



Intraguild Predation, Invertebrate Predators, and Trophic Cascades in Lake Food Webs

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The top-down and bottom-up properties of model food webs that include intraguild predation and self-limiting factors such as cannibalism are investigated. Intraguild predation can dampen or even reverse the top-down effects predicted by food chain theory. The degree of self-limitation among the intraguild prey is a key factor in determining the direction and strength of the top-down response. Intraguild predation and self-limiting factors can also substantially alter the bottom-up effects of enrichment. These results can help explain the disparate results of trophic cascade experiments in lakes, where cascades are usually seen when large *Daphnia* are the primary herbivores, but not when smaller-bodied herbivores are dominant. Top-down manipulations should cascade at least modestly to phytoplankton in those lakes whose food web can be reasonably approximated by a chain (typically, those where *Daphnia* is the dominant herbivore), as predicted by food chain theory. On the other hand, smaller-bodied zooplankton are often preyed upon heavily by invertebrate predators as well as by planktivorous fish, thereby introducing elements of intraguild predation into these food webs. In this case, conventional food chain theory is likely to give incorrect predictions. Very large cascade effects may be due primarily to regime shifts between intraguild predation-dominated food webs and those that more resemble food chains, rather than due to the simple food chain cascade usually considered.

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Introduction

The effect of top predators on lower trophic levels has long been an important aspect of ecological theory (Hairston *et al.*, 1960). Classical food chain models (Fretwell 1977, Oksanen *et al.*, 1981) predict that changes in the top level of a chain should cascade without dissipation down the chain, with the direction of the interaction alternating between levels. These

models also predicts that changes in the growth rate of the bottom of the food chain (which might be induced by increases in nutrients) will affect only the top level of the chain and those an even number of levels below.

There has been considerable work in recent years testing these predictions in lake food webs (e.g. Carpenter & Kitchell, 1988, 1993; Reynolds, 1994; Brett & Goldman, 1996, 1997; Leibold *et al.*, 1997). These studies give limited support for food chain theory. For example, manipulation of fish had a strong effect on phytoplankton only in about one-third of the studies surveyed by Brett & Goldman (1996).

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Model predictions for “bottom-up” control also have not been totally confirmed. Changes in nutrient loading often (but not always) increase the biomasses of all trophic levels, and not just those an even number of levels from the top (McQueen *et al.*, 1986; Ginzburg & Akçakaya, 1992; Sarnelle, 1992; Mazumder, 1994; Leibold *et al.*, 1997).

Why is there so much variation in the top-down responses of different systems? It has been observed that transmission of top-down effects from fish to phytoplankton is more common in those lakes where *Daphnia* spp. are the dominant grazers (Pace, 1984; McQueen *et al.*, 1986; Leibold, 1989; Strong, 1992; Reynolds, 1994; Polis & Strong, 1996; Dettmers & Stein, 1996; Leibold *et al.*, 1997), although some exceptions have been reported (e.g. Leibold, 1989; Turner & Mittlebach, 1992). It has been suggested that the enhanced ability of *Daphnia* to transmit top-down effects is due to its superior feeding capabilities, allowing it greater ability to reduce phytoplankton biomass (Carpenter & Kitchell, 1984; Gliwicz, 1990; Strong, 1992; Reynolds, 1994). However, many studies have indicated that smaller zooplankton are capable of reducing phytoplankton to levels at or below those observed in *Daphnia*-dominated systems (Dodson, 1974; DeMott, 1982; Bogden & Gilbert, 1984; Tessier & Goulden, 1987; Neill, 1988; Turner & Mittlebach, 1992; Declerck *et al.*, 1997), or that *Daphnia* are only competitively superior in eutrophic lakes (Romanovsky, 1984; Hansson *et al.*, 1998). Hence, while differences in grazing capabilities among zooplankton assemblages may sometimes play a role in their ability to transmit top-down effects, they cannot provide a full explanation for the varying results of cascade experiments.

This article explores an alternative hypothesis: the outcome of top-down manipulations depends on food web structure. Classical cascade models are only applicable in those systems where the food web can be well approximated by a simple food chain. Besides phytoplankton, herbivorous zooplankton, and fish, lake food webs often contain invertebrate predators such as insect larvae and predatory crustaceans that both compete for food with, and are prey for, planktivorous fish (Dodson, 1974; Hall *et al.*,

1976; Kerfoot & DeMott, 1984; Elser *et al.*, 1987; Riessen *et al.*, 1988; Edmondson & Abella, 1988; Soranno *et al.*, 1993; Wissel & Benndorf, 1998; Wissel *et al.*, 2000; Benndorf *et al.*, 2000). Food webs where invertebrate predators are important cannot be modeled as a simple chain; food chain models may therefore give incorrect predictions in this situation. Since large zooplankton such as *Daphnia* are often too large for many invertebrate predators to consume, *Daphnia* are generally less vulnerable to invertebrate predators than are smaller zooplankton (Kerfoot, 1977; Zaret, 1980; Elser *et al.*, 1987; Riessen *et al.*, 1988; Gliwicz & Umana, 1994). Thus, the fact that cascade effects occur most often in *Daphnia*-dominated lakes may be due to the fact that these food webs can often be well approximated as a simple chain, whereas this would not be a good approximation in many lakes where small-bodied zooplankton are prevalent.

Adding a compartment for invertebrate predators into lake food chain models introduces an element of “intraguild predation” (IGP) into these models (Polis *et al.*, 1989; Holt & Polis, 1997; see Fig. 1). Intraguild predation occurs when a consumer of a resource (the IG predator) also preys upon on a second consumer of that

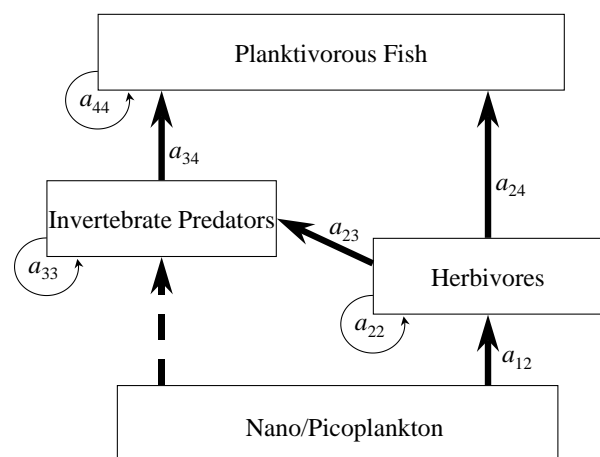


FIG. 1. Schematic of the basic food web models. In the Lotka–Volterra model, there is no link between invertebrate predators and phytoplankton, but self-limitation may occur in each of the three consumer compartments. In the simulation model, the invertebrate predators are assumed to be omnivorous, and self-limitation occurs only among the invertebrate predators and herbivores. The rate coefficients in the Lotka–Volterra model that correspond to a given interaction are also shown.

resource (the IG prey). In Fig. 1, fish are the IG predators, and invertebrate predators are the IG prey. If the invertebrate “predators” are actually omnivorous, and feed both on herbivores and phytoplankton, the invertebrate predators and herbivores would form a second IG predator–prey pair.

It is important to distinguish between IGP models where the IG predator and prey are in different model compartments, as in Fig. 1, and where they are in the same compartment. The former type of model allows for independent changes in the IG predator and prey compartments, and combines elements of both predator–prey and competitive interactions. This is the most common way of modeling IGP (Holt & Polis, 1997; Gismervik & Andersen, 1997; Diehl & Feissel, 2000; Mylius *et al.*, 2001). By contrast, in IGP models where the IG predator and prey are in the same compartment, IGP acts as a self-limiting factor (McCann *et al.*, 1998). This type of model process can represent not only intracompartamental IGP, but also intraspecific cannibalism and many other types of density-dependent self-limiting factors. In this article, I will restrict the use of the term “intraguild predation” to the cases where the IG predator and prey are in different compartments. I will refer to consumption of a compartment upon itself as “intracompartamental predation” or, more generally, as a “self-limiting factor”. Both intraguild predation and self-limiting factors have been shown to affect the strength and even the direction of top-down and bottom-up manipulations (Mittlebach *et al.*, 1988; Gatto, 1991; Gleeson, 1994; Palomares *et al.*, 1995; McCann *et al.*, 1998).

The effects of intraguild predation and self-limiting factors on the top-down and bottom-up properties of food webs are explored here using three models. The first is a modified version of the basic intraguild predation model of Holt & Polis (1997). The other two specifically model a pelagic food web consisting of phytoplankton, herbivores, invertebrate predators, and planktivorous fish. The former model has linear functional responses, allowing for analytic results to be obtained, while the latter has more realistic functional responses, and was studied numerically.

Basic Intraguild Predation Model

I first consider the basic intraguild predation model of Holt & Polis (1997), modified to include terms for self-limitation in the IG predator and prey compartments:

$$\frac{dx_1}{dt} = [r(1 - x_1/K) - a_{12}x_2 - a_{13}x_3]x_1, \quad (1)$$

$$\frac{dx_2}{dt} = [a_{12}b_{12}x_1 - a_{22}x_2 - a_{23}x_3 - m_2]x_2, \quad (2)$$

$$\frac{dx_3}{dt} = [a_{13}b_{13}x_1 + a_{23}b_{23}x_2 - a_{33}x_3 - m_3]x_3, \quad (3)$$

where x_1 , x_2 , and x_3 represent the levels of basal resource, intraguild prey, and intraguild predator, respectively. Stability properties and the effect of bottom-up perturbations on this system (in the absence of self-limitation of the IG predator and prey) were analysed in Holt & Polis (1997) and Diehl & Feissel (2000).

The intraguild predation equations (1)–(3) can be solved for their non-trivial equilibrium point (x_1^*, x_2^*, x_3^*) . The equilibrium value of the basal resource x_1^* is

$$x_1^* = \frac{K}{D} [r(a_{22}a_{33} + a_{23}^2b_{23}) + m_2(a_{12}a_{33} + a_{13}a_{23}b_{23}) + m_3(a_{13}a_{22} - a_{12}a_{23})], \quad (4)$$

where $D = r(a_{22}a_{33} + a_{23}^2b_{23}) + K(a_{12}^2b_{12}a_{33} + a_{13}^2b_{13}a_{22} + a_{12}b_{12}a_{13}a_{23}b_{23} - a_{12}a_{13}b_{13}a_{23})$.

It can be shown, using the same argument as Holt & Polis (1997), that D must be positive at any stable equilibrium, so it will be assumed here that $D > 0$. The effect of a change in mortality rate of the IG predator, m_3 , on the basal resource equilibrium biomass x_1^* will depend on the value of

$$\frac{\partial x_1^*}{\partial m_3} = \frac{K}{D} (a_{13}a_{22} - a_{12}a_{23}). \quad (5)$$

Note the important role of the IG prey self-limitation term a_{22} in controlling the strength and direction of the response. In the absence of such self-limitation, an increase in the IG predator mortality m_3 will always induce a

somewhat counterintuitive decrease in basal resource abundance.

The effects of enrichment on the basal resource can be assessed by computing $\partial x_1^*/\partial K$ and $\partial x_1^*/\partial r$. Calculating the first of these quantities gives

$$\frac{\partial x_1^*}{\partial K} = x_1^* \left[\frac{1}{K} - \frac{1}{D} (a_{12}^2 b_{12} a_{33} + a_{13}^2 b_{13} a_{22} + a_{12} b_{12} a_{13} a_{23} b_{23} - a_{12} a_{13} b_{13} a_{23}) \right]. \quad (6)$$

Since $a_{23}^2 b_{23} > 0$, the second term on the right-hand side can be estimated as

$$\begin{aligned} & \frac{1}{D} (a_{12}^2 b_{12} a_{33} + a_{13}^2 b_{13} a_{22} + a_{12} b_{12} a_{13} a_{23} b_{23} - a_{12} a_{13} b_{13} a_{23}) \\ &= \frac{K}{KD} (a_{12}^2 b_{12} a_{33} + a_{13}^2 b_{13} a_{22} + a_{12} b_{12} a_{13} a_{23} b_{23} - a_{12} a_{13} b_{13} a_{23}) \\ &< \frac{r(a_{22} a_{33} + a_{23}^2 b_{23}) + K(a_{12}^2 b_{12} a_{33} + a_{13}^2 b_{13} a_{22} + a_{12} b_{12} a_{13} a_{23} b_{23} - a_{12} a_{13} b_{13} a_{23})}{KD} \\ &= \frac{D}{DK} = \frac{1}{K}. \end{aligned} \quad (7)$$

Hence, $\partial x_1^*/\partial K > 0$. In contrast to a two-level Lotka–Volterra food chain, the intraguild predation model predicts that there will always be a positive bottom-up effect on the basal resource. Computation of $\partial x_1^*/\partial r$ gives similar results.

Table 2(a) gives the responses of each compartment to an increased mortality rate of the IG predator or prey, or to an increased growth rate of the basal resource. These are compared to conventional two- and three-level food chains with linear functional responses. The behavior of the IGP model is different from either of the chain models.

Four-Compartment Lotka–Volterra Model

The other two models considered here are four-compartment fish – invertebrate predator – herbivore – phytoplankton (pico/nanoplankton) systems, as shown in Fig. 1. In these models, (planktivorous) fish are predators of herbivores, invertebrate predators, and (possibly) their own young; invertebrate predators can consume herbivores, other invertebrate predators, and in the second model, phytoplankton. Herbivores feed on phytoplankton and possibly other herbivores. In order to be tractable analytically, the first model (the “Lotka–Volterra model”)

has linear functional responses and no link from phytoplankton to the invertebrate predator. This model can be considered an extension of the basic intraguild predation model given above. The model equations are

$$\frac{dx_1}{dt} = \left[r \left(1 - \frac{x_1}{K} \right) - a_{12} x_2 \right] x_1, \quad (8)$$

$$\frac{dx_2}{dt} = [a_{12} b_{12} x_1 - a_{22} x_2 - a_{23} x_3 - a_{24} x_4 - m_2] x_2, \quad (9)$$

$$\frac{dx_3}{dt} = [a_{23} b_{23} x_2 - a_{33} x_3 - a_{34} x_4 - m_3] x_3, \quad (10)$$

$$\frac{dx_4}{dt} = [a_{24} b_{24} x_2 + a_{34} b_{34} x_3 - a_{44} x_4 - m_4] x_4, \quad (11)$$

where x_1, x_2, x_3 , and x_4 represent phytoplankton, herbivore, invertebrate predator, and fish biomass, respectively. In Appendix A, these equations are solved for their non-trivial equilibrium point and the stability of this point is considered.

Top-down effects can be explored by examining how a change in the fish death rate m_4 affects lower trophic levels. The change in phytoplankton biomass with respect to a change in m_4 can be computed from eqn (22) (see Appendix A) as

$$\frac{\partial x_1^*}{\partial m_4} = \frac{K a_{12}}{\Delta} (a_{23} a_{34} - a_{24} a_{33}). \quad (12)$$

Thus, an increase in the fish death rate (and hence a decrease in fish biomass) will have a negative effect on the phytoplankton biomass when

$$a_{24} a_{33} > a_{23} a_{34} \quad (13)$$

and will have a positive effect if the inequality is reversed. Note the importance of a high invertebrate predator self-limitation rate a_{33} in inducing a positive correspondence between fish and phytoplankton biomass. It can be similarly computed that the effect of an increase in fish mortality on herbivores is opposite in sign to that of phytoplankton, and always increases the invertebrate predator biomass. Also, an increase in invertebrate predator mortality m_3 always decreases phytoplankton biomass and increases herbivore biomass, while its effect on fish could be either positive or negative [see Table 2(b)].

Bottom-up effects in this model can be computed as in the Holt and Polis model. For example,

$$\frac{\partial x_1^*}{\partial r} = \frac{K - x_1^*}{\Delta} [a_{23}a_{24}a_{34}(b_{23}b_{34} - b_{24}) + a_{22}a_{34}^2b_{34} + a_{24}^2b_{24}a_{33} + a_{23}^2b_{23}a_{44} + a_{22}a_{33}a_{44}]. \quad (14)$$

Bottom-up effects are more complex than those predicted by simple food chain models. Self-limitation at any level increases the positive effect of enrichment on phytoplankton. On the other hand, if there is no self-limitation in the consumer compartments, and the conversion efficiencies b_{24} and b_{34} are equal, enrichment would actually decrease phytoplankton biomass.

Table 2(b) shows the responses of this model to increases in mortality in each of the consumer compartments, and also to increased nutrient levels. The behavior of this model is not totally analogous to either a three- or a four-level chain [see Table 2(a) and 2(b)]. Many of the responses depend on the exact choices of parameters.

Simulation Model

MODEL DESIGN

The two models considered above assume linear functional responses that are at best crude approximations near equilibrium. To test the generality of the conclusions given above in a more realistic setting, a simulation model was developed based on a typical food web of a small-bodied zooplankton lake, as represented by that of Lake Kinneret in northeastern Israel.

This model has nonlinear functional responses, an omnivorous invertebrate “predator” compartment, and no fish intracompartamental predation; these assumptions correspond with the actual Lake Kinneret food web (Hart *et al.*, 2000). It was parameterized to the average summertime conditions in this lake during the period 1989–1992. General information about Lake Kinneret can be found in Serruya (1978) and Hart *et al.*, (2000), and the references therein. The base of the Lake Kinneret food web was comprised of nano- and picoplankton, consisting mostly of nanophytoplankton and heterotrophic bacteria. There were often high levels of large net phytoplankton, but these were almost completely inedible by zooplankton, and thus were excluded from this model. The herbivore compartment was dominated by small cladocerans, but rotifers and ciliated protozoa were also present. The main invertebrate predator in this system was the copepod *Mesocyclops ogunnus*. It is primarily herbivorous during its naupli and early copepodite stages, but carnivorous in later stages (Gophen, 1977). For simplicity, the copepods were modeled as a single omnivorous compartment rather than stage-structured. The fish compartment consisted primarily of the “Kinneret sardine” *Acanthobrama terraesanctae*, which consumes both herbivorous zooplankton and copepods (Gophen & Threlkeld, 1989). There were also fish in Lake Kinneret that are primarily herbivorous, but these fish consume little, if any, nanophytoplankton, and so are of minor importance for the questions of interest here. Hence, it was assumed that the fish are strict zooplanktivores.

The nano/picoplankton compartment was modeled to grow logistically. Grazing by herbivores on nano/picoplankton was modeled by a prey-dependent Holling type-II functional response that has been shown to be reasonably accurate for filter-feeding cladocerans (Porter *et al.*, 1982; McCauley *et al.*, 1988). The dominant herbivores are relatively unselective filter-feeders, and interference competition is unlikely to be strong. Thus, no good case can be made to include predator dependence in the herbivores’ functional response (Diehl *et al.*, 1993).

The situation is different, however, for predation by fish and invertebrate predators. Zooplankton respond to heavy fish predation by diel vertical migrations, reduced size and visibility, and other defensive techniques that make them less vulnerable to visually foraging fish (Zaret, 1980; Havel, 1987; Lampert, 1987; O'Brien, 1987; Scheffer, 1997). On the other hand, heavy predation by invertebrates elicits defensive responses in herbivorous zooplankton such as increases in size, changes in shape, and growth of spines that make them more difficult for gape-limited invertebrate predators such as copepods to consume (Kerfoot, 1977; Zaret, 1980; Scheffer, 1997). Note that the defenses against fish predation are not generally effective against invertebrate predators and vice versa. The result of these defensive responses is that at the same level of prey biomass, the fish per capita consumption rate will be lower when there is heavy fish predation pressure than when fish predation is modest, and similarly for invertebrate predators (Ives & Dobson, 1987; Abrams, 1993; Abrams & Ginzburg, 2000). This means that the functional responses for the top two compartments will depend on predator as well as prey density. Besides antipredator defenses, spatial heterogeneities in predator densities (e.g. due to fish schooling), predator interference, and ontogenetic niche shifts may also contribute to predator dependence in the functional response (Mittlebach *et al.*, 1988; Cosner *et al.*, 1999; Abrams & Ginzburg, 2000).

These predator-dependent functional responses were modeled by assuming that they are of Monod form, with predator dependence of the type proposed by Hassell & Varley (1969) (termed "Hassell and Varley type II model" by Jost & Ellner, 2000). This leads to a functional response of the form

$$f(x, p) = \frac{rx/p^\gamma}{1 + \alpha x/p^\gamma} = \frac{rx}{p^\gamma + \alpha x}, \quad (15)$$

where x and p represent prey and predator density, and r , α , and γ are constants. The exponent γ represents the level of predator dependence in the functional response; $\gamma = 0$ gives a prey-dependent Holling type-II response, whereas $\gamma = 1$ leads to a full "ratio-dependent"

functional response (Ginzburg & Akçakaya, 1992; Sarnelle, 1994). For the reasons discussed above, the predator-independent case $\gamma = 0$ can be ruled out, while the full ratio-dependent response $\gamma = 1$ is also likely to be unrealistic (Diehl *et al.*, 1993; Abrams, 1994; Abrams & Ginzburg, 2000). The middle value of $\gamma = 1/2$ was chosen here. This choice allows for predator dependence in the functional response while avoiding many of the problems of full ratio-dependent response since the functional response still depends more strongly on prey than predator density. For example, if both the predator and the prey biomasses tend to zero in a proportional way, then eqn (15) implies that the predation rate would tend to zero, rather than to a non-zero constant as in a full ratio-dependent model.

In the actual model, both invertebrate predators and fish consume more than one prey type. If x_k represents the predator biomass, and x_1, \dots, x_k represents its potential prey, then a multi-prey version of eqn (15) is

$$f_k(x_1, \dots, x_k) = \frac{r_k \sum_i \alpha_{ik} x_i}{\sum_i \alpha_{ik} x_i + \sqrt{x_k}}. \quad (16)$$

Based on these considerations, the simulation model is given by four equations below. These equations, together with the parameter values given in Table 1, will be referred to as the standard simulation model:

$$\begin{aligned} \frac{dx_1}{dt} = & \left[r_1(1 - x_1/K) - \frac{r_2 \alpha_{12} x_2}{1 + \alpha_{12} x_1 + \alpha_{22} x_2} \right. \\ & \left. - \frac{r_3 \alpha_{13} x_3}{\alpha_{13} x_1 + \alpha_{23} x_2 + \alpha_{33} x_3 + \sqrt{x_3}} \right] x_1, \end{aligned} \quad (17)$$

$$\begin{aligned} \frac{dx_2}{dt} = & \left[\frac{r_2 [\beta_2 \alpha_{12} x_1 + (\beta_2 - 1) \alpha_{22} x_2]}{1 + \alpha_{12} x_1 + \alpha_{22} x_2} - d_2 \right. \\ & - \frac{r_3 \alpha_{23} x_3}{\alpha_{13} x_1 + \alpha_{23} x_2 + \alpha_{33} x_3 + \sqrt{x_3}} \\ & \left. - \frac{r_4 \alpha_{24} x_4}{\alpha_{24} x_2 + \alpha_{34} x_3 + \sqrt{x_4}} \right] x_2, \end{aligned} \quad (18)$$

TABLE 1

Parameters and estimated average summertime biomasses (in units of mg C m⁻²) for the standard four-compartment simulation model

		Compartment							
		1		2		3		4	
r		0.78		2.7		2.0		0.047	
β				0.24		0.13		0.12	
d				0.071		0.053		0.0042	
K		10 000							
eqnbrm biomass		5200		1250		400		2000	
		Subscript							
		12	22	13	23	33	24	34	
α		1.8×10^{-4}	4.6×10^{-5}	5.5×10^{-3}	0.011	6.4×10^{-3}	0.077	0.096	

$$\frac{dx_3}{dt} = \left[\frac{r_3[\beta_3(\alpha_{13}x_1 + \alpha_{23}x_2) + (\beta_3 - 1)\alpha_{33}x_3]}{\alpha_{13}x_1 + \alpha_{23}x_2 + \alpha_{33}x_3 + \sqrt{x_3}} - \frac{r_4\alpha_{34}x_4}{\alpha_{24}x_2 + \alpha_{34}x_3 + \sqrt{x_4}} - d_3 \right] x_3, \quad (19)$$

$$\frac{dx_4}{dt} = \left[\frac{r_4\beta_4(\alpha_{24}x_2 + \alpha_{34}x_3)}{\alpha_{24}x_2 + \alpha_{34}x_3 + \sqrt{x_4}} - d_4 \right] x_4. \quad (20)$$

Parameters were chosen so that the biomasses of the compartments, the rates of predation, and the rate of nano/picoplankton production at the non-trivial equilibrium point correspond to their mean summer levels in Lake Kinneret over the period 1989–1992, as estimated by Hart *et al.*, (2000). It was also assumed that the zooplankton compartments were half-saturated at the mean summer biomasses of their prey, representing a situation where they are mildly food limited. Fish were taken to be feeding somewhat closer (75%) to their saturation levels, consistent with their role as top predator. The parameters used are given in Table 1. The equations were solved numerically for their non-trivial equilibrium point using these parameters. The equilibrium values were asymptotically stable, except when the system was enriched by increasing K and r . At high values of enrichment, a Hopf bifurcation occurred and small stable oscillations about the

equilibrium point were seen. By contrast, the system would be unstable if simple Holling type-II responses were used for all consumers at realistic parameter values.

SIMULATION MODEL RESULTS

Top-down effects in this model are given in Fig. 2. Figure 2(a) is a plot of the phytoplankton equilibrium values as a function of the fish mortality rate d_4 , with all other parameters as in Table 1. The increase in d_4 from 0.0035 to 0.0055 d^{-1} had a large negative impact on fish biomass. This effect is transmitted to zooplankton, at least to some extent. Invertebrate predator biomass increased with decreasing fish biomass, due to the fact that they are both prey and competitors of fish. The net effect of the increase in invertebrate predators and decrease in fish on herbivores was slightly negative. This resulted in an increase in nano/picoplankton as the fish biomass declined.

The results from the Lotka–Volterra models suggest that invertebrate predator self-limitation may strongly influence the level and direction of top-down interactions. To test this idea in the simulation model, I increased the invertebrate predator self-limitation parameter to five times that of the estimated natural rate, with all other parameters as in Fig. 2(a) (see Table 1). The results are shown in Fig. 2(b). As suggested by the Lotka–Volterra model, high invertebrate

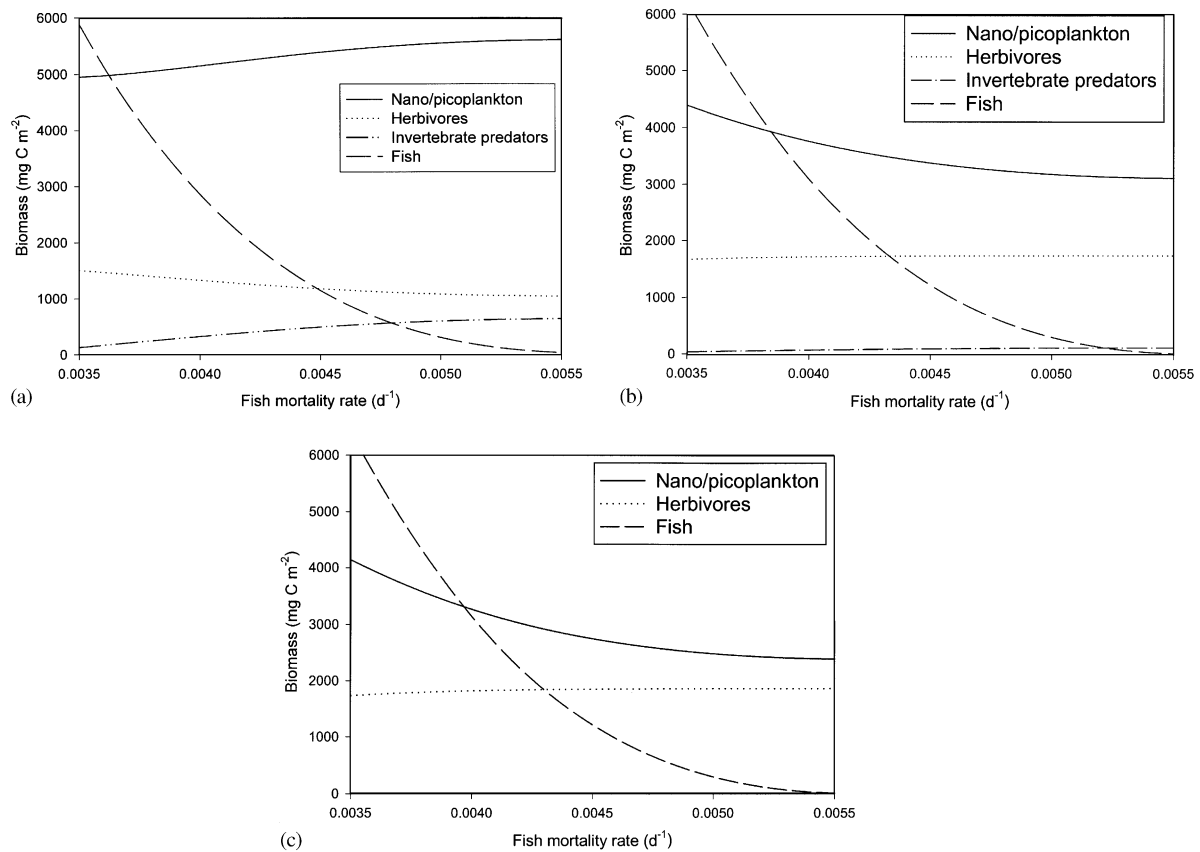


FIG. 2. The effect of a change in fish mortality rate on the biomass levels of each compartment in: (a) the standard four-compartment simulation model; (b) the simulation model with invertebrate predator self-limitation at five times the estimated natural level; and (c) the simulation model with the invertebrate predator compartment removed. Note that the direction of the effect of fish planktivory on the nano/picoplankton in (a) is opposite to that predicted by a simple food model such as (c), and that invertebrate predator self-limitation tends to push the IGP four-compartment model toward a positive relation between fish planktivory and phytoplankton biomass.

predator self-limitation induced a positive correlation between fish and nano/picoplankton. It also decreased the equilibrium biomass x_3^* of the invertebrate predator, itself causing a reduction in pico/nanoplankton biomass.

To simulate the situation where the dominant herbivores are invulnerable to invertebrate predators, the model was run with the invertebrate predator compartment removed, but with all other parameters as in Table 1 [Fig. 2(c)]. A change in the fish death rate cascaded in a more conventional manner to herbivores and phytoplankton under this scenario. Note also that phytoplankton levels are considerably lower here than in Fig. 2(a), indicating that the invertebrate predators themselves have a substantial top-down influence on phytoplankton levels.

Figure 3 shows the bottom-up response of the simulation models, in which both r and K were increased proportionately by a factor p . This parameter can be considered as a surrogate for the input level of a limiting nutrient. Figure 3(a) shows the results of runs with p varying from 0.6 to 1.4. In contrast to top-down effects, it is apparent that bottom-up effects remained strong in all but the invertebrate predator compartment. Fish and herbivores displayed the strongest response to enrichment. The Lotka-Volterra model suggested that self-limitation in consumer compartments can enhance the bottom-up effect on the basal compartment. To check this, I reran the model with herbivore and invertebrate predator intracompartamental predation increased by a factor of two [Fig. 3(b)]. As predicted, the increase in self-limitation

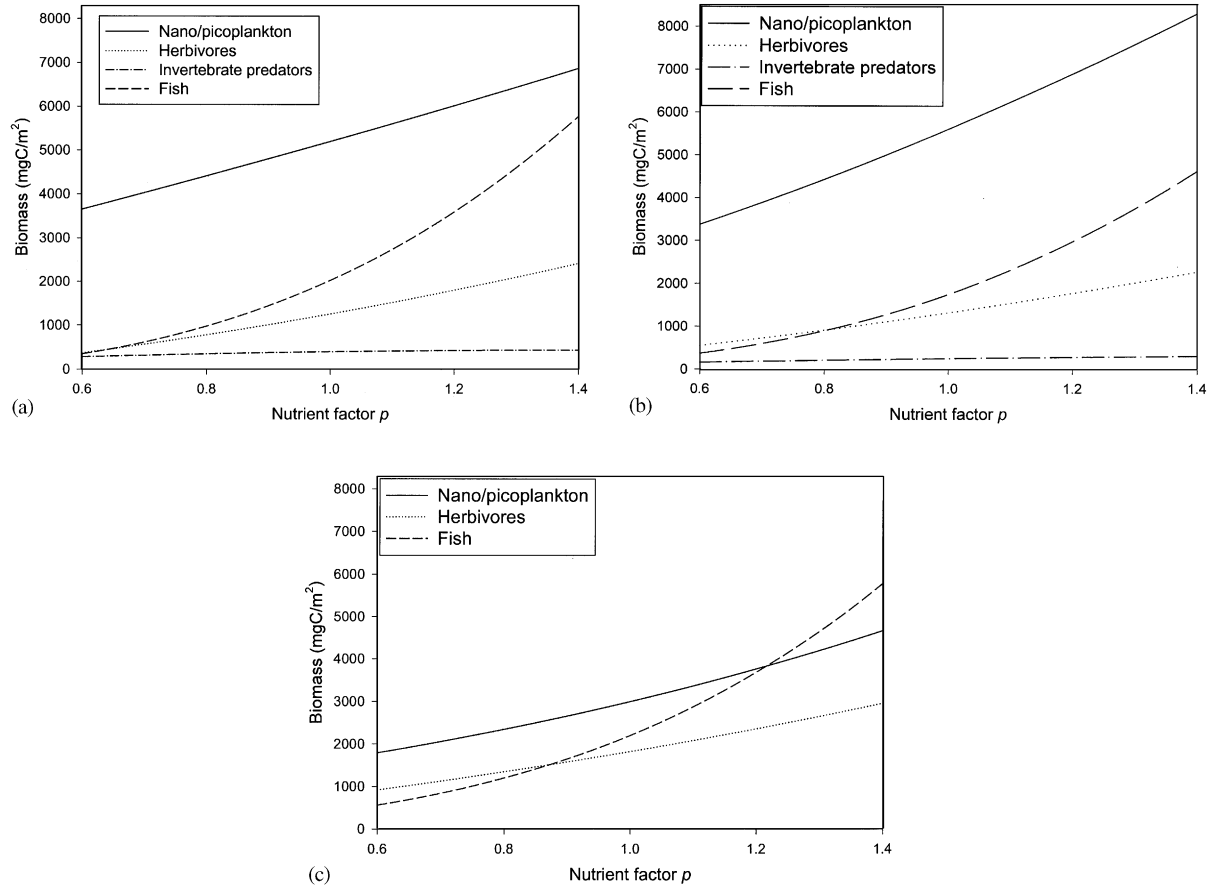


FIG. 3. The effect of changes in the growth rate of the basal nano/picoplankton compartment on the equilibrium biomass of each compartment of the simulation models: (a) the standard four-compartment model; (b) the four-compartment model with herbivore and invertebrate predator self-limitation increased by a factor of two; and (c) the simulation model with the invertebrate compartment removed. The “nutrient factor” p indicates the relative growth rate of the nano/picoplankton compartment compared to that of natural conditions. Note that unlike classic food chain models with prey-dependent functional responses, these models generally predict positive relationships between nutrients and the biomasses of all trophic levels. Also, the response of herbivore biomass to increased nutrients is especially strong in the IGP model (a), and increased zooplankton self-limitation tends to enhance the response of phytoplankton biomass to enrichment.

induced an enhanced response of the nano/picoplankton compartment to enrichment. Figure 3(c) shows the effects of enrichment when the invertebrate predator compartment was removed. Enrichment increased the biomass of all levels, and was most evident in fish.

Table 2(c) gives the response of the standard and three-compartment (without invertebrate predators) simulation models to increased fish, invertebrate predator, or herbivore mortality, or to increased nutrients. The responses of the three-compartment simulation model to increased mortality in any of the consumer compartments qualitatively resemble those of simple tri-trophic food chains, while the

four-compartment model was qualitatively more similar to a simple four-level chain. Enhanced nutrient levels increased the biomasses of all compartments in both models. This is in conformance with most experimental observations, but not with simple food chain models with prey-dependent functional responses.

Discussion

THEORETICAL IMPLICATIONS OF INTRAGUILD PREDATION TO FOOD WEB THEORY

The analysis of the basic Holt and Polis intraguild predation model indicates that in the absence of self-limitation among IG prey, an

TABLE 2

The effect of various perturbations on the basic IGP model, the four-compartment Lotka–Volterra model, the three- and four-compartment simulation models, and on two-, three- and four-level food chain models with linear functional responses

(a)	IGP model			Two-level L–V chain		Three-level L–V chain		
	T-M	G-M	N	T-M	N	T-M	G-M	N
T (IG predator)	–	?	+	–	+	–	–	+
G (IG prey)	+	–	?	N/A	N/A	+	0*	0†
B (basal resource)	–‡	+	+	+	0†	–	0†	+

(b)	L–V Four-compartment IGP model				Four-level L–V chain			
	F-M	I-M	H-M	N	F-M	I-M	H-M	N
F (fish)	–	?	–	+	–	–	–	+
I (invertebrate predator)	+	–	?	?	+	0§	0§	0¶
H (herbivores)	–	+	–	+	–	0¶	–	+
P (nano/picoplankton)	+**	–	+	?	+	0††	+	0††

(c)	Four-compartment simulation				Three-compartment simulation		
	F-M	I-M	H-M	N	F-M	H-M	N
F (fish)	–	–	–	+	–	–	+
I (invertebrate predator)	+	–	+	+	N/A	N/A	N/A
H (herbivores)	–	+	–	+	+	–	+
P (nano/picoplankton)	+	–	+	+	–	+	+

Note: For the food chain models in (a), “T” represents the top predator, “G” is the intermediate predator (for the three-level chain), and “B” represents the basal resource. For the four-level Lotka–Volterra chain [Fig. 2(b)], “P” represents the bottom level, while “H”, “I”, and “F” represents primary, secondary, and tertiary consumers, respectively. The manipulation “X–M” indicates an increase in the mortality of compartment X, while manipulation “N” represents an increase in the growth rate (i.e. an increase in r or K) of the basal resource. Responses are indicated as “+” for an increase in equilibrium biomass, “–” for a decrease in equilibrium biomass, “0” for no change, and “?” if the result could be an increase or a decrease in equilibrium biomass, depending on parameters.

‡ Positive if G self-limitation is sufficiently large.

† Positive if T self-limitation > 0.

* Negative if T self-limitation > 0.

|| Positive if I self-limitation is sufficiently large.

** Negative if I self-limitation is sufficiently large.

§ Negative if F self-limitation > 0.

¶ Positive if F self-limitation > 0.

†† Positive if either F or H self-limitation > 0.

increase in IG predator mortality will always induce a rather surprising decrease in their basal resource prey, due to an overcompensatory increase in predation by the IG prey. This is in agreement with the age-structured model of Palomares *et al.* (1995), and shows that their result did not depend on the details of their lynx–mongoose–rabbit system (except for the lack of self-limitation in the IG prey compartment), but is a general property of intraguild predation systems.

This result can be conceptualized in the following way. The IG prey must be superior competitors for the basal resource (Holt & Polis, 1997), and hence they are capable of reducing the basal resource to a lower level than the IG predators. An increase in the IG predator mortality will decrease the biomass of the IG predator, and hence increase that of the competitively superior IG prey, resulting in a lower basal resource abundance.

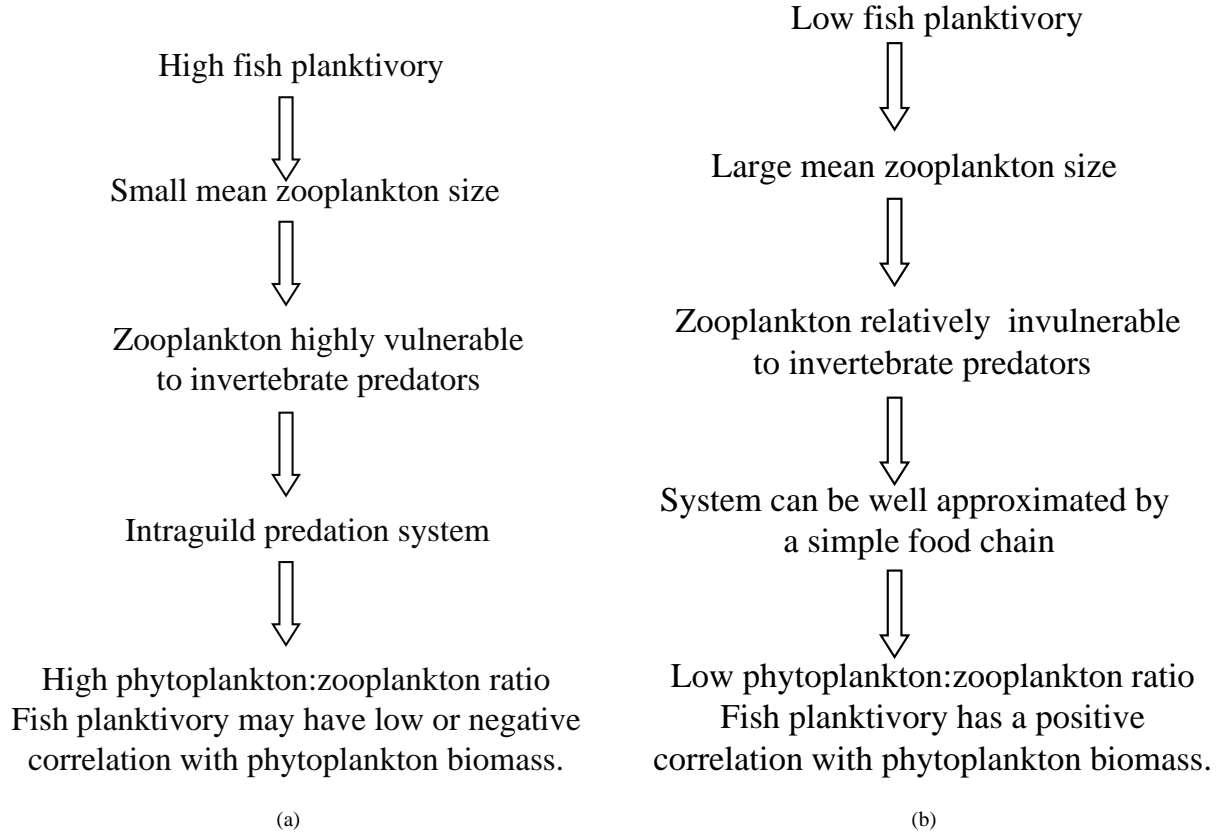


FIG. 4. Schematic representation of two alternative lake food web states. In (a), high fish planktivory induces a small mean zooplankton size, substantial IGP predation via invertebrate predators, and hence a high phytoplankton : zooplankton ratio and unconventional responses to top-down manipulation. In (b), low fish planktivory induces a system that more closely resembles a simple food chain, with large mean zooplankton size, a low phytoplankton : zooplankton ratio, and a top-down response similar to that predicted by food chain theory. The very large “cascade” effects sometimes observed are likely induced primarily by a regime shift from (a) to (b), rather than the simple food chain effects usually considered.

Self-limitation in the IG prey compartment can strongly affect top-down responses. An increase in IG predator mortality will induce a decrease in the basal resource when

$$a_{12}a_{23} > a_{13}a_{22} \quad (21)$$

and will increase the basal resource when this inequality is reversed. The term on the left-hand side of this inequality, $a_{12}a_{23}$, is a measure of the strength of the three-level chain: basal resource \rightarrow IG prey \rightarrow IG predator. When this chain is relatively strong, it is intuitively clear that an increase in IG predator mortality should decrease basal resource biomass. However, even when this chain is weaker than the direct consumption of basal resource by the IG

predator, an increase in IG predator mortality will only induce an increase in the basal resource if IG prey self-limitation is sufficiently strong (i.e. if $a_{13}a_{22}$ is sufficiently large). Thus, the dynamics of this system cannot be inferred by just considering its constituent food chains, but must be analysed in its entirety.

Responses to enrichment can also be influenced by intraguild predation and self-limiting factors. In all of the models, self-limitation of any compartment enhanced the bottom-up effect of enrichment on the base of the food web. Intraguild predation can also sometimes induce such an effect, as the analysis of the Holt and Polis model shows. However, in a tri-trophic chain, where enrichment normally increases the biomass of the base of chain, the addition of an

intraguild predation component (e.g. invertebrate predators) can weaken the response of phytoplankton to enrichment.

The overly simplistic functional responses in the two Lotka–Volterra type models may be another reason that some simple food chain models fail to predict positive responses to enrichment at all levels (Ginzburg & Akçakaya, 1992; Abrams & Ginzburg, 2000). Indeed, the three-compartment simulation model displayed strong responses at all levels [Fig. 3(c)], while the responses were strong in the four-compartment simulation model in all but the invertebrate predator compartment [Fig. 3(a)]. Thus, modest levels of self-limitation and predator dependence in the functional responses of the top predator(s) are sufficient to induce positive responses to enrichment (see also Sarnelle, 1994).

It has been noted by Gismervik & Andersen (1997) that IGP systems with Holling type-II responses are stable only in a limited parameter range, at low productivity (see also Mylius *et al.*, 2001). They proposed a prey-switching mechanism, leading to a Holling type-III response, as a mechanism for stabilizing IGP models. Here, predator dependency in the functional response, induced by anti-predator defenses, was shown to be another mechanism that stabilizes models with intraguild predation. Predator-dependent functional responses are likely to be common in natural systems (Abrams, 1993; Cosner *et al.*, 1999; Abrams & Ginzburg, 2000), and may be an important mechanism for stabilizing complex food webs. Interestingly, the four-compartment IGP simulation model was stable over a larger range of parameter values than was the corresponding three-level chain, and intracompartamental predation also enhanced food web stability. These results support the recent idea that omnivory can often be stabilizing (Fagan, 1997).

RELATIONSHIP OF MODEL RESULTS TO EXPERIMENTAL EVIDENCE IN LAKE FOOD WEBS

Differences in food web structure may explain why trophic cascades are observed more often in *Daphnia*-dominated lakes than in lakes with mostly small zooplankton, because substantial

levels of invertebrate predation are more likely to occur in the latter type of lake. This is in opposition to the conventional explanation based on the “size-efficiency hypothesis” (Brooks & Dodson, 1965; Hall *et al.*, 1976). Under the latter viewpoint, cascades occur in *Daphnia*-dominated lakes because these animals are more efficient herbivores than are smaller zooplankton (Carpenter & Kitchell, 1984; Declerck *et al.*, 1997). While the results of some studies have supported the size-efficiency hypothesis (Hall *et al.*, 1976; Gerritsen, 1984; Gliwicz, 1990; Gliwicz & Lampert, 1993), others have not (Dodson, 1974; Lynch, 1978; DeMott, 1982; Bogdan & Gilbert, 1984; Peters & Downing, 1984; Tessier & Goulden, 1987; Turner & Mittlebach, 1992; Peters, 1992), or have suggested that it applies only under eutrophic conditions (Romanovsky, 1984; Hansson *et al.*, 1998).

Turner & Mittlebach (1992) tested whether zooplankton size has a direct effect on trophic cascades. In their experiment, they used lake water where the natural macrozooplankton assemblage had been removed, after which either *Daphnia* or the smaller cladoceran *Ceriodaphnia* were added. They found that *Ceriodaphnia* were just as effective in transmitting top-down effects as were *Daphnia*. These results cannot be explained by the size-efficiency hypothesis, which would predict that steady-state phytoplankton biomass would be lower in the *Daphnia* treatments because of their putative competitive superiority. On the other hand, the results are in full agreement with the models presented here. Because invertebrate predators were excluded from the enclosures, the food webs in these experiments could be approximated by simple food chains, and hence trophic cascades would be expected in all treatments.

The analyses presented here also indicate that invertebrate predators themselves exert a strong top-down influence on phytoplankton. The simulation model indicates that the presence of invertebrate predators can almost double the level of nano/picoplankton compared with a similar system that lacks these predators. This suggests that the successful introduction of an invertebrate predator will reduce herbivorous zooplankton abundance. Such a phenomenon

has been observed after the introduction of the opossum shrimp *Mysis relicta* into a number of lakes (Goldman *et al.*, 1979; Rieman & Falter, 1981; Chipps & Bennett, 2000).

It has been observed that lakes dominated by large zooplankton tend to have a lower phytoplankton:zooplankton ratio than those lakes with mostly small zooplankton (Pace, 1984; Sterner, 1989; Carpenter *et al.*, 1991; Havens, 1998; Jeppesen *et al.*, 2000), which again has been attributed to more efficient grazing by large zooplankton (Carpenter & Kitchell, 1984; Carpenter *et al.*, 1991). However, these observations may instead be explained by variations in food web structure. The phytoplankton:zooplankton ratios seen in the four-compartment simulation model [Fig. 2(a)] are considerably higher than when the invertebrate predator compartment has been removed [Fig. 2(c)], due to the top-down influence of invertebrate predators in the four compartment model. Note that the per capita herbivore grazing rates in these two simulations are the same. Thus, differences in relative vulnerability to invertebrate predators may be an important factor in explaining the observed patterns in the phytoplankton:zooplankton ratio.

Even the food chain model given here predicts only a modest effect of fish on phytoplankton [Fig. 2(c)]. The dramatic changes seen in a minority of trophic cascade experiments may be due to a more complex mechanism than the simple food chain cascade usually considered. Changes in fish planktivory often induce concomitant changes in zooplankton species composition (Hrbáček *et al.*, 1961, Brooks & Dodson, 1965; Zaret, 1980; Kerfoot & DeMott, 1984). Because large cladocerans are more vulnerable to fish predation, they will be eliminated at high levels of fish planktivory. On the other hand, such large cladocerans are likely to become dominant at low levels of fish planktivory because their size allows them to escape most predation by invertebrates (Dodson, 1970, 1974; Zaret, 1980). Thus, after a fish manipulation, a system may transition from a small zooplankton/intraguild predation system at high levels of planktivorous fish [Fig. 2(a)] to a large zooplankton/food chain system at low levels of such fish. Comparison of the left-hand

side of Fig. 2(a) with the right-hand side of Fig. 2(c) shows that if a system undergoes such a food web shift, phytoplankton would be reduced by about half. This is in good quantitative agreement with that observed in the minority of cascade experiments in which there were large changes in phytoplankton abundance (Brett & Goldman, 1996).

The above ideas are summarized in Fig. 4. Systems where fish planktivory is high are characterized by small mean zooplankton size and substantial invertebrate predation on zooplankton [Fig. 4(a)]. Such systems will have high phytoplankton:zooplankton ratios and a change in fish planktivory will have a negative or negligible effect on phytoplankton biomass. Systems with low fish planktivory will typically have a large mean zooplankton size and invertebrate predators will often not play an important role [Fig. 4(b)]. In this case, a low phytoplankton:zooplankton ratio would be expected and cascade effects should follow those predicted by food chain theory. Very large changes in phytoplankton biomass, however, would be induced primarily by a regime shift from the system depicted in Fig. 4(a) to that given in Fig. 4(b), rather than the simple food chain cascade usually considered.

The models predict that a decrease in fish planktivory should be accompanied by increases in predation of zooplankton by invertebrates. This prediction is consistent with many experimental and observational studies (Hrbáček *et al.*, 1961; Hurlbert *et al.*, 1972; Kerfoot & DeMott, 1984; McQueen *et al.*, 1986; Benndorf, 1987; Elser *et al.*, 1987; Hansen & Jeppesen, 1992; Findlay *et al.*, 1994; González & Tessier, 1997; Wissel & Benndorf, 1998) that found increases in invertebrate predators following decreases in fish planktivory. The models also predict that in systems where invertebrate predation is substantial, planktivory by fish may have a negative correlation with phytoplankton biomass. This phenomenon was observed in Lake Washington (Edmundson & Abella, 1988) and in biomanipulation experiments in Germany (Wissel & Benndorf, 1998; Wissel *et al.*, 2000; Benndorf *et al.*, 2000).

Many empirical studies have shown a strong correlation between the levels of primary

production and the standing stocks of higher trophic levels (e.g. McQueen *et al.*, 1986; Sarnelle, 1992; Ginzburg & Akçakaya, 1992; Mazumder, 1994), in reasonable agreement with the results of the simulation models. In contrast to conventional tri-trophic models, the four-compartment Lotka–Volterra and simulation models both predict positive responses of herbivores to enrichment (see Fig. 3). Intraguild predation and self-limiting factors can therefore substantially affect bottom-up responses of food webs.

The models analysed here were deliberately kept as simple as possible, so that they could be easily compared to simple food chain models. Factors not modeled here such as inedible algae, nutrient cycling, and nutrient limitation of consumers are likely to induce behavior that may differ from that predicted by classic food chain theory (e.g. Liebold, 1989; Elser *et al.*, 2000). Another phenomenon that is not fully considered here is trophic ontogeny (Mittlebach *et al.*, 1988). Juvenile invertebrate “predators” are often actually herbivorous. These juveniles are likely to be inferior competitors to the dominant herbivores (Kerfoot & DeMott, 1984). Other juvenile invertebrate predators feed on microzooplankton that are often also inferior competitors to larger herbivores. In either case, competition from the dominant herbivores can prevent the invasion of invertebrate predators into a system where they were absent (Kerfoot & DeMott, 1984; Benndorf, 1987; Neill, 1988). On the other hand, once invertebrate predators are established, their top-down influence can increase levels of phytoplankton biomass, thus preventing such competitive “bottlenecks” on their juveniles. This leads to the possibility of hysteresis (alternative steady states) that has sometimes been observed in aquatic food webs (Polis *et al.*, 1989; Scheffer *et al.*, 1993).

Conclusions

The models analysed here indicate that the trophic cascades observed in lake food webs are more complex than those suggested by simple food chain models. Invertebrate predators can introduce intraguild predation and self-limiting

factors into these webs. These phenomena can not only affect the predictions of food chain theory (Table 2), but shifts in the levels of intraguild predation may itself induce large changes in phytoplankton biomass. The dynamics of intraguild predation systems is not analogous to any simple food chain, nor can it be correctly predicted by any combination or approximation of food chains.

Intraguild predation and self-limiting factors are often ignored in trophic models for the sake of simplicity, despite being nearly ubiquitous in natural systems (Polis *et al.*, 1989). The results presented here indicate that these phenomena can crucially influence both bottom-up and top-down properties of food webs, and thus need to be taken into account in modeling any system where such processes are substantial.

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APPENDIX A

Equations (8)–(11) can be solved for their non-trivial equilibrium point by setting the derivatives to zero and solving the resulting set of linear equations:

$$\begin{aligned} x_1^* &= \frac{K}{\Delta} [ra_{23}a_{24}a_{34}(b_{23}b_{34} - b_{24}) \\ &\quad + r(a_{22}a_{34}^2b_{34} + a_{24}^2b_{24}a_{33} \\ &\quad + a_{23}^2b_{23}a_{44} + a_{22}a_{33}a_{44}) \end{aligned} \quad (\text{A.1})$$

$$\begin{aligned} &+ m_2a_{12}(a_{34}^2b_{34} + a_{33}a_{44}) \\ &- m_3a_{12}(a_{23}a_{44} + a_{24}a_{34}b_{34}) \\ &+ m_4a_{12}(a_{23}a_{34} - a_{33}a_{24})], \end{aligned}$$

$$\begin{aligned} x_2^* &= \frac{r}{\Delta} [Ka_{12}b_{12}(a_{33}a_{44} + a_{34}^2b_{34}) \\ &- m_2(a_{34}^2b_{34} + a_{33}a_{44}) + m_3(a_{23}a_{44} \\ &+ a_{24}b_{34}a_{34}) + m_4(a_{33}a_{24} - a_{23}a_{34})], \end{aligned} \quad (\text{A.2})$$

$$\begin{aligned} x_3^* &= \frac{1}{\Delta} [Kra_{12}b_{12}(a_{23}b_{23}a_{44} - a_{34}a_{24}b_{24}) \\ &+ m_2r(a_{24}b_{24}a_{34} - a_{23}b_{23}a_{44}) \\ &- m_3(a_{12}^2b_{12}a_{44} + ra_{24}^2b_{24} + ra_{22}a_{44}) \\ &+ m_4(Ka_{12}^2b_{12}a_{34} + ra_{23}b_{23}a_{24} + ra_{22}a_{34})], \end{aligned} \quad (\text{A.3})$$

$$\begin{aligned} x_4^* &= \frac{1}{\Delta} [Kra_{12}b_{12}(a_{23}b_{23}a_{34}b_{34} + a_{24}b_{24}a_{33}) \\ &- m_2r(a_{23}b_{23}a_{34}b_{34} + a_{24}b_{24}a_{33}) \\ &+ m_3(ra_{23}a_{24}b_{24} - ra_{22}a_{34}b_{34} - Ka_{12}^2b_{12}a_{34}b_{34}) \\ &- m_4(ra_{22}a_{33} + Ka_{12}^2b_{12}a_{33} + ra_{23}^2b_{23})], \end{aligned} \quad (\text{A.4})$$

where

$$\begin{aligned} \Delta &= r[a_{23}a_{24}a_{34}(b_{23}b_{34} - b_{24}) + a_{22}a_{34}^2b_{34} \\ &+ a_{24}^2b_{24}a_{33} + a_{23}^2b_{23}a_{44} + a_{22}a_{33}a_{44}] \\ &+ Ka_{12}^2b_{12}(a_{34}^2b_{34} + a_{33}a_{44}). \end{aligned} \quad (\text{A.5})$$

Since an increase in fish mortality will decrease the fish equilibrium biomass x_4^* (this can be seen rigorously by performing a perturbation analysis as described in Yodis, 1988), $\partial x_4^*/\partial m_4 = -(ra_{22}a_{33} + Ka_{12}^2b_{12}a_{33} + ra_{23}^2b_{23})/\Delta$ must be negative. This implies that Δ must be greater than 0 at any positive equilibrium.

The stability of this point can be analysed by considering the characteristic polynomial

$$p(\lambda) = \lambda^4 + c_3\lambda^3 + c_2\lambda^2 + c_1\lambda + c_0 \quad (\text{A.6})$$

of the Jacobian matrix J associated with this system.

The coefficients of this polynomial can be calculated as

$$c_0 = \Delta x_1^* x_2^* x_3^* x_4^* / K,$$

$$c_1 = [a_{12}^2 b_{12} a_{33} + r(a_{22} a_{33} + a_{23}^2 b_{23})/K] x_1^* x_2^* x_3^*$$

$$+ (a_{24}^2 b_{24} + a_{22} a_{44}) x_2^* x_4^*$$

$$+ r(a_{12}^2 b_{12} a_{44} + a_{22} a_{44} + a_{24}^2 b_{24}) x_1^* x_2^* x_4^*/K$$

$$+ (a_{33} a_{44} + a_{34}^2 b_{34}) x_3^* x_4^*,$$

$$+ r(a_{33} a_{44} + a_{34}^2 b_{34}) x_1^* x_3^* x_4^*/K$$

$$c_3 = r x_1^*/K + a_{22} x_2^* + a_{33} x_3^* + a_{44} x_4^*. \quad (\text{A.7})$$

$$+ [a_{22}(a_{34}^2 b_{34} + a_{33} a_{44}) + a_{23} a_{24} a_{34}(b_{23} b_{34} - b_{24})$$

$$+ a_{23}^2 b_{23} a_{44} + a_{24}^2 b_{24} a_{33}] x_2^* x_3^* x_4^*,$$

$$c_2 = (a_{12}^2 b_{12} + r a_{22}/K) x_1^* x_2^*$$

$$+ r(a_{33} x_1^* x_3^* + a_{44} x_1^* x_4^*)/K$$

$$+ (a_{22} a_{33} + a_{23}^2 b_{23}) x_2^* x_3^*$$

According to the Routh–Hurwitz criteria (see e.g. Edelstein-Keshet, 1988), the equilibrium will be stable if $c_i > 0$, $i = 0, \dots, 3$ and $c_1 c_2 c_3 > c_1^2 + c_3^2 c_0$. Since c_0, c_2 , and c_3 are all positive, $c_1 > 0$ provided that the final inequality is also satisfied. Hence, the criterion for stability of the equilibrium point is that $c_1 c_2 c_3 > c_1^2 + c_3^2 c_0$. This last inequality may or may not be satisfied, depending on the parameter choices (c.f. Holt & Polis, 1997, Diehl & Feissel, 2000).