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PRIMARY-PRODUCTIVITY GRADIENTS AND SHORT-TERM POPULATION DYNAMICS IN OPEN SYSTEMS

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Abstract. We present three models representing the trophic and behavioral dynamics of a simple food chain (primary producers, grazers, and predators) at temporal scales shorter than the scale of consumer reproduction, and at the spatial scales typically employed in field experiments. These models incorporate flexible behavioral responses of organisms to their predators and resources in spatially heterogeneous environments that are open to immigration and emigration. The basic models include passive immigration at all trophic levels, producer growth rates and losses to grazer consumption, grazer emigration rate as a behavioral response to producer and predator densities, grazer losses to predator consumption, and predator emigration as a function of grazer density. We model this system as: (1) a set of ordinary differential equations (“well-mixed model”); (2) a set of partial differential equations describing a population of discrete grazers foraging on discrete patches of primary producers (“discrete-grazer model”); and (3) a set of simulation rules describing the movement and foraging of individual grazers and the growth of primary producers on discrete patches in explicit space (“individual-based model”). The ordinary differential-equation models produced similar results to individual-based models with well-mixed producers, and the discrete-grazer and individual-based models produced similar results when grazers possessed a long-term memory of patch reward rates. The well-mixed and discrete-grazer models thus represent specific, limiting cases of the general individual-based model.

Multiple equilibria and sustained oscillations are possible but are less likely in the discrete-grazer and individual-based models than in the well-mixed model, because localized foraging of discrete grazers leads to the rapid development of spatial heterogeneity in producer biomass and, hence, to a decrease in overall primary production. All models predict that stable equilibrium densities of all trophic levels increase with enrichment, provided grazers increase their emigration rates as predator density increases. If increasing predator density leads to decreasing grazer-emigration rates, predator and grazer densities increase, but producer biomass may increase or decrease with enrichment. These results contrast with predictions from models that assume ideal free distributions of grazers and/or predators with respect to their resources. Our models also predict that densities at all trophic levels will increase with increasing producer immigration, and that producer density will decline with increasing grazer immigration and increase with increasing predator immigration. Our qualitative findings on enrichment are used to interpret an experiment dealing with the short-term dynamics of a stream community open to grazers and predators.

Key words: discrete-grazer model; food-chain dynamics; grazers; individual-based models; population dynamics in open systems; primary producers; primary-productivity gradients; trophic and behavioral dynamics.

INTRODUCTION

Simple models of trophic dynamics have played a significant role in increasing our understanding of mechanisms influencing community and ecosystem structure. Models of food chains in closed systems have proven particularly instructive, owing to their sharp

predictions concerning the responses of higher trophic levels to changes in the fundamental quantities—light and inorganic nutrients—controlling primary production. Assuming that individuals do not interfere with each other, and hence that competition within consumer trophic levels is mediated only through effects of consumers on their resources, these models predict that increases in primary productivity translate into increased equilibrium biomasses of the top trophic level and even-numbered trophic levels below it, whereas the equilibrium biomasses of trophic levels at odd-numbered positions below the top level do not change (Rosenzweig and MacArthur 1963, Smith 1969, Oksanen et al. 1981; but see Abrams and Roth [1994a, b]

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for systems with unstable equilibria). These predictions constitute a particularly powerful "null hypothesis" for comparisons to data, as deviations provide the starting point for evaluating the importance of the many complicating features of natural systems not included in the basic model.

In this paper, we explore the short-term population consequences of three deviations from the assumptions of simple food-chain models: (1) most systems are open, i.e., population dynamics are affected by not only birth and death rates but also by migration and dispersal processes (Cooper et al. 1990, Gaines and Bertness 1993); (2) the behavior of many (if not most) organisms is flexible and adaptive, so that dispersal rates are influenced by the environment; (3) many systems are not well mixed, and over many spatial scales populations consist of heterogeneously distributed individuals (Levin 1992, Cooper et al. 1997a and references therein) and interactions are more likely to take place among neighbors than among spatially distant organisms (McAuliffe 1984, Pacala and Silander 1990).

Few attempts have been made to explore the population consequences of *any* of these factors in systems with more than two trophic levels (e.g., the open food-chain models of Ross et al. [1993, 1994], and Abrams' [1984, 1992] models of flexible individual dispersal behavior). Nor, to the best of our knowledge, have there been any theoretical studies of the *combined* effects of system openness, spatial heterogeneity, and the behavioral flexibility of organisms on consumer-resource interactions. In many environments, these features are closely linked, because movement within and across system boundaries is partly or totally under the behavioral control of individual organisms.

Such theory would be potentially applicable in a wide range of habitats (e.g., streams, marine benthos) and, with minor modifications, would also be applicable to the detritus food chain. The particular models presented in this paper are motivated by our empirical work in stream systems consisting of benthic algae, invertebrate grazers, and vertebrate and invertebrate predators (Cooper et al. 1997b). Most organisms drift and/or move actively in streams, making migration a significant factor affecting local population dynamics (Townsend and Hildrew 1976, Cooper et al. 1990). Emigration of grazers and predators out of local patches is mostly under the behavioral control of these organisms and related to foraging return and predation risk (Kohler 1985, Kohler and McPeck 1989, Sih et al. 1992). Also, in temperate streams, algae grow continuously for much of the year, whereas reproduction of many grazers and predators occurs annually. Thus we model local population dynamics over time scales at which grazers and predators do not reproduce, and equilibria are determined only by algal growth rates and by consumer dispersal and feeding rates.

Different species of grazers show a variety of movement patterns during foraging, with important conse-

quences for spatial heterogeneity in their algal resources (Kohler 1992, Schmitt 1996). We therefore use different modeling approaches that explore the extreme cases of grazer foraging strategies, including grazers that skim off local peaks in algal biomass and tend to equalize standing stocks of algae over their foraging range, and grazers that totally deplete local foraging patches before they move on, thereby enhancing spatial heterogeneity in algal biomass.

Our first family of models is formulated as ordinary differential equations (ODEs). The use of the ODE formalism presupposes that population sizes are large, that organisms are homogeneously distributed within the system, and, consequently, that the dynamics of the system can be described using *per capita* rates of feeding, growth, and migration that depend on *average* population densities. From an individual-based perspective, ODE models assume a *well-mixed* system in which all organisms of a particular species experience the same average environment at any particular time. This also corresponds to a situation where individual grazers forage in a way that effectively homogenizes the biomass of sessile algae.

Over certain spatial scales, it may be reasonable to think of producer density as a continuous variable, but to recognize *discrete grazers*. An example in our stream system would be a mat of microalgae with mayflies as grazers. Several recent papers have shown (using spatially explicit simulations) that models of interacting populations of discrete individuals may exhibit dynamics that differ qualitatively from those of the analogous systems of ODEs (e.g., Wolff 1988, DeRoos et al 1990, McCauley et al. 1993, Durrett and Levin 1994, D. D. Donalson and R. M. Nisbet, *unpublished manuscript*). Our second family of models, *discrete-grazer* models, assumes that discrete grazers forage in a way that leads to the rapid development of a spatially heterogeneous producer distribution. Mathematical tractability is achieved through the use of an idealization that allows us to describe the dynamics in terms of partial differential equations (PDEs) similar to those used to describe the dynamics of structured populations (e.g., Metz and Diekmann 1986).

Finally, and critical to establishing the credibility and limitations of the previous two families of models, we use a spatially explicit, *individual-based* simulation model (IBM), which follows the movement and feeding of individual organisms on a grid of discrete resource patches.

We start by exploring the dynamic behavior of a two-trophic-level system containing only primary producers and grazers and show that multiple equilibria and sustained oscillations are possible with the "well-mixed" model. In contrast, multiple equilibria and oscillations are less likely in the "discrete-grazer" models, consistent with results from IBM simulations. We then explore the responses of two- and three-trophic-level systems to gradients in enrichment and in im-

migration rates, and use our results to examine experiments involving primary productivity gradients in streams.

MODEL FORMULATIONS

We model the population dynamics of benthic algae, grazers, and predators within a fixed region of space (e.g., stream reach), and over a limited period of time during which reproduction of grazers and predators does not occur. Immigration at all trophic levels is assumed to be governed by external factors and to be independent of population densities within the system. In contrast, emigration rates of consumers may depend on the densities of their resources and/or predators, and feeding rates of consumers depend on the densities of their resources. Growth of primary producers (algae) depends on their own density. Note that we incorporate no direct consumer density dependence (*sensu* Murdoch 1994) as no per capita rates affecting a particular consumer's dynamics depend directly on the density of that consumer (Kratz 1996).

"Well-mixed producer" model

The structure of the "well-mixed" model is summarized in Table 1. The state variables are biomass density of producers (i.e., dry mass of producers per unit area), and numerical density (i.e., number of individuals per unit area) of grazers and predators. We use numerical densities of consumers in order to be able to legitimately include behavior such as emigration, which involves decisions by individuals, not biomass units. The model equations involve functions describing producer growth, and consumer feeding and migration. For maximum generality, we initially do not assume particular functional forms. Instead, we assume that these functions obey certain inequalities, listed in Table 1 and discussed below.

Producer dynamics.—The model allows for both passive recruitment (at a constant rate I_A per unit area) and internal growth of producers. The specific growth rate is written in the form $r\rho(A, K)$, where r represents the maximum attainable growth rate, attained only when A is close to zero, and K is the carrying capacity, set by light or nutrients depending on the system under study. The function $\rho(A, K)$, is the fractional reduction from this maximum growth rate at biomass density A , and is assumed to be a decreasing function of A and an increasing function of K . If, for example, algal growth is logistic, the function would be

$$\rho(A, K) = (1 - A/K). \quad (1)$$

Producers leave the system only through consumption by grazers.

Grazer and predator dynamics.—Grazers and predators enter the system at constant rates I_G and I_P per unit area. Grazers leave the system both through consumption by predators and by emigration. Based on empirical work in streams (Malmqvist and Sjöström

TABLE 1. The basic (well-mixed producer) model and its components. All immigration rates are constant; emigration rates are a response to the local environment.

A. Definitions	
Variables	
$A(t)$	Density of producers at time t (biomass per unit area)
$G(t)$	Density of grazers at time t (no. of grazers per unit area)
$P(t)$	Density of predators at time t (no. of predators per unit area)
Passive immigration	
I_A	Total producer supply rate from external sources (biomass per unit area per unit time)
I_G	Total grazer supply rate from external sources (grazers per unit area per unit time)
I_P	Total predator supply rate from external sources (predators per unit area per unit time)
B. Dynamic equations	
$\frac{dA}{dt}$	$= I_A + rA\rho(A, K) - f_G(A)G$ (Producers)
$\frac{dG}{dt}$	$= I_G - e_G(A, P)G - f_P(G)P$ (Grazers)
$\frac{dP}{dt}$	$= I_P - Pe_P(G)$, where (Predators)
Feeding and growth	
$\rho(A, K)$	Proportion of maximum specific growth rate of producers
$f_G(A)$	Functional response of grazers (producer biomass per grazer per unit time)
$f_P(G)$	Functional response of predators (grazers per predator per unit time)
Emigration behavior	
$e_G(A, P)$	Per capita emigration rate of grazers
$e_P(G)$	Per capita emigration rate of predators
Parameters	
r	Maximum specific growth rate of producers
K	Producer carrying capacity (biomass per unit area)
σ	Grazer attack coefficient $\left[= \lim_{A \rightarrow 0} \frac{f_G(A)}{A} \right]$ (area per grazer per unit time)
Assumptions	
$\frac{\partial \rho}{\partial A} < 0$ and $\frac{\partial \rho}{\partial K} > 0$	for all $A, K > 0$ (Producer growth)
$\frac{\partial e_G(A, P)}{\partial A} \leq 0$; $\frac{\partial e_G(A, P)}{\partial P} \geq 0$	(Grazer emigration)
$\frac{\partial e_P(G)}{\partial G} \leq 0$	(Predator emigration)
$\frac{\partial f_G}{\partial A} > 0$; $\frac{\partial f_P}{\partial G} > 0$	(Functional responses)

1987, Kohler and McPeck 1989, Forrester 1994, K. W. Kratz 1996 and personal communication), we assume that grazer per capita emigration rates increase in response to predator density and decrease in response to

TABLE 2. Partial differential equations (PDEs) and definitions for the "discrete-grazer" model. Further mathematical details are in Appendix A.

Variables	
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
$a(\tau, t)$	Producer biomass on a patch aged τ at time t
$A(t) = \int_0^\infty a(\tau, t)n(\tau, t)d\tau$	total producer biomass at time t
$G(t)$	Total grazer density at time t
Rates	
$\mu(t)$	Attack rate per patch at time t
$g(t)$	Biomass growth rate on a patch aged τ at time t
PDEs	
$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial \tau} - \mu(t)n$	
$\frac{\partial a}{\partial t} = -\frac{\partial a}{\partial \tau} + g(a, \tau)$	
Boundary conditions	
$n(0, t) = \mu(t)$	
$a(0, t) = 0$	
Functions	
$\mu(t) = \frac{\sigma G(t)}{1 + \sigma bA(t)}$	
$g(a, t) = I_A + ra\left(1 - \frac{a}{K}\right) - \varepsilon a + \varepsilon A$	

producer density but are independent of grazer density. For example, we might have

$$e_G(A, P) = e_{G0}(1 + \nu P)\exp[-\alpha A] \quad (2)$$

where e_{G0} is the grazer emigration rate from an empty system (i.e., no producers or predators present) and α and ν are parameters that describe how this rate changes in response to producer and predator densities. Similarly, the per capita rate of predator emigration is assumed to be a decreasing function of grazer density. We revisit these assumptions on emigration rates later in the paper.

The functional responses of the grazers and predators are increasing functions of their arguments, an assumption that is normally plausible, but may be invalid with certain foraging mechanisms (Abrams 1989, 1990); however for much of our analysis it is not necessary to further restrict their shape (e.g., Holling types I, II, and III are all permissible). Where specificity is necessary (e.g., in comparing the predictions of our three models), we use a type II functional response with

$$f_G(A) = \frac{\sigma A}{1 + \sigma bA} \quad (3)$$

where σ represents the area searched per grazer per unit time (Table 1), and b represents the handling time per unit of producer biomass. Note that as we do not model consumer growth or reproduction, the "functional response" may include all losses caused by the consumers, not only true feeding losses. Thus, for example, in a stream model we might choose a form that included sloughing export of algae disturbed by grazers.

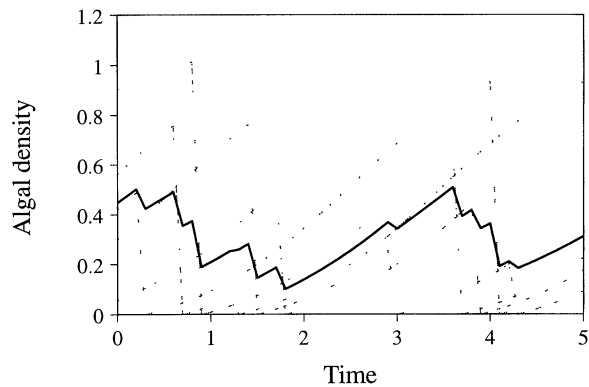


FIG. 1. Schematic concept of discrete-grazer model. Broken lines represent producer biomass on individual patches, which drops to zero when a grazer visits the patch. The bold continuous line is the average producer biomass.

"Discrete-grazer" model

The equations for the "discrete-grazer" model are listed in Table 2. We represent "space" as an arena made up of a large number of very small patches. Individual grazers move randomly among patches and feed on primary producers. We assume that the individual primary producers are much smaller than the grazers (e.g., microalgae and aquatic invertebrate grazers), and that each patch is large enough to allow us to model producer dynamics *within the patch* as a continuous process, but small enough that *all* producer biomass in the patch is consumed if the patch is visited by an individual grazer. The importance of individual grazers is that they generate a *distribution* of producer densities over the large number of small patches. Fig. 1 shows how this distribution arises: immediately after an attack by a grazer on a particular patch, the producer density on that patch is reset to zero, but the density on other patches is unchanged. Following an attack, the local producer density recovers in accordance with the same ordinary differential equation (ODE) that we use to describe producer dynamics in the well-mixed system.

The global producer dynamics are described using equations similar to those introduced by Hastings (1991) in a theoretical study of metapopulation dynamics in a system with intermittent, uncorrelated catastrophes on individual patches. Producer patches are characterized by their "age," τ where "age" means time elapsed since the last visit by a grazer. We require two functions: $n(\tau, t)$, the age distribution of the cells at time t , and $a(\tau, t)$, the producer density on a patch of age τ at time t . Like Hastings, we assume the number of patches to be sufficiently large that the age-distribution function may be regarded as continuous. For example, when modeling mayflies grazing on a mat of algae covering 10 m² of stream, an appropriate "patch" in this model might typically have an area of a few square millimeters, leading to $\sim 10^6$ patches. With such

a large number of patches, partial differential equations provide a good approximation to the dynamics of the age distribution. The equations we use are very similar to those used to model size-structured populations (e.g., Metz and Diekmann 1986, de Roos 1997), and the reader is referred to that literature for mathematical details. The precise biological interpretation of the terms in the equations differs from these previous models, as here we are modeling the distribution of producer biomasses on a collection of patches rather than the age or size distribution of a collection of individual organisms. The form taken by the equation in Table 2 for $\partial n/\partial t$ arises because two factors lead to changes in the number of patches of age τ : aging (associated with the term $\partial n/\partial \tau$), and grazing (the term $\mu(t)n$). The boundary condition $n(0, t)$ takes a very simple form, because the total rate of loss of patches through grazing is exactly equal to the rate of creation of new patches of age zero. The equation for $\partial a/\partial t$ has two terms on the right-hand side because growth and aging occur simultaneously.

We achieve a corresponding major simplification in modeling grazer dynamics if we assume that the total number of grazers is sufficiently large that demographic stochasticity (Nisbet and Gurney 1982) is unimportant, so that we can treat the *total* number of grazers in the system, $G(t)$, as a continuous variable. In our previous example of the mayflies in a stream, this idealization would be reasonable if the mayfly population in the study area consisted of around 100 or more individuals. Grazers are assumed to “explore” the system rapidly and to attack patches randomly at a rate $\mu(t)$ that may depend on the average producer density in the system, $A(t)$ (for example through satiation), but is independent of local producer density; thus the rate $\mu(t)$ at which grazers attack cells is equal to $G(t)$ times some function of $A(t)$. For example, with a type II functional response, we have

$$\mu(t) = \frac{\sigma G(t)}{1 + \sigma b A(t)}. \quad (4)$$

Similarly, the rate $e_G(t)$ at which grazers leave the system is assumed to depend only on the average producer density, $A(t)$, and/or on the density of predators in the system, $P(t)$, e.g., through the function represented in Eq. 2. Thus grazers obey the same ODEs as in the well-mixed system (Table 1). A similar argument applies to predators.

Thus far, the model allows no mixing of producers among patches. This is deliberate: our aim is to construct a model that will highlight the consequences of deviations from the common assumption of perfect mixing. However, for the purpose of comparison with the other models, it is useful to incorporate (imperfect) mixing by assuming that a fraction, ε , of producer biomass is constantly lost from each patch to a hypothetical “pool” that is mixed and redistributed evenly among patches. If ε is large compared with all other rates in the system, at any given time, all patches will

TABLE 3. Notation for the individual-based model. The rules are described in the text.

Symbol	Definition
t	Time
Δt	Time increment in simulations (small)
N	Total number of algal patches
a_i	Algal density in patch i
r	Intrinsic growth rate of algae (takes same value for all patches)
K	Carrying capacity for a patch
I_A	Producer immigration rate per patch
V	Speed of grazer movement
ϕ	Probability per unit time that grazer changes direction
R	Maximum gut content of grazer
b	Handling time during which grazer empties gut
γ	Memory parameter
T_π	Minimum residence time for grazer on a patch

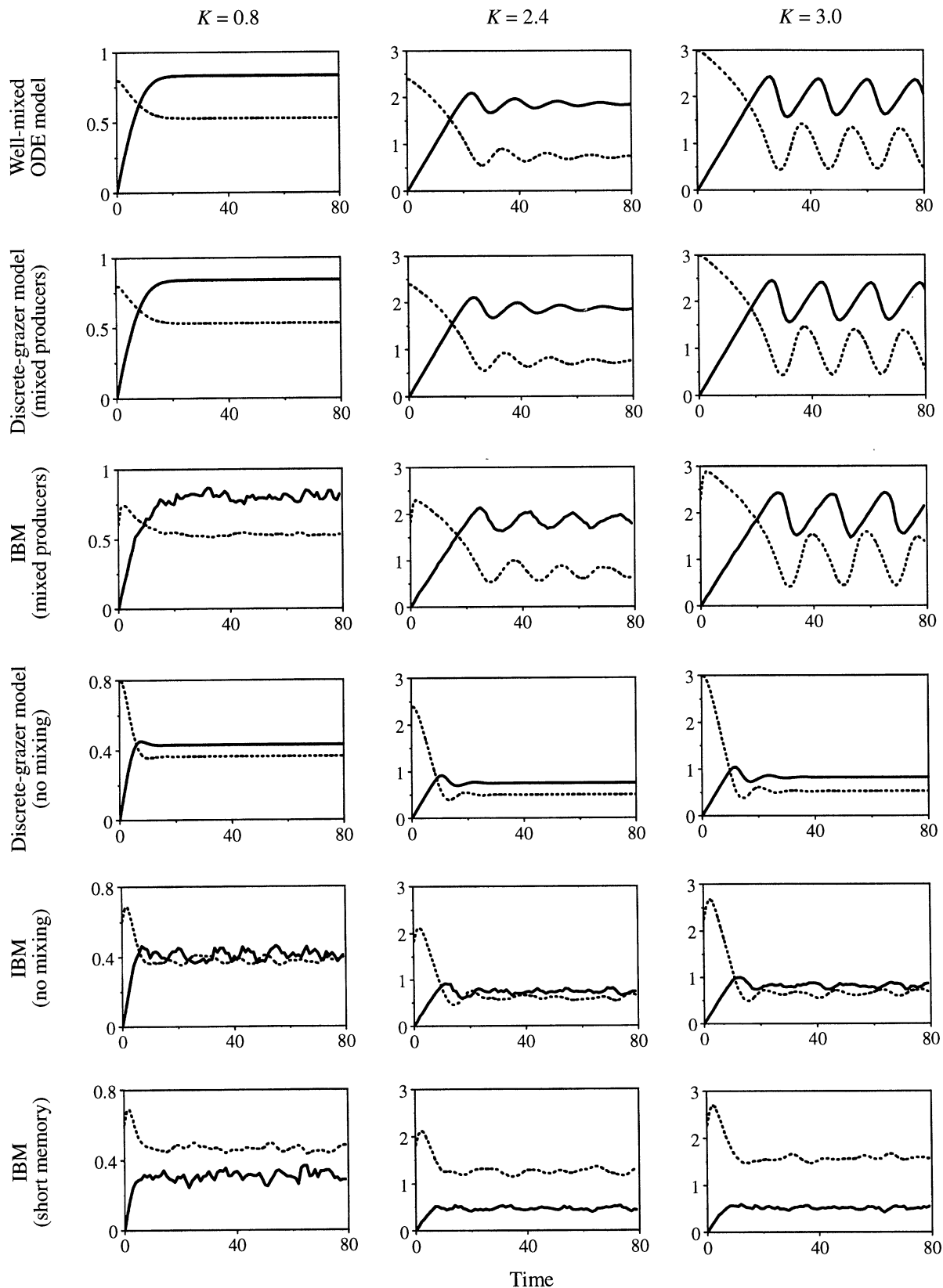
have essentially the same producer biomass, and we expect the dynamics to resemble those of the well-mixed producer model. We emphasize that this representation of mixing is introduced in order to facilitate model comparison, and is *not* a serious representation of the biology of the stream systems that motivated this study.

Spatially explicit, individual-based model

The notation for the individual-based model is listed in Table 3. This model differs from the previous “discrete-grazer” model in that the patches containing primary producers now have well-defined locations in space, being arranged on a square 128×128 lattice. Each grid square has unit area. For computational convenience, we use cyclic boundary conditions, i.e., the lattice has the topology of a torus. Individual grazers, which are characterized by the two state variables gut content and location in space, move around and feed on primary producers, emptying any patch they attack. We restrict our studies of this model to the case where there are no predators in the system.

Time advances in small discrete steps of duration Δt . At the beginning of each simulation step the producer biomass in each patch is incremented by an amount $\Delta a_i = [I_A + r a_i (1 - a_i/K)] \Delta t$, where a_i is the producer biomass in patch i . This is a discrete-time analog of the local ODE in the discrete-grazer model. If $a_i + \Delta a_i > K$ (overshooting by discretization), the updated patch biomass is set to K . Primary producers do not grow laterally into neighboring patches.

Grazers move in straight lines at a fixed speed V , and have a probability $\phi \Delta t$ of changing direction at each time step. If there is a change in direction, the new direction is uncorrelated with the previous direction, chosen at random from a uniform distribution over $0-360^\circ$. After each time step, every grazer’s spatial coordinates are matched to a specific patch i . Unless the grazer is sated, all of the producer biomass in this patch is consumed by the grazer; consequently the patch’s producer biomass is set to zero, and the grazer’s



gut content is incremented by a_i . On the rare occasions where two or more grazers occupy the same patch, the first grazer to be matched with the patch consumes all of the producers. After consuming R biomass units of algae, the grazer is assumed to be sated, irrespective of the time taken for this consumption, and it enters a latent period of duration b during which it continues to move around on the lattice but does not consume algae. This is the implementation of a Type II functional response used by de Roos et al. (1990). Provided we choose $V > 2/\Delta t$ (as we did in all simulations reported in this paper), the grazer will never be in the same patch at successive time steps, and the area visited per unit time ($1/\Delta t$) is independent of V .

During each time step, a constant number of $I_G \Delta t$ new grazers enters the system from outside. Immigrants are assumed to have gut content zero and are placed randomly on the lattice. The probability for an individual grazer to leave the lattice (emigrate) during a particular time step does not depend on the average producer biomass (as in the previous two models), but depends on that particular grazer's estimate, π , of average producer biomass. Thus we require rules describing how a grazer "learns" the state of its environment, and "computes" the instantaneous value of π .

Our principal assumption is that the grazer's estimate of producer biomass is based only on knowledge obtained from patches it has visited. Upon immigration, the grazer's π value is set equal to the producer biomass in the patch on which it settles. At later times, the value of π for a grazer on patch i is updated according to the rule

$$\pi_{i+\Delta t} = \gamma a_{i+\Delta t} + (1 - \gamma)\pi_i. \quad (5)$$

The parameter γ ($0 < \gamma \leq 1$) characterizes the grazer's "memory"; an individual with $\gamma = 1$ has no memory, whereas an individual with $\gamma = 0$ would never update its estimate from the instant it arrives on the lattice. With intermediate values of γ , the individual grazer is estimating its environment by exponential smoothing, with significant "memory" of its experience over a number of time steps of order $1/\gamma$. Exponential smoothing is described in detail in most texts on time-series analysis (e.g., Chatfield 1975); it is arguably the simplest approach to forecasting the value of a fluctuating variable from a single, short, time series, and is a natural, if simplistic, way to describe learning. In order to allow sufficient time for a reasonable initial estimate

of the "average" producer biomass, we arbitrarily require that, after settling on the lattice, individuals remain for a certain minimum time T_π before emigration is allowed. After that time has elapsed, a grazer emigrates in accordance with the same rule used in the previous models, except with π replacing A . Thus the emigration probability per time step is $e_{G0} \exp(-\alpha\pi)\Delta t$ (cf. Eq. 2). Because sated grazers continue to move around and assess the environment, we assume that gut status does not directly affect a grazer's probability of emigrating.

DYNAMICS OF THE PRODUCER-GRAZER SYSTEM

The repertoire of possible dynamical behavior in our models is very great, and an exhaustive mathematical analysis would be a major undertaking. Previous work on linear food chains (e.g., Hastings and Powell 1991) leaves little doubt that there will be choices of functions and regions of parameter space for which chaotic dynamics can occur; however, the primary focus of this paper is stable equilibria, and we restrict our analysis to establishing that there is a wide range of situations in which unique, stable equilibria can be expected. For simplicity, we work primarily with the two-level models that are obtained if there are no predators, and identify those circumstances under which the equilibria are either (a) non-unique, or (b) locally unstable.

Intuition on the dynamics produced by the three types of models is helped by establishing connections among them. Thus we start by establishing that the well-mixed-producer model is a limiting case of the other two if reassortment of producers among patches is sufficiently rapid, and that the discrete-grazer model is a good approximation to the individual-based representation provided grazers base their decision to emigrate on a sufficiently large number of patches. We then study two problems related to equilibria: non-uniqueness (i.e., existence of more than one possible equilibrium), and local instability leading to oscillations.

Interrelationships among the models

The discrete-grazer model should behave like the well-mixed ordinary differential equation (ODE) model if the mixing rate among patches, ε , is very large. Similarly, if producers were redistributed evenly among all patches on the lattice at the beginning of each time step, the individual-based model (IBM)

←

FIG. 2. Simulations illustrating the relationship among the three models. For detailed explanation see *Dynamics of the producer-grazer system: Interrelationships*. . . . Parameters for the well-mixed ODE (ordinary differential equation) model are: $I_A = 0.02$, $r = 1.5$, $e_{G0} = 1.0$, $\alpha = 4$, $\sigma = 1$, $b = 1$, and $I_G = 0.1$ (row 1). The discrete-grazer model runs used these parameters together with $\varepsilon = 50$ (row 2) and $\varepsilon = 0$ (row 4). The IBM (individual-based model) runs used the well-mixed model parameters, except for $\sigma (= 1/\Delta t)$; see *Model formulation: Spatially explicit individual-based model* and b , and in addition had $\Delta t = 0.01$, $V = 0.022$, $R = 3$, $b = 0.03$, and $\phi = 0.1$. The IBM runs in rows 3 and 5 had $\gamma = 0.1$ and $T_\pi = 0.1$. The "short-memory" runs in row 6 had $\gamma = 0.9$ and $T_\pi = 0$. In all panels, the broken line represents producer density, the continuous line grazer density. (For definitions of most variables see Tables 1 and 3.) In all cases the y axis represents relative population density.

would be expected to exhibit broadly similar dynamics to the well-mixed ODE model.

The top three rows of Fig. 2 confirms the validity of these claims for runs using all three models with the model functions given by Eqs. 1–3. The only exception occurred with parameter combinations for which the ODE model produced weakly damped oscillations of algae and grazers ($K = 2.4$ in Fig. 2). The corresponding IBM runs exhibited sustained oscillations. We identified the hunger state of immigrant grazers as the primary reason for this discrepancy. In the ODE model, immigrants are identical to residents in that both respond to mean algal density. In the IBM, immigrants have gut content zero and feed in accordance with their individual hunger states, which are different from the mean hunger state of residents (McCauley et al. 1993). During periods of low algal densities and declining grazer densities, immigrants with zero gut content constitute an increasingly large proportion of the grazer population, resulting in a higher overall grazing rate than in the ODE model. This tends to accentuate population troughs and may inhibit the decay of oscillations.

Rows 4 and 5 of Fig. 2 compare discrete-grazer and IBM outputs for a situation where the IBM's individuals have long memory ($\gamma = 0.1$). The IBM results show demographic stochasticity due to the finite lattice used in the simulations, but the plots confirm that the discrete-grazer representation is consistent with the individual-based behavior, provided that individuals base their decision to emigrate on the average resource environment experienced over many time steps. The importance of the memory of individual grazers is demonstrated by the plots in the bottom row of Fig. 2, which come from IBM runs for individuals with very short memory ($\gamma = 0.9$). The equilibria in these simulations have fewer grazers and higher producer biomass than those from the runs with long memory, since grazers encountering even a single low-density patch have a high probability of leaving.

Multiple equilibria

We first establish that multiple equilibria are possible in the well-mixed producer model. To demonstrate this property in the simplest possible context, we initially make one additional assumption, namely that the emigration rate of grazers is independent of producer biomass. Thus the equilibrium grazer density is simply

$$G^* = I_G/e_G. \quad (6)$$

Once the grazer equilibrium is known, the producer equilibrium is obtained from the equation for producer dynamics, namely

$$I_A + rA^*\rho(A^*, K) - f_G(A^*)G^* = 0. \quad (7)$$

Depending on the form of the functions $\rho(A, K)$ and $f_G(A)$ this equation may have many solutions (e.g., Noy-Meir 1975, May 1977). In the special case where $I_A =$

0, one of these is always $A^* = 0$. This zero solution is stable if

$$r < \sigma G^*. \quad (8)$$

The parameter σ , formally defined in Table 1, can be interpreted as the area searched per grazer per unit time. Thus if the equilibrium grazer density is sufficiently high, the primary producers are unable to persist in the system.

At equilibrium the total grazing rate must balance the combined effects of producer immigration and growth. Fig. 3 illustrates the possibilities with logistic producer growth and three possible forms of functional response for the grazers: type I, type II, and type III. With a type I functional response in a system closed to input of producers ($I_A = 0$), there are only two possibilities: if $r > \sigma G^*$ (Fig. 3a), there is a unique, stable producer equilibrium, but if this inequality is reversed (Fig. 3b), the equilibrium grazing rate exceeds the maximum possible producer growth rate and the producers are eventually cleared from the system. If $I_A > 0$ (not shown), there is always a stable producer equilibrium.

With a type II functional response, two stable equilibria are possible only if $r < \sigma G^*$ (Fig. 3f and g). In this case, the grazers may drive the producers extinct if $I_A = 0$. If $I_A > 0$, the lower of the stable producer equilibria is nonzero and represents primarily a balance between producer immigration and grazing losses. The higher equilibrium is present in all cases considered (Fig. 3b, c, f, and g), if grazer satiation reduces the grazing rate sufficiently. In the absence of producer immigration, only a type III functional response can produce two, nonzero, stable equilibria (Fig. 3h).

If grazer emigration rate is a function of producer biomass, the equilibria cannot be described using Fig. 3, and it is necessary to consider zero isoclines. The previous assumption of grazer emigration being independent of producer biomass yields a grazer isocline parallel to the producer axis. In contrast, if *per capita* grazer emigration is a decreasing function of producer biomass, the grazer isocline has a positive slope (Fig. 4). The slope of the grazer isocline has quantitative implications for the producer and consumer equilibria (see *Effects of enrichment and immigration . . . : Effects of enrichment*, below), but does not affect the qualitative conclusions on the number and stability of equilibria derived from Fig. 3. This can be seen easily by comparing the corresponding panels of Figs. 3 and 4 (i.e., Figs. 3c vs. 4a, 3f vs. 4b, 3g vs. 4c).

Multiple equilibria are also possible with the discrete-grazer model, but are *much* less likely (in the sense that they are found in a much smaller region of parameter space). This is most easily demonstrated by calculating the total rate of increase of the producer population (=total primary production, the integral in Eq. A.2 [see Appendix A]) and comparing the result with that for the well-mixed model. Numerical calculations show that the effect of heterogeneity in producer

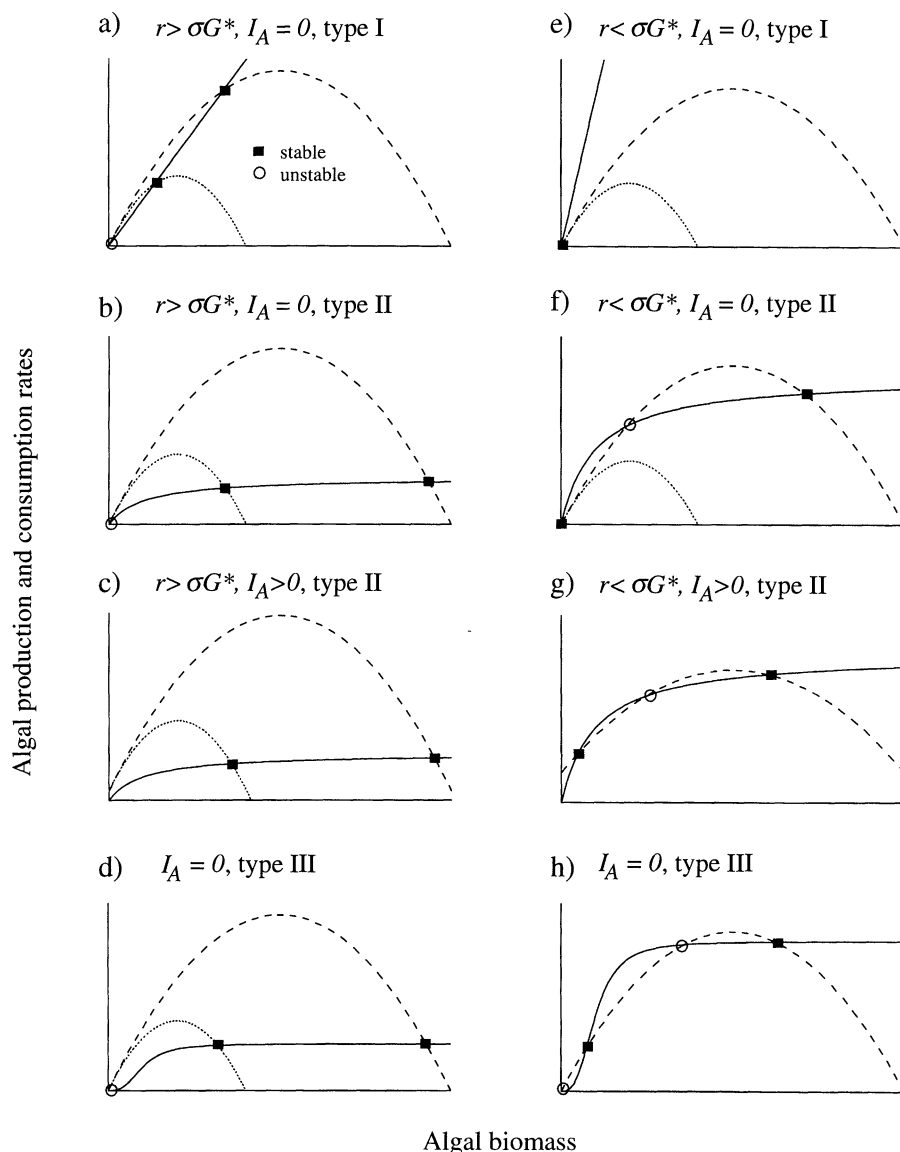


FIG. 3. Number and stability of equilibria in a producer-grazer system with logistic growth of the algae and grazer emigration independent of algal density. Hump-shaped curves represent producer production rates at low K (.....) and high K (—), respectively; — = total producer loss rates caused by grazing, assuming linear (type I), type II, or type III functional responses of the grazers; \circ = locally unstable equilibria, \blacksquare = locally stable equilibria.

biomass among patches is always to reduce total primary production (Fig. 5a), and that the producer isocline is then much less likely to have a significant "hump" (Fig. 5b). Thus, multiple equilibria are always less likely in the discrete-grazer model than in the well-mixed model.

We have also investigated the occurrence of multiple equilibria with our individual-based model. For consistency with the previous analyses, we fixed the number of grazers on the lattice. In the case of constant mixing of the system, the IBM produces multiple stable equilibria with domains of attraction that closely match the solutions of the corresponding ODEs, but as with

the discrete-grazer model, these multiple equilibria commonly disappear when mixing is removed.

Producer-grazer oscillations

If grazer emigration rate depends on producer biomass (e.g., by Eq. 2), then the system may exhibit sustained oscillations similar to those found in standard consumer-resource models of closed systems (with consumer reproduction). Fig. 2 (top row) shows a specific example where increases in K gradually destabilize a well-mixed system and eventually produce population cycles through a similar mechanism to the paradox of enrichment in closed-system, multi-generation,

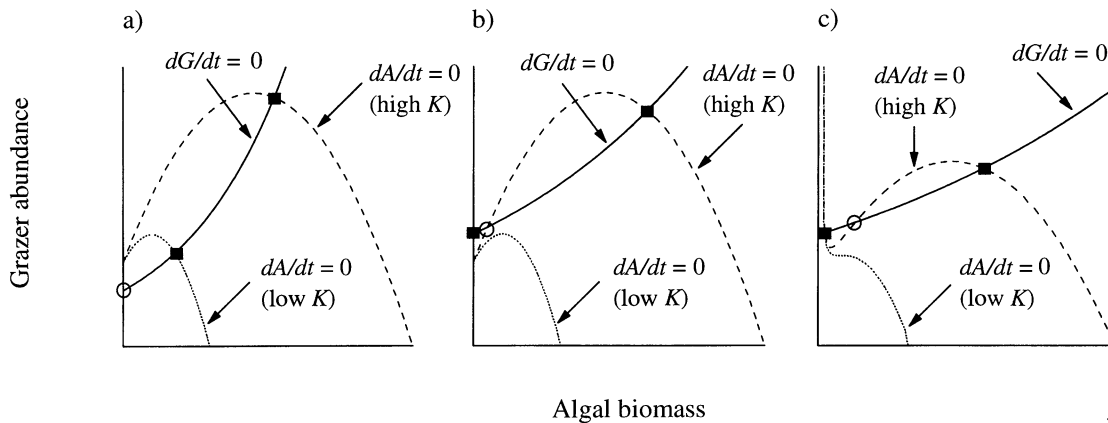


FIG. 4. Examples of the effects of increasing producer carrying capacity (K) on equilibrium levels of producers and grazers in a producer–grazer system with grazers having a type II functional response and grazer *per capita* emigration being a decreasing function of producer density. Lines (isoclines) represent combinations of producer and grazer densities at which populations do not change. Producer densities (.....; —) increase (decrease) below (above) the isoclines ($dA/dt = 0$). Grazer populations (—) increase (decrease) to the right (left) of the isoclines ($dG/dt = 0$). Where producer and grazer isoclines intersect, the system is at an equilibrium; \circ = locally unstable equilibria; \blacksquare = locally stable equilibria. In the absence of producer immigration (a, b), the intersection of the grazer isocline with the grazer axis is also an equilibrium. (a) Producer immigration rate $I_A = 0$, low grazer immigration. The system has a stable equilibrium that will eventually become unstable, yielding limit cycles if K increases even more than shown. (b) $I_A = 0$, high grazer immigration. At low K , grazers exclude producers from the system. At high K , two stable equilibria are possible, but one has zero producer density. (c) $I_A > 0$, high grazer immigration. The system can have two stable equilibria at which producer biomass is nonzero. In all cases, the equilibrium levels of both producers and grazers increase with K for stable equilibria (with nonzero producer biomass).

population dynamics (Rosenzweig 1971). Cycles occur through the “prey-escape” mechanism (de Roos et al. 1990): the producer population escapes the control of the consumer population and grows rapidly until self-limited. Once producers become self-limited and start to decline, emigration of grazers is too slow to prevent rapid decline of the producers to levels well below equilibrium. Eventually, enough consumers emigrate for the producer recovery to start and the cycle is repeated.

Small-scale producer heterogeneity makes oscillations less likely. We have already shown that if producer biomass is homogenized at each time step, the discrete-grazer model and the IBM exhibit similar dynamics to the well-mixed model (Fig. 2). The lower panels in Fig. 2 show an example of the stabilizing effect of producer spatial heterogeneity. We have not attempted a formal local-stability analysis of the discrete-grazer model, but the plots of producer productivity and producer isoclines in Fig. 5 suggest that the explanation may be similar to that invoked to explain the reduced likelihood of multiple equilibria: a reduction in productivity removing the “hump” from the isocline. This argument is not rigorous, as there is no simple interpretation of points above and below the isoclines with the discrete-grazer model. For example, values of G and A above the line may represent a system in which A is increasing or decreasing, depending on the instantaneous biomass distribution.

EFFECTS OF ENRICHMENT AND IMMIGRATION ON EQUILIBRIUM DENSITIES

Effects of enrichment

One important property of simple models of *closed* two-level producer–consumer systems is that the equilibrium density of producers is set solely by parameters describing properties of the consumer. Consequently, an increase in the values of r or K (the parameters describing producer growth) leads ultimately to an increase solely in consumer density, provided the equilibrium remains stable. Fig. 4 shows isoclines for a well-mixed *open* producer–grazer model with producer growth and grazer feeding and emigration described by Eqs. 1–3. Three situations are displayed. In Fig. 4a, there is only one stable equilibrium irrespective of the value of K , whereas Fig. 4b and c depicts situations where increasing the value of K leads to the appearance of multiple stable equilibria. These figures suggest that stable, nonzero, equilibrium levels of both producers and consumers will increase with increasing K , provided the equilibrium is locally stable.

This result does not depend on the specific functional forms chosen to describe grazing, emigration and/or producer growth. In Appendix B we show that it is possible to determine the signs of a sufficient number of elements of the Jacobian matrix of the general model described by the inequalities in Table 1 to prove, for locally stable equilibria, the generality of the positive relationship between K and the equilibrium densities

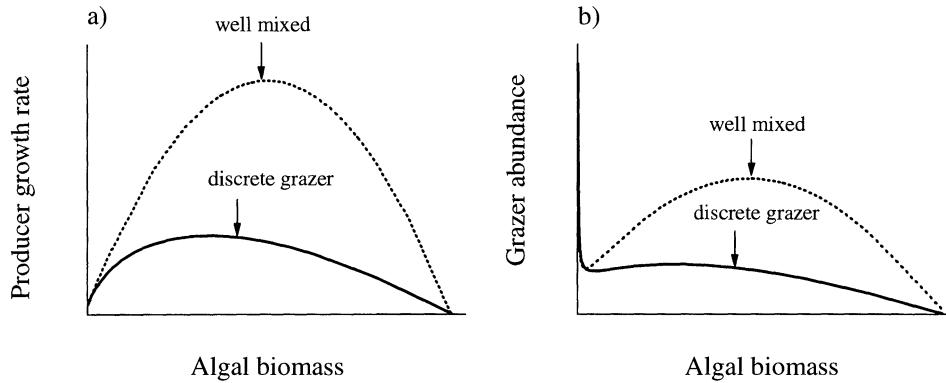


FIG. 5. Typical forms for (a) producer growth curves and (b) producer isoclines for the well-mixed model and discrete-grazer model.

of producers and consumers. In Appendix C we then use the same method to establish that this prediction extends to three-level systems. For our most general ODE (ordinary differential equation) model of an open three-level food chain (Table 1), equilibrium levels of producers, grazers, and predators all increase with K , provided the equilibrium is locally stable (Fig. 6a,b).

An analogous result cannot be proved rigorously for the discrete-grazer model without performing a local stability analysis, which as already noted is beyond the

scope of this paper. However, in all cases studied numerically, equilibrium densities of all trophic levels increase with K , a result we suspect is general. We have not conducted an exhaustive check of the K dependence of equilibria in the IBM (individual-based model), but previous demonstrations that this model's dynamics are broadly similar to those of the discrete-grazer model make it likely that here, too, all stable equilibria increase with enrichment.

The assumption that grazers increase their emigra-

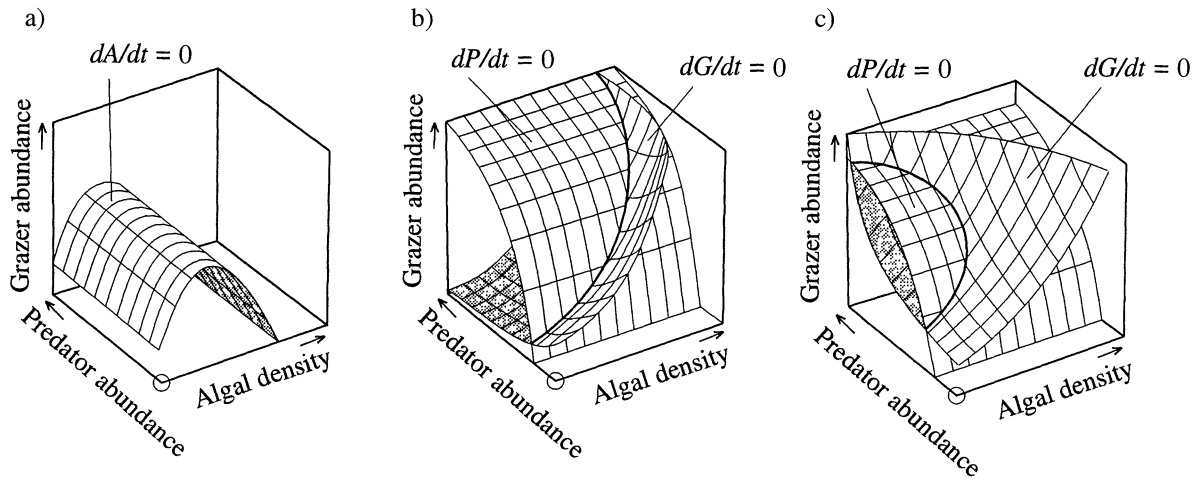


FIG. 6. Examples of isoclines of a producer-grazer-predator system. For clarity of presentation, the producer isocline is shown separately from the grazer and predator isoclines. In all panels, the origin is marked with \circ . (a) Producer isocline ($dA/dt = 0$). Producers increase when the system is below the isocline and decrease when the system is above the isocline. Producer immigration is assumed to be zero. Nonzero producer emigration would yield a three-dimensional extension of the producer isocline in Fig. 4c. With increasing K , the producer isocline moves upward and to the right. (b) and (c) Grazer ($dG/dt = 0$) and predator ($dP/dt = 0$) isoclines for two different assumptions about grazer emigration behavior. Grazers increase when the system is below the grazer isocline and decrease when the system is above the grazer isocline. Predators increase when the system is above the predator isocline and decrease when the system is below the predator isocline. The system is at an equilibrium where producer, grazer, and predator isoclines intersect. In (b) grazers increase their emigration rates with increasing predator abundance, as assumed in our well-mixed model. In that case, stable equilibria are associated with the descending limb of the algal isocline. Consequently, as K increases, the stable equilibrium moves up along the thick solid line, i.e., the equilibrium densities of algae, grazers, and predators all increase. In (c) grazers are assumed to decrease their emigration rates with increasing predator abundance. In that case, stable equilibria can be associated with either the ascending or the descending limb of the producer isocline. Stable equilibria associated with the descending limb of the producer isocline move up and to the right along the front part of the thick solid line. Stable equilibria associated with the ascending limb of the producer isocline move up and to the left along the distant part of the thick solid line. Consequently, with increasing K , grazer and predator equilibrium densities always increase, but producers may either increase or decrease.

tion rates in response to increasing predator density is probably not universally valid. Depending on predator foraging mode (e.g., benthic or drift feeding), some prey taxa may actually decrease their emigration rates in the presence of predators (Andersson et al. 1986, Bechara et al. 1993, Douglas et al. 1994, Wooster and Sih 1995, Dahl and Greenberg 1996). If so, the grazer isocline will shift upward and to the left (compare grazer isoclines in Fig. 4b and c), creating the potential for two alternative stable equilibria, one of which behaves as above with producers, grazers, and predators all increasing with K . The second equilibrium, which only occurs if the peak of the hump in the producer isocline is relatively high, but which may be the only equilibrium if K is high, occurs at a lower producer biomass and higher abundances of grazers and predators than the first equilibrium. In this case, grazers and predators still increase, but producers decrease with increasing K . Thus, the direction of change of the producer level with changing K is indeterminate, as can be shown analytically using the method outlined in Appendix C. The dynamics of a three-level model with a negative relationship between grazer emigration and predator density may in reality be even more complex, because the emigration and foraging behavior of grazers are probably not independent. A grazer that reduces its emigration rate in response to predators is likely to reduce all risky activities, thereby affecting grazing rates and predator feeding and emigration rates.

Effects of immigration rates

With the ODE model, the same approach used to analyze the effects of changes in K on equilibrium densities can, in principle, also be used to analyze the effects of changes in immigration rates on equilibrium densities of all trophic levels. Again, the analysis applies only to equilibria that are locally stable. The effects of changes in algal immigration rate on the equilibrium densities of all trophic levels are equivalent to the effects of changes in K , i.e., equilibrium densities of producers, grazers, and predators all increase with increasing I_A .

Because the sign of the effect of producers on their own growth rate at equilibrium is undetermined in both the two- and three-level models, we can only make limited predictions of the effects of changes in consumer immigration rates (see Appendices B and C). Increases in grazer immigration rate have a negative effect on equilibrium producer biomass in both the two- and three-level models. Producer biomass always increases in response to increases in predator immigration rate. The analyses in Appendices B and C show that the effects of changes in consumer immigration rates on consumer densities cannot be determined, and it is possible that the signs of these effects are contingent on the equilibrium densities. Under most conditions, increasing I_G (the total grazer supply from external sources) will either increase G^* (the equilibrium

grazer density) or, if G^* decreases, will destabilize the equilibrium (and our analysis no longer applies). However there are cases where an increase in I_G decreases G^* . For example, consider $I_A = 0$; $r = 1.5$; $K = 2.5$; $e_{G0} = 0.5$; $\alpha = 4$; $\sigma = 1$; $b = 1$; $I_G = 0.045$ and $I_G = 0.5$ (see Table 1 for symbol definitions).

Effects of passive immigration vs. ideal free distributions: comparisons to empirical data

The prediction that the abundances of all trophic levels should increase with the carrying capacity of the basal resource crucially depends on the assumption that immigration into the system at all trophic levels is independent of the system's internal state. Alternative predictions arise if we consider the open systems of our models as components ("habitats") within the larger range of a highly mobile top consumer and if we assume that top consumers distribute themselves among habitats in an ideal free manner (sensu Fretwell and Lucas 1970). The latter assumption implies that, at equilibrium, the levels of the top consumers' resources are equal among habitats and independent of habitat productivities (Gilliam and Fraser 1988, Wootton and Power 1993, Hugie and Dill 1994, Oksanen et al. 1995). Applied to a three-level stream system, a model assuming an ideal free distribution of predators would predict constant grazer abundances across productivities, but positive relationships between habitat productivity and the abundances of algae and predators (Wootton and Power 1993). Similarly, in a two-level system, algal biomass should be independent of productivity, whereas grazer abundance should increase with productivity (Sarnelle 1992, Oksanen et al. 1995).

Empirical data that can be used to discriminate among models assuming passive vs. ideal free immigration of stream organisms are scarce, because stream enrichment studies have often been conducted in systems that were closed to grazer migration (Hill and Harvey 1990, Rosemund 1993, Rosemund et al. 1993), or did not report the responses of consumers (Stockner and Shortread 1978, Perrin et al. 1987, Stewart 1987). Organisms that move actively up and down streams may be able to achieve ideal free habitat distributions. For example, the distributions of grazing catfish among pools in a Panamanian stream conformed to an ideal free model, and the catfish kept algal biomass constant across pools differing in algal productivity (Power 1984, Oksanen et al. 1995). Similarly, algal standing stocks in Tennessee streams responded to small-scale (20×20 cm) enrichment only in grazer-exclusion treatments. In treatments open to grazer migration, grazing snails aggregated in enriched sites and kept algal biomass similar across productivities (Hill et al. 1992). In contrast, when whole-stream sections (120–150 m) were enriched, both algae and grazing snails showed positive responses after 100 d (Elwood et al. 1981), suggesting that ideal free distributions can only be ex-

pected at spatial scales close to the ranges of active movement of consumers.

In contrast to fish, many stream invertebrates in their aquatic stages have limited capacities to move upstream, but can drift kilometers downstream over a 1-mo period (Hershey et al. 1993). Drifting invertebrates probably have limited abilities to assess habitat quality downstream, and the assumption of our models that immigration into a habitat is unidirectional and independent of that habitat's quality is likely to be valid for most drifting invertebrates. In accordance with our model predictions, Hart and Robinson (1990) observed an increase in the abundances of both periphyton and grazing caddisfly larvae in enriched, open in situ stream channels (0.3×3 m) compared to open, unenriched, control channels. Similarly, the abundances of both periphyton and grazing mayflies increased downstream of experimental fertilization in an Alaskan stream (Peterson et al. 1993), owing to reduced per capita emigration of mayflies at the enriched site (Hershey et al. 1993). Unfortunately, these results cannot be interpreted in the framework of our models, because predatory fish were prevented from moving between enriched and control sites.

To our knowledge, the only study of enrichment in an open stream system that reports abundance responses of three trophic levels was performed by Wootton and Power (1993). Wootton and Power created a gradient of primary productivity through differential shading of 0.7×3 m cages, which excluded secondary carnivores (large fish), but did not restrict the movement of grazers and their predators (small fish, predatory invertebrates). Biomasses of all trophic levels remained roughly constant between days 30 and 55, suggesting that experimental cages had reached equilibrium. Both algae and predators increased with increasing productivity (irradiation). Grazer biomass also increased with increasing productivity, but the relationship was not statistically significant, leading Wootton and Power (1993) to conclude that there was no relationship between irradiation and grazer biomass. It can be argued, however, that the lack of statistical significance reflected low statistical power rather than the lack of a relationship. In fact, the positive relationship between irradiation and grazer biomass on day 55 becomes statistically highly significant after the removal of one outlier that is responsible for >70% of the unexplained variance (Fig. 7). Note that the slope of the regression line is only slightly affected by the removal of this outlier. The positive relationship between productivity and grazer biomass suggests that passive immigration might be a reasonable assumption for at least some of the grazers and their predators.

DISCUSSION

Implications of open system boundaries and the temporal and spatial scales of empirical studies

Open system boundaries allow short-term equilibria to be set by the balance of population gains (immigra-

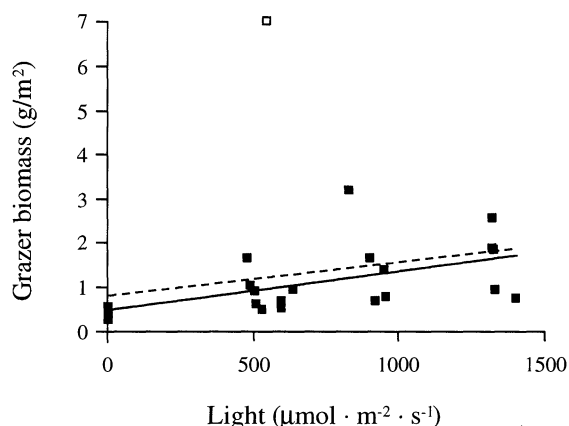


FIG. 7. Relationship between manipulated light level (irradiation, a correlate of primary productivity) and biomass of invertebrate grazers on day 55 of the experiment by Wootton and Power (1993). Hatched line: linear regression including all 25 data points (Grazer biomass = $0.81 + 0.0008(\text{Light})$, $r^2 = 0.06$, $P = 0.23$). Solid line: linear regression excluding the outlier marked by \square (Grazer biomass = $0.48 + 0.0009(\text{Light})$, $r^2 = 0.31$, $P = 0.005$). Data from Wootton and Power (1993).

tion) and losses (emigration, mortality) of consumers. The short response time for the approach to equilibrium makes model predictions highly testable at the temporal and spatial scales at which field experiments are routinely conducted. For example, the experiments by Hart and Robinson (1990) and Wootton and Power (1993) were carried out in 3-m-long channels and lasted three and two months, respectively, which was probably long enough to yield equilibria for taxa with high per capita drift rates.

It is important to note that per capita emigration rates as treated in our models are sensitive to the size of the system (e.g., the size of channels or cages used in experiments). The spatial scale of a study is a crucial determinant of the equilibrium population densities and of the time until equilibrium is reached. For example, in a stream system, immigration and emigration are defined as the rates at which organisms cross the upstream and downstream boundaries. Expressed on a per capita basis, migration rates decrease rapidly with system length. System length will therefore affect a system's rate of approach to equilibrium as well as the equilibrium population densities. Consequently, our models should be most useful when the size of the system is scaled to a relevant biological property, e.g., the median distance drifted per day by the species/trophic level with the shortest drift distance. When the size of the system is large, assumptions of our models (e.g., that immigrants are equally likely to settle at any point within the system) are violated. Modeling the short-term dynamics of populations over larger spatial scales would require modified or different models.

Our models were created for time scales on which reproductive responses of consumers are negligible.

The investigation of longer-term dynamics is beyond the scope of this paper. It is clear that the temporal scale of such a population model will, again, be intimately related to its spatial scale. For many open systems, long-term dynamics can only be meaningfully studied at large spatial scales, because reproductive stages (e.g., terrestrial stages of many stream insects) disperse over large distances. One potential way of approaching long-term dynamics could be a model of subsystems (similar to our models) linked by drift, which settle to short-term equilibria. Periodically, the subsystems generate an overall reproductive output of consumers that is then redistributed over the global system, possibly resetting subsystems to initial conditions away from their short-term equilibria. Such a resetting of the global system could also be used to model periodic or stochastic disturbance events.

*Implications of behavioral flexibility
in emigration rates*

Our simple models allow only two ways in which the abundance of a consumer trophic level can be decoupled from the carrying capacity of its resource. Either the consumer's predators must be able to distribute themselves in an ideal free manner among habitats (as in the model of Wootton and Power 1993), or the consumer's emigration rate must be independent of resource density. In the former case the consumer isocline is a straight line parallel to the consumer axis (Oksanen et al. 1995), whereas in the latter case the consumer isocline is a straight line parallel to the producer axis. We have argued that ideal free distributions are unlikely for unidirectionally drifting organisms, because drift immigration into a system is probably independent of that system's internal state. However, we do assume that consumers are able to assess the quality of the habitat after they have arrived and respond to it by adjusting their emigration rates. It is this behavioral flexibility in combination with uninformed, passive immigration that creates slanting isoclines of both grazers and predators and thus causes all trophic levels to change with increasing carrying capacity of the producers.

Our model predictions rely on two further assumptions about the emigration behavior of consumers that are supported by empirical data. First, both grazers and predators may decrease their per capita emigration rates in response to increasing levels of their respective resources (Kohler 1985, 1992, Richards and Minshall 1988, Hershey et al. 1993, Kratz 1996). Second, grazers increase their emigration rates with increasing predator levels (Walde and Davies 1984, Malmqvist and Sjöström 1987, Peckarsky 1988, Kohler and McPeck 1989, Forrester 1994, Kratz 1996). Both of these assumptions are sufficient to yield the prediction that, for stable equilibria, all trophic levels increase with an increase in the carrying capacity of the primary producers. However we noted earlier that grazers do not always in-

crease their emigration rates in response to increasing predator density, and that, in this situation, producer density may increase or decrease with increasing K (Wooster and Sih 1995, Dahl and Greenberg 1996).

Effects of enrichment in detritus-based food chains

The predictions from our ODE (ordinary differential equation) models of the effects of enrichment on equilibrium biomasses of trophic levels are only valid under conditions when equilibria are stable. Uncertainty about the stability of equilibria arises from the density dependence in the production of the basal resource. If we assume that the food chain is not based on primary producers but on detritus from external sources, all ambiguities disappear, because the per capita rate of change of the basal resource (in Appendices B and C) will normally be a negative function of its own density. Thus the equilibria of detritus-based systems with two and three trophic levels are always stable (no sustained oscillations), and the prediction that all trophic levels increase with enrichment (increased input of detritus) is general (see empirical verification in Richardson 1991). For the same reasons, all ambiguities regarding the effects of increased immigration rates of consumers on equilibrium densities disappear in a detritus-based system. When detritivore immigration rates increase, detritus always decreases and detritivores and predators always increase. When predator immigration increases, detritivores always decrease, and detritus and predators always increase.

Implications of grazer foraging behavior

The discrete-grazer model suggests that the mechanism for the likely absence of multiple equilibria and of sustained oscillations in individual-based model (IBM) simulations of a two-level system is the rapid development of spatial variability in producer biomass due to the localized foraging of discrete grazers. Two key assumptions of both models are that grazer movement among producer patches is random and that grazers remove all primary producers from a patch before they move on. These assumptions produce a maximum in the spatial heterogeneity of producer biomass produced by grazing, and represent a limiting case of grazer foraging behavior (remove all producer biomass per patch, but visit few patches per unit time), which Schmitt (1996) termed "area-intensive grazing." At the opposite end of the behavioral continuum are grazers that search non-randomly, move quickly among high-resource patches, and do not deplete all of the algal biomass in a patch ("area extensive grazing," Schmitt 1996). In the limiting case of optimal patch choice and patch residence time (Charnov 1976), this foraging behavior results in the dynamics of our ODE model. Thus, the spatial scale at which consumer foraging should be modeled may depend on foraging strategies. If grazing is area intensive, this should increase spatial heterogeneity in algal biomass and a discrete-grazer model may be necessary

to describe algae-grazer dynamics. If grazing is area extensive, this should tend to homogenize spatial differences in algal biomass, and an ODE model may be a good approximation.

We conclude by noting that *all* our results rest on critical assumptions regarding spatial scale. Our discrete-grazer and individual-based models incorporate variability at the small scales on which individual grazers forage (Scrimgeour et al. 1991, Sinsabaugh et al. 1991, Downes et al. 1993, 1995), but we have investigated neither small-scale heterogeneity caused by environmental variables, such as shading from terrestrial vegetation, current speed, and substrate composition (see references in Cooper et al. 1997b), nor any forms of heterogeneity over larger scales. Of particular interest in streams are large-scale, smooth gradients in enrichment, and sharp discontinuities in flow regime (e.g., riffle, pool). We have work in progress exploring these issues.

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APPENDIX A

EQUILIBRIA AND ISOCLINES FOR THE DISCRETE-GRAZER MODEL

The model equations are set out in Table 2. The total producer biomass density is obtained by recognizing that $n(\tau, t)a(\tau, t) d\tau$ represents the contribution to biomass density from patches aged τ to $\tau + d\tau$ at time t . Thus the total algal biomass density is

$$A(t) = \int_0^\infty n(\tau, t)a(\tau, t) d\tau. \quad (\text{A.1})$$

By similar reasoning the contribution to producer growth rate from patches aged τ to $\tau + d\tau$ at time t , is $n(\tau, t)g(\tau, t) d\tau$. All patches are equally likely to be visited by a grazer. Thus the total biomass density loss rate is $\mu(t)A(t)$, and we conclude that

$$\frac{dA}{dt} = \int_0^\infty n(\tau, t)g(a(\tau), t) d\tau - \mu(t)A(t). \quad (\text{A.2})$$

The same result can be obtained more formally by differentiating Eq. A.1 to obtain

$$\frac{dA}{dt} = \int_0^\infty \left(n \frac{\partial a}{\partial \tau} + a \frac{\partial n}{\partial \tau} \right) d\tau. \quad (\text{A.3})$$

A few manipulations involving integrations by parts and substitutions from the partial differential equations in Table 2 lead to Eq. A.2.

If μ^* denotes the attack rate on patches when the grazer and producers are at equilibrium, the equilibrium age distribution of the patches is given by

$$n^*(\tau) = \mu^* \exp(-\mu^* \tau). \quad (\text{A.4})$$

Substituting from Eq. A.4 into Eq. A.2, using the property that $dA/dt = 0$ at equilibrium, we obtain

$$A^* = \int_0^\infty e^{-\mu^* \tau} g(a(\tau)) d\tau = \mu^* \int_0^\infty e^{-\mu^* \tau} a(\tau) d\tau \quad (\text{A.5})$$

(the second equality involving an integration by parts).

Thus the general recipe for numerical evaluation of the equilibria in the producer-grazer system is to solve simultaneously three equations: Eq. A.5, the equation defining μ ,

$$\mu^* = \frac{\sigma G^*}{1 + \sigma b A^*} \quad (\text{A.6})$$

and the equation obtained by setting $dG/dt = 0$ (see Table 2),

$$I_G + e_G(A^*)G^* = 0. \quad (\text{A.7})$$

Calculating the equilibria for the three-level system simply involves including a fourth equation—obtained by setting $dP/dt = 0$.

The isocline $dA/dt = 0$ in the A - G plane is defined parametrically by Eqs. A.5 and A.6. The only difficulty is that Eq. A.5 requires knowledge (numerical or analytic) of the producer growth curve, $a(\tau)$, on a patch. For all the graphs shown in this paper, we assumed that

$$\frac{da}{d\tau} = I_A + r a \left(1 - \frac{a}{K} \right) \quad (\text{A.8})$$

with $a = 0$ when $\tau = 0$. Eq. A.8 can be solved to give

$$a(\tau) = \frac{K \alpha \beta (e^{r(\alpha + \beta)\tau} - 1)}{\beta + \alpha e^{r(\alpha + \beta)\tau}} \quad (\text{A.9})$$

with

$$\alpha = \frac{\sqrt{1 + 4\gamma} - 1}{2} \quad (\text{A.10})$$

$$\beta = \frac{1 + \sqrt{1 + 4\gamma}}{2} \quad (\text{A.11})$$

and

$$\gamma = I_A / (rK).$$

APPENDIX B

ANALYSIS OF THE TWO-LEVEL ODE MODEL

In the absence of predators, our basic model takes the form i.e.,

$$\frac{dA}{dt} = I_A + rA\rho(A, K) - f_G(A)G \quad (\text{B.1})$$

$$\frac{dG}{dt} = I_G - e_G(A)G. \quad (\text{B.2})$$

If we define

$$\theta_1(A, G, K) = I_A + rA\rho(A, K) - f_G(A)G \quad (\text{B.3})$$

$$\theta_2(A, G) = I_G - e_G(A)G \quad (\text{B.4})$$

then at equilibrium

$$\theta_1(A, G, K) = 0 \quad \text{and} \quad \theta_2(A, G) = 0.$$

We want to know whether the equilibrium values of A and G increase or decrease as K increases. Consider a small change δK in K . The corresponding changes δA and δG can be determined by implicit differentiation:

$$0 = \delta\theta_1 = \frac{\partial\theta_1}{\partial A}\delta A + \frac{\partial\theta_1}{\partial G}\delta G + \frac{\partial\theta_1}{\partial K}\delta K \quad (\text{B.5})$$

$$0 = \delta\theta_2 = \frac{\partial\theta_2}{\partial A}\delta A + \frac{\partial\theta_2}{\partial G}\delta G \quad (\text{B.6})$$

$$\mathbf{J}_2 \begin{bmatrix} \delta A \\ \delta G \end{bmatrix} = - \frac{\partial\theta_1}{\partial K} \begin{bmatrix} \delta K \\ 0 \end{bmatrix} \quad (\text{B.7})$$

where

$$\mathbf{J}_2 = \begin{bmatrix} \frac{\partial\theta_1}{\partial A} & \frac{\partial\theta_1}{\partial G} \\ \frac{\partial\theta_2}{\partial A} & \frac{\partial\theta_2}{\partial G} \end{bmatrix}. \quad (\text{B.8})$$

Note that the (Jacobian) matrix \mathbf{J}_2 on the left hand side of Eq. B.7 is the matrix that appears in routine local-stability analyses. Thus if we are describing a locally stable equilibrium, the determinant

$$\Delta \equiv \frac{\partial\theta_1}{\partial A} \frac{\partial\theta_2}{\partial G} - \frac{\partial\theta_1}{\partial G} \frac{\partial\theta_2}{\partial A} \quad (\text{B.9})$$

must necessarily be positive. From this point on, we assume $\Delta > 0$, which implies that \mathbf{J}_2 has an inverse. Eq. B.7 can thus be solved to give

$$\begin{bmatrix} \delta A \\ \delta G \end{bmatrix} = - \frac{\partial\theta_1}{\partial K} \mathbf{J}_2^{-1} \begin{bmatrix} \delta K \\ 0 \end{bmatrix}. \quad (\text{B.10})$$

Using the rules for forming an inverse matrix,

$$\mathbf{J}_2^{-1} = \Delta^{-1} \begin{bmatrix} \frac{\partial \theta_2}{\partial G} & -\frac{\partial \theta_1}{\partial G} \\ -\frac{\partial \theta_2}{\partial A} & \frac{\partial \theta_1}{\partial A} \end{bmatrix}. \tag{B.11}$$

The inequalities in Table 1, together with the assumption that $\Delta > 0$, then imply that the signs of the elements of \mathbf{J}_2^{-1} are:

$$\mathbf{J}_2^{-1} = \begin{bmatrix} - & + \\ - & ? \end{bmatrix} \tag{B.12}$$

where “?” means that the sign of the matrix element is undetermined. It follows from Eqs. B.10–B.12 that

$$\delta A = -\Delta^{-1} \frac{\partial \theta_1}{\partial K} \frac{\partial \theta_2}{\partial G} \delta K \Rightarrow \frac{\delta A}{\delta K} > 0 \tag{B.13}$$

$$\delta G = \Delta^{-1} \frac{\partial \theta_1}{\partial K} \frac{\partial \theta_2}{\partial A} \delta K \Rightarrow \frac{\delta G}{\delta K} > 0. \tag{B.14}$$

Thus if the system is at a locally stable equilibrium, the effect of an increase in the value of K is to increase the equilibrium values of G and A . However, increasing K may also lead to oscillatory instability as the sign of $\partial \theta_1 / \partial A$ is not fixed and hence the trace of the Jacobian matrix may change sign.

Similar reasoning can be used to determine the effects of a change in I_G , the result being

$$\begin{bmatrix} \delta A \\ \delta G \end{bmatrix} = -\frac{\partial \theta_2}{\partial I_G} \mathbf{J}_2^{-1} \begin{bmatrix} 0 \\ \delta I_G \end{bmatrix} \tag{B.15}$$

from which it follows that

$$\delta A = \Delta^{-1} \frac{\partial \theta_2}{\partial I_G} \frac{\partial \theta_1}{\partial G} \delta I_G \Rightarrow \frac{\delta A}{\delta I_G} < 0. \tag{B.16}$$

The corresponding expression for δG is

$$\delta G = -\Delta^{-1} \frac{\partial \theta_2}{\partial I_G} \frac{\partial \theta_1}{\partial A} \delta I_G \tag{B.17}$$

but here the sign of δG is undetermined, since the sign of $\partial \theta_1 / \partial A$ is undetermined.

APPENDIX C

ANALYSIS OF THE THREE-LEVEL ODE MODEL

We follow the same approach as in Appendix B. The full model takes the form:

$$\frac{dA}{dt} = I_A + rA\rho(A, K) - f_G(A)G \tag{C.1}$$

$$\frac{dG}{dt} = I_G - e_G(A, P)G - f_P(G)P \tag{C.2}$$

$$\frac{dP}{dt} = I_P - e_P(G)P. \tag{C.3}$$

We define

$$\theta_1(A, G, K) = I_A + rA\rho(A, K) - f_G(A)G \tag{C.4}$$

$$\theta_2(A, G, P) = I_G - e_G(A, P)G - f_P(G)P \tag{C.5}$$

$$\theta_3(G, P) = I_P - e_P(G)P \tag{C.6}$$

and at equilibrium

$$\theta_1(A, G, K) = 0; \quad \theta_2(A, G, P) = 0; \quad \theta_3(G, P) = 0.$$

We again consider a small change δK , and find that

$$0 = \delta \theta_1 = \frac{\partial \theta_1}{\partial A} \delta A + \frac{\partial \theta_1}{\partial G} \delta G + \frac{\partial \theta_1}{\partial K} \delta K \tag{C.7}$$

$$0 = \delta \theta_2 = \frac{\partial \theta_2}{\partial A} \delta A + \frac{\partial \theta_2}{\partial G} \delta G + \frac{\partial \theta_2}{\partial P} \delta P \tag{C.8}$$

$$0 = \delta \theta_3 = \frac{\partial \theta_3}{\partial G} \delta G + \frac{\partial \theta_3}{\partial P} \delta P \tag{C.9}$$

i.e.,

$$\mathbf{J}_3 \begin{bmatrix} \delta A \\ \delta G \\ \delta P \end{bmatrix} = -\frac{\partial \theta_1}{\partial K} \begin{bmatrix} \delta K \\ 0 \\ 0 \end{bmatrix} \tag{C.10}$$

where the Jacobian matrix \mathbf{J}_3 is defined by

$$\mathbf{J}_3 = \begin{bmatrix} \frac{\partial \theta_1}{\partial A} & \frac{\partial \theta_1}{\partial G} & 0 \\ \frac{\partial \theta_2}{\partial A} & \frac{\partial \theta_2}{\partial G} & \frac{\partial \theta_2}{\partial P} \\ 0 & \frac{\partial \theta_3}{\partial G} & \frac{\partial \theta_3}{\partial P} \end{bmatrix}. \tag{C.11}$$

Again, this is the matrix that appears in local-stability analyses. Its determinant is given by

$$\Gamma \equiv \frac{\partial \theta_1}{\partial A} \frac{\partial \theta_2}{\partial G} \frac{\partial \theta_3}{\partial P} - \frac{\partial \theta_1}{\partial G} \frac{\partial \theta_2}{\partial A} \frac{\partial \theta_3}{\partial P} - \frac{\partial \theta_1}{\partial A} \frac{\partial \theta_2}{\partial P} \frac{\partial \theta_3}{\partial G} \tag{C.12}$$

and at a stable equilibrium, Γ must be negative. The signs of all the matrix elements except J_{11} can be determined from the inequalities in Table 1, the result being

$$\mathbf{J}_3 = \begin{bmatrix} ? & - & 0 \\ + & - & - \\ 0 & + & - \end{bmatrix}. \tag{C.13}$$

The signs of some of the elements of the inverse matrix \mathbf{J}_3^{-1} are now determined:

$$\mathbf{J}_3^{-1} = \Gamma^{-1} \begin{bmatrix} + & - & + \\ + & ? & ? \\ + & ? & ? \end{bmatrix}. \tag{C.14}$$

Using these signs in Eq. C.10 and noting that $\Gamma < 0$, $\partial \theta_1 / \partial K > 0$, we find

$$\frac{\delta A}{\delta K} > 0; \quad \frac{\delta G}{\delta K} > 0; \quad \frac{\delta P}{\delta K} > 0.$$

Thus, as with the two-level system, we find that an increase in K leads to an increase in the values of stable equilibria for all three trophic levels.

Again, we can use the same approach to explore the effects on equilibrium densities of changes in I_G and I_P . As in the two-level model, the signs of the effects of consumer im-

migration can only be determined unequivocally for the producers, the relationships being

$$\frac{\delta A}{\delta I_G} < 0; \quad \frac{\delta A}{\delta I_P} > 0.$$

The signs of the effects of consumer immigration on consumer equilibrium densities remain undetermined for both grazers and predators.