\frac{dN}{dt} = bcRN - mN,$$

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - cRN, \qquad (2)$$

where $R(t)$ and $N(t)$ are the resource and consumer densities at time t, respectively.

As discussed in Section 2.1 the time, resource, and consumer reference values are $1/m$, $R^\star = m/(bc)$, and $N^\star = (r/c)(1 - m/(bcK))$, respectively. With these values the non-dimensionalized version of (2) is given by the consumer-resource system

$$\frac{d\tilde{N}}{d\tilde{t}} = (\tilde{R} - 1)\tilde{N},$$

$$\varepsilon \frac{d\tilde{R}}{d\tilde{t}} = \tilde{R}(1 - \beta\tilde{R}) - (1 - \beta)\tilde{R}\tilde{N},$$

where

$$\varepsilon = \frac{m}{r}, \qquad (3)$$

and

$$\beta = \frac{m}{bcK}. \qquad (4)$$

Table 1
Model functions for resource growth and consumer functional response.

Resource type	$g(R)$	Functional response	$f(R)$
Abiotic	$i - eR$	Linear	cR
Biotic	$rR\left(1 - \dfrac{R}{K}\right)$		
Biotic + Migration	$rR\left(1 - \dfrac{R}{K}\right) + i - eR$	Saturating	$\dfrac{cR}{1 + chR}$

a

b

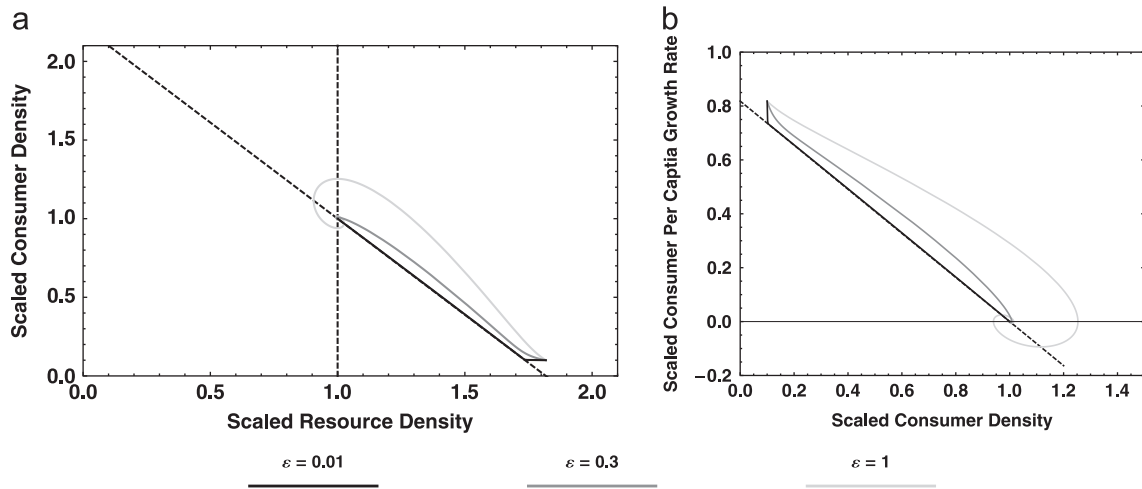$\varepsilon = 0.01$ $\varepsilon = 0.3$ $\varepsilon = 1$

Fig. 1. (a) Phase plot for the scaled biotic resource and linear consumer functional response model with $\beta = 0.55$, $\tilde{N}_0 = 0.1$, and $\tilde{R}_0 = 20/11$. Black dashed lines represent the resource and consumer nullclines. At the smallest values of ε the resource quickly adjusts to and remains at quasi-equilibrium as assumed for accuracy of model (6). (b) Consumer per capita growth rate curves corresponding with the trajectories seen in (a). The dashed line is the logistic PCGR curve predicted by model (6), and is very accurate for the smallest value of ε. When damped oscillations occur, there are consumer densities where the PCGR curve takes on multiple values. These values are determined by the resource density at the time and are highly sensitive to initial conditions. Note, it is not always the case that the PCGR curves will be a simple transformation of the phase plot; the addition of handling time, for example, will further distort this transformation.

An ecological interpretation of $\varepsilon \ll 1$ reveals a more precise definition of when the resource response is "fast" compared to that of the consumer. Eq. (3) can be written as

$$\varepsilon = \frac{1/r}{1/m} = \frac{\tau_{RB}}{\tau_N}, \tag{5}$$

where τ_N may be thought of as the expected consumer lifespan and τ_{RB} is the time it takes for the resource to increase by one unit when rare and consumer-free, henceforth referred to as the resource's "intrinsic growth time". For $\varepsilon \ll 1$, it must be that $\tau_{RB} \ll \tau_N$. If the resource's intrinsic growth time is short compared with the lifespan of the consumer, then ε will be a small parameter. Equivalently, if the intrinsic per capita growth rate of the resource is very large relative to the consumer's per capita death rate, then resource dynamics will be occurring on a fast time scale. Under these circumstances, we set $\varepsilon = 0$ and solve for $\tilde{R}$ in terms of $\tilde{N}$. Substituting the result for $\tilde{R}$ into the consumer equation, the first order approximation of the consumer's dynamics is given by the function $\tilde{N}(\tilde{t})$ that solves the initial value problem (IVP)

$$\frac{d\tilde{N}}{d\tilde{t}} = \rho\tilde{N}(1-\tilde{N}), \quad \tilde{N}(0) = \tilde{N}_0 < \frac{1}{1-\beta}, \tag{6}$$

where

$$\rho = \frac{1-\beta}{\beta}, \quad 0 < \beta < 1.$$

In other words, the dynamics of the consumer are represented by the solution to the logistic equation with intrinsic growth rate ρ and an equilibrium density of one. Since the coexistence steady-state equilibrium of the system is stable for $\beta < 1$, only the values $0 < \beta < 1$ are considered. Notice from (4) that

$$\beta = \frac{m/bc}{K} = \frac{R^\star}{R^\star_{abs}}, \tag{7}$$

where $R^\star_{abs}$ is the equilibrium population density of the unscaled resource population in the absence of the consumer. Hence, for the consumer resource-system to be stable the resource equilibrium in the presence of the consumer must be smaller than the equilibrium in the absence of the consumer. Intuitively, it makes sense that consumption of a population would result in a lower equilibrium population density. When β is close to zero, ρ is very large.

As β approaches one, ρ approaches zero. Hence, the scaled intrinsic growth rate, $\rho = (R^\star_{abs} - R^\star)/R^\star$, may take on any positive value.

If the presence of the consumer alters the resource density significantly, then β is small and the consumer density grows rapidly towards equilibrium. This will likely be the case if the consumer's attack rate is high, the consumer's lifespan is long, and the resource population is only weakly self-limiting. While we have assumed that the consumer's lifespan is long relative to the resource's intrinsic growth time, this does not mean that we expect β to always be small. If the consumer's attack rate or the resource's carrying capacity are of the same magnitude as the consumer's per capita death rate, then the consumer will have less of an effect upon the resource density and β will not be small. If the addition of a consumer population has little effect upon the resource density, then $\beta \approx 1$ and the consumer will have a low growth rate ($\rho \approx 0$). In any case, the growth is predicted to be approximately logistic. Moreover, the smaller the value of ε, or the smaller the resource's intrinsic growth time τ_{RB} is compared with the consumer's lifespan τ_N, the closer the actual dynamics of the consumer will be to the logistic dynamics predicted by (6). However, how small $\varepsilon \ll 1$ needs to be for the logistic model to be a good approximation differs by case, as it is dependent on the parameter β.

When β is small, slight changes in the consumer's density, require large changes in the resource density for the system to remain at quasi-equilibrium. If β is small enough, the consumer's growth rate ρ will be so large that changes in consumer density will occur too rapidly for the resource to completely maintain quasi-equilibrium. Damped oscillations converging to the coexistence equilibrium then result. Hence, the smaller the value of β, the more likely damped oscillations will occur and the smaller ε must be for the dynamics of the consumer-resource system to be non-oscillatory. In other words, when the consumer's attack rate is high or the resource's carrying capacity is large, the resource's intrinsic growth rate must be extremely large for the consumer's actual dynamics to be monotonic as predicted by the logistic model.

While the logistic model cannot exhibit damped oscillations, it remains a good approximation whenever the damped oscillations are small and irrelevant to the use of the model. Stability analysis shows that damped oscillations will occur

whenever $\varepsilon > \beta^2/(4(1-\beta))$. When ε is very small but just slightly larger than the right hand side of this inequality, then the magnitude of the oscillations are small and, for small β, the dynamics converge to equilibrium quickly, often within a few generations. The magnitude of these damped oscillations also depends on the initial conditions of the system. For a system just slightly perturbed from its equilibrium, the oscillations are smaller and die down more rapidly. For a system where damped oscillations are expected, if ε is quite a bit larger than the right hand side of the given inequality or at least one of the densities starts far from equilibrium, then the damped oscillations will be greater in magnitude and take longer to approach equilibrium. These cases and any others where damped oscillations cannot be ignored are examples in which a time-invariant single-species model cannot capture the dynamics of the consumer-resource system.

As β increases in value towards one, the system becomes more stable and no damped oscillations are expected for small ε. Therefore, compared to when the consumer has a large effect on resource density, when the consumer only slightly alters the resource density the logistic model is expected to be a good approximation for higher ratios of the resource's intrinsic growth time, τ_{RB}, to the consumer's lifespan, τ_N. The smaller the consumer's attack rate and the resource's carrying capacity, the wider the range of $\varepsilon \ll 1$ for which model (6) makes good predictions of the actual consumer dynamics. For large values of ε, no matter what the value of $0 < \beta < 1$, the consumer's system dynamics will differ from those predicted by logistic model (6). In some of these cases, depending on how the predictions will be used, it is possible that a logistic model may still be an appropriate estimate of dynamics. However, even in these few cases, it is likely that the intrinsic growth rate parameter that best fits the actual consumer dynamics will differ from the intrinsic growth rate ρ predicted in model (6). In general, the robustness of model (6) to changes in small ε are strongly linked with the degree of stability of the given consumer-resource system. As the stability of the consumer-resource system's coexistence steady-state weakens, the robustness of the single-species model decreases.

2.3. Abiotic resource and linear functional response

The same type of analysis can be performed on the following model, which represents a consumer that relies upon an abiotic resource:

$$\frac{dN}{dt} = bcRN - mN,$$

$$\frac{dR}{dt} = i - eR - cRN. \tag{8}$$

The equation governing consumer density, N, has not changed; the only difference between (8) and (2) occurs in g, the rate of change of the resource density in the absence of the consumer, which is now non-logistic. The non-dimensionalized model is

$$\frac{d\tilde{N}}{d\tilde{t}} = (\tilde{R} - 1)\tilde{N},$$

$$\varepsilon\beta\frac{d\tilde{R}}{d\tilde{t}} = 1 - \beta\tilde{R} - (1-\beta)\tilde{R}\tilde{N}, \tag{9}$$

where

$$\varepsilon = \frac{m}{e} \tag{10}$$

and

$$\beta = \frac{em}{bci}. \tag{11}$$

Both parameters, ε and β, have ecological interpretations related to those explained in Section 2.2 with a biotic resource. The meaning of β has not changed; it is still the ratio of the resource equilibrium value in the case of coexistence to the resource equilibrium value in the absence of the consumer

$$\beta = \frac{m/(bc)}{i/e} = \frac{R^\star}{R^\star_{abs}}. \tag{12}$$

Similar to (3), ε compares a consumer rate to a resource rate. Here, the natural death rate of the consumer is compared with the natural decline rate of the abiotic resource. These values can also be thought of as times

$$\varepsilon = \frac{1/e}{1/m} = \frac{\tau_{RA}}{\tau_N}. \tag{13}$$

In contrast to (5), τ_{RA} in the abiotic case measures the expected retention time of one resource density unit within the resource pool when the consumer is absent.

For $\varepsilon \ll 1$, it must be that $\tau_{RA} \ll \tau_N$, or, the average lifespan of the consumer is much larger than the retention time of the resource within the resource pool when consumer-free. In other words, the smaller the per capita death rate of the consumer, m, and the larger the per capita decline rate of the resource, e, the smaller ε will be. Assuming ε is a small parameter, the consumer's order one dynamics are given by the solution to the IVP

$$\frac{d\tilde{N}}{d\tilde{t}} = \rho\tilde{N}\left(\frac{1-\tilde{N}}{1+\rho\tilde{N}}\right), \quad \tilde{N}(0) = \tilde{N}_0, \tag{14}$$

where

$$\rho = \frac{1-\beta}{\beta} = \frac{R^\star_{abs} - R^\star}{R^\star}, \quad 0 < \beta < 1.$$

The inequality $0 < \beta < 1$ restricts the system to parameter values for which the coexistence steady-state equilibrium of (9) is stable.

Eq. (14) is a scaled version of a single-species density-dependent model that was introduced by Smith (1963), but see also Birch (1999). Smith derived the model by starting from the logistic equation and taking into account the food consumption rate not currently being utilized by the consumer population. We derived the model by starting with a consumer-resource system and taking into account the two different time scales of the resource and the consumer. Our results are equivalent to a previous time scale analysis of the same system with different density scales (Thieme, 2003). This model is often cited as an alternative to the logistic model (Wu et al., 2009; Tsoularis and Wallace, 2002), and its use in the literature will be discussed in Section 3. Unfortunately, (14) does not have an algebraic solution in terms of $\tilde{N}$ as a function of $\tilde{t}$, and dynamics must be calculated numerically. Fig. 2 shows the per capita growth rate (PCGR) curves for different values of ρ and their associated consumer dynamics.

When ρ is large (β small), the consumer's growth rate when rare is very large. Moreover, the deviation of the consumer's per capita growth rate from a logistic curve is also large. Thus, if the resource value of the coexistence equilibrium is much smaller than the resource consumer-absent equilibrium value, then the consumer is expected to grow quickly when rare and have dynamics that deviate from a logistic curve. In other words, if on average the consumer harvests a large quantity of abiotic resource within its lifetime (drastically changing the resource's density), then we expect the consumer population to grow rapidly in a non-logistic way.

On the other hand, as ρ decreases to zero ($\beta \to 1$) the consumer's PCGR curve becomes more and more logistic looking (linear), albeit with a very small scaled growth rate. Consequently, if the resource coexistence equilibrium deviates very little from the resource equilibrium in the absence of the consumer, then the
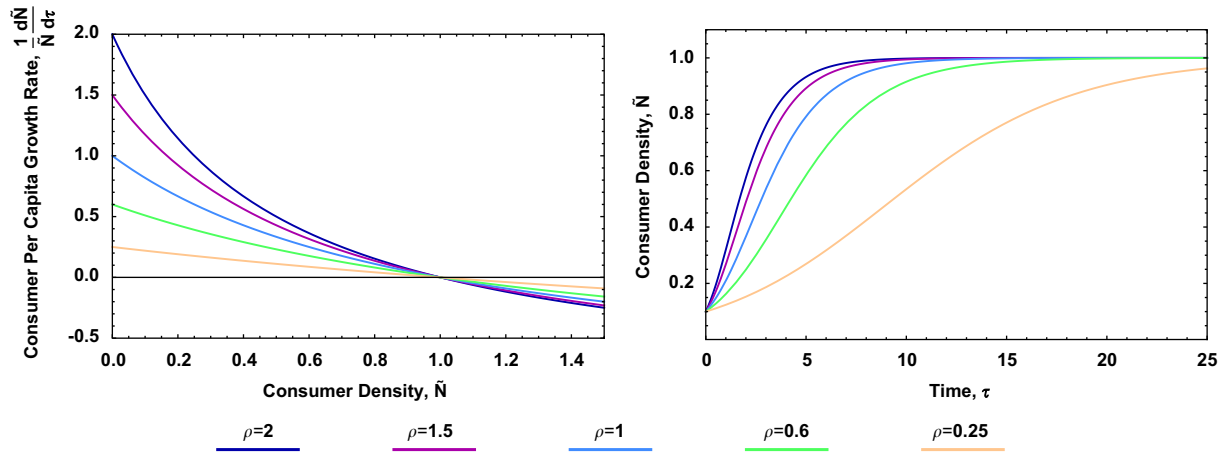
Fig. 2. Consumer per capita growth rate curves (left) and consumer dynamics over time when $N_0 = 0.1$ (right) for the abiotic resource and linear functional response model (14) at different values of $\rho = (1-\beta)/\beta$.

consumer will grow slowly when rare, taking more time to reach its coexistence equilibrium value. In this case the consumer has very little affect upon the resource population density and its dynamics could be predicted, within reasonable accuracy, by a logistic curve with a small intrinsic growth rate.

As in Section 2.2, the robustness of model (14) to changes in $\varepsilon \ll 1$ is directly tied to the stability of the system. Unlike the case with a biotic resource, analysis of the Jacobian matrix after linearizing around the coexistence steady-state shows that damped oscillations are not expected for $\varepsilon < 1$ when the resource is abiotic. Observations of the full nonlinear system reveal that a consumer population may grow rapidly, overshooting its equilibrium density, and then monotonically decrease to equilibrium. Single-species model (14) cannot capture such dynamics; however, this behavior is highly unlikely or small in magnitude for reasonable parameter values and initial conditions. Hence, we can expect a much wider range of acceptable values of small ε, than those seen in Section 2.2. In some cases, model (14) is even a good approximation for ε values close to one.

2.4. Biotic resource, migration, and linear functional response

In an open system, a biotic resource will not only grow but will also have the opportunity to migrate into or out of the observed area of study. The system

$$\frac{dN}{dt} = bcRN - mN,$$

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) + i - eR - cRN, \tag{15}$$

models this type of resource when it is being predated upon by a consumer with a linear functional response. Utilizing the reference scaling values as described in Section 2.1, the equivalent non-dimensionalized system is

$$\frac{d\tilde{N}}{d\tilde{t}} = (\tilde{R} - 1)\tilde{N},$$

$$\varepsilon \frac{d\tilde{R}}{d\tilde{t}} = \alpha - \delta\tilde{R} + \tilde{R}(1 - \beta\tilde{R}) - (\alpha - \delta + 1 - \beta)\tilde{R}\tilde{N},$$

where

$$\varepsilon = \frac{m}{r}, \tag{16}$$

$$\alpha = \frac{bci}{mr}, \tag{17}$$

$$\delta = \frac{e}{r}, \tag{18}$$

and

$$\beta = \frac{m}{bcK}. \tag{19}$$

Eqs. (16) and (19) are the same as (3) and (4) from Section 2.2 where a non-migratory biotic resource and a consumer with a linear functional response were considered. The interpretations of ε and β must only be altered slightly from those presented in Section 2.2 by noting that r and $R^\star_{abs}$ are the resource intrinsic growth rate and resource equilibrium density, respectively, given that the consumer is absent and there is no migration. Two new parameter values α and δ have been added to take into account the level of immigration and emigration, respectively.

Eq. (18) is the ratio of the resource's per capita emigration rate to its per capita intrinsic growth rate. When ε is small, it is very likely that r is large; therefore, δ is only an important parameter if the emigration rate of the resource is comparable to r. This is to be expected, since if there is only a small amount of emigration it will have little effect on how the population grows.

Since the immigration rate is constant, it can only be compared with the intrinsic per capita growth rate at a specific resource density level. Eq. (17) uses the system's coexistence equilibrium resource density to translate the constant immigration rate into a per capita immigration rate. This resource "per capita immigration rate", $(bci)/m$, is compared with the biotic resource's intrinsic per capita growth rate. The larger the value of α, the more likely immigration will alter the consumer's dynamics from those expected for model (2).

Given that ε is a small parameter, or $m \ll r$ the order one consumer dynamics are described by a novel single-species model

$$\frac{d\tilde{N}}{d\tilde{t}} = \frac{1}{2}\left((A-1)\tilde{N} - (A+B)\tilde{N}^2 + \sqrt{\left((A+1)\tilde{N} - (A+B)\tilde{N}^2\right)^2 + 4B\tilde{N}^2}\right), \tag{20}$$

$$\tilde{N}(0) = \tilde{N}_0,$$

where

$$A = \frac{1-\delta-\beta}{\beta}, \quad B = \frac{\alpha}{\beta}, \quad \text{and} \quad -B < A.$$

While ecologically $B > 0$, it is possible for A to be negative. In the cases were A is negative the consumer's order one PCGR curves look like Fig. 2 from the abiotic resource and linear functional consumer response. In particular, when $A < -1$, then $r < e$. In other
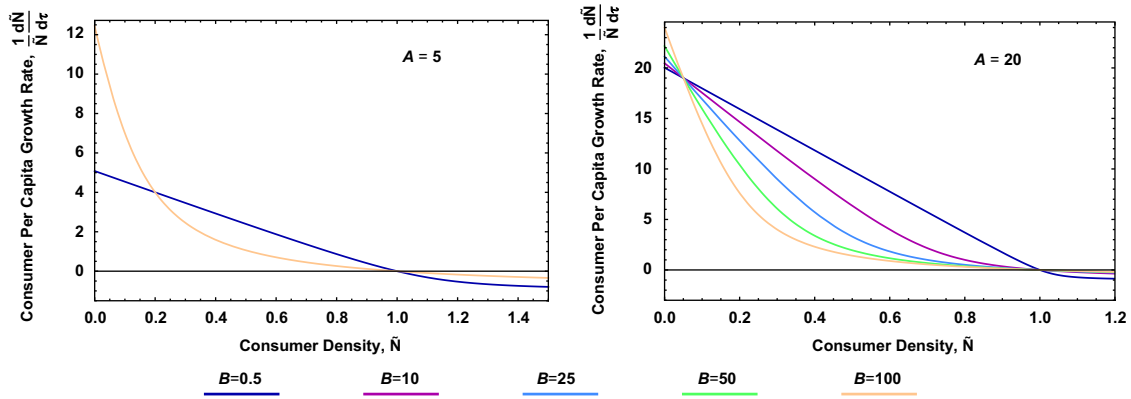
Fig. 3. Consumer per capita growth rate curves from the biotic resource with migration and consumer linear functional response model (20) for $A=5$ (left), $A=20$ (right), and the given range of B.

words, emigration of resource out of the observed area is so high that the natural births from biotic growth cannot compensate for it. Instead, the population is being sustained by immigration of the resource into the area of study. The area of study can be considered a sink patch for the resource, and the resource dynamics will be dominated by migration. Since the form of migration we have considered is the same form as that for an abiotic resource, it is not surprising that the resulting PCGR curves resemble Fig. 2 in this case.

When $A > 0$, the biotic growth rate of the population can overcome emigration, at least at small densities, and the population is no longer a sink. In this case the consumer's PCGR curves range from linear to concave up in a different manner than that seen in Fig. 2. Fig. 3 highlights this difference. For fixed A an increase in B can be thought of as an increase in the level of immigration, i. At small values of B the biotic growth processes dominate the resource dynamics and the consumer's PCGR curve is essentially linear for densities below the equilibrium. As B increases, immigration becomes a more dominant process and the consumer's PCGR curves become more concave up, representing early-acting density-dependence.

As in the previous cases, the robustness of model (20) is linked with the stability of the system and ranges between the cases seen in Sections 2.2 and 2.3 depending on the parameter values. Damped oscillations are possible and are likely when there is little resource immigration and emigration combined with either a large consumer attack rate or a large resource carrying capacity. However, a large immigration or emigration rate can prevent large magnitude damped oscillations even when β is small.

2.5. Abiotic resource and saturating functional response

A saturating consumer functional response to an abiotic resource is exemplified by the model

$$\frac{dN}{dt} = \frac{bcRN}{1+chR} - mN,$$

$$\frac{dR}{dt} = i - eR - \frac{cRN}{1+chR}. \tag{21}$$

In the absence of the consumer, the abiotic resource reacts the same as in model (8). However, the consumer now exhibits a Holling Type II functional response, which takes into account the time it takes the consumer to handle one unit of resource, h.

The non-dimensional model is given by

$$\frac{d\tilde{N}}{d\tilde{t}} = \frac{(\tilde{R}-1)\tilde{N}}{1+\gamma\tilde{R}},$$

$$\varepsilon\beta\frac{d\tilde{R}}{d\tilde{t}} = 1 - \beta\tilde{R} - (1-\beta)(1+\gamma)\frac{\tilde{R}\tilde{N}}{1+\gamma\tilde{R}}, \tag{22}$$

where

$$\varepsilon = \frac{m}{e}, \tag{23}$$

$$\beta = \frac{em}{ci(b-mh)}, \tag{24}$$

and

$$\gamma = \frac{mh}{b-mh}. \tag{25}$$

While (24) differs from (12) of model (9), the meaning of β has not changed. Indeed,

$$\beta = \frac{m/(bc-cmh)}{i/e} = \frac{R^\star}{R^\star_{\text{abs}}}$$

is the ratio of the coexistence resource equilibrium value to the consumer-absent resource equilibrium value. As in (9), the coexistence equilibrium of (22) is an ecologically reasonable stable node for values of $0 < \beta < 1$.

The additional parameter, γ, is a measure of how the handling time alters the resource coexistence equilibrium value. To see this, denote $R^\star_L$ as the coexistence equilibrium value of model (8), where resource growth is abiotic and the consumer's functional response is linear. Therefore,

$$R^\star_L = \frac{m}{bc} \quad \text{and} \quad R^\star = \frac{m}{bc-cmh}$$

are the resource coexistence equilibriums for models (8) and (21), respectively. Using this notation,

$$\gamma = \frac{R^\star - R^\star_L}{R^\star_L}.$$

The parameter γ represents the difference between the resource equilibrium when the consumer has a saturating response and when the consumer has a linear functional response, scaled by the resource's equilibrium value when the consumer's functional response is linear. Requiring $R^\star > 0$, implies that $\gamma > 0$. Hence, for conditions under which a stable (steady-state) coexistence equilibrium occurs, $R^\star > R^\star_L$. In other words, with all else being equal, a consumer population with a negligible handling time will cause a greater reduction in the resource population density than a consumer population with a significant handling time. This matches our intuition. The rate of resource consumption will be less for the consumer with the greater handling time, allowing the resource population to persist at higher densities. As the handling time approaches its ecological maximum, the consumer

equilibrium density approaches zero while the resource equilibrium density approaches $R_{\text{abs}}^{\star}$.

Notice (23) is the same as (13) from the equivalent model with no handling time, model (9). Therefore, the meaning of ε is the same as in the discussion concerning the retention time of the abiotic resource under the specific conditions (see Section 2.3). When $\varepsilon \ll 1$, or equivalently $\tau_{RA} \ll \tau_N$, the resource responds quickly relative to the consumer. Separating time scales, the resource tracks it quasi-equilibrium while the consumer dynamics play out according to the IVP,

$$\frac{d\tilde{N}}{d\tilde{t}} = \frac{\beta+\gamma}{2\gamma(1-\beta)} + \frac{1-\gamma}{2\gamma}\tilde{N} - \sqrt{\left(\frac{\gamma-\beta}{2\gamma(1-\beta)} - \frac{1+\gamma}{2\gamma}\tilde{N}\right)^2 + \frac{\beta}{\gamma(1-\beta)^2}}, \quad (26)$$

$$\tilde{N}(0) = \tilde{N}_0,$$

for $0 < \beta < 1$ and $0 < \gamma$. This is a novel single-species density-dependent model. While the form is not simple, the model has some nice properties. The per capita growth rate decreases monotonically with consumer density and approaches a negative horizontal asymptote (see Section 2.8). A wide range of PCGR curve shapes are possible for different values of β and γ in (26).

As expected, when γ, the effect of handling time, approaches zero, the PCGR curves converge to those determined by a linear functional response (14). Indeed, for small values of γ with $\gamma < \beta$, the handling time is negligible and the PCGR curves of the consumer are nearly identical to the concave up curves found in Fig. 2. In cases where γ is very small but $\beta < \gamma$, the PCGR curves still look very similar to those in Fig. 2; however, there is a small range of consumer density values near zero where the two differ. For this range of density values, the PCGR curve of a consumer with a saturating response is concave down, resulting in a noticeably smaller intrinsic growth rate compared to the same consumer with a linear functional response. In either of these cases, the consumer exhibits early-acting density-dependence. The only difference between these two cases, is when $\beta < \gamma$ the strongest density-dependent effects do not occur for a small range of densities very close to zero.

For large γ values, where $\gamma > 1/\sqrt{\beta}$, the consumer's PCGR curve is concave down for all consumer density values smaller than the equilibrium density (Fig. 4). The consumer exhibits late-acting density-dependence, where the steepest decline in the PCGR curve occurs at high densities. These dynamics may be understood with respect to the handling time. The consumer's per capita growth rate will be most affected by a large handling time when the resource is plentiful. Since the resource responds
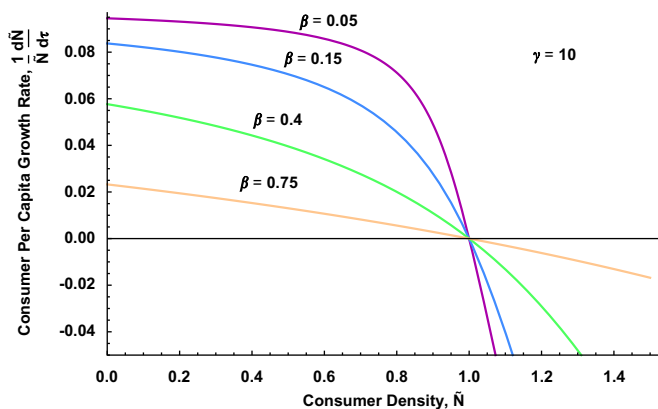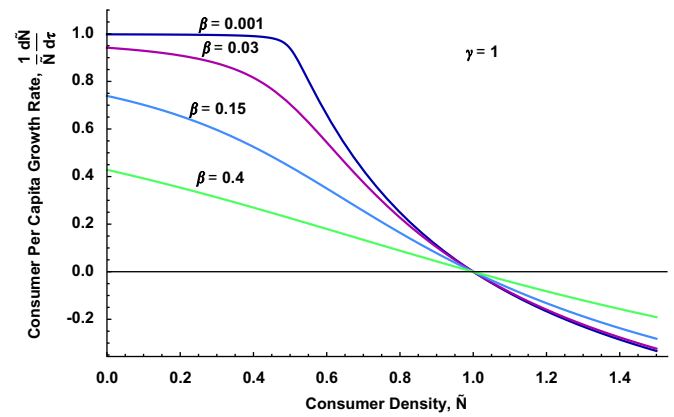
Fig. 5. Consumer per capita growth rate curves from the abiotic resource and saturating functional response model (26) for $\gamma = 1$. The strongest effects of density-dependence are found at the inflection point, which occurs at mid-range densities prior to the equilibrium density of 1. As $\beta \to 1$ the curves become more logistic looking for consumer densities where the population is growing.

quickly to the consumer, the resource is the most plentiful when the consumer's density is low. As the consumer's density increases, the resource density decreases, forcing the consumer to spend more and more time trying to acquire the abiotic resource on which it depends. At high consumer densities, the resource has become so sparse that the ratio of the handling time to the total time spent acquiring and handling the resource is insignificant. The consumer's per capita growth rate then becomes strongly density-dependent, taking on a shape similar to that of Fig. 2 from the abiotic resource and linear functional response model. The larger the handling time (the larger γ) the higher the consumer density value at which this transition takes place. As expected, the larger γ, the smaller the consumer's intrinsic growth rate.

A popular single-species model, the θ−logistic model (Gilpin and Ayala, 1973), also exhibits either early-acting ($\theta < 1$) or late-acting ($\theta > 1$) density-dependence. Single-species model (26), however, lifts the constraint that the strongest effects of density-dependence must only be found at the extremes of the consumer's density range. For $\beta < \gamma < 1/\sqrt{\beta}$, the consumer exhibits the strongest density-dependence at mid-range densities (Fig. 5). For this range of γ the handling time is large enough to matter at small densities, but transitions to being insignificant prior to the consumer population reaching its equilibrium density. As γ approaches β, density-dependence transitions from mid-acting to early-acting, while as γ approaches $1/\sqrt{\beta}$ it transitions to late-acting.

Similar to the abiotic resource model with a linear functional response, the shape of the consumer's PCGR curve differs as β increases to one. In this case—when the resource coexistence equilibrium deviates very little from its consumer-absent equilibrium—the consumer's PCGR curve becomes more linear and the intrinsic growth rate becomes smaller. In other words, if the consumer has very little affect upon the resource population density then its dynamics could be accurately represented by a logistic model with a small intrinsic growth rate.

For $\varepsilon < 1$ no damped oscillations are expected and the robustness of model (26) to increases in small ε is similar to that when the functional response is linear. Additionally, as handling time is increased, the consumer's effect on the resource is lessened, broadening the situations in which the resource response is considered fast and model (26) serves as a good approximation for consumer dynamics.
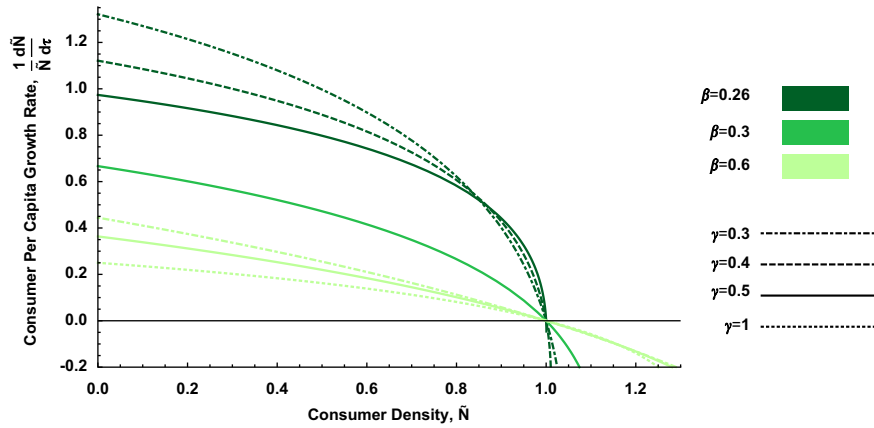
Fig. 4. Consumer per capita growth rate curves from the abiotic resource and saturating functional response model (26) for $\gamma = 10$. The strongest effects of density-dependence occur at high consumer densities (late-acting). As $\beta \to 1$ the curves become more logistic looking for consumer densities where the population is growing.

Fig. 6. Consumer per capita growth rate curves from the biotic resource and saturating functional response model (31) for several values of β and γ, as shown. These PCGR curves only result in late-acting density-dependence.

2.6. Biotic resource and saturating functional response

A biotic resource taken up by a consumer with a Type II functional response may be modeled as

$$\frac{dN}{dt} = \frac{bcRN}{1+chR} - mN,$$
$$\frac{dR}{dt} = rR\left(1-\frac{R}{K}\right) - \frac{cRN}{1+chR}, \tag{27}$$

where, as in (2), we assume that the resource dynamics in the absence of the consumer are accurately represented by a logistic model. As the handling time h approaches zero, model (2) is recovered. Non-dimensionalizing (27) results in the model

$$\frac{d\tilde{N}}{d\tilde{t}} = \frac{(\tilde{R}-1)\tilde{N}}{1+\gamma\tilde{R}},$$
$$\varepsilon\frac{d\tilde{R}}{d\tilde{t}} = \tilde{R}(1-\beta\tilde{R}) - (1-\beta)(1+\gamma)\frac{\tilde{R}\tilde{N}}{1+\gamma\tilde{R}},$$

where

$$\varepsilon = \frac{m}{r}, \tag{28}$$

$$\beta = \frac{m}{cK(b-mh)}, \tag{29}$$

and

$$\gamma = \frac{mh}{b-mh}. \tag{30}$$

Notice that Eq. (30) describing the non-dimensional parameter γ is the same as Eq. (25), from the model with an abiotic resource and a consumer with a Type II functional response. Indeed, (30) may be written as

$$\gamma = \frac{R^\star - R_L^\star}{R_L^\star},$$

where $R_L^\star$ is the resource equilibrium value of model (27) with a handling time of zero, i.e. the resource equilibrium value of model (2). Hence, γ indicates the effect of the handling time h has on the system in the same manner as described in Section 2.5.

Also, since (28) and (29) may be rewritten as

$$\varepsilon = \frac{1/r}{1/m} = \frac{\tau_{RB}}{\tau_N} \quad \text{and} \quad \beta = \frac{m/(bc-cmh)}{K} = \frac{R^\star}{R_{abs}^\star},$$

respectively, it is clear that ε and β share the same meaning as their counterparts from the biotic resource and linear functional response model, or Eqs. (5) and (7), respectively. For ecological situations when the biotic resource's time to increase one

unit when rare and consumer-free is much smaller than the consumer's lifespan, the consumer's dynamics are approximately described by the IVP

$$\frac{d\tilde{N}}{d\tilde{t}} = \frac{-(\beta+\gamma)}{2\gamma^2(1-\beta)} + \frac{\tilde{N}}{\gamma} + \sqrt{\left(\frac{\beta+\gamma}{2\gamma^2(1-\beta)}\right)^2 - \frac{\beta(1+\gamma)\tilde{N}}{\gamma^3(1-\beta)}}, \tag{31}$$

$$\tilde{N}(0) = \tilde{N}_0 < \tilde{N}_{max},$$

where

$$0 < \gamma < \frac{\beta}{1-2\beta} \quad \text{for } 0 < \beta < \frac{1}{2} \quad \text{and} \quad 0 < \gamma \quad \text{for } \frac{1}{2} \leq \beta < 1.$$

These last two conditions must be met to ensure stability of the steady-state coexistence equilibrium.

This novel single-species, density-dependent model is much more complex and unintuitive than its related model with no handling time, which is logistic. As expected, the PCGR curves converge to a line as γ approaches zero. However, in general, model (31) results in a per capita growth rate curve that is monotonically decreasing and concave down on its domain (Fig. 6). Unlike (26), the shape of the PCGR curves resulting from different parameter ranges of β and γ have relatively little variation, with density-dependence always acting most strongly at high densities.

With all else being equal, an increase in γ, or an increase in the effect of handling time, has three consequences: (1) a decrease in the consumer's intrinsic per capita growth rate, (2) a decrease in the effect of density-dependence at lower consumer values, (3) an increase in the severity of the effects of density-dependence at higher consumer values, i.e. those closer to equilibrium. The first two consequences also occurred in model (26), where an increase in γ likewise represented an increase in the time it takes the consumer to handle its resource. Therefore, the same explanations described in Section 2.5 apply to model (31) for these consequences. The third consequence, is a result that has to do with the end behavior of (31), which will be discussed in more detail in Section 2.8.

As with all of the models presented here, the robustness of model (31) to increases in the small parameter ε is tied to stability. Similar to the biotic resource and linear functional response case, a suppression-stability tradeoff (Murdoch et al., 2003) leads to damped oscillations in the consumer-resource system when the consumer significantly depresses the resource density. Stability analysis reveals that varying handling time can have different results for robustness, depending on how large or small of an effect the consumer has on the resource population.

2.7. Biotic resource, migration, and saturating functional response

The remaining combination of resource type and functional response type considered is a system where a consumer with a saturating functional response preys upon a biotic resource that migrates into and out of the area considered. This open system may be written as

$$\frac{dN}{dt} = \frac{bcRN}{1+chR} - mN,$$
$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) + i - eR - \frac{cRN}{1+chR}. \tag{32}$$

The analysis of system (32) as laid out by the procedure described in Section 2.1 is complex. Abrams (2009a) presented this system as a density-dependence peculiarity that clearly could not be closely approximated by a θ−logistic model. Abrams' second figure in Abrams (2009a) shows the inverse of the consumer's PCGR curve—with consumer density as a function of consumer per capita growth rate—of system (32). Note that this function is not one-to-one for the particular choice of parameter values, indicating that the consumer's PCGR curve is not a function. Indeed, for certain parameter values and at certain consumer densities, the time scale separation problem has alternative stable quasi-equilibrium states to which the resource could rapidly grow or decline. This translates into the existence of alternative per capita growth rates at some consumer densities (Fig. 7). While phase plane analysis can determine which density the resource is rapidly heading towards, it cannot do so without knowledge of the resource density—something we lack when utilizing a density-dependent single-species model for the consumer. Hence, the "correct choice" of consumer per capita growth rate for the given consumer density depends on the current state of the full system and may vary greatly for initial resource conditions that are close to one another (see Fig. A.1).

How often quasi-equilibrium bistability will arise for model (32) under parameter ranges found in natural systems is unclear. Preliminary analysis has shown that its occurrence may be linked to the stability of the system. In general, since this problem did not arise for the same model when the consumer's functional response was linear, it is important to note that this situation requires the consumer to have a significant, possibly very large, handling time.

Regardless, a population that starts at a low consumer density will trace a per capita growth rate curve with a stark mid-density threshold. The PCGR curves for this model can have a small region of consumer densities where density-dependence acts the strongest. Fig. 7 clearly shows intense mid-acting density-dependence. Mid-acting density-depen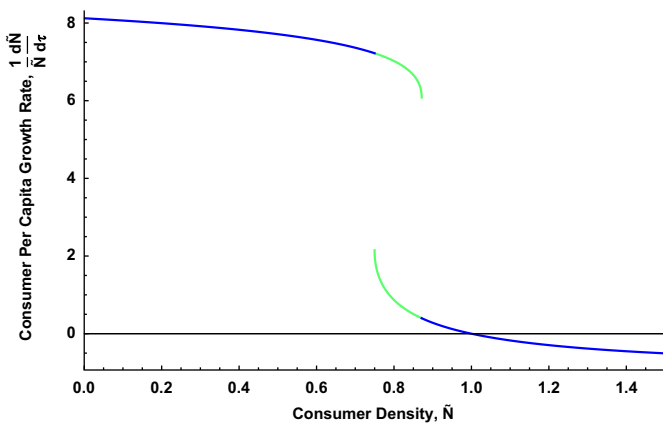dence is seen in only one of the other abstracted models presented here, the abiotic resource and saturating functional response model. Hence, a consumer with a saturating functional response could experience mid-acting density-dependence whether or not it consumes an abiotic or biotic resource, as long as the biotic resource experiences some migration.

In general, having multiple quasi-equilibrium choices prevents the construction of a clear consumer PCGR function that depends on consumer density alone. However, given the initial resource value a single-species model for the consumer could be constructed. For parameter ranges where these complications do not arise, a single-species model can be constructed as described in Section 2.1; however, the formula for determining the PCGR curve is complex and has been omitted.

2.8. High densities

Often, PCGR curves are used to understand information on how a population grows to its equilibrium density. While the order one single-species consumer models that were derived in the previous sections have had many interesting differences when considering consumer densities below equilibrium, they also differ at densities above the equilibrium. One criticism of the logistic model (Fig. 8, top left) is that the per capita growth rate decreases without bound as consumer density increases. This can make the logistic model unsuitable for predicting the ways in which a population will decline. Interestingly, none of the PCGR curves presented in Sections 2.2–2.6 have this property (Fig. 8).

When the resource is abiotic, both a linear and a saturating consumer functional response lead to PCGR curves with a horizontal asymptote. As the density increases to very high densities above equilibrium, the per capita death rate asymptotically approaches -1 (scaled) or $-m$ (unscaled). This is also the case when a consumer with a linear functional response utilizes a biotic resource whose density is affected by migration. While this system can have PCGR curves that are approximately linear at consumer densities smaller than its equilibrium value, these same curves do not remain linear at high densities, in contrast to the logistic. Instead they become concave up and approach a horizontal asymptote of -1 (see bottom right in Fig. 8).

For a consumer that specializes on a biotic resource (no migration), the end behavior is piecewise but still bounded. A biotic resource without migration will always have the vertical line $\tilde{R} = 0$ as a nullcline. For consumer densities greater than some $\tilde{N}_{max} > 1$, the second resource nullcline is not defined in the positive plane and resource density declines rapidly towards its quasi-equilibrium at zero. Since real ecological systems face both demographic and environmental stochasticity, it is possible that the resource would not recover from it's population density crashing to and remaining at densities close to zero for an extended period of time. Here, we proceed under the assumption that the resource density is still positive and only considered zero up to first order. Substituting $\tilde{R}(\tilde{N}) = 0$ for all $\tilde{N} > \tilde{N}_{max}$ results in a scaled consumer per capita growth rate of -1 at high densities. When the consumer has a linear functional response, the PCGR curves of the classical logistic model would be truncated at $\tilde{N}_{max} = 1/(1-\beta)$ and continued as a horizontal line with value -1. When the consumer's functional response is saturating (bottom left of Fig. 8), the value of $\tilde{N}_{max}$ depends on both how much the consumer depresses the resource density (β) and the relative effect of the consumer's handling time (γ).

In the full consumer-resource system, when consumer densities are larger than $\tilde{N}_{max}$ and ε is a small parameter, the resource density does drop extremely rapidly towards zero, often remaining at very low densities before increasing to its equilibrium again (see
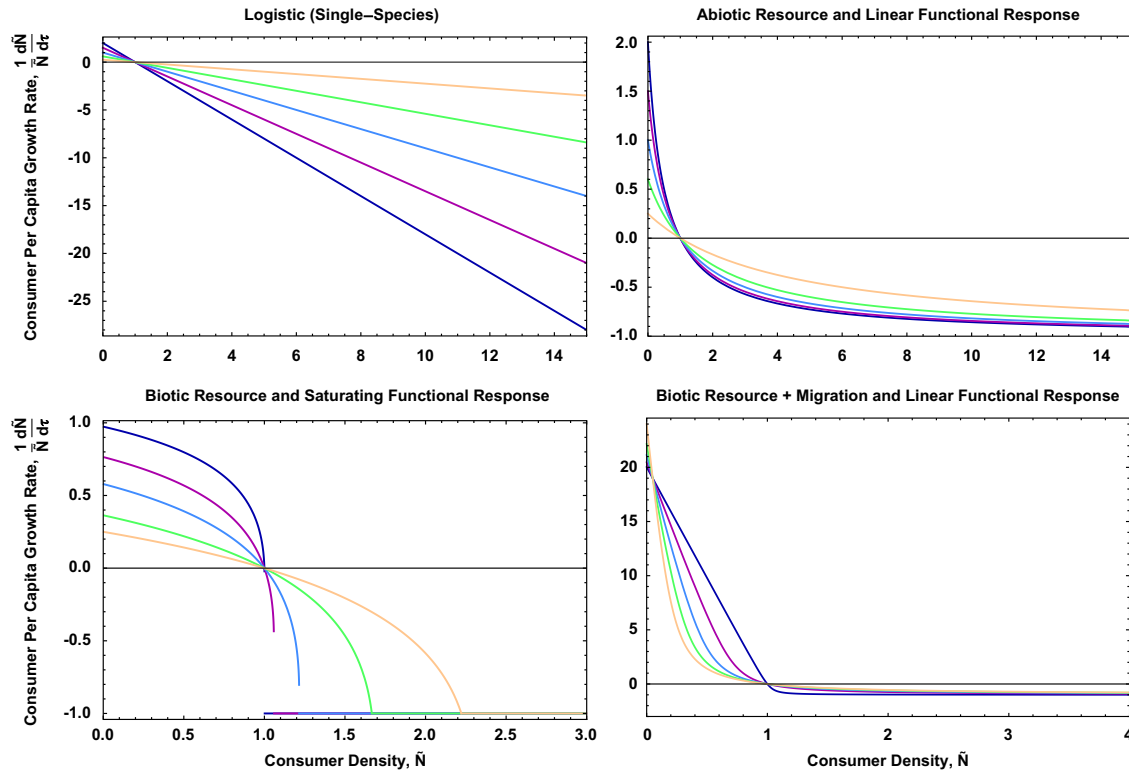
Fig. 7. A consumer per capita growth rate curve from the biotic resource with migration and consumer saturating functional response model (32). Notice that there is a region of consumer densities for which the two curves overlap.

Fig. 8. The end behavior of some consumer PCGR curves for: (top left) the logistic model with ρ as in Fig. 2, (top right) model (14) with ρ as in Fig. 2, (bottom left) model (31) with $\gamma = 0.5$ and $\beta = 0.26, 0.35, 0.45, 0.6,$ and 0.7, and (bottom right) model (20) with parameters as in Fig. 3 (right). Besides the logistic model, the end behavior of all of the models is bounded at large consumer density values.

Fig. A.2). While the piecewise approach to a single-species model described above captures the rapid decline in resource, it is not as good of an approximation of the dynamics that occur after this (even for parameter values where the model was very good at predicting consumer growth). As resource levels decrease towards zero, they are reaching the same magnitudes as ε and the order one solutions cannot capture the dynamics projected by the full system. In this case, the limitations of the order one population growth model are made very clear.

3. Discussion

When the resource responds quickly a single-species model can be analytically derived which approximates the dynamics of the consumer from an equivalent consumer-resource model. When resource dynamics are biotic via the logistic model and the consumer's functional response is linear, the consumer's single-species dynamics are also logistic. When the resource dynamics are abiotic and the consumer's functional response is linear, the consumer's single-species per capita growth rate (PCGR) curve is concave up, representing early-acting density-dependence. If resources are biotic with migration, consumers can exhibit PCGR curves that span the range from linear to concave up for densities prior to the equilibrium. When handling time becomes significant, the consumer can exhibit later acting density-dependence. For abiotic resources and a saturating functional response, the consumer's single-species per capita growth rate curve can have a concave down region at low densities and a concave up region at high densities, perhaps best described as mid-acting density-dependence. With biotic resources and a saturating functional response, the relationship is always concave down, i.e. late-acting density-dependence. Finally, in the case of a biotic resource with migration and a saturating functional response, the single-species

consumer PCGR curve can have a concave down region at low consumer densities and a concave up region at high densities connected by a sharp drop in growth rates or even overlapping growth rates, where the choice amongst them depends on the current density of the resource.

In biotic resources, a reduction in density due to consumer predation leads to compensation in the population—the resource either grows more or dies less at lower densities. In contrast, when the resource is abiotic, the same amount of resource is entering the system with each additional consumer but is being divided over more consumers. Consequently, abiotic resources result in the concave up relationship with the steepest drop in consumer per capita growth rates occurring as consumers increase from low densities. Saturating functional responses result in density-dependence acting at high densities because, in contrast to linear functional responses, consumers have limited effect on the resource at low consumer densities. However, at higher consumer densities the resource population has been reduced to a level where handling time becomes less important, allowing the density-dependent effects to play a strong role. Many of the patterns observed in the specific models are combinations of these general patterns.

Our derivation of a single-species model from a system where a consumer predates upon a biotic resource was based on the assumption that the biotic resource's dynamics were logistic in the absence of the consumer. It should be noted that the logistic model is itself a phenomenological single-species density-dependent model. Since this paper is addressing situations in which it is appropriate to estimate the dynamics of a population with a single-species density-dependent model, it may seem circular that such a model is assumed to be the base of a consumer-resource system. On one hand, this illustrates how ubiquitous the logistic equation is in ecology. However, it is not only the extensive use of the logistic model that warrants its use. Singular perturbation

analysis of a consumer-resource model, where an abiotic renewable resource did not have logistic dynamics, shows the order one dynamics of the consumer to be logistic (Lakin and Van Den Driessche, 1977). Hence, the logistic model may be considered an appropriate approximation for this type of biotic consumer in the absence of predation. The biotic consumer, however, may serve as a biotic resource for another organism as in (2).

Instead of assuming the biotic resource has logistic dynamics, one could examine a biotic resource which exhibits the nonlinear per capita growth derived in Eq. (14). When this type of biotic resource is paired with a consumer that has a linear functional response, the single-species consumer per capita growth rate would also have the same form as that shown in (14). Thus it is not always the case that a biotic resource and a linear functional response result in a linear per capita growth rate for the consumer. The shape of the consumer's PCGR curve is dependent on how the biotic resource is compensating for its own density loss.

Despite differences in the shape of the PCGR curves, the time dynamics projected by each of the models we derived differ little in that they all go to a stable equilibrium. For the same initial condition, the consumer's path en route to the long-term equilibrium will differ amongst models; however, the dynamics will be qualitatively similar in that they all asymptotically rise to the equilibrium in a monotonic way. It is interesting that the models we derived can have such different PCGR curves, yet if they were all parameterized as to best fit the same time series data set, then the consumer dynamics that result from these PCGR curves may be practically indistinguishable. However, distinguishing features of the models, such as the location of the inflection point, can have consequences for how these models behave when displaced from their solo equilibrium. Differences in the shape of density-dependence likely matter a great deal when embedded back into food webs, during harvesting, or when interacting with variable environments (Leirs et al., 1997). In some situations, the dynamics or behavior of the system may by very sensitive to the exact shape of the PCGR curve (Fussmann and Blasius, 2005). In these situations, there might be large consequences amongst the different single-species models we characterize.

This work is related to previous work on the topics of abstracting single-species models from larger systems and other works looking at density-dependence in a consumer-resource system. Our work is an example of what Schaffer (1981) termed "ecological abstraction." In our case, we have considered a system of two interacting species, which we have presumed to be accurately described by the given model, and reduced this system to an ecological model considering only one species, the consumer. The method in which we have chosen to carry out this process is different from that proposed by Schaffer (1981) in that we did not linearize about the equilibrium. Hence, under the assumption of fast resource dynamics and sufficient stability conditions, our models serve as a good approximation for consumer dynamics even when the consumer's initial density is much lower than its equilibrium value. Whereas Schaffer's method of reduction only derives logistic single-species models, we have shown that order one time-scale separation methods can derive single-species models with non-logistic forms.

Besides the logistic model, only single-species model (14) has been noted in previous work. Model (14) is a scaled version of the model developed by Smith (1963) (see also Birch, 1999). This same functional form was noted by Schoener (1973) when exploring different ways of looking at near equilibrium per capita growth rates of system (8)—the same model from which we derived (14). Additionally, Thieme (2003) derived this functional form by applying time scale separation to two different starting models: consumer-resource model (8) and a model of adults cannibalizing juveniles. While model (14) is often cited as an alternative to the

logistic model (Wu et al., 2009; Tsoularis and Wallace, 2002), it is comparatively under-utilized (but see Li, 2012; Pan and Wan, 2009). In many cases the logistic model is used in place of it (Tanner 1966). Our work provides support for the increased use of model (14) in ecology.

The analytical work presented in this paper compliments the single-species density-dependence work by Abrams (2009a). Our work strengthens and confirms the ideas put forth by Abrams, yet reframes some of the results in a format which can be more widely utilized by others. The approach Abrams used to look at the form of density-dependence of a consumer in a consumer-resource system resulted in finding the inverse of what we have been calling a consumer's PCGR curve. Typically one thinks of a population's per capita growth rate as a function of density, i.e. a particular population density value determines the per capita growth rate. However, in Abrams' work the inverse of this relation was plotted, i.e. consumer population density was plotted as a function of per capita growth rate. Ideally, both cases should contain all the important information; however, due to the ease of comparison to previous knowledge and PCGR curves, there is a value to transposing the figures. By writing per capita growth rate as a function of density, early-, late-, and mid-acting density-dependence can be clearly identified and the analytical expression for a single-species model is obvious. Furthermore, having an explicit single-species equation describing the consumer's dynamics is of value. It allows for particular properties of individual models derived from different consumer-resource systems to be individually analyzed in detail and compared. Moreover, it provides an equation that could be used in modeling or to fit data.

Our analysis, which can be more rigorously grounded in singular perturbation theory, upholds Abrams' results and numerical findings. The curves determined using Abrams' method are exactly the inverse of the PCGR curves derived by first order time scale separation. Furthermore, our analysis strengthens the one provided by Abrams, as it discusses when such curves are expected to be accurate. In each of the six scenarios we considered, the derived models were only order one approximations. These models were only expected to be descent approximations when ε, a specified ratio between a consumer rate and a resource rate, was small. In all cases, this ratio being small meant that the resource responded rapidly relative to the consumer. Since it can be shown that the order one consumer PCGR curves derived via time scale separation are the inverses of Abrams' derivations, Abrams' results are also the most accurate when the resource response is fast. Moreover, model robustness to slight decreases in resource response speed varied with the stability of the system, being most robust when damped oscillation were not expected and less robust as the system approached a neutral center.

In both Abrams' work and our work, the scenario of a saturating functional response and a biotic resource that migrates can lead to PCGR curves that have consumer densities for which multiple per capita growth rates are possible. There are other interesting aspects within the same, or nearly the same, range of consumer densities. When considering Abrams' approach to graph the relationship between density and per capita growth rate it becomes clear that there is a region of per capita growth rate values which were calculated from a system that has an unstable steady-state but stable consumer-resource cycles. Outside of this region, the per capita growth rate values were calculated from a consumer-resource system that tends to a stable steady-state coexistence equilibrium. A given consumer-resource system of this type, however, may tend to a stable steady-state equilibrium or cycle around an unstable node. The observed system is not expected to do both unless there has been a change in parameter values over time. Time scale analysis revealed that the per capita growth rates in this region of Abrams' graph correspond to

unstable resource quasi-equilibriums, and therefore, these values have been omitted from our PCGR curve (Fig. 7) for this model. Nonetheless, the functional form of the consumer's dynamics and density-dependence in this scenario were found to be unclear in both Abrams' and our analysis.

For much of this paper we have emphasized the conditions under which a single-species model is a good approximation of the consumer dynamics. However, in a consumer-resource system with a generally slow response of the resource there can be lots of cycling time-dynamics, sometimes sustained. These dynamics will have large departures from the proposed single-species models, which can never capture such cycling. Of course, this all depends on how close of an approximation is adequate. The single-species models presented here may be adequate to characterize the average behavior of a moderately cycling system as shown by Abrams (2009a).

Our results raise many interesting and unresolved questions. What type of consumer dynamics can be expected when the resource or consumer equation involves a mechanistic derivation of an Allee effect? What changes can we expect to see in consumer density-dependence with other functional responses, such as a Holling Type III or those proposed in Abrams (1990). Can lower levels of food webs be approximated by the single-species models we present, or do they need to be mechanistic at all lower trophic levels? Can a single-species model be abstracted from an even broader food web?

For example, if a continuous single-species model can be abstracted from a three-species model (as has been done with discrete models Geritz and Kisdi, 2004), then we could consider the following situation. If a consumer with a linear functional response specializes on an abiotic resource, we expect its dynamics to be of form (14). Imagine that this same consumer is now exposed to a predator. Using (14) as the base for the consumer model and adding in loss due to predation, a predator-consumer system could be constructed. If the consumer responds quickly relative to the predator, then a single-species model for the predator could be derived. Is the single-species model for the predator the same model as would be derived given the full three-species system with a focus on the predator? If not, in what ways do these models differ? Indeed, similar questions could be raised about single-species abstractions from models when other trophic level relationships, such as competition, are considered. It is possible that other species in the food web are interacting with the focal species in such a way that the single-species models derived here cannot be used to approximate the consumer dynamics. However, time series analysis of empirical data sets suggests single-species models are adequate for generalist consumers (Murdoch et al., 2002). The case of multiple resources can result in even more complex per capita growth rate curves (Abrams, 2009b).

More broadly, there are a variety of basic model assumptions utilized in our work which could be examined. The deterministic, unstructured models used in this work simplify reality in many ways. For example, they ignore spatial and temporal heterogeneity, environmental and demographic stochasticity, age and stage structure, genetic variation, and phenotypic plasticity. Some features such as age structure may be difficult to capture if the system is not in a stable age distribution. However, other elements such as individual variation in demographic parameters, otherwise known as frailty, have been successfully captured in simple models under certain circumstances (Vaupel et al., 1979). Following the lead of Abrams (2009a), we examined density-dependence that can arise as a consequence of resource utilization. Several other mechanisms could lead to density-dependence, for example nest sites or habitat limitation. Even in the case of resources, classic categorizations such as contest competition could be examined in

contrast to the scramble competition implied in classic consumer-resource dynamics.

There are many situations in which a single-species model can be used to approximate the dynamics of the consumer in a consumer-resource model. In some cases, the form of this model matches existing models of density-dependence. In other cases it takes on more complex forms. However, in many situations the form of the per capita growth rate curve can be derived and the shape of that curve can be understood as the result of late-acting and early-acting components. Our work provides a justification for some existing forms of density-dependence as well as provides some new equations for use in future research.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2013.08.025.

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