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IMPLICATIONS OF SPATIAL HETEROGENEITY FOR THE PARADOX OF ENRICHMENT[1]

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Abstract. We analyze a simple model to show that spatial heterogeneity of zooplankton can explain discrepancies between the behavior of classical predator–prey models and the patterns observed in natural planktonic systems. We use a Lotka–Volterra type model of *Daphnia* and algae. *Daphnia* occupies only part of a total volume whereas the algae grow in the entire volume and diffuse between the two compartments. This simple spatial structure suffices to explain the observations that (1) natural *Daphnia*–algae systems tend to be relatively stable up to high nutrient values, and that (2) in the presence of *Daphnia* edible algae do increase with enrichment. Additionally, the model trivially explains confusing observations of oscillating *Daphnia* densities in the presence of a practically constant density of edible algae. The model is supported by the results of a laboratory experiment with a cascade of zooplankton–phytoplankton containers, devised originally to test ratio-dependent foraging. We derive minimalizations of our model, which no longer explicitly account for the spatial structure, but still preserve the essential behavior of the full model.

Key words: Daphnia; *functional response; spatial structure; stability.*

INTRODUCTION

Populations of large herbivorous zooplankters of the genus *Daphnia* are long since known for their tendency to oscillate (e.g., Pratt 1943). The driving force behind the oscillations is a delayed response of the population to the depletion of the algal food (Goulden and Hornig 1980). Thus, the observed oscillations can be considered predator–prey cycles as produced in a simple form by the classical Lotka–Volterra type minimal models (Caughley and Lawton 1981). For "realistic" parameter values, such models only have a stable equilibrium if the productivity of the algae is very low. Increasing productivity leads to the so-called "paradox of enrichment" (Rosenzweig 1971, Gilpin 1972): the equilibrium becomes the unstable focus of a limit cycle. The oscillations tend to become so large that the algae and *Daphnia* populations would run the risk of extinction.

From extensive reviews of *Daphnia* dynamics, McCauley and Murdoch (1987, 1990) conclude that coupled oscillations of *Daphnia* and algae are indeed common in the field. However, contrary to the paradox of enrichment predictions, the amplitudes of the oscillations are typically small (i.e., $2 \leq N_{max}/N_{min} \leq 4$), and destabilization with increasing nutrient level hardly occurs. Another deviation between model and data that has recently received much attention is that even in the presence of *Daphnia*, algal density increases with nutrient level (e.g., Sarnelle 1992). The simple models employed in the original paradox of enrichment papers (Rosenzweig 1971, Gilpin 1972) have a strictly vertical predator nullcline, and thus predict that the algae should not increase with enrichment.

In this paper we show that the relative stability of natural *Daphnia*–algae systems and the increase of grazed algae with enrichment can be accounted for by the classical minimal models if we allow for a simple spatial structure. We assume that *Daphnia* occupies only part of the total volume and that the algae diffuse between the grazed and the ungrazed part.

Indeed, spatial aggregation seems to be the rule rather than the exception in lake zooplankton. The animals are often concentrated in dense swarms (e.g., Kuenne 1925, Colebrook 1960, Klemetsen 1970, Johnson and Chua 1973, Malone and McQueen 1983, Jakobsen and Johnsen 1988). In addition, zooplankton in deep lakes usually exhibit diel vertical migration, concentrating in deep water layers during daytime and at the surface during night (e.g., Gliwicz 1986). In shallow lakes, a similar diel migration is found. During daytime the animals concentrate in vegetation stands, and at night they swim out to the adjacent open water (Timms and Moss 1984, Schriver et al. 1995).

With respect to food competition, aggregation should be unfavorable. Indeed, it has been shown that in zooplankton swarms algal densities can be considerably reduced (Tessier 1983, Jakobsen and Johnsen 1988). Reduction of predation risk is generally considered the reason why the animals nevertheless aggregate. This has been discussed extensively with respect to swarm formation (Heller and Milinski 1979, Jakobsen and Johnsen 1987, 1988, Young et al. 1994), as well as with respect to the diel migration to deep water (Gliwicz 1986, Leibold 1990, Loose and Dawidowicz

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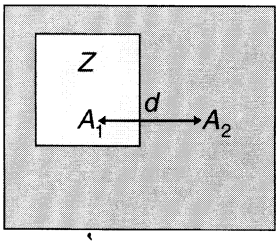

FIG. 1. The spatial configuration represented in the model. Zooplankton (Z) is confined to one part of the space. Their algal food (A_1 and A_2) grows over the whole volume, and diffuses (d) between both compartments.

TABLE 1. Parameter values and dimensions for the full model (Eqs. 1–3). Algal growth is (r and K) parameterized for a euthrophic system (Harris 1986). Values for zooplankton parameters (e, g, h, and m) are chosen in the middle of the literature range for *Daphnia* given by Rose and Swartzman (1988). Densities of zooplankton (Z) and algae (A) are in milligrams dry mass (DM) per litre.

r	0.5	day^{-1}
K	10	mg DM/L
e	0.6	
g	0.4	day^{-1}
h	0.6	mg DM/L
m	0.15	day^{-1}

1994) and vegetation refuges (Timms and Moss 1984, Schriver et al. 1995).

Although the specific spatial structure that we propose has not been analyzed before, many models have shown a stabilizing effect of partial isolation of habitat patches on predator–prey dynamics (e.g., Gurney and Nisbet 1978, Nisbet et al. 1989). Other models have been formulated to show that consumer–prey oscillations can be stabilized if the consumers aggregate in patches with high food levels (e.g., Hassel and May 1974). Stabilization can also be achieved by limiting the speed of movement of individuals in individual-based, spatially explicit, predator–prey models (De Roos et al. 1991). All of these mechanisms are in fact closely related. The space outside the patches where the predator is concentrated can be considered a "partial refuge" where predation pressure is low. This also holds for the model developed in this paper.

MODEL

We consider a volume, e.g., a lake, consisting of two hypothetical compartments (see Fig. 1). The predator (*Daphnia*) is only present in one compartment, while the prey (algae) is present in both compartments. We define f to be the fraction of the total volume that is inhabited by *Daphnia* and assume a passive flow d (expressed as a fraction of the total volume per day) to cause an exchange of algae between the two compartments. Algal growth is logistic with a maximum growth rate r and carrying capacity K. And the consumption of algae by *Daphnia* is described by a standard type 2 functional response (e.g., DeMott 1982). Thus, for the algae in the grazed compartment we write:

$$\frac{dA_1}{dt} = rA_1\left(1 - \frac{A_1}{K}\right) - gZ\frac{A_1}{h + A_1} + \frac{d}{f}(A_2 - A_1), \quad (1)$$

where g is the maximum grazing rate, and h is the half-saturation constant of the Monod function; for the algae in the ungrazed compartment:

$$\frac{dA_2}{dt} = rA_2\left(1 - \frac{A_2}{K}\right) + \frac{d}{(1 - f)}(A_1 - A_2), \quad (2)$$

and for the zooplankters:

$$\frac{dZ}{dt} = egZ\frac{A_1}{h + A_1} - mZ, \quad (3)$$

where e is the efficiency at which the predator converts food into growth, and m is the rate of mortality plus respiration. The default parameter values were chosen to represent a eutrophic *Daphnia*–algae system. Values, sources, and dimensions are listed in Table 1.

RESULTS

Stabilizing effect of patchy consumers.—The behavior of the model strongly depends on the fraction of the volume f occupied by zooplankton and the exchange d of algae between the two compartments (Fig. 2). If the consumer compartment is completely isolated, i.e., $d = 0$, A_2 remains at its carrying capacity, while A_1

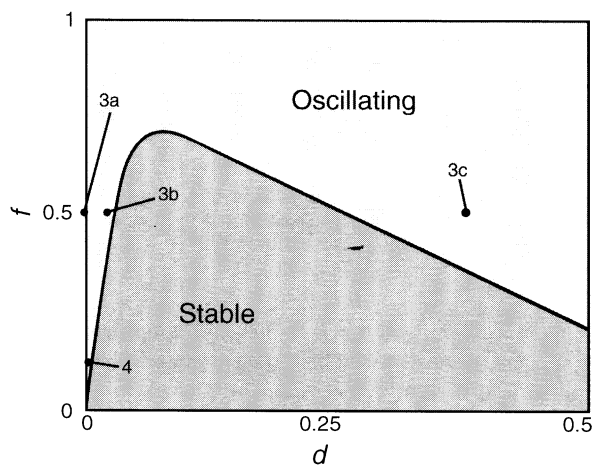

FIG. 2. A two parameter continuation of the Hopf bifurcations with f and d as bifurcation parameters. The curve defines the borderline in parameter space between oscillatory and stationary behavior. The steady state is stable when the grazed fraction f is sufficiently small and the exchange rate d is intermediate. Stabilization becomes increasingly difficult if the consumer occupies a larger part of space. The parameter settings for which the behavior is shown in Figs. 3a–c and Fig. 4 are indicated.

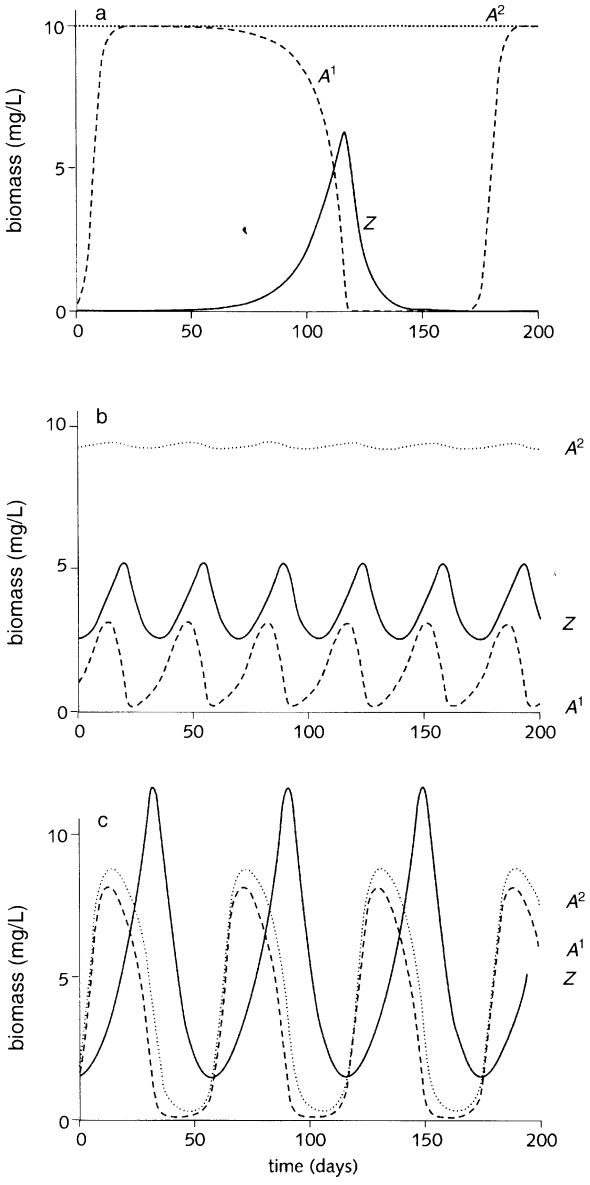

FIG. 3. Time plots showing the behavior of the models for the parameter settings indicated in Fig. 2. Parameters: $f = 0.5$ and $d = 0.0$, 0.02, and 0.4 for panels a–c, respectively.

and Z are involved in a stable high-amplitude limit cycle. Increasing the exchange rate d stabilizes the system (for sufficiently low values of f), i.e., at a critical value of d the limit cycle disappears through a Hopf bifurcation. Increasing d further, however, leads to a second Hopf bifurcation at which the behavior becomes oscillatory again. This destabilization can be understood as a result of the fact that the system approaches the nonspatial limit case of a well-mixed system again.

Fig. 3 shows the behavior of the model for various points indicated in the parameter space of Fig. 2. If the compartments are completely isolated ($d = 0$) we find the unnaturally high amplitude limit cycles that are

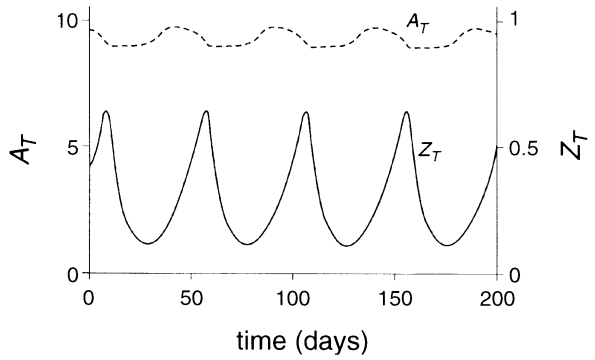

FIG. 4. Time plot showing the dynamics of the concentrations of zooplankton (Z_T) and algae (A_T) averaged over space when the flow and the grazed fraction are small, i.e., $d = 0.001$ and $f = 0.1$. Zooplankton oscillates while their algal food stays practically constant.

characteristic for the classical predator–prey models with a type 2 functional response (Fig. 3a). The period of the limit cycle is long due to the slow recovery from near extinctions. A slight increase of the flow rate (Fig. 3b) stabilizes the system: the amplitude and the period of the limit cycles are reduced. Driven by an oscillatory influx A_2 now oscillates also. A further increase of the exchange between the two compartments leads the system through a Hopf bifurcation to a stationary state (see Fig. 2). Increasing the flow rate even further leads to destabilization again. Due to the high mixing rate, the dynamics of A_1 and A_2 become increasingly alike. Zooplankton reaches high densities in this situation due to the inflow of extra food from the other compartment (Fig. 3c).

Oscillating consumers of stable prey.—In addition to oscillatory and stationary behavior, McCauley and Murdoch in their review of *Daphnia* dynamics (1987) report a rather elusive pattern termed "single species oscillations." In this case zooplankton densities oscillate whereas the densities of edible algae remain practically constant. To see how this pattern can be understood from our model, we have to consider the effect of sampling. Biologists usually describe the dynamics of natural populations by sampling at various points at a lake, and averaging the samples. In the model we can do the same by studying the population densities averaged over the total volume:

$$A_T = fA_1 + (1 - f)A_2, \quad \text{and} \quad Z_T = fZ. \quad (4a, b)$$

The conditions that give rise to the "single species oscillations" can be inferred easily. If the grazed fraction f is small, i.e., $A_T \simeq A_2$, oscillations of *Daphnia* will hardly affect the overall algal density. In order to maintain the oscillatory behavior of zooplankton in that case, exchange d needs to be small too (see Fig. 2). A simulation (Fig. 4) confirms this almost trivial explanation for the mysterious behavior reported by McCauley and Murdoch (1987). Indeed, this explanation is supported by observations in stock tanks where a

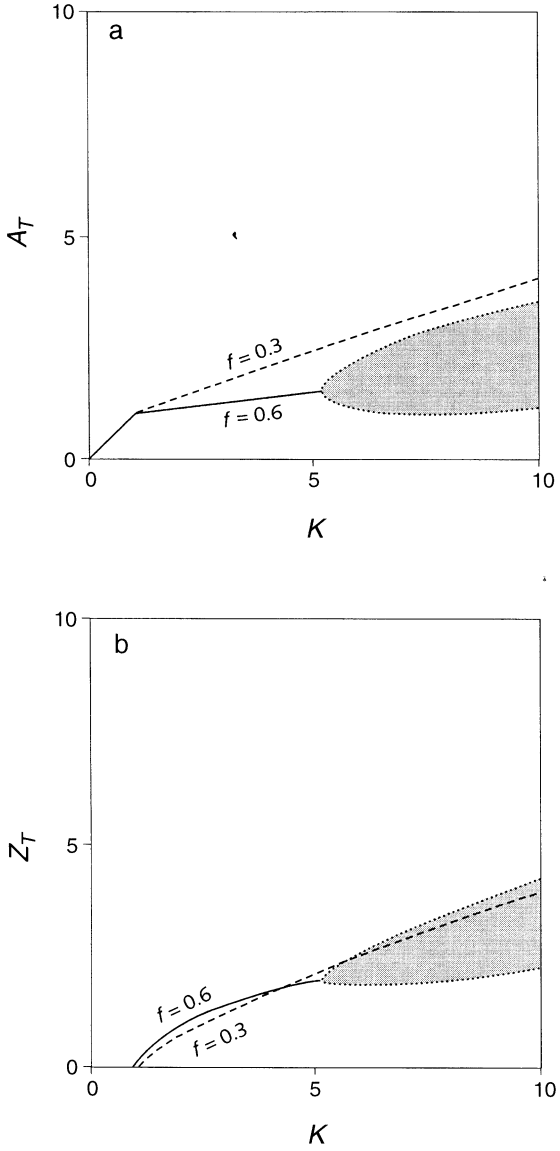

FIG. 5. Response to enrichment of the space-averaged equilibrium density of algae A_T (a) and zooplankton Z_T (b) for $d = 0.2$. In the shaded area the equilibrium is unstable and we plot the amplitude of the limit cycles.

cloud of aggregated *Ceriodaphnia* showed strong oscillations apparently due to local depletion of algae, whereas the algal biomass in the rest of the tank was hardly affected (E. McCauley, *personal communication*).

Response to enrichment.—We study the effect of enrichment on our model by plotting algal and *Daphnia* densities as a function of the carrying capacity K (Fig. 5). For very low values of K the algal equilibrium density is too low to sustain zooplankton, and the algal equilibrium density traces the carrying capacity. In the presence of *Daphnia*, i.e., beyond the transcritical bifurcation, algal densities modestly increase with enrichment. This "intermediate control" of algae by *Daphnia* is indeed what is observed in most field data and laboratory experiments (Sarnelle 1992, Watson et al. 1992; W. W. Murdoch et al., *unpublished manuscript*). Fig. 5 also illustrates that, while enrichment can destabilize the system, the amplitude of the cycles remains limited.

Behavior of a cascade of systems.—Arditi and colleagues (Arditi et al. 1991, Arditi and Saïah 1992) recently conducted a set of experiments with heterogeneously distributed zooplankton to provide evidence for a ratio-dependent functional response. Their interpretation has been criticized because the results can also be explained with a classical functional response if the heterogeneity is accounted for (Abrams 1994). Here, we show that the experimental results strongly support our model.

The experiments involved a cascade of five containers in which cladocerans fed upon algae. From each container there was a flow of water with algae to the next container. The first container received water with algae from a reservoir. Each container was seeded with zooplankters. Depending on the experimental setup, zooplankters were either distributed uniformly or heterogeneously. The prediction of the classical predator models is that, if zooplankters are distributed uniformly, the zooplankters in the first container will equilibrate at such a level that the outflow of algae from that container is too low to sustain zooplankters in the next container. In the uniformly distributed cases the experiment confirmed this classical prediction. However, when the zooplankters were unevenly distributed, they were found in all five containers (Arditi et al. 1991, Arditi and Saïah 1992). The latter is consistent with the prediction from the ratio-dependent model that zooplankton equilibrium density Z^*_i should decrease geometrically with the rank number i of the container:

$$Z^*_1 > 0, \text{ and } z^*_{i+1} = \alpha z^*_i, \text{ for } i = 2, 3, \ldots, 5 \quad (5)$$

with $\alpha < 1$.

The experimental setup is easily mimicked by our model. Adding the flow of algae between the containers we employ our Eqs. 1–4 for modeling one container. Thus for the five containers we write for the total algae in container i

$$A_{Ti} \equiv fA_{i1} + (1 - f)A_{i2}, \quad (6)$$

for the algal population in the grazed compartment

$$\frac{dA_{i1}}{dt} = rA_{i1}\left(1 - \frac{A_{i1}}{K}\right) - gZ_i\frac{A_{i1}}{h + A_{i1}} + \frac{d}{f}(A_{i2} - A_{i1}) + s(fA_{Ti-1} - A_{i1}), \quad (7)$$

for that in the ungrazed compartment

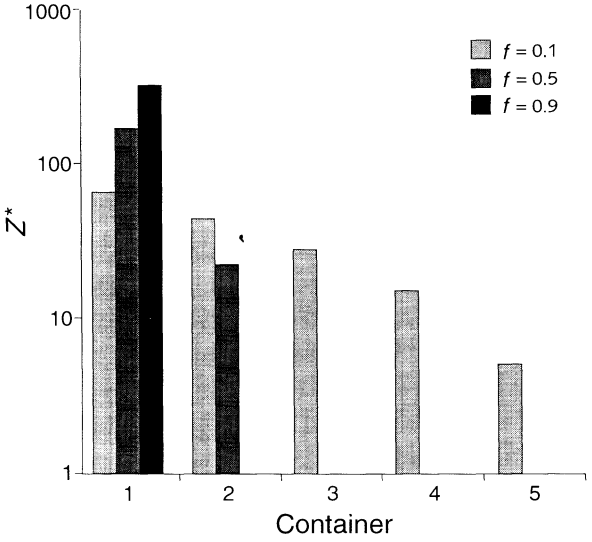

FIG. 6. Equilibrium densities of zooplankton (Z) produced our model describing the dynamics in a cascade of five containers (Eqs. 6–9). The first container receives a constant inflow of algae. A continuous flow transports algae but no zooplankters to the subsequent containers. If zooplankton occupies only a small fraction of the volume in each container ($f = 0.1$), zooplankton survive in all containers. If the animals employ a large fraction of the volume, i.e., $f = 0.5$ or $f = 0.9$, zooplankton populations go extinct in the later containers.

$$\frac{dA_{i2}}{dt} = rA_{i2}\left(1 - \frac{A_{i2}}{K}\right) + \frac{d}{1 - f}(A_{i1} - A_{i2}) + s[(1 - f)A_{Ti-1} - A_{i2}], \tag{8}$$

and for the zooplankters

$$\frac{dZ_i}{dt} = egZ_i\frac{A_{i1}}{h + A_{i1}} - mZ_i, \tag{9}$$

where $i = 1, 2, \ldots, 5$. Here A_0 is the concentration of algae in the reservoir and s is the flow rate between the containers. For the simulations we choose $A_0 = 10$, $s = 10$, and $d = 0.2$.

Fig. 6 demonstrates that the model results are exactly in line with the experimentally obtained patterns. For $f = 0.9$, i.e., a system with a largely uniform distribution of zooplankters, we only find zooplankters in the first container. For $f = 0.1$, i.e., a system in which the grazed fraction is small we find zooplankters in all containers. Additionally, we confirm Eq. 5b because $Z^*_i \simeq \alpha Z^*_{i-1}$. For intermediate values, e.g., $f = 0.5$, we find zooplankters in the first two containers only. Note that the exact values of f at which we find these different distributions depend on the other parameter values, which could thus be used to fit the results to the data.

SIMPLIFICATION

In this section we study how the spatial effects that we are interested in can best be represented in a minimal model of two differential equations. Our approach is based upon a quasi steady-state assumption for A_2, i.e., the algae in the ungrazed compartment. The full solution of Eq. 2 is

$$A_2^{\pm} = \frac{\beta \pm \sqrt{\beta^2 + (1 - f)4rKdA_1}}{2r(1 - f)}, \tag{10}$$

where $\beta = K[r(1 - f) - d]$. Because $1 - f > 0$ the square-root term is larger than β. Hence, only the A_2^+ solution is positive and physically meaningful.

Two Taylor approximations.—The above solution is obviously too complex to be attractive for use in a minimal model. We therefore approximate Eq. 10 by a Taylor expansion for small values of d. For $d = 0$ its first- and second-order approximations are

$$A_2 = K, \tag{11a}$$

and

$$A_2 = K - \frac{d}{r(1 - f)}(k - A_1), \tag{11b}$$

respectively. Eq. 11b is physically meaningful when $A_2 > 0$ only. Because $1 - f > 0$ this is most critical when $A_1 = 0$. For $A_1 = 0$ we solve

$$K\left(1 - \frac{d}{r(1 - f)}\right) > 0 \tag{12a}$$

to obtain

$$f < \frac{r - d}{r}, \tag{12b}$$

as a parameter constraint for the validity of Eq. 11b. In fact, Eq. 12b defines a transcritical bifurcation at which the equilibrium value of A_2 with $A_1 = 0$ becomes negative.

The two forms of Eq. 11 can be substituted into the growth equation of A_1 (Eq. 1) to reduce the model to two differential equations for the total system. The first-order approximation, i.e., $A_2 = K$ (Eq. 11a), assumes that A_2 is not affected by the leakage to the grazed compartment. Eq. 11b has a leakage term that increases when A_1 is small, i.e., when the difference between the algal concentrations in the two compartments is large.

Immigration model.—Because the effect of diffusion on the growth of A_1 is largest when A_1 is small we can simplify further by ignoring the outflow from the grazed compartment which is negligible in that situation. Thus, we substitute $A_2 = K$ and $A_1 = 0$ in the diffusion term of Eq. 1 and write for the growth of the algae in the grazed compartment

$$\frac{dA_1}{dt} = A_1\left(1 - \frac{A_1}{K}\right) - gz\frac{A_1}{h + A_1} + \frac{Kd}{f}, \tag{13}$$

where Kd/f plays the role of an independent immigration term. A predator–prey model with immigration that is identical to our Eqs. 3 and 13 was devised and analyzed before by May (1977).

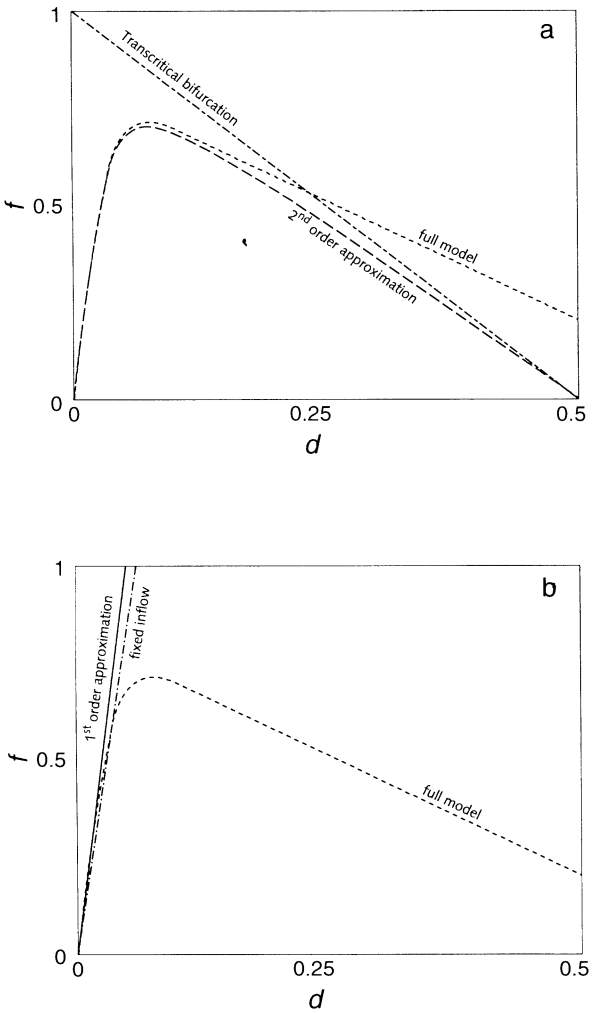

FIG. 7. Two parameter continuations of the Hopf bifurcations of the simplified models. (a) The second-order approximation of Eq. 11b with that of the full model. The diagonal line is the parameter constraint defined by Eq. 12b. The second-order approximation becomes negative above this line. (b) The first-order approximation of Eq. 11a, the migration model of Eq. 13 with that of the full model.

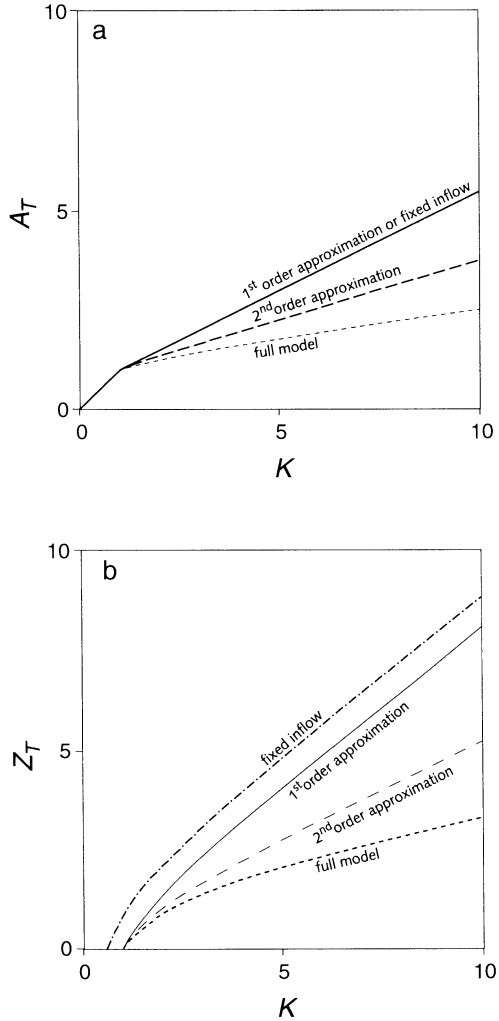

FIG. 8. Response to enrichment of the space-averaged equilibrium density of algae A_T (a) and zooplankton Z_T (b) for the three simplified models as compared to the response of the full model ($f = 0.5$ and $d = 0.2$).

IMPLICATIONS OF SIMPLIFICATIONS

One way to study the effects of the simplifications on the model behavior is to apply the same bifurcation analysis that we used for the full model. The two parameter continuation of the Hopf bifurcation of the second-order approximation (Eq. 11b) closely mimics that of the full model (see Fig. 7a). However, for high values of d the Hopf bifurcation occurs very close to the parameter constraint defined by Eq. 12b. This is not surprising as the Taylor approximation is only valid for small values of d.

With respect to the other simplifications we have to restrict ourselves to small values of d, i.e., to compartments that are not well mixed. In this parameter region, the Hopf bifurcation occurs for very similar values of f and d in the full model, the first- (Fig. 7b) and second- (Fig. 7a) order approximation, and in the immigration model (Fig. 7b). Thus, for systems with compartments that are not well mixed, the usage of either simplification seems reasonable.

With respect to the paradox of enrichment, we again employ Eq. 4a, b to average over the total volume. In Fig. 8 the densities A_T and Z_T are calculated from our various simplifications. (Here we only have stable equilibria because $f = 0.5$, cf. Fig. 5.) As in the full model, the response of algal biomass to enrichment is modest. There are, however, quantitative differences between results of the different models. The degree of grazer control appears to be especially affected by the simplifications. The stronger our simplification the weaker the control of algae by *Daphnia* (Fig. 8a). This makes sense because the indirect repercussion of grazing on A_2 becomes increasingly weak when we simplify.

Discussion

Our analysis suggests that a patchy distribution of zooplankton can explain two major discrepancies between the patterns observed in nature and the behavior of classical prey–predator models (see the *Introduction*): (1) natural systems oscillate less than predicted by simple models; (2) algal biomass is reduced by *Daphnia* but still increases with enrichment. In the following discussion we will refer to those deviations as "enhanced stability" and "intermediate grazer control" for short. Since patchy zooplankton distributions are the rule rather than the exception in nature (see the *Introduction*), patchiness seems to be a good explanation for the observations. However, several other mechanisms have been proposed. A detailed review of alternative explanations is presented by W. W. Murdoch et al. (*unpublished manuscript*). We limit our discussion to four alternatives: the presence of inedible algae, fish predation on zooplankton, a sigmoidal functional response, and *Daphnia* interference.

At high nutrient concentrations large inedible species tend to dominate the algal community (e.g., Watson et al. 1992). Obviously, the presence of inedible algae is likely to affect the dynamics of zooplankton and edible algae (Leibold 1989, Sarnelle 1992, Kretzschmar et al. 1993). The effect of the inedible algae can be twofold: (1) they compete for resources with the edible algae, thus lowering the "effective carrying capacity" of the edible algae, and (2) some species reduce the efficiency with which zooplankton can consume the edible algae. Kretzschmar et al. (1993) analyze a model to show that both mechanisms give rise to the enhanced stability and the intermediate algal response. Their results with respect to enrichment are questionable as they do not consider a competitive advantage of inedible algae under eutrophic conditions which is likely to cause the observed switch to inedibles in real lakes (M. Scheffer et al., *unpublished manuscript*). It seems likely, however, that the presence of inedible algae contributes to the stability of *Daphnia* populations in eutrophic lakes where inedible algae are abundant.

Predation on *Daphnia* by fish can also stabilize *Daphnia*–phytoplankton dynamics (Scheffer 1992), and explain the intermediate response of edible algae to enrichment (Gatto 1991, Scheffer 1992). Interestingly, the reduction of predation risk is precisely the reason why zooplankton concentrates in patches (see the *Introduction*). Thus, fish may be expected to cause those patterns not only by consuming *Daphnia*, but also by increasing *Daphnia* patchiness.

Stability is greatly enhanced by using a sigmoidal functional response (Holling's type 3 response) rather than a simple saturating one. This has been considered a proper solution to account for the stabilizing effect of "partial" and "real" refuges of the prey (e.g., Begon et al. 1986). Indeed, the nullclines of our simplifications are very similar to those of a model with a sigmoidal functional response (not shown). However, since careful measurements of *Daphnia* functional responses show a simple Holling type 2 response (e.g., DeMott 1982), it seems awkward to tamper with these experimental results just to account for the desired behavior.

With respect to grazer interference, it is clear that any form of additional (i.e., direct) competition among *Daphnia* changes the vertical grazer nullcline. This can account for the enhanced stability as well as the intermediate algal response. Grazer interference (mostly termed "predator interference") can either be incorporated by modeling direct interactions between the animals (Rosenzweig 1971, Gilpin 1972) or by using a grazer-dependent functional response (Beddington 1975, DeAngelis et al. 1975, Ruxton et al. 1992, Abrams 1994). A special case of grazer dependence is a ratio dependent functional response (Arditi and Ginzburg 1989). Predator dependence has to our knowledge never been observed in *Daphnia*–algae interactions, but it is unclear how carefully it has been looked for. W. W. Murdoch et al. (*unpublished manuscript*) show that a predator-dependent functional response could reasonably account for observed *Daphnia*–algae dynamics.

Thus, we reject the use of a sigmoid functional response, but acknowledge that several mechanisms besides patchiness may contribute to the observed patterns. Although enhanced stability is observed in stock tanks in the absence of inedible algae or fish (W. W. Murdoch et al., *unpublished manuscript*), and *Daphnia* interference has not been observed yet, these mechanisms cannot be ruled out in general, as they may prove important in other circumstances. Unfortunately, distinguishing between alternative explanatory mechanisms on the basis of field data is extremely difficult (Quinn and Dunham 1983, Roughgarden 1983, Scheffer and Beets 1994). The above mechanisms will often act in concert in lakes and, as Quinn and Dunham (1983) note, "it is not possible to perform 'critical tests' to distinguish between the 'truth' of processes occurring simultaneously." However, in view of the fact that zooplankton are rarely distributed homogeneously, we think patchiness is both a simple and a strong candidate for explaining the enhanced stability and the intermediate algal response to enrichment.

Acknowledgments

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