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PLANKTON ABUNDANCE AND DYNAMICS ACROSS NUTRIENT LEVELS: TESTS OF HYPOTHESES

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Abstract. In lakes and reservoirs in which *Daphnia* is able to suppress the biomass of edible algae far below the level set by nutrients, the interaction is stable across the range of nutrient-poor to nutrient-rich environments. This phenomenon contradicts standard consumer–resource models, which predict that dynamics should become increasingly unstable with enrichment. We test four hypotheses that might account for stability at high-nutrient levels: (1) greater abundance of inedible algae with enrichment interferes with *Daphnia*'s feeding; (2) *Daphnia*'s death rate increases with enrichment; (3) *Daphnia*'s death rate increases with *Daphnia* density; (4) *Daphnia*'s functional response depends on *Daphnia*'s density. All hypotheses are rejected because they predict much higher biomass of edible algae at high-nutrient levels than is observed. Additional evidence on *Daphnia* death rates strengthens the case against hypotheses (2) and (3). We consider other hypotheses and conclude that three in particular would repay further investigation. (a) Inedible algae act as a nutrient "sponge," reducing the effective carrying capacity for edible algae; (b) limited spatial movement can enhance stability through a metapopulation-like effect, and (c) stochastic variation among individuals can be stabilizing. The central problem investigated here is a general one, with implications for many consumer–resource systems.

Key words: Daphnia; freshwater; models; paradox of enrichment; plankton; population dynamics.

Introduction

This paper concerns the following mismatch between theory and real systems. Most simple consumer–resource (i.e., predator–prey) models predict extreme instability when the prey population is in a nutrient-rich environment but is suppressed far below the carrying capacity by the predator. This is sometimes called "the paradox of enrichment" (Rosenzweig 1971, Gilpin 1972). Instability is especially marked in Lotka-Volterra-type models, embodying a tension between a stabilizing process in the prey population (e.g., density-dependent growth) and a destabilizing process in the predator population (e.g., a time lag or a type 2 functional response). The result is large-amplitude cycles in which the prey is periodically suppressed by the predator to extremely low densities and then "escapes" to its carrying capacity before the predator catches up and suppresses it again. In contrast with theory, many real prey populations fail to show the predicted instability. They are continuously suppressed by their predators far below the limits set by their resources, yet show little fluctuation in density. Examples are common in both natural insect populations and those under biological control (Murdoch 1994). Much of the history of predator–prey modeling can be seen as attempts to complicate models in ways that damp instability and

hence mimic well-regulated real populations. The list of potential complications, e.g., switching predators, aggregation, physical refuges, and spatial heterogeneity, is extensive, even if we have few well-documented demonstrations of how any one mechanism actually regulates a particular population.

We use the interaction between *Daphnia,* a freshwater zooplankter, and its algal food supply to explore this dilemma. The *Daphnia*–algal system is ideal in several ways. First, planktonic communities have been viewed as likely exemplars of the paradox of enrichment (Rosenzweig 1971, McAllister et al. 1972). Second, *Daphnia* is one of the best-studied organisms in ecology at all levels from physiology to population ecology (McCauley and Murdoch 1987, McCauley et al. 1990), and we have developed a model of individual *Daphnia* energetics that provides a sound basis for parameterizing individual-based population models (Gurney et al. 1990). Third, there is strong evidence that the dynamics in many field situations result from the predator–prey interaction between *Daphnia* and algae and not from interactions with other components of the community (McCauley and Murdoch 1987). Fourth, we have done experiments in simple mesocosms (stock tanks) that allow us to look at the system's dynamics in the absence of many of the complications that have been offered as explanations for stability, such as predators of *Daphnia* and spatial refuges for the prey. The dynamics in the tanks appear congruent with those seen

in natural systems (McCauley and Murdoch 1987, 1990).

Our emphasis here is different from many previous analyses of planktonic systems, which have largely been concerned with a different inconsistency between theoretical and real populations (Oksanen et al. 1981, McCauley et al. 1988, Leibold 1989, Sarnelle 1992), namely that Lotka-Volterra-like theory predicts that edible algal biomass should not increase as nutrient levels increase, whereas in real systems edible algal biomass has been observed to increase, albeit weakly (Watson and McCauley 1988, Watson et al. 1992). The issue of edible biomass is key to our analysis, however, because we require hypotheses seeking to explain stability to be consistent with the observed low edible biomass at high-nutrient levels.

Daphnia can be prevented from suppressing edible algae by its own predators. We concentrate, therefore, on systems in which there is little predation on *Daphnia.*

The paper is organized as follows. The next section summarizes field data on stability and edible algal biomass in relation to nutrient levels. We then present four hypotheses that compete to explain stability. In that section we describe a Basic Model lacking the hypotheses, a set of simple modifications incorporating the hypotheses, and the predictions that flow from them. The next section describes tests of the hypotheses. The Discussion evaluates the hypotheses, explores alternatives, and broadens the context.

The four hypotheses tested are among the main explanations offered either for the increase in edible algal biomass with enrichment or for stability. They are: (1) greater abundance of inedible algae with enrichment interferes with *Daphnia*'s feeding; (2) *Daphnia*'s death rate increases with enrichment; (3) *Daphnia*'s death rate increases with *Daphnia* density; and (4) *Daphnia*'s functional response depends on *Daphnia*'s density. We also discuss several hypotheses we are not able to test. Several seem quite strong candidates—for example hypotheses 8 and 9, below. These other hypotheses are: (5) element recycling sequesters some of the "excess" nutrients, (6) *Daphnia* has a type 3 functional response, (7) *Daphnia* has an alternative food source, (8) inedible algae act as a sponge for "excess" nutrients, (9) spatial heterogeneity and/or "environmental stickiness" stabilizes the interaction, (10) *Daphnia*'s physiology changes at low-food levels, and (11) stochastic variation among individuals is stabilizing. Even this list, though long, is of course not exhaustive, but it includes those hypotheses that have been given serious consideration.

The logic of the paper is as follows. (1) At low nutrient levels, both the real and the Basic Model populations are "stable" (more formally: the model equilibria are stable), and the model also correctly predicts edible algal abundance. Thus the simplest model appears to be a good descriptor of the observed abundance

and dynamics at low nutrients. (2) As nutrients increase, real populations remain stable, but model equilibria become unstable. The model is therefore wrong. (3) Versions of the model that incorporate each of the four tested hypotheses can yield stable equilibria at the higher nutrient levels, but only when the models have parameter values that yield unrealistically abundant edible algae. These variants must therefore also be wrong. We explore other processes that might be able to retain the ability of the Basic Model to get edible algal abundance correct over a broad range of nutrient levels and, at the same time, account for stability at high-nutrient levels.

The Problem

Field observations

Daphnia's ability to ingest algae is largely determined by cell size, and we define edible algae as those species <50 μm in maximum dimension; inedible species are larger (Burns 1968, Gliwicz 1977, Porter 1977, McCauley and Briand 1979, Reynolds et al. 1982). (We discuss the distinction between edible and inedible algae, and other issues relating to *Daphnia*'s food supply, in the Appendix.) By "enrichment" we mean an increase in total phosphorus, which is in general the resource limiting algal growth in north-temperate freshwater environments (Dillon and Rigler 1974, Schindler 1977, Smith 1982, McCauley et al. 1989).

In this section we summarize the evidence on the effects of enrichment on the stability and mean density of plankton populations. Before doing so, we note that the populations in our analyses are close to the pure two-trophic-level interaction portrayed in the predator–prey theory under discussion. First, because there is little or no predation on *Daphnia* in these systems, *Daphnia* suppresses the edible algal population far below the limits set by algal resources; for example, *Daphnia* maintained the biomass of algae in stock tank experiments at Santa Barbara at ~1% of the density reached by the algae when *Daphnia* was absent. Second, *Daphnia* in turn exists at the edge of starvation. Thus, while *Daphnia* can attain clutches of 20–40 eggs given ample food, the average clutch size in summer in the experimental and natural populations we discuss was typically <1 egg; even recruitment pulses are driven by average clutches of <2 eggs (McCauley and Murdoch 1987).

Lack of large-amplitude cycles in the face of enrichment.—McCauley and Murdoch (1990) reviewed data from natural environments and showed that the dynamic patterns were remarkably consistent across nutrient levels: stable populations are not restricted to low-nutrient environments and, where algae or *Daphnia* cycle, the small-cycle amplitudes do not increase with nutrient level. The interaction remains stable up to an algal carrying capacity (K) of at least 3 mg carbon/L (Fig. 7, and see Appendix). McCauley and

TABLE 1. Basic Model, equilibria, and stability criterion, and parameters. The parameter values and their derivation are discussed in Nisbet et al. (1991).

Variables	E = Density of edible algae (mg carbon/L)
	D = Density of *Daphnia* (mg carbon/L)
Equations	$dE/dt = rE(1 - E/K) - I_{max}ED/(E + E_h)$
	$dD/dt = eI_{max}ED/(E + E_h) - (m + b)D$
Equilibria	$E^* = E_h(m + b)/(eI_{max} - m - b)$
	$D^* = [r/I_{max}](1 - E^*/K)(E_h + E^*)$
Positive D^* requirement	$K > E_h(m + b)/(eI_{max} - m - b)$
Local stability requirement	$K < E_h(eI_{max} + m + b)/(eI_{max} - m - b)$

Daphnia parameters

Parameter	Value	Interpretation
I_{max}	1 d^{-1}	Maximum intake rate
E_h	0.16 mg C/L	Half-saturation density of edible algae
e	0.5	Assimilation efficiency
b	0.09 d^{-1}	Respiration (maintenance) rate
m	0.03 d^{-1}	Minimum mortality rate in field

Murdoch (1990) also showed that the interaction was not made less stable when nutrients were increased experimentally in stock tank communities.

The small-amplitude cycles sometimes found in *Daphnia* and algal populations have a max/min ratio of ~2–4, and a period comparable in duration to *Daphnia*'s generation time, typically ~30 d (Murdoch and McCauley 1985, McCauley and Murdoch 1987). They are most likely caused by time lags in *Daphnia* development (Nisbet et al. 1989) and are unrelated to the ''paradox of enrichment'' type of instability that concerns us here. The latter produces algal cycle max/min ratios of 10^3–10^9, and periods of 100 d or so, in the range of nutrient levels that interest us. For simplicity, we will refer hereafter to real populations as stable, taking this to include populations showing small-amplitude cycles.

One study (Borgmann et al. 1988) appears to challenge our claim that enrichment does not lead to cycles. They found fluctuating dynamics in enriched large-volume microcosms with edible algae and *Daphnia magna.* However, the algae fluctuated over a wide range of abundance even in the containers without *Daphnia,* i.e., any putative increase in instability with phosphorus loading did not require *Daphnia.* Even in the high-phosphorus population with *Daphnia,* after the initial transient, fluctuations in abundance were small amplitude (approximately fivefold) with a short period (~2 wk) close to that seen in the algae-only population.

Limited increase in algal biomass with enrichment.—We take as our estimate of equilibrium ''prey'' abundance the mean biomass of edible algae (measured as cell volume) in a lake over summer, i.e., over the period following the spring peak and preceding the fall decline. We denote this average by $\langle E \rangle$. Nutrient level, defined as the algal carrying capacity, $K,$ is the maximum potential biomass of edible algae in summer in

the absence of competitors and grazers. Unfortunately it is never measured directly and we estimate it by the maximum biomass of edible algae in spring when zooplankton are rare, except where it was measured directly in summer in stock tanks lacking *Daphnia.* The spring measure gives a minimum estimate (Appendix), which is conservative in the sense of making it harder to reject the hypotheses we will consider.

Watson et al. (1992) analyzed data from >100 lakes in the north-temperate region and showed that $\langle E \rangle$ increases with nutrient level. The increase is small: a factor of only 1.8 over a 10-fold increase in total phosphorus (TP). In contrast, mean inedible algal biomass, *I,* increases sixfold over the same range (Watson et al. 1992). Inedible algae increase from ~0.05 mg carbon/L at $K = 0.3$ mg carbon/L, to almost 0.3 mg carbon/L at $K = 1.2$ mg carbon/L.

Failure of theory

We now illustrate the failure of standard predator–prey theory, using both a simple model and two others that are more realistic, to predict maintenance of stability with enrichment.

Basic Model.—Nisbet et al. (1991) derived, from a consideration of individual energetics, a model of *Daphnia* and edible algae that is a standard Lotka-Volterra-type model with a destabilizing (type 2) functional response and a stabilizing logistic prey. The model variables and equations, together with equations for equilibria, the condition for local stability of the equilibria, and the parameters and their values are in Table 1.

Both *Daphnia* and algal densities are expressed in the common currency of carbon per unit volume (i.e., milligrams carbon per liter). The key assumptions of the model follow. (a) Algal population growth rate in the absence of *Daphnia* is logistic, with intrinsic per
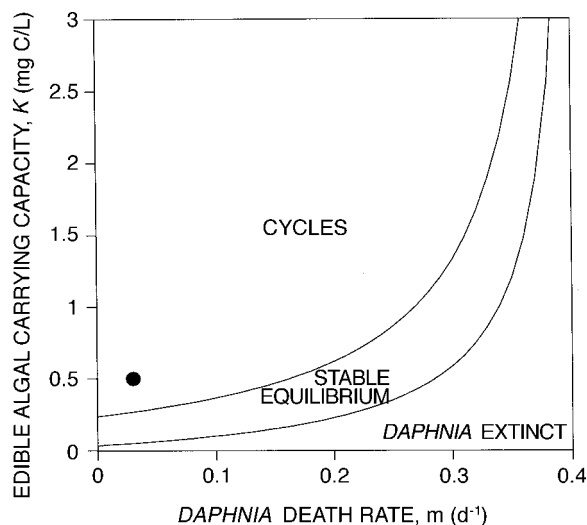
FIG. 1. Stability behavior of the Basic Model in terms of the nutrient level of the environment, K, and $Daphnia$'s death rate, m. K ranges from 0.15 to at least 3 mg C/L in real systems, and m in principle can vary from 0.03 to 0.41 d^{-1}, though the maximum in real systems is likely to be smaller. $Daphnia$ parameter values are in Table 1. Large-amplitude cycles (Fig. 2a) occur throughout most of this parameter space. The point on the graph indicates the origin of the simulations in Fig. 2a.

capita rate of increase, r, and carrying capacity, K. (b) At a given food level, an individual $Daphnia$'s ingestion rate (functional response) is proportional to its carbon content; as food level varies, $Daphnia$'s functional response is type 2, with a half-saturation constant, E_h, which takes the same value for all individuals, irrespective of size (McCauley et al. 1990 and references therein). (c) $Daphnia$ converts food to new $Daph$-

nia biomass with an efficiency, e, that is independent of the nature (eggs or body) of the new biomass. This conversion efficiency takes account of the metabolic costs. (d) The basal metabolic rate of an individual $Daphnia$ is proportional to its carbon content.

Enrichment of the prey environment is defined as an increase in algal carrying capacity, K. As is well known, enrichment of the prey environment rapidly destabilizes the model equilibrium (Table 1), and the Basic Model cannot account for the population stability observed over a wide range of nutrient levels. Fig. 1 shows the dynamical behavior of the model as a function of $Daphnia$ death rate (m) and the nutrient status of the environment (K). Observed values of m range from 0.03 (George and Edwards 1974) to 0.17 d^{-1} (McCauley et al. 1988), and an absolute upper limit of 0.41 is set by $m = eI_{max} - b$ (Table 1). The model predicts unstable equilibria in virtually all of this parameter space. The unstable region is characterized by limit cycles (''paradox of enrichment'' cycles) whose amplitude increases very rapidly as the system passes beyond the stability boundary. For example, even with modest enrichment ($K = 0.5$ mg C/L, $r = 0.5$ d^{-1}), the cycle amplitude (ratio of maximum to minimum density) of the algae is 2.5×10^3 and that of $Daphnia$ is 25 (period 52 d) (Fig. 2a); at still realistic nutrient levels ($K = 1$, $r = 0.5$) these values change, respectively, to 10^9 and 10^3 (period $\sim$100 d).

As is also well known, the model predicts that enrichment increases the predator ($Daphnia$) equilibrium, D^*, but does not affect the prey (edible algae) equilibrium, E^* (Table 1). As noted, it appears that the density of edible algae does increase, although weakly, from nutrient-poor to nutrient-rich lakes.

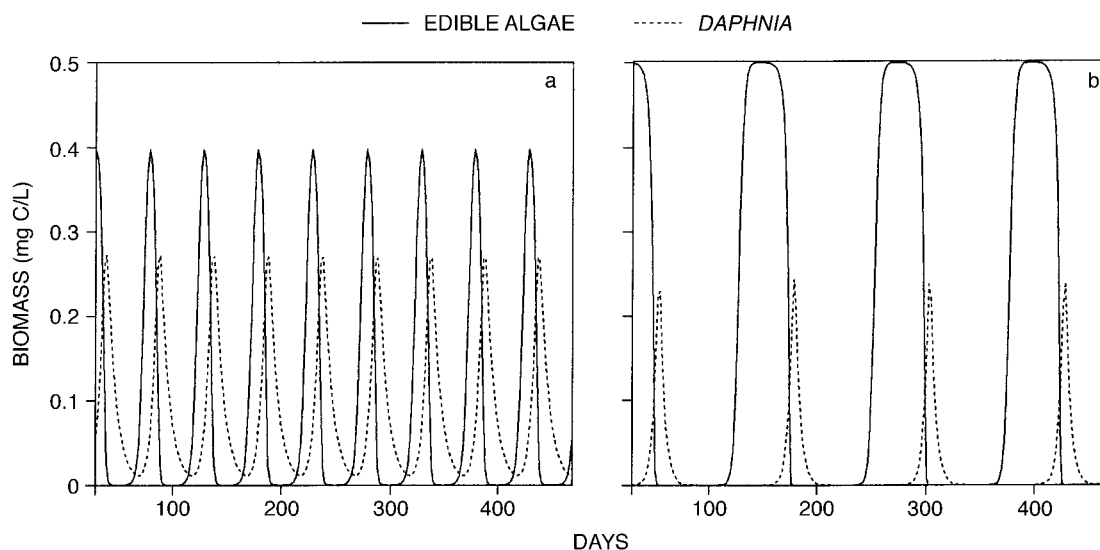*Models with more realistic* Daphnia *physiology.*—

FIG. 2. Simulations of $Daphnia$/algal models with $K = 0.5$ mg C/L and $r = 0.5$ d^{-1}. (a) Simulation of the Basic Model with the $Daphnia$ parameter values in Table 1, at the point indicated in Fig 1. (b) Simulation of the stage-structured model described in Nisbet et al. (1991), with $Daphnia$ parameter values given there.

The basic model makes simplistic assumptions about *Daphnia* energetics. In particular, the assumptions that ingestion and metabolic rates are proportional to size, and that assimilate is converted to *Daphnia* biomass with a fixed efficiency, take no account of the constraints associated with real life cycles. We have developed a stage-structured model (Nisbet et al. 1989) of the *Daphnia*–algal interaction, which is based on more plausible representations of individual energetics and the *Daphnia* life cycle. The model follows the density of *Daphnia* eggs, juveniles, and adults. The model and its dynamic behavior are fully described in Nisbet et al. (1989), and it has successfully predicted the dynamics of laboratory populations of *Daphnia* supplied with nongrowing algae (McCauley et al. 1996).

Adding stage structure, however, does not solve our problems. The model's stability behavior is broadly similar to that of the Basic Model. At the same values of r and K as we used to illustrate cycles generated by the Basic Model, the model also shows large-amplitude and long-period limit cycles (Fig. 2b). Indeed, the larger amplitudes in Fig. 2b relative to those in Fig. 2a suggest that the more realistic model may be even less stable than its simple counterpart since both were parameterized on the basis of the same experimental data. A model of an age-structured *Daphnia*–algal interaction, based on different energetics and rates of development, shows the same generic results (DeRoos et al. 1992). This model also predicts that the equilibrium algal density should not respond to enrichment.

These results suggest that the failure of standard theory to account for the observations lies in the fundamental assumptions, rather than in missing details of *Daphnia* life history. In the remainder of this paper we will therefore use modifications of our Basic Model to test various hypotheses that have been proposed to account for the maintenance of stability with enrichment.

Four Hypotheses and Resulting Predictions

We describe four hypotheses, present a model for each, describe its equilibrium and stability properties, and then develop predictions of the models. All four hypotheses were first proposed as possible explanations for the small observed increase in edible algal biomass with enrichment.

The hypotheses and the models

1. *Inedible algae reduce* Daphnia's *filtering rate.*—McCauley et al. (1988) suggested that the observed increase in edible algal density with enrichment might be caused by a decrease in *Daphnia*'s attack rate, caused in turn by increasing interference with *Daphnia*'s filtering mechanism as the concentration of inedible algae increases. As shown below, this is also a stabilizing process.

This is a feasible hypothesis. First, it is well established that inedible algae increase with enrichment (Watson and McCauley 1988, Watson et al. 1992). Second, McCauley et al. (1988) referred to considerable experimental evidence that inedible algae interfere with *Daphnia*'s food handling and this is supported by more recent evidence (Hawkins and Lampert 1989, Gilbert and Durand 1990).

With the standard interpretation of a type 2 functional response, the effect of reducing filtering rate is to increase the parameter E_h while leaving I_{max} unchanged. We have no empirical basis for defining a relationship between E_h and K, and assume it increases linearly with K, i.e.,

$$E_h = E_{h0} + \alpha K \qquad (1)$$

where E_{h0} is the half-saturation value at $K = 0$. The equilibria are now

$$E^* = (E_{h0} + \alpha K)/(A - 1)$$

$$D^* = [r/I_{max}](E^* + E_{h0} + \alpha K) \qquad (2)$$

where $A = eI_{max}/(m + b)$, with local stability of that equilibrium if

$$K < E_{h0}(A + 1)/[A(1 - \alpha) - (1 + \alpha)]. \qquad (3)$$

Eqs. 2 and 3 show that hypothesis 1 leads to an increase in the region of parameter space in which the equilibrium is stable as well as to an increase in E^*.

In the *Discussion* we examine another way in which inedible algae might stabilize the interaction, namely by taking up nutrients (Kretzschmar et al. 1993). Although it is a likely hypothesis, we do not discuss it here since we could not develop a critical test.

2. Daphnia *death rate increases with enrichment.*—McCauley et al. (1988) also suggested that the observed increase in the density of edible algae with enrichment might result from an increase in *Daphnia*'s death rate with enrichment. The potentially stabilizing effect of increasing *Daphnia* death rate is seen in Fig. 1.

Increased mortality with enrichment could arise from an increase in zooplanktivorous fish populations, and McCauley et al. (1988) provided empirical evidence that *Daphnia*'s death rate is higher in more eutrophic lakes. Persson et al. (1992) suggested that increases in zooplankton mortality in high-nutrient environments could occur as a result of a decrease in the fraction of fish that are piscivorous and hence an increase in zooplanktivorous fish, a pattern they observed in Swedish lakes. However, we concentrate below on systems lacking significant predation on *Daphnia* and, though we know of no mechanism that might produce such an increase in mortality other than predation, here we simply investigate the effect of an increase in death rate without hypothesizing a particular source. We discuss fish predation under *Tests of hypotheses.*

As an aside, it is known that *Daphnia*'s death rate in the laboratory increases at very high food levels. The food concentrations at which this occurs, however, are higher by two orders of magnitude than the edible-algal equilibrial densities experienced by *Daphnia* in

rich environments, and increased mortality associated with high algal densities (as distinct from high-nutrient levels) is not a feasible explanation.

There are no good data from which to derive an empirical relationship between *Daphnia* mortality and level of enrichment, K. Consequently we assume that death rate rises linearly with nutrient level, i.e.,

$$m = m_0 + \beta K \qquad (4)$$

where m_0 is the death rate at $K = 0$. The equation for D^* is unchanged and E^* is now

$$E^* = E_h(m_0 + \beta K + b)/(eI_{max} - m_0 - \beta K - b). \qquad (5)$$

The equilibrium is locally stable if

$$\beta > [(b + m_0)(E_h + K)$$
$$+ eI_{max}(E_h - K)]/K(E_h + K). \qquad (6)$$

Eqs. 5 and 6 establish that hypothesis 3 has a general stabilizing effect, which could have been anticipated from Fig. 1, as well as causing E^* to increase. This model can serve as a simple portrayal of increases in death rate with enrichment owing to increases in the density of zooplanktivorous fish, since fish abundance does not respond to short-term changes in *Daphnia* abundance within a season (Murdoch 1993).

3. Daphnia *death rate is density dependent.*—Density dependence of *Daphnia* vital rates could both stabilize the interaction and lead to increased $\langle E \rangle$ with K. However, although density dependence in the parasitoid attack rate is a common assumption in models of parasitoid–host systems in insects (e.g., Hassell 1978), it has long been rejected by plankton ecologists because there is no known mechanism that would induce density dependence (e.g., Slobodkin 1954).

Recently, density dependence in *Daphnia*'s death rate has been proposed to account for the observed increase in algae with enrichment (Gatto 1991). It is difficult to find evidence for a mechanism that might produce such density dependence. Slobodkin's (1954) evidence for a linear dependence of *Daphnia* density on food level in laboratory populations argues strongly against a mechanism involving *Daphnia* behavior. Gatto (1991) proposed that switching behavior in fish predators of *Daphnia* is a likely mechanism, though Murdoch and Bence (1987) have argued that density-dependent mortality is unlikely to arise from switching in predators of zooplankton. Murdoch and McCauley (1985) and McCauley and Murdoch (1990) showed that stability in nutrient-rich stock tanks did not require predation on *Daphnia*.

Following Gatto (1991), we assume linear dependence of *Daphnia* death rate on *Daphnia* density, and modify the Basic Model accordingly:

$$m = m(0) + \chi D. \qquad (7)$$

Formal analysis of equilibria and local stability for this model have been done by Hainzl (1988). Its dynamical
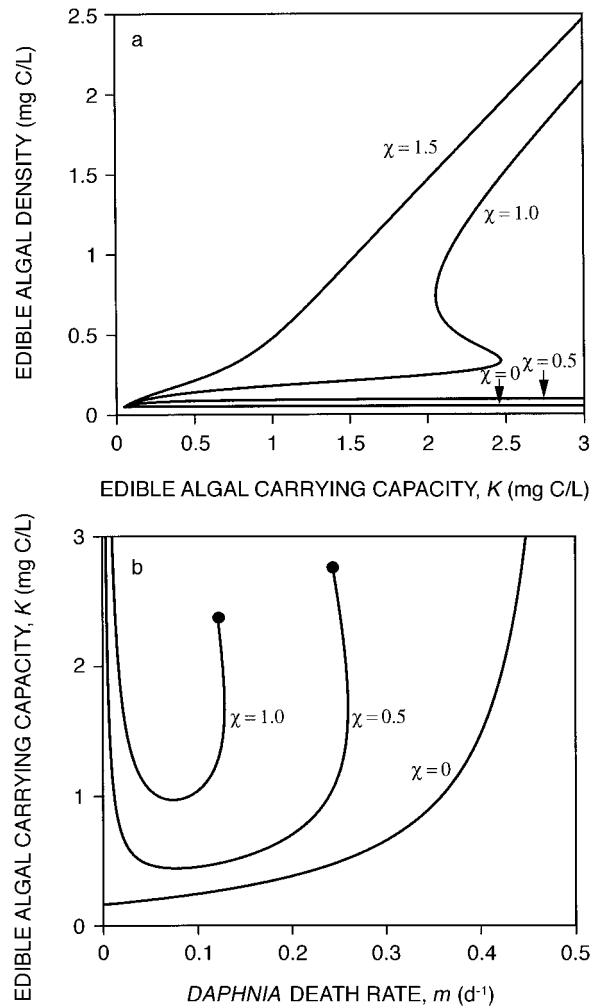

FIG. 3. Equilibrium and stability properties of the model with density-dependent *Daphnia* mortality. Parameter values are in Table 1; χ measures the strength of density dependence. (a) Variation of edible algal density with K for four values of the parameter χ. (b) Local stability boundaries for three values of χ (cf. Fig. 1). The stability behavior of this model is exceedingly complex (Hainzl 1988) owing to the possibility of multiple equilibria; near the points marked ●: one branch of equilibria "bends back" on itself [as in (a) when $\chi = 1.0$], and the diagram is not helpful in characterizing the dynamics.

behavior is complicated, because at large values of K multiple equilibria appear. Fig. 3 illustrates some of the properties that are significant for the present paper.

4. Daphnia *functional response depends on* Daphnia *density.*—Arditi et al. (1991) suggested that a functional response that depends on the ratio of prey to predators can explain both the observed increase in $\langle E \rangle$ and the persistence of stability with enrichment. For the reasons presented in the *Discussion,* we examine here the broader idea of a functional response that depends on the density of the predator rather than on the predator:prey ratio. Dependence on predator density might arise, approximately, if *Daphnia* interfered with
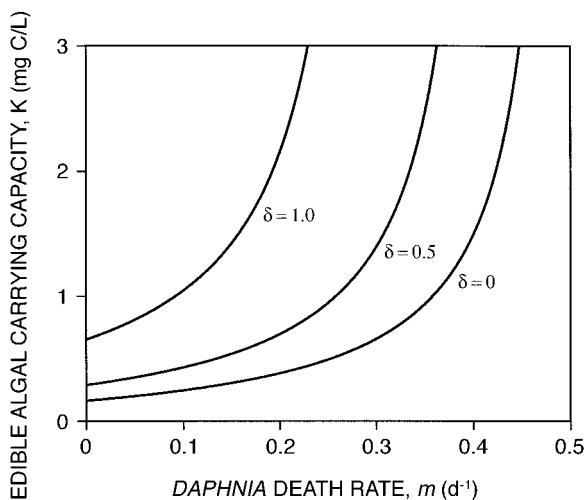
FIG. 4. Stability properties of the model with the functional response dependent on predator density, in terms of the nutrient status of the environment, *K,* and *Daphnia*'s death rate, *m* (cf. Fig. 1). The parameter δ measures the strength of density dependence.
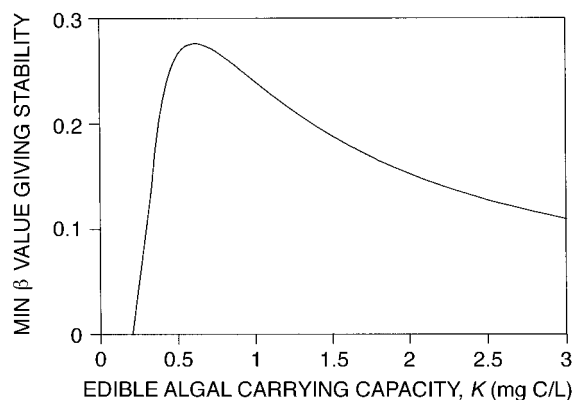

FIG. 5. Minimum value of the free parameter, β, needed for stability in the model when *Daphnia* mortality increases linearly with *K* (Eq. 4). The free parameter has a maximum at an intermediate nutrient level, so that stability at $K = 3$ mg C/L does not ensure stability at intermediate levels of *K*.

each other (Ruxton et al. 1992), though there is no evidence for interference in real *Daphnia.* R. M. Nisbet et al. (*unpublished manuscript*) show predator dependence can arise as an approximation in some circumstances in a model in which prey individuals can move in and out of a physical refuge. Scheffer and DeBoer (1995) have shown similar dynamics in a plankton model.

The form of our predator-density-dependent functional response is due to Beddington (1975). Intake, *I,* is

$$I = EI_{max}/(E + E_h + \delta D). \qquad (8)$$

It can be derived as an approximation by assuming predators interfere with each other, and hence lose time from searching (Ruxton et al. 1992). These authors demonstrate that quite restrictive assumptions or relatively strong approximations are required for interference between predators to lead to precisely Eq. 8. More realistic assumptions lead to a more complex functional response whose effects on stability, however, are similar to those of Eq. 8.

With our assumed form of density dependence, there is only a single equilibrium given by the (positive) root of a cumbersome, and uninstructive, quadratic equation. The local stability analysis is even more cumbersome and does not give a simple formula in terms of *K,* however numerical calculation of stability boundaries from the Routh-Hurwitz criteria is straightforward. Adding this type of density dependence has the expected stabilizing effect: increasing the intensity of interference among individual *Daphnia* (δ) expands the stable region (Fig. 4), with a concomitant increase in ⟨*E*⟩.

Derivation of predictions

All hypotheses can be tested by comparing observed and predicted relationships between ⟨*E*⟩ and *K,* with the constraint that the equilibria must be stable for all *K* values considered. The interaction remains stable up to at least $K = 3$ mg C/L (data in Fig. 7). A procedure for testing each hypothesis, simple in principle, is as follows. (1) Determine the maximum (target) value of *K* for which we know real systems are stable; this is $K = 3$ mg C/L. The hypotheses thus need to explain stability at all nutrient levels up to $K = 3$. (2) Set all parameters to their known values, except for the parameter that defines the "strength" of the mechanism being examined, which is a free parameter. Determine the minimum value of this parameter (i.e., the weakest form of the mechanism) that yields stability at $K = 3$. (3) Calculate the relationship between ⟨*E*⟩ and *K* that is predicted when this minimum parameter value is substituted into the appropriate equation predicting ⟨*E*⟩.

This approach is appropriate for hypothesis 1, but a difficulty arises for the three remaining hypotheses. Nonlinearities in the model cause the minimum value of the free parameter needed for stability to be larger at intermediate values of *K*. Fig. 5 shows the case for *Daphnia* death rate increasing with *K* (hypothesis 3): stability at $K = 3$ can be achieved with $\beta = 0.11$, but stability over the range $0 < K < 3$ requires $\beta = 0.28$.

These nonlinearities create a dilemma. When the free parameter is assigned its peak value, none of the three hypotheses is remotely consistent with the data: they all predict ridiculously high ⟨*E*⟩ values when *K* is > 1. On the other hand, if we assign the value needed to generate stability at $K = 3$, there is always some intermediate range of *K,* for reasonable values of *r,* at which the model exhibits very large amplitude fluctuations (e.g., Fig. 6).

We resolved the dilemma by assigning to the free parameter the minimum value that yields stability at *K*
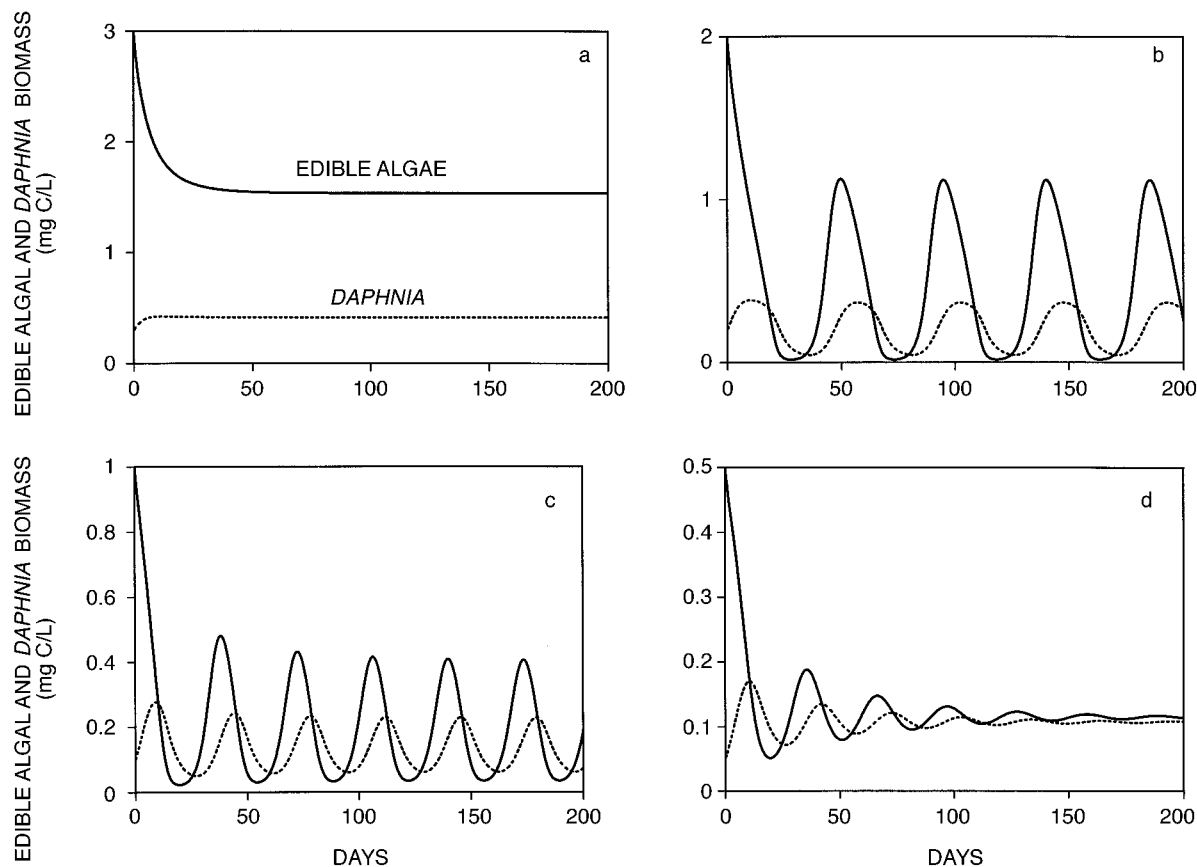
FIG. 6. Simulations of the model with density-dependent *Daphnia* mortality (Fig. 3). The strength of density dependence is determined by the free parameter, χ (Eq. 7), which was set at the value (0.8) that gives stability at $K = 3$ mg C/L. This results in large-amplitude cycles at intermediate values of K. The values of K in (a), (b), (c), and (d) are, respectively, 3.0, 2.0, 1.0, and 0.5 mg C/L.

$= 3$. This is conservative, i.e., it makes it more difficult for us to reject the hypotheses. We illustrate the procedure using hypothesis 1, whose stability criterion is defined in Eq. 3. Substituting $K = 3$ in Eq. 3 gives $\alpha = 0.56$, i.e., α must be ≥ 0.56 to achieve stability up to $K = 3$. From Eq. 2 we then calculate E^* as a function of K, with $\alpha = 0.56$. This gives line 1 in Fig. 7.

The above predictions were generated by adding the hypotheses to the Basic Model. Here we provide justification for using this simple model.

Nisbet et al. (1997) have shown that the Basic Model, parameterized as here from independent experiments on the behavior, physiology, and performance of individual *Daphnia* (Nisbet et al. 1991), is able to predict with good accuracy the equilibrium biomass (but not the detailed stage structure) of *Daphnia pulex* and *D. galeata* in laboratory populations at high- and low-food concentrations. The model was also able to predict both coexistence of *Daphnia* and *Bosmina* and the fact that their dominance in the mixture was reversed between 2-d low-food transfers and 4-d high-food transfers.

Next we turn to the stage-structured model to confirm the robustness of the predictions based on the Basic

Model. McCauley et al. (1996) have shown that the stage-structured model is capable not only of predicting the correct equilibrium biomass, but also the stage structure and detailed dynamics of laboratory populations of *Daphnia galeata*. To compare this model with the Basic Model we used the stage-specific parameter set for *D. pulex* derived in Nisbet et al. (1989).

First, we note that the picture of stability in relation to key parameters is broadly the same for the Basic and stage-structured models (Fig. 8). To the extent that the models differ, there is a *larger* region of unstable parameter space in the stage-structured model. We would expect this, since adding stage structure adds time lags to the consumer population. This implies, for any of the four hypotheses, that it will be at least as difficult to reach a stable equilibrium in the stage-structured model as it is in the Basic Model, and hence that the minimum edible algal equilibrium, for a given value of K, will be *at least* as large in the stage-structured as in the Basic Model. (The stage-structured model also predicts a small region of parameter space in which occur small-amplitude single-generation cycles not seen in the Basic Model. These are tantalizingly like
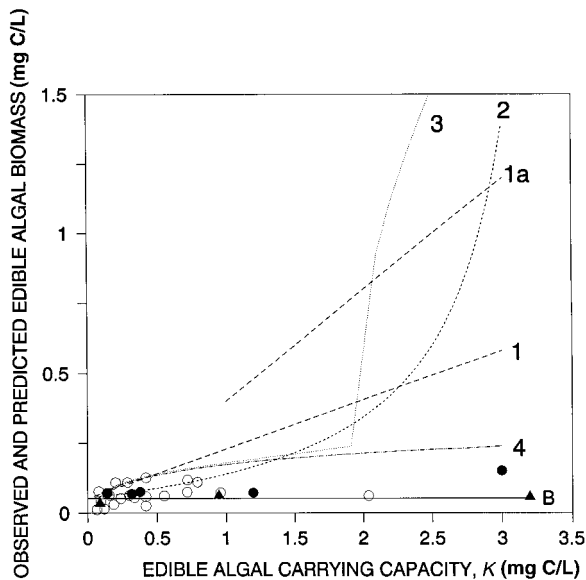
FIG. 7. Predicted equilibrial values of edible algae, E^*, and observed values of average edible algal biomass, $\langle E \rangle$, over a wide range of nutrient levels, K. The observations fall into those used to test the hypotheses (closed symbols) and those used to demonstrate that these observations are consistent with a larger data set ($\triangle$). Among the former, $\blacktriangle$ are data from experimental stock tanks at Santa Barbara and Calgary, and $\bullet$ are from lakes and a reservoir (Appendix). The numbers on the curves correspond to the hypothesis number: (1) E_h increases with K, (2) m increases with K, (3) m depends on *Daphnia* density, and (4) the functional response depends on *Daphnia* density. Line 1a is predicted by the stage-structured model for hypothesis 1. Line B is from the Basic Model.

the cycles seen in the field and mentioned earlier, but we have not yet demonstrated that they are the same.)

We confirmed that the minimum predicted stable edible algal equilibria are at least as large in the stage-structured model by adding hypothesis 1 (filtering rate decreases with K), to this model for values of $K > 1$. At each value of K, we simulated the model for a range of values of the free parameter α in Eq. 1. As expected, oscillations like or larger than those in Fig. 2b are seen for small values of α (i.e., where the stabilizing effect is small). We then calculated the edible algal equilibrium reached when the value of α was just large enough to produce damped oscillations instead of limit cycles. This yielded line 1a in Fig. 7, which confirms that the predicted minimum values for stable equilibria using the Basic Model are certainly not higher than they would be if we used the more detailed model as the test vehicle.

Tests of Hypotheses

In the previous section we noted that a variant of the Basic Model with the independently derived set of parameter values correctly predicted the equilibrium biomass observed in laboratory populations. We can further test the accuracy of the parameter values by asking whether the Basic Model as parameterized can correctly predict $\langle E \rangle$ in oligotrophic environments, where the model equilibrium is stable and none of the four hypotheses operates. The constant value predicted by the Basic Model is $E^* = 0.05$ mg C/L. The estimated values for $\langle E \rangle$ in the most oligotrophic of our four lakes are between 0.05 and 0.09 mg C/L (solid circles, Fig. 7). The lower figure is obtained by assuming a carbon/volume ratio of 0.08, which is likely to be correct in this environment (Appendix). These observations are thus consistent with the model as parameterized.
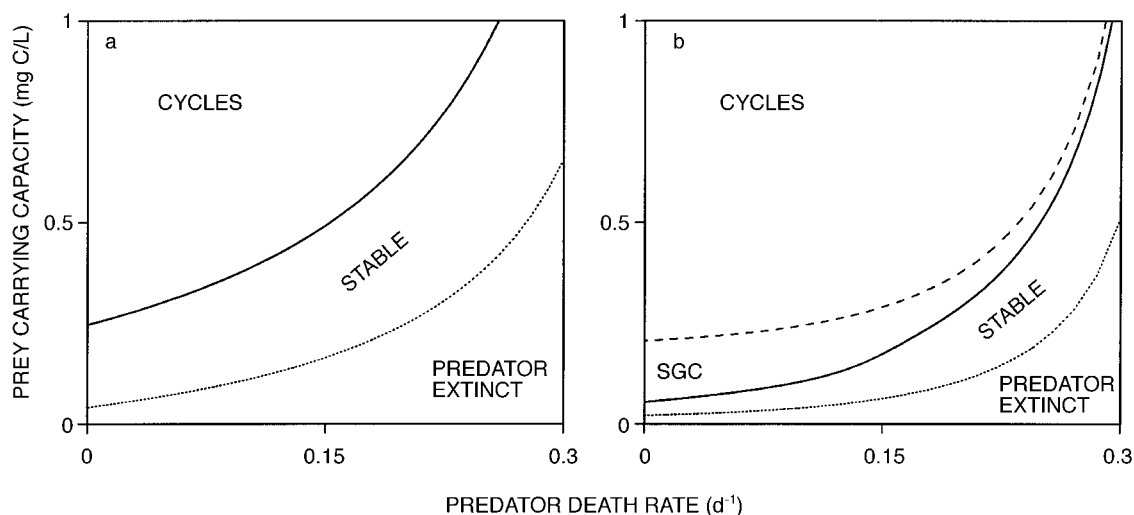

FIG. 8. Comparison of stability properties of (a) the Basic Model and (b) the stage-structured model in terms of the nutrient level of the environment, K, and *Daphnia*'s death rate, m. Cycles with a period approximately equal to a *Daphnia* generation are found in the area marked SGC in (b).

In testing the hypotheses, below, we therefore fix the parameter values and do not allow them to vary as free parameters in examining model fits to the data from nutrient-rich environments. It turns out in any case that the differences between model predictions and data are so large that small variation in parameter values is irrelevant.

We now test the hypotheses by comparing predicted and observed relationships between $\langle E \rangle$ and K. We then use information on *Daphnia* death rate to make further tests and to comment on the potential role of fish predation. The data used to test the hypothesis are only the closed symbols in Fig. 7; the other data (open circles) are discussed later.

$\langle E \rangle$ vs. K: observed vs. predicted relationship

The predictions are constrained by the requirement that the system be stable for $K = 3$. All four hypotheses are rejected by the comparisons between the data (solid symbols) and the predicted curves in Fig. 7. Each curve in Fig. 7 describes the *minimum* edible algal biomass, for each value of K, that is consistent with the requirement that the system be stable at $K = 3$. For K much above 1, these predicted values are all substantially higher than are ever observed. Hypothesis 4, that the functional response depends on *Daphnia*'s density, performs best. However, as noted above, the curve would be much above the data if we required the equilibrium to be stable for the whole range of K between 0.05 and 3. The other three hypotheses are strikingly inconsistent with the data even when we require only that the system be stable at $K = 3$.

The Santa Barbara stock tank data provide an especially useful test. The nutrient level was extremely high ($K = 3.2$) and it is well established that the populations were stable (Murdoch and McCauley 1985). Yet the mean edible algal biomass of these populations was the same as that observed in the most oligotrophic environment and is the value predicted by the Basic Model (line B in Fig. 7). The $\langle E \rangle$ estimated for the very eutrophic Eglwys Nynydd reservoir ($K = 3$) is also well below the predicted values, thus indicating that the Santa Barbara stock tank result is not idiosyncratic in this regard (Appendix). The somewhat higher value for the reservoir relative to the stock tank is consistent with the presence of inedible algae in the reservoir and with hypothesis 1, which predicts that E^* should increase in the presence of inedible algae.

Evidence from Daphnia's death rates

Observations on *Daphnia*'s death rate show that the two hypotheses requiring high death rates in rich environments (hypotheses 2 and 3) can be rejected. First, in both the Santa Barbara stock tanks and Eglwys Nynydd reservoir (George and Edwards 1974), nutrient level was high ($K \approx 3$), the populations were stable (McCauley and Murdoch 1987), yet the death rates were very low (~ 0.03 d^{-1}); in fact they were close to

the rates seen in optimal laboratory conditions (Appendix). These observed death rates are much lower than those required by hypotheses 2 and 3 for stability in rich environments. For hypothesis 2 the required death rates are in the range of 0.25–0.36 d^{-1} for $2 < K < 3$. For hypothesis 3 and $K = 3$, death rate needs to be ≥ 0.36 d^{-1}, and even higher values are needed for $K = 1$ or 2.

Potential role of fish predators of Daphnia.—The test data (solid symbols) in Fig. 7 are from environments where predators of *Daphnia* were either absent (the stock tanks) or did not cause much mortality. Clearly, predation on *Daphnia* is not a necessary factor for stability, though it is possible that when fish cause substantial predation this ''replaces'' the stabilizing mechanism(s) that exist in the purer *Daphnia*–algal interaction. We think this hypothesis, which provides a specific mechanism for hypothesis 2, is unlikely for the following reasons.

The model thus formulated requires *Daphnia* death rates in the region of 0.25–0.36 d^{-1} for $2 < K < 3$, as noted above. These death rates are substantially greater than the largest (0.17) found by McCauley and Murdoch (1987). They are also not feasible given the demography of the field populations studied. First, they imply mean life expectancies for *Daphnia* of 3–4 d, whereas the *Daphnia* take ~ 20 d just to become mature. Second, they are not consistent with observed birth rates that are an order of magnitude lower. Thus, while deaths from fish predation may contribute to the stability of the *Daphnia*–algal interaction in some environments, they do not appear to be able to explain it.

DISCUSSION

Status of the four tested hypotheses

Our fundamental observations are that *Daphnia*-edible algal systems occur in nutrient-rich environments in which (1) there are no large-amplitude oscillations in abundance and (2) the edible algae remain at very low mean biomass. Predation on *Daphnia* is low in many of these systems, so this consumer–resource interaction has a stable equilibrium in the absence of substantial effects from higher trophic levels.

These observations are inconsistent with the hypotheses tested here: all four require much higher than observed edible algal biomass if they are to account for stability. Of the four hypotheses, a functional response dependent on *Daphnia*'s density (hypothesis 4) is the most consistent with the data, but is inconsistent if we require the hypothesis to account for stability over the observed range of nutrient values, rather than only at the end of the range. Furthermore, the observed low *Daphnia* death rates in these systems are inconsistent with the high rates required by hypotheses 2 (death rate increases with enrichment) and 3 (death rate increases with *Daphnia* density); they are also inconsistent with a hypothesis that requires substantial pre-

dation on *Daphnia* as an explanation for stability. It is possible that interference from inedible algae and increasing death rate with enrichment both contribute to stability in some nutrient-rich systems, but they appear unable to provide a general explanation.

Both inedible algae and increasing death rates may also contribute to the small observed increase in edible algal biomass, and there is direct evidence from stock tank experiments that inedible algae have this effect. McCauley and Murdoch (1990) described an experiment in which nutrients in stock tanks containing only *Daphnia* and algae were set at one of two levels: edible algal biomass ($\langle E \rangle$) was higher at the higher nutrient level (McCauley and Murdoch 1990: Table 1) and so was the biomass of inedible algae (E. McCauley, *unpublished data*). This does not establish that inedibles were the cause of the higher edible biomass, but it is consistent with that hypothesis, and the tanks contained no other factors except nutrients that could have had the effect.

Although we found only five natural lakes with appropriately measured variables, these environments appear to be representative of northern temperate lakes and reservoirs in general. The biomass of edible algae in our five habitats was not exceptionally low compared with a larger set of 15 lakes analyzed by Watson et al. (1992). This larger data set also fails to show the strong response of edible algae to nutrient status predicted by the hypotheses (open circles in Fig. 7).

Our conclusions are unlikely to rest on the assumed linearity in our portrayals of each of the four hypotheses (e.g., death rate was assumed to increase linearly with K in hypothesis 2) since, for stability, $\langle E \rangle$ still needs to reach the same absolute values at high K, regardless of the shape of the relationship at lower values of K (Fig. 7).

Although we have tried to test the above hypotheses as rigorously as possible, some difficulties remain. They need to be borne in mind both in evaluating our results and in developing better tests to explain the observed phenomena. First, *Daphnia*'s food supply in nature cannot be defined as precisely as we would like (see Appendix). Issues that are not wholly resolved include the extent to which the various ingested algae are assimilated and whether there may be variation in their quality as a resource. We need more accurate measures of algal carrying capacity (see Appendix). Finally, it is always possible that some combination of these hypotheses (or including those discussed below) might be consistent with the data; we believe it makes sense, however, to begin with simpler explanations.

Three less likely hypotheses

Element recycling.—Instability in the Basic Model is caused in part by the capacity for near-exponential algal growth when the algae are kept well below K by *Daphnia*. It is conceivable that in real systems the limiting resource (phosphorus) is bound up in another component of the system (e.g., *Daphnia,* decaying bodies, particulate phosphorus) and is released as free phosphorus only slowly.

We have examined this hypothesis using a model of the *Daphnia*–alga–phosphorus interaction in a closed system. In addition to phosphorus in algae and *Daphnia,* which is represented as phosphorus quotas per unit of carbon, the model recognizes three other forms of phosphorus: soluble inorganic, soluble organic, and feces plus corpses. Uptake of phosphorus by plankton obeys Michaelis-Menten kinetics. All excretion processes, the decomposition of feces and corpses, and conversion of organic to inorganic phosphorus obey first-order kinetics. Phytoplankton growth rate depends on phosphorus quota. Uptake of phosphorus by phytoplankton is assumed fast relative to other processes so the density of free inorganic phosphorus is small and in pseudoequilibrium.

The results show that this mechanism is not compatible with the known fast recycling of phosphorus via excretion and decomposition, which implies that *Daphnia* or other components cannot sequester a significant fraction of the total phosphorus in the system (Nisbet et al. 1991). The model has a stable equilibrium over only a narrow low-nutrient range of parameter values corresponding approximately with the stable regime in the Basic Model (Fig. 1). It thus appears that this is not a viable hypothesis to explain stability in nutrient-rich environments.

Type 3 functional response by Daphnia.—The available evidence suggests this is not a viable hypothesis. Most of the evidence points to a type 2 response in *Daphnia* (McCauley et al. 1990). In particular, the best data are those of DeMott (1982) and a type 2 response explains 98% of the variance (McCauley et al. 1990). A redrawing of Porter's data (Porter et al. 1982) from a semi-log to an arithmetic plot shows an initially accelerating response, but the data are sparse, and the accelerating portion is over a very narrow range of algal densities and would provide little scope for damping large perturbations in density. There is also no evidence for a type 3 response in recent experiments (Urabe and Watanabe 1991, Rothhaupt and Lampert 1992).

Daphnia *has an alternative food source other than inedible algae.*—There is some evidence that *Daphnia* can use bacteria in the field as an additional source of food, albeit with very low efficiency and little absolute energy gain. Consumer–resource models such as those explored here can be stabilized by adding a food source for the consumer, especially if the dynamics of the source are little affected by the interaction. The model of Kretzschmar et al. (1993), although formulated with inedible algae in mind as the alternative food, is applicable here. There is as yet little evidence to sustain this hypothesis. However, alternative foods were not measured in the Santa Barbara stock tank experiments, discussed below, and the presence of such food is a potential explanation for the stability seen in these ex-

periments. A major difficulty with this hypothesis, however, is that alternative food for *Daphnia* would lead to an equilibrium density of edible algae below that predicted by the Basic Model, and this was not the case.

Four viable hypotheses

1. *Inedible algae act as a nutrient sponge.*—Instability in the Basic Model at high nutrient levels is caused, in part, by the fact that *Daphnia* suppress edible algae far below their carrying capacity, thus allowing periodic existence of a very high "unused capacity for increase" for the algae. However, in lakes both the absolute concentration and the proportion of inedible algae increase with enrichment (Watson et al. 1992). Inedible algae, by competing for and taking up nutrients, might greatly reduce the effective K for edible algae and so stabilize the interaction.

Kretzschmar et al. (1993) developed a model for interacting populations of *Daphnia* and competing edible and inedible algae. The model yields stable dynamics over a very wide range of parameter values, essentially because as the environment is enriched (total K increases), inedible algae increase and thereby reduce the effective K for edible algae. We were not able to develop testable predictions for this model because the effect on edible algal equilibrium depends on unknown details of the competition between edible and inedible algae and on whether the "inedibles" are 100% inedible. The predicted equilibrium biomass of edible algae depends on these details, and indeed with judicious choice of parameter values this model can predict stability at high nutrient levels with no increase in edible algal biomass. This model is thus in principle able to account for all observations from natural environments, because it can explain both stability at all nutrient levels and, in combination with inedibles interfering with *Daphnia*'s feeding (hypothesis 1), it can explain the small increase in edible algal biomass with enrichment.

This hypothesis is not compatible with the data from the Santa Barbara stock tanks. This very high-nutrient system (Fig. 7) was stable even though it contained no inedible algae. Two interpretations are thus consistent with the results so far. First, inedible algae may stabilize all natural environments that are otherwise predicted to be unstable, mainly by being a sink for nutrients. In this interpretation, the stability of the Santa Barbara stock tanks was caused by some special feature of the tanks that is not relevant in nature. We have not been able to come up with a likely special feature. For example, we saw no algal growth on the sides of the tanks that might have provided *Daphnia* with a steady alternative source of food. *Daphnia* might have grazed on debris, or sediments, or other organisms present in the water column but not sampled. Unfortunately, this experiment was not designed to explore the hypotheses discussed here and cannot serve as a definitive test.

The role of inedible algae cannot be resolved until there are better controlled experiments in simple environments at high-nutrient levels.

The second interpretation is that any universal explanation of stability in nutrient-rich systems must account for the results from the Santa Barbara tanks. In that case we cannot accept the inedible-algal hypotheses.

2. *Spatial heterogeneity and environmental "stickiness."*—Spatial heterogeneity might potentially stabilize the system in several ways. First, there might be a spatial refuge for the algae (Nisbet et al. 1989, Scheffer and DeBoer 1995, Abrams and Walters 1996). This is possible in lakes, but not likely in the stock tanks, including those done at Calgary, which were better controlled than the Santa Barbara tanks.

Second, the system could be composed of subpopulations fluctuating out of phase and being maintained by metapopulation or "ensemble" dynamics. Again, while this mechanism may be operating and contributing to stability in some natural environments, it seems unlikely to be important in the small and simple stock-tank environments.

Third, recent work with spatially explicit individual-based models has shown that small-scale differences in space, combined with restricted movement of individuals (environmental "stickiness"), can also lead to stability via metapopulation-like dynamics (deRoos et al. 1991). McCauley et al. (1993) show that the effect is greater if prey movement, rather than predator movement, is restricted, so this mechanism might operate even on the small spatial scale of stock tanks since individual algal cells move so little.

Finally, Neary et al. (1994) and Coddington and McCauley (1994) have demonstrated that *Daphnia* can respond to gradients of food concentration. Although aggregation to patches of locally high prey density has been suggested as a possible stabilizing mechanism (Hassell and May 1973), it is more likely to be destabilizing in a continuously reassorting system such as the *Daphnia*–alga interaction (Murdoch and Stewart-Oaten 1989, Murdoch et al. 1992, Rohani et al. 1994).

Although spatial heterogeneity and/or restricted movements may play a role in stabilizing our planktonic systems, there is at present no evidence for any of this suite of mechanisms.

3. *Changes in* Daphnia *physiology at low-resource levels.*—There is evidence that *Daphnia* responds with an increase in efficiency to lowered food levels. For example, a very low rate of ingestion leads to increased assimilation efficiency (probably via food taking longer to pass through the gut), and lowered maintenance (Appendix). S. A. L. M. Kooijman (*personal communication*) suggests two other mechanisms: a decrease in the ratio of reserves to structural biomass and a decrease in the rate of rejecting ingested food, at low-food levels. These changes can be incorporated into the Basic Model by making the conversion efficiency,

e, a decreasing function of algal density and making maintenance, *b,* an increasing function of algal density. These changes reduce E^* at low-nutrient levels but do not enhance stability, hence they cannot solve the problem. However, until there is a complete account of *Daphnia*'s response to low-food levels, and these are examined in a more detailed model, the possibility of some stabilizing change in physiology cannot be excluded.

4. *Individual variation in* Daphnia.—In the field, there is differential selection on *Daphnia* clones through the season (e.g., Carvalho and Crisp 1987). In addition, we have seen quite marked variation, at low-food levels, in growth and survival of genetically identical individuals given the same strictly controlled environment (E. McCauley, *unpublished data*). Kooijman et al. (1989), Kooijman (1993), and DeAngelis and Rose (1992) showed that models that include stochastic variation (by keeping track of all individuals in the population), may predict very different dynamics from deterministic individual-based models if there is significant variation in the environment experienced by individuals and/or significant variation in individual response to a common environment. We have not yet formulated models that include such variation, and it is a possible source of stability that we intend to check.

The general problem

The problem of accounting for stability in systems where the consumer greatly depresses its resource population is ubiquitous. While it is easy to develop mechanisms that are stabilizing in theory, it has been much harder to establish that any particular mechanism actually regulates a particular system. Murdoch (1994) and Murdoch et al. (1996) provide an example in red scale, an agricultural insect pest that is controlled by a parasitoid, and there is still much controversy over the mechanisms that stabilize such systems.

The insect and plankton examples also underline a difficulty in developing a general explanation: it is not likely to rest on mechanisms that relate to particular features of the life history. For example, while stability in red scale may be enhanced by its having a long-lived adult stage that is invulnerable to attack by the parasitoid (Murdoch et al. 1987), edible algae do not have a long-lived invulnerable stage. Three apparently viable alternative stabilizing mechanisms discussed in the previous section—among-individual variation, spatial heterogeneity, and an environment that is ''sticky'' for the prey—are promising because they are largely independent of life history details. But much empirical and theoretical exploration remains to be done to determine whether they operate in real systems.

One hypothesis that makes strong claim to generality, ''ratio dependence,'' has been the subject of much recent writing (e.g., Arditi et al. 1991, Berryman 1992, Abrams 1994). We found a poor fit of the data with a more general form of this hypothesis, namely dependence of the functional response on predator density.

The recent focus on ratio dependence rather than on a more general form of predator dependence is unfortunate because, although it is difficult to defend ratio dependence as a representation of known behavioral or physiological mechanisms, dependence on predator density does arise as an approximation in at least two instances. The first potential, behavioral, source of predator dependence is interference among feeding predators. Ruxton et al. (1992) have shown that this behavior leads as an approximation, not to ratio dependence in the functional response, but to its dependence on predator density as in Eq. 8. Even this approximation, however, requires quite strong assumptions.

A second potential source of predator dependence is spatial heterogeneity. Arditi and Ginzburg (1989) argued that ratio dependence can arise as the average of consumer foraging in a spatially heterogeneous environment. However, such a result has not been derived and, as pointed out by Oksanen et al. (1992), there is a fundamental incompatibility of time scales in writing differential-equation models for consumer–resource dynamics in which consumption is meant to reflect a long-term average. An absolute physical refuge, however, can lead as an approximation to predator-density dependence of the form in Eq. 8, provided prey move into and out of the refuge at random (R. M. Nisbet et al., *unpublished manuscript*).

Additional difficulties with ratio dependence, and with predator dependence, as they relate to planktonic systems are presented in Diehl et al. (1993), Sarnelle (1994), and Abrams (1994). To these we would add that the Ginzburg and Akcakaya (1992) analysis of field data ignores distinctions that are crucial to the hypothesis, namely those between edible and inedible algae, between lakes where zooplankters are likely to be controlling the abundance of phytoplankton and those in which fish suppress the zooplankton to levels at which they have little effect on the algae, and between planktivorous and piscivorous fish (cf. Persson et al. 1992).

In sum, we have found evidence to reject four of the major hypotheses that might account for the maintenance of stability of the *Daphnia*–algal interaction in the face of enrichment. Among other hypothesis discussed, several remain viable. In particular, inedible algae may in many situations dispel the problem by sequestering nutrients that would otherwise be available to the interacting populations, and spatial heterogeneity and ''environment stickiness'' represent a potential explanation in this and many other systems. Our exploration makes no claim, of course, to being exhaustive, and the real mechanism may lurk in some so far poorly explored area of the interaction itself or the larger food web in which it resides.

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APPENDIX

Sources of Data and Parameter Estimates

We first explain the criteria used for selecting studies against which to test the hypotheses, and briefly describe the studies. We then discuss measurements of K and $\langle E \rangle$. Finally we describe the source of the *Daphnia* parameter estimates.

Studies used to test hypotheses

Suitable studies of natural environments are those finding a single species of *Daphnia* and either no vertebrate predators of *Daphnia* or low predation on *Daphnia* (e.g., Murdoch and McCauley 1985, McCauley and Murdoch 1987). Under these conditions, *Daphnia*–algal dynamics are internally generated (McCauley 1993). Also needed are (1) reliable estimates, in carbon units (i.e., measures of cell volume), of algal concentration in both the spring peak (to estimate K) and over summer (to give $\langle E \rangle$); (2) separate estimates of edible and inedible algae if the latter are present; and (3) summer measurements over a long enough period to confirm that the populations were stable. Thus, while there are numerous estimates of average summer algal biomass from natural environments (Watson et al. 1992), most of them are not useful for one or more of the following reasons: *Daphnia* was absent, the fraction edible was not measured, and factors such as predation on *Daphnia* both varied and were not well measured. In addition, we used only studies in which $\langle E \rangle$ was measured as cell volume.

We found only four studies of natural environments that meet the criteria. These are, from least to the most eutrophic: Lake Maarsseveen (Koning and Dorgelo 1982), Hall Lake (Taylor 1981), Lake Constance (Lampert and Schober 1978), and Lake Washington for the year 1978 (Edmondson and Litt 1982). We also calculated expected values for a fifth environment, Eglwys Nynydd reservoir (George and Edwards 1974). We were not able to confirm the appropriateness of data from field experiments in which nutrient levels and other factors have been manipulated (e.g., data reviewed by Leibold 1989, Sarnelle 1992). We also used data from studies of experimental stock tanks in Santa Barbara and Calgary, in which there were no predators of *Daphnia*. The Santa Barbara tanks were very nutrient-rich environments that contained only a single edible algal species, *Chlamydomonas reinhardii* and no inedible algae (Murdoch and McCauley 1985, McCauley and Murdoch 1987). *Daphnia pulex* was the only or the overwhelmingly dominant cladoceran.

The Santa Barbara stock tank experiment was not designed to look primarily at *Daphnia*-algal interactions, but to examine the effects of the backswimming bug, *Notonecta,* on *Daphnia* dynamics. (We report here only on tanks without *Notonecta.*) As a result, there was less control over the nutrient regime than we would like. In March 1981 the tanks were scrubbed, filled with deionized water, and received 5 mL of plant nutrient medium, and an inoculation of *Chlamydomonas rheinhardii* from a culture tank. Regular checking of samples under the microscope throughout the experiment confirmed that no inedible algae invaded the tanks. *Daphnia pulex* taken from a culture tank were added in several 1-L aliquots in June. During this period tanks were also stirred and water transferred among them to make them more similar. We cannot be certain that *Daphnia* had no food other than edible algal cells in the water column. We did not see algae on the sides or bottom of the tanks, but the bottoms accumulated detritus that conceivably could have yielded a source of food.

The tanks were sampled from 20 June for ~90 d, until the end of summer. We report the means of seven populations. Chlorophyll *a* (chl *a*) was estimated once per week in replicated samples by in vivo fluorescence and calibrated against estimates using acetone-extraction techniques (Strickland and Parsons 1972). K was estimated in two tanks lacking *Daphnia*. These became a ''pea soup'' of edible algae.

Daphnia abundance, clutch size, and size structure were estimated twice a week, the entire sample or 100 individuals (whichever was smaller) being measured to the nearest 0.025 mm. Each of two samples was taken as follows. The tank was stirred and then a 500-mL jar was held upside-down ~15 cm under the water and then inverted. The contents were transferred to a bucket. This procedure was repeated at a grid of nine positions in the tank. The contents of the bucket were well mixed and a 500-mL sample taken. This process was then repeated to provide a duplicate sample.

The Calgary stock tanks were studied over summer in a greenhouse; details of the experiment are given in McCauley and Murdoch (1990). The tanks contained *Daphnia pulex* and a mixture of edible and inedible algal species. Nutrient level was manipulated by adding different initial quantities of phosphorus and nitrogen.

Our aim was to include studies done over the widest possible range of nutrient levels, but the richest lake had $K = 1.6$ mg C/L, which is only moderately eutrophic. The Santa Barbara stock tanks were very nutrient rich, with $K > 3$ mg C/L. As a check that the results from the stock tanks were in line with those from field environments, we examined results from an equally rich natural environment, Eglwys Nynydd reservoir, $K \approx 3$ mg C/L (George and Edwards 1974), which had stable populations (McCauley and Murdoch 1987) and offered a reliable, if indirect, method for estimating $\langle E \rangle$.

To determine whether the relationship between K and $\langle E \rangle$

found in the above set of studies is more general, we used data compiled by Watson et al. (1992). These authors established values for total phosphorus and total algal biomass in over 100 lakes and reservoirs spread throughout the northern temperate region. A time series for edible algae that included spring data, and hence provides an estimate of *K,* was available for 14 of these environments (Border, Cayuga, Central, Constance, Erie, Hertel, Indian, Lake 226, Lake 239, Langvattn, Paajarvi, Scugog, Washington, and Whitefish), and we were able to find data for one additional lake (Lake Mendotae [Lathrop and Carpenter 1992]). Some lakes provided data for more than one year and each lake-year provides one observation in Fig. 7 (open circles). These data cannot be used to test the hypotheses, however, since (1) information on plankton dynamics is incomplete, (2) there were several to many species of cladocera and copepods rather than a single dominant *Daphnia* species as in the lakes we selected, and (3) details on fish populations or the importance of fish predation are not available. Nevertheless, the plankton data showed no evidence of large-amplitude fluctuations other than the spring peak.

Estimates of E* and K

Summer average edible algal biomass in carbon units (mg C/L), *E**, can be estimated from total cell volume, since the carbon : volume ratio varies between 0.08 and 0.12. The ratio increases with nutrient level, but a quantitative relationship has not been established (Reiman et al. 1989).

Unfortunately, standard practice is to estimate algal abundance as total chlorophyll *a,* including the contribution of inedible algae. Such data cannot provide estimates of edible algal biomass in environments with different nutrient levels because the fraction edible is not estimated and the fraction of chlorophyll *a* in algal cells varies with nutrient level (e.g., Watson et al. 1992).

Reliable estimates of edible cell volume can be made if measurements of edible chl *a* are available and either (a) we also know total phosphorus, or (b) the environment is nutrient rich. Condition (a) allows us to use an algorithm developed by Watson et al. (1992), based on the relationships among chl*a,* TP, and cell volume of edible algae, over more than 100 lakes. In situation (b) the chl *a*/cell volume ratio is known accurately (Watson et al. 1992).

Estimates of ⟨*E*⟩ in the four natural lakes were based on direct counts of cell volume. The estimates in the stock tanks were based on measures of edible chl *a.* In the Calgary stock tanks both the fraction edible and TP were measured. We also calculated an estimate of ⟨*E*⟩ from the study by George and Edwards (1974). These authors measured TP, and the system was very eutrophic, so there is a reliable algorithm for predicting cell volume from TP (Watson et al. 1992). In all cases we calculated the range of estimates of milligrams of carbon per liter obtained by multiplying cell volume by 0.08 and 0.12. This range is covered by the points in Fig. 7.

As a check on the congruence between estimates from the lakes and the overall relationship between trophy and ⟨*E*⟩ established by Watson et al. (1992), we calculated the expected ⟨*E*⟩ for the three lakes where total phosphorus was measured. The two sets of estimates overlap.

Ideally, *K* (edible algal carrying capacity) would be estimated as the average summer biomass of edible algae (in milligrams of carbon per liter) that would exist if there were no competitors, no limiting factors other than nutrients, and no zooplankton. This direct estimate was available for the stock tanks, but not for the other environments, so we substituted estimated spring maximum algal biomass in these cases. In temperate lakes this is typically the maximum biomass achieved during the entire year and the algal community is often dominated by edible species at that time.

K was estimated in the stock tanks from measures of edible algae in the absence of *Daphnia.* All other estimates used measures of spring algal peak, when edible species predominate and when crustacean zooplankton are relatively scarce. Spring counts in Lakes Hall and Maarsseveen were in cell volume. The Watson et al. (1992) algorithm that makes use of TP measurements was used to convert chl *a* to cell volume in Lakes Washington and Constance, in the Calgary tanks, and in Eglwys Nynydd reservoir. The UCSB tank estimate again relied on the conversion from edible chl *a* to cell volume in high-nutrient conditions. We used a factor of 0.12 to convert estimates of cell volume to carbon in all cases where *K* > 1 mg C/L and 0.08 when *K* < 1.

The peak biomass of edible algae in spring is probably not an accurate measure of summer *K.* However, we require only that it not be a gross overestimate, i.e., that the points in Fig. 7 for which *K* ≫ 1 are not from environments in which the true *K* values are <1. In fact, it seems more likely that the spring peak underestimates summer *K.*

First, the spring algal peak most likely underestimates spring *K.* Peak algal abundance is likely to be below the limit set by nutrients because in northern temperate lakes, in spring, light or temperature are likely to be limiting factors. In addition, in some lakes herbivorous zooplankton may have been grazing over winter, and certainly do so in spring. Second, an alternative approach gives estimates of summer *K* in nutrient-rich lakes that are higher than those based on spring algal peak. We made these estimates using measured phosphorus in summer, and first define the fraction of TP potentially available to edible algae. TP consists of a particulate fraction, which is almost entirely algae, and dissolved phosphorus. Some part of the latter is in principle available to algae, but only at high energetic cost and, to keep our estimates of summer *K* conservative, we ignored the dissolved fraction, which is typically ~40% of TP in nutrient-rich lakes (those with TP > 16 μg/L; e.g., Nalewajko et al. 1981, Peters 1983, and Prepas and Vickery 1984). We also need to exclude from our calculations the phosphorus bound up in inedible algae, since this is not available to edible algae. The regressions of Watson et al. (1992) establish that 20–25% of the algae are edible in lakes in the range of trophy studied here. The direct estimates available for two rich lakes confirm this: Lake Constance with 21% and Lake Memphremagog with 28% (Watson et al. 1992). Again, we chose a conservative estimate of 20% edible algae. Thus, the phosphorus potentially available to edible algae is only 0.12 (0.2 × 0.6) of TP.

With this as background, we calculated summer *K* as follows. The standard model for algal growth, used broadly by limnologists and algal physiologists, is

$$\mu = \mu_{max}(1 - k_Q/Q) \qquad (A.1)$$

where μ is the instantaneous per head rate of cell division per unit time, *Q* (in moles of phosphorus per milligram of carbon) is the concentration of phosphorus in the cell, i.e., the "cell quotient," and k_Q is the threshold cell quotient needed for maintenance (Droop 1974). If *T* is the total phosphorus available for uptake by edible algae in the absence of grazers, T/k_Q provides an estimate of *K.*

The usefulness of this estimate is made transparent by rewriting Eq. A.1 in a form suitable for the field. μ_{max} is equivalent to *r,* the maximum per head algal growth rate in our Basic Model, and in the field *Q* = *T/E,* where *E* is the average edible algal density. Substitution in Eq. A.1 gives the per head rate of increase of the algal population in the same form as in the Basic Model:

$$dE/dt = rE(1 - E/K). \qquad (A.2)$$

Values for total summer phosphorus (TP) are available for two lakes that span the spring-estimated *K* values for the nutrient-rich lakes in Fig. 7. For Lake Constance TP = 60 μg P/L and for Eglwys Nynydd TP = 130 μg P/L of which 7.2 and 15.6 μg P/L, respectively, are available to the edible algae. So the phosphorus available to edible algae, in moles

of phosphorus per liter, is $T = 2.25 \times 10^{-7}$ for Lake Constance and $T = 4.9 \times 10^{-7}$ for Eglwys Nynydd.

Finally, the modal volume of edible algae (based on the distribution of biomass with size) in nutrient-rich lakes is $\sim$500 μm^3 (e.g., Sprules et al. 1983). Table 1 in Shuter (1978) shows that a cell of approximately this volume has a threshold cell quota of 3.7×10^{-15} mol P/cell and a carbon content of 3.8×10^{-12} mol C/cell, giving 9.7×10^{-2} mol P/mol C. This converts to $k_Q = 0.8 \times 10^{-7}$ mol P/mg C. Thus, from $K = T/k_Q$, the estimated summer K values range from 2.8 mg C/L (Lake Constance) to 6.1 mg C/L (Eglwys Nynydd). The K values based on the spring peak are, respectively, 1.6 mg C/L and $\sim$3 mg C/L, which suggests that the estimates of K based on the spring algal peak are underestimates, and at least are not gross overestimates.

Two alternative calculations give similar answers. (1) Shuter (1978) establishes a regression for threshold P quota per cell as $a(V)^b$, where V is cell volume in cubic micrograms, $b = 0.69$, and $\log a = -1.229$; this yields a cell quota of 4.3×10^{-15} mol P/cell. The standard relationship for carbon content, C (in picograms), is $C = 0.12V^{1.051}$, giving $C = 82.4 \times 10^{-12}$ per cell, i.e., 6.9×10^{-12} mol C/cell. This now gives 6.3×10^{-3} mol P/mol C, giving $k_Q = 0.52 \times 10^{-7}$ mol P/mg C, and hence increasing the estimates of K in Lake Constance and Eglwys Nynydd to, respectively, 4.33 and 9.42 mg C/L. (2) Smith and Kalff (1982) estimate the parameters in the regression for the threshold P cell quota as $b = 0.70$ and $\log a = -0.72$. The authors note that this regression overestimates threshold cell quota because the algae were still growing when the estimates were made. However, even if we use the resulting overestimate of $k_Q = 14.8$ mol P/cell, we still obtain estimates of K for the two lakes as 1.3 and 2.7 mg C/L, which are only marginally lower than the estimates based on the spring peak.

Daphnia *parameters*

We earlier developed a parameter set for a model of acquisition and allocation of energy in individual *Daphnia pulex* that successfully predicted individual growth, development, ultimate size, and fecundity over a range of moderate to high food densities (Gurney et al. 1990, McCauley et al. 1990). Nisbet et al. (1991) used these values to parameterize the Basic Model. Here we have changed two values in the light of more recent work. Bohrer and Lampert (1988) and Glazier and Calow (1992) showed that respiration cost, b, is slightly smaller under low food than we had originally estimated. Nisbet et al. (1991) set $b = 0.12$ d^{-1}, but present data are consistent with 0.08 d$^{-1} < b < 0.12$ d^{-1}, and our laboratory studies suggest $b = 0.09$ d^{-1}. Nisbet et al. set $m = 0.02$ d^{-1}, since 50 d is a reasonable estimate of average longevity of *Daphnia* in laboratory conditions. We use $m = 0.03$ d^{-1} since this is the lowest death rate observed in field populations (George and Edwards 1974).