LETTER

Discrete consumers, small scale resource heterogeneity, and population stability

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Abstract

We present a consumer-resource model in which individual consumers subsist on a continuum of resource distributed over a very large number of small "bite-sized" patches, each patch being sufficiently small that all its resource is eaten whenever a consumer visits. This form of consumer–resource interaction forces a heterogeneous distribution of resource among the patches, and may dampen out the large amplitude, consumer-resource cycles that are predicted by traditional models of well-mixed, spatially homogeneous systems. The resource equilibrium does not increase with enrichment, a prediction that distinguishes this model from models that invoke direct or indirect consumer density dependence as a stabilizing mechanism.

Keywords

Consumer-resource, equilibrium, paradox of enrichment, predator-prey, stability.

INTRODUCTION

Many simple models of coupled prey-predator or consumer-resource systems predict large-amplitude cycles in both populations whenever the equilibrium density of the resource in the presence of consumers is much lower than its carrying capacity K (e.g. Rosenzweig & MacArthur 1963; May 1972; Murdoch & Oaten 1975; Brauer 1979; de Roos *et al.* 1990; Murdoch 1994; Gurney & Nisbet 1998; Murdoch *et al.* 1998). This phenomenon has come to be known as the "paradox of enrichment," because if K is interpreted as a measure of enrichment, there is an implication that increases in K will lead to unstable equilibrium and large cycles – contrary to observations on many systems (Murdoch *et al.* 1998 and references therein). The instability involves the resource (prey) population growing faster than the consumer following a perturbation; for this reason the cycles are sometimes called "prey escape cycles" (e.g. de Roos *et al.* 1990).

In this letter, we introduce a consumer–resource model that recognizes individual consumers subsisting on a continuum of resource distributed over a very large number of small "bite-sized" patches, each patch being sufficiently small that all its resource is eaten when a consumer visits. This form of consumer–resource interaction ensures local resource extinction on the smallest meaningful spatial scale, yielding a heterogeneous distribution of resource among the patches. This heterogeneity may dampen out the large consumer–resource cycles predicted by analogous ordinary differential equation (ODE) models. The resource equilibrium density does not increase with enrichment, a prediction that distinguishes the mechanisms in the new model from alternative stabilizing mechanisms that involve density dependence of the consumer vital rates.

MODEL FORMULATION

The paradox of enrichment is commonly demonstrated using a model put forward by Rosenzweig & MacArthur (1963); for an elementary treatment of this model, see Gurney & Nisbet (1998). In the absence of consumers, the resource grows logistically with parameters r and K. Consumers have a type II functional response with search rate σ and handling time b, and a density-independent per capita death rate m. Resource is converted into new consumers with efficiency ψ. There is no explicit consumer density dependence (*sensu* Murdoch 1994). The

dynamics of the resource density $X(t)$ and the consumer density $C(t)$ are given by two ODE:

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right) - \frac{\sigma XC}{1 + \sigma bX}, \tag{1}$$

$$\frac{dC}{dt} = \frac{\psi\sigma XC}{1 + \sigma bX} - mC. \tag{2}$$

The new discrete-consumer model embodies the same assumptions, except that the resource is not assumed to be well mixed. It is a variant of a model developed by Nisbet *et al.* (1997) to describe short-term (intragenerational) consumer–resource dynamics in open systems, and the reader is referred to that paper for a more detailed account of the model concepts. The resources are modelled as a metapopulation distributed over a large number of cells, each of which is assumed large enough to allow us to model resource dynamics *within the cell* as a continuous process, but small enough that *all* resource biomass in the cell is consumed if the cell is visited by a consumer. Thus, following an attack on a cell by an individual consumer, the resource density on that cell is set to zero. We have in mind examples like a benthic mat of microalgae with invertebrate consumers that completely clear any local area they attack.

The model equations (Table 1) are based on formalism used by Hastings (1991) to describe metapopulation

Table 1 PDE for the "discrete consumer" model

τ = "age" of a patch (time since last attack)
$n(\tau,t)d\tau$ = fraction of patches aged $\tau \rightarrow \tau + d\tau$ at time t
$x(\tau,t)$ = resource density on a patch aged τ at time t
$X(t) = \int_0^\infty x(\tau,t)n(\tau,t)d\tau$ = average resource density at time t
$C(t)$ = consumer density at time t
$\mu(t)$ = attack rate per patch at time t
$g(t)$ = biomass growth rate on a patch aged τ at time t

$$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial \tau} - \mu(t)n$$

$$\frac{\partial x}{\partial t} = -\frac{\partial x}{\partial \tau} + g(x,\tau)$$

$$n(0,t) = \mu(t)$$
$$x(0,t) = 0$$

$$\mu(t) = \frac{\sigma C(t)}{1 + \sigma bX(t)}$$

$$g(x,\tau) - rx\left(1 - \frac{x}{K}\right) - \varepsilon x + \varepsilon X$$

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dynamics in a system with intermittent, uncorrelated, local catastrophes. Each cell is characterized by its age, τ, where "age" refers to the time since the last visit by a consumer, and we define $n(\tau,t)$ to be the "age distribution" of cells at time t. This allows the resource dynamics to be described by a partial differential equation (PDE), very similar to those used in age structured population dynamics (e.g. Metz & Diekmann 1986; Tuljapurkar & Caswell 1996). If the dynamics within a patch subsequent to a visit by a consumer are deterministic, then all patches of the same age have the same biomass density and we can define a continuous variable $x(\tau,t)$ to represent the resource density on *any* patch aged τ at time t. This variable also obeys a PDE (Table 1).

Resource can only start growing on an empty patch if it is "seeded" from elsewhere in the system. Thus we assume that there is a continuous redistribution of resource. A cell with resource density $x(\tau,t)$ loses resource at a rate $\varepsilon x(\tau,t)$; resource is mixed uniformly and is immediately redistributed equally among all cells, so that individual cells receive resource at a rate $\varepsilon X(t)$, where $X(t)$ represents the average resource density at time t. Following recolonization, the local resource density exhibits logistic growth as in the well-mixed system, modified by these redistribution terms. The parameter ε characterizes the rate of resource mixing in the system.

To model the consumer dynamics we assume that the number of cells is sufficiently large that, although we treat consumers as discrete on the scale of an individual cell, we can treat the total density of consumers in the system as a continuous variable. Consumers attack cells randomly at a rate $\mu(t)$ that may depend on average resource level $X(t)$ (through satiation), but is independent of local resource density, i.e. the consumers exercise no foraging preference. In summary, the consumers obey the same ODE as in the well mixed system.

RESULTS

The qualitative dynamics of the Rosenzweig–MacArthur (ODE) model are controlled by three dimensionless groups of parameters: $m' = m/r$, $\Psi' = \Psi/bm$, and $K' = \sigma bK$. These parameters represent, respectively, the ratio of per capita consumer death rate to intrinsic growth rate of the resource (m'), the ratio of the maximum per capita consumer birth and death rates (Ψ'), and the ratio of resource carrying capacity to the half saturation constant in the consumer's type II functional response (K'). The dynamics of the discrete grazer model involve a fourth dimensionless group, $\varepsilon' = \varepsilon/r$, representing the ratio of the interpatch mixing rate to the resource's intrinsic growth rate.

The dynamics of the Rozenzweig–Macarthur model are well documented (see earlier references). It has a unique equilibrium state with positive values for both populations provided $K' > m'/(\varepsilon' + m')$. The resource equilibrium level is obtained from the consumer eqn 2, and hence does not involve the parameters that characterize resource growth. The equilibrium is stable only if $K' > (\varepsilon'-m')/(\varepsilon' + m')$; otherwise the system exhibits stable limit cycles. This result is the basis of the paradox of enrichment; high enrichment (large K) has no effect on the equilibrium resource density, but implies instability.

The analysis of the discrete discrete consumer model is much more complex. The equilibrium level of the average resource density, X, is again obtained from eqn 2, and is thus unaffected by enrichment. With considerable algebraic effort, it is possible to linearize the dynamic equations, and obtain a condition for the transition from stability to instability (for details of the mathematical approach, see de Roos 1996). From the linearized equations, it can be proved that as the scaled mixing rate, ε', becomes very large, the stability condition approaches that of the Rosenzweig–MacArthur model. Lower values of ε' stabilize the system in the sense that for any given value of Ψ', the transition from stability to instability occurs at larger values of scaled resource carrying capacity and/or consumer death rate. This is illustrated in Fig. 1.

DISCUSSION

The discrete grazer model introduced in this letter is of course a caricature of any real consumer–resource system. However, the idealization of an immobile resource with small enough individuals that its local density may be treated as a continuous variable, interacting with a population of highly mobile, discrete consumers, has wide applicability. We already mentioned the example of a
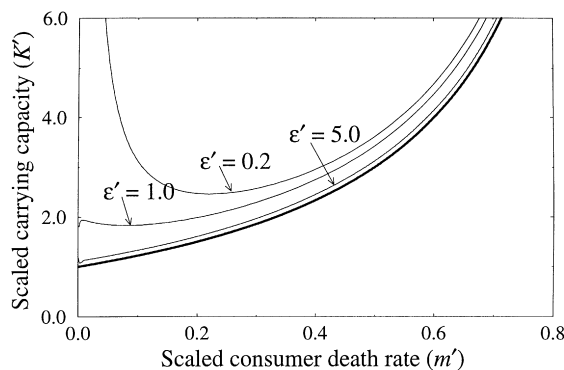
benthic mat of microalgae with invertebrate consumers, but the continuous/discrete distinction may even be important at the smallest spatial scales when considering the interaction of single cells with the continuum of substrate that limits their growth.
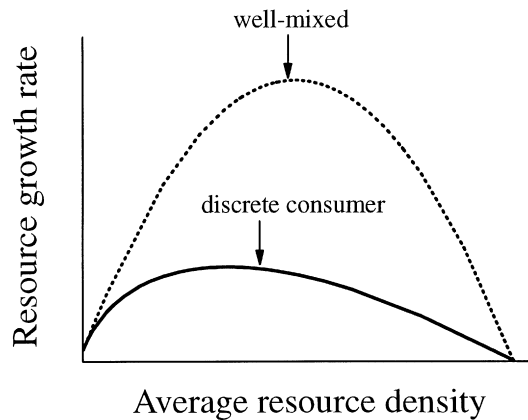
Traditional ODE models are appropriate if population sizes are large and organisms are homogeneously distributed within the system, so that all per capita rates depend on average population densities. This idealization is never wholly plausible; in particular, many spatially explicit, individual-based, consumer–resource models exhibit much more stable dynamics than their ODE counterparts, (e.g. de Roos *et al.* 1991; McCauley *et al.* 1993; Wilson 1996; Donalson & Nisbet 1998). Stability in these models arises because the limited spatial range of interactions desynchronizes local dynamics in different regions of the system. Two recent papers (Wilson *et al.* 1998; Gurney *et al.* 1998) suggest that ephemeral regions of local extinction of consumer or resource may play a key role in achieving this decoupling of local from global dynamics. In the present model, such local extinction is forced by the feeding rules.

However, more than one stabilizing mechanism is possible in models with resource heterogenity. Many mechanisms lead to stability via some form of density dependence that reduces the effectiveness of the consumer at high consumer density. In such models, equilibrium resource density increases with enrichment. An example is a model by de Roos *et al.* (1998), similar to ours except that the time spent by consumers on resource patches is much longer than the handling time per resource item, so that the functional response depends on local resource density. The stabilizing mechanism described here is very different: the efficiency of the consumers is unaffected by the resource heterogeneity, but there is a reduction in the total rate of *resource* production, relative to the well-mixed situation. This is illustrated in Fig. 2.

Finally, we note that mechanisms capable of stabilizing consumer–resource interactions, commonly also promote coexistence of multiple consumers competing for a single resource. Wilson *et al.* (in preparation) show that the "discrete consumer" mechanism indeed has this potential, provided the competitors reduce the resource level to different thresholds after attacking a patch.

Figure 1 Stability boundaries for the discrete consumer model with scaled parameter $\Psi' = 1$. The equilibrium is unstable above the lines.

Figure 2 Continuous curve, typical form for a plot of equilibrium value of the total rate of resource production in the discrete consumer model (equal to

$$\int_0^\infty rx(\tau)\left[1-\frac{x(\tau)}{K}\right]\exp(-\mu\tau)\mathrm{d}\tau$$

where $x(\tau)$ is the resource density on a cell of age t and m is the rate of attack on patches by consumers) against average resource density X. Broken curve, analogous plot for the well-mixed (ODE) model.

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BIOSKETCH

Roger Nisbet's recent research has emphasized individual-based population models that relate population dynamics to the physiology and behaviour of individual organisms. These models, as well as more traditional population models, are being used in studies of population regulation and response to environmental stress.