

# Effects of Multi-chain Omnivory on the Strength of Trophic Control in Lakes

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## ABSTRACT

Omnivory has been implicated in both diffusing and intensifying the effects of consumer control in food chains. Some have postulated that the strong, community level, top-down control apparent in lakes is not expressed in terrestrial systems because terrestrial food webs are reticulate, with high degrees of omnivory and diverse plant communities. In contrast, lake food webs are depicted as simple linear chains based on phytoplankton-derived energy. Here, we explore the dynamic implications of recent evidence showing that attached algal (periphyton) carbon contributes substantially to lake primary and secondary productivity, including fish production. Periphyton production represents a cryptic energy source in oligotrophic and mesotrophic lakes that is overlooked by previous theoretical treatment of trophic control in lakes. Literature data demonstrate that many fish are multi-chain omnivores, exploiting food chains

based on both littoral and pelagic primary producers. Using consumer-resource models, we examine how multiple food chains affect fourth-level trophic control across nutrient gradients in lakes. The models predict that the stabilizing effects of linked food chains are strongest in lakes where both phytoplankton and periphyton contribute substantially to production of higher trophic levels. This stabilization enables a strong and persistent top down control on the pelagic food chain in mesotrophic lakes. The extension of classical trophic cascade theory to incorporate more complex food web structures driven by multi-chain predators provides a conceptual framework for analysis of reticulate food webs in ecosystems.

**Key words:** top down control; omnivory; littoral-pelagic coupling; consumer-resource models; trophic cascades; food webs.

## INTRODUCTION

Predator-induced top-down control of resources and omnivory have persisted in uneasy coexistence as two dominant themes of food web theory. In particular, omnivory has thwarted attempts by ecologists to reduce trophic interactions into simple chain-like dynamics, complicating models of top

down control that are predicated on discrete trophic levels (Strong 1992; Polis and Strong 1996; Persson 1999; Polis and others 2000). Trophic cascades are the extreme form of top-down control in which top predators suppress their prey and cause alternate control by and release from predation across successively lower trophic levels, ultimately to the level of primary producers. Multi-channel omnivory, or allochthonous energy subsidies from adjacent ecosystems, can facilitate or attenuate trophic cascades (Polis and others 2000), and

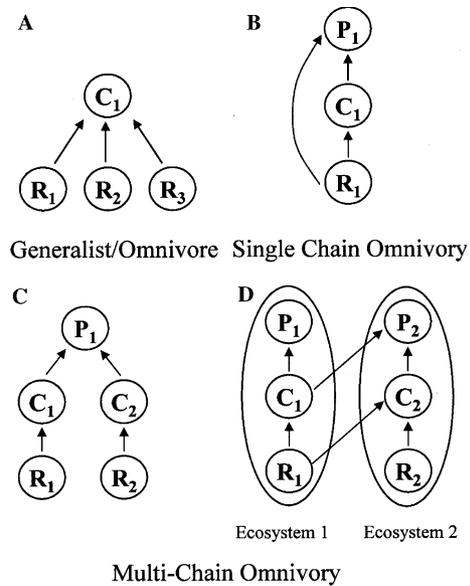
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predator exploitation of multiple resources within ecosystems profoundly affects the expression of top-down control (Schindler and others 1996; Estes and others 1998; Post and others 2000; Ramcharan and others 2001). In this paper, we use consumer-resource models to explore how the dependence of omnivorous predators on multiple food chains affects the strength and stability of top-down trophic control across eutrophication gradients in lakes.

Omnivory is a common feature of food webs that reflects consumers' flexibility in energy acquisition (Yodzis 1984). Inclusive definitions equate omnivory with generalist foraging (Figure 1A), but the most widely accepted definition is that omnivores feed on more than one trophic level within a single food chain (Pimm and Lawton 1978), (Figure 1B). However, ecosystem structure can rarely be reduced to single food chains (Polis and Strong 1996), and predators, prey and resources often cross habitat and ecosystem boundaries (Polis 1991). This diversity of trophic pathways leading to top predators has motivated researchers to look beyond omnivory within simple linear food chains (Nakano and Murakami 2001; Roemer and others 2002) to develop concepts appropriate for more complex food web structures. Notable among these is Polis and Strong's (1996) "multi-channel omnivory", in which organisms feed off different trophic levels embedded in multiple energy channels or pathways. Here, we use "multi-chain" instead of "multi-channel" simply because a food chain is a historically acknowledged subunit of a food web. We use the term multi-chain omnivores for generalist predators that exploit multiple food chains based on different primary producer functional groups, including detritus (Figure 1C, D). This modern taxonomy of omnivory includes Pimm and Lawton's (1978) definition (Figure 1B) but also addresses Polis and Strong's (1996) insightful concerns with modern overemphasis on a single (focal) food chain perspective (Figure 1C, D). This extension of the single food chain concept is fundamental to understanding how large, mobile predators affect various food chains at ecologically meaningful temporal and spatial scales.

Like omnivory, dynamic trophic control of resources has been a dominant theme in ecologists' exploration of food webs, but top-down regulation is not expressed similarly in all ecosystems (Pace and others 1999; Persson 1999; Polis and others 2000; Power 2000; Schmitz and others 2000). In streams and pelagic ecosystems, strong top-down control sometimes results in community level trophic cascades that substantially alter the distribution of total biomass among all trophic levels



**Figure 1.** Development of concepts of omnivory **A**) omnivory defined as a consumer (C) that feeds on multiple resources (R); **B**) single chain omnivory was originally restrictively defined as a predator (P) that fed on both plants and animals, but now encompasses the most common modern definition, an organism that feeds on more than one trophic level within a food chain (Pimm and Lawton 1978); Polis and Strong (1996) pointed out that omnivory can occur across food chains either **C**) within an ecosystem or **D**) across ecosystem boundaries.

(Power and others 1985; Power 1990; Carpenter and Kitchell 1993; Jeppesen and others 1998; Jeppesen and others 1999; Carpenter and others 2001). This contrasts with the more isolated, chain-like cascades described for terrestrial ecosystems that lead to changes in species composition and sometimes to changes in biomass distribution (Pace and others 1999; Schmitz and others 2000). It has been argued that linear food chains, homogeneous trophic levels, and the isolated nature of lake food webs contribute to the common occurrence of trophic cascades in aquatic ecosystems compared to terrestrial ecosystems (Hairston and Hairston 1993; Polis and others 2000). The generalization that simple food web structures in aquatic systems enable trophic cascades whereas reticulate food webs in terrestrial ecosystems attenuate them has been challenged on an empirical basis (Chase 2000; Power 2000). Furthermore, such proposed simple, linear food chains are actually likely to lead to heightened consumer-resource instability and what Strong (1992) terms "runaway consumption", especially as ecosystem productivity increases (Rosenzweig 1971).

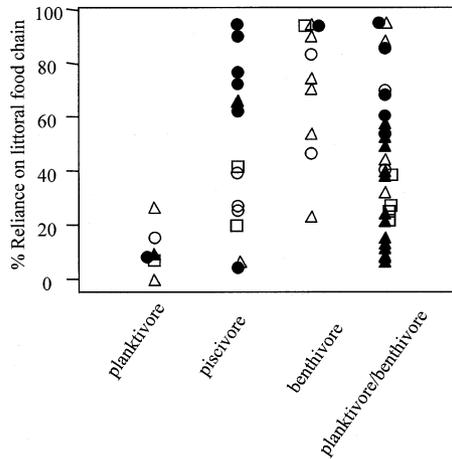
Despite the potential instability of strong top-down control, experiments in lakes and streams demonstrate that trophic cascades in which entire trophic levels respond to the addition or removal of top predators do persist over ecologically meaningful time scales (Power 1990; Jeppesen and others 1998; Carpenter and others 2001). This has prompted a search for factors that stabilize consumer-resource interactions in aquatic ecosystems and alter the expression of top-down control (Persson and others 1996). Stabilizing factors include: single-chain omnivory (Fagan 1997; McCann and Hastings 1997), consumer-mediated nutrient recycling (Drenner and others 1996; Pérez-Fuentetaja and others 1996; Ramcharan and others 1996; Vanni and Layne 1997), and prey refuges (Balciunas and Lawler 1995; Agrawal 1998). It is notable that the best-studied mechanisms that alter the expression of trophic cascades in lakes tend to enhance third level trophic control (planktivore dominance) and phytoplankton productivity. For example, planktivorous fish that feed on phytoplankton detritus strongly suppress zooplankton biomass while being maintained by a donor controlled phytoplankton detrital pathway (Stein and others 1995; Vanni 1996), and nutrient regeneration by fishes in planktivore-dominated lakes enhances phytoplankton productivity (Vanni 1996; Vanni and Layne 1997). In terrestrial ecosystems, control by top predators on individual food chains is strengthened when alternate prey sources are available and predators readily move across habitat boundaries (Terborgh and others 2001; Murakami and Nakano 2002; Roemer and others 2002). We suggest that similar dynamics may be induced by piscivorous fish that exploit both littoral and pelagic food chains in lakes.

Previous theoretical treatment of lake food webs assume a single primary production source – phytoplankton. This simple assumption may obscure critical food web dynamics that energetically link littoral and pelagic habitats (Schindler and Scheuerell 2002; Vadeboncoeur and others 2002). Piscivorous fish undergo ontogenetic diet shifts and even as adults are generalists that consume both benthic and pelagic prey, and this exploitation of zoobenthos potentially affects the expression of top down control (McQueen and others 1986; Persson and others 1991; Schindler and others 1996). Despite the historical emphasis on phytoplankton-based food webs in lakes, carbon stable isotope analysis has demonstrated that attached algae (periphyton) are a significant energy source for zoobenthos and ultimately for fish (Hecky and Hesslein 1995; Bootsma and others 1996; France

and Steedman 1996; Campbell and others 2000; Vander Zanden and Vadeboncoeur 2002). We augmented Hecky and Hesslein's (1995) comprehensive data set to illustrate that a wide variety of fish, regardless of feeding habits, are functionally multi-chain omnivores, deriving energy from both periphyton- and phytoplankton-based food chains (Figure 2). Among lakes, only planktivores show a consistent energetic link to their presumed, phytoplankton-based, food chain. Piscivores, benthivores, and benthic fish that can exploit pelagic prey exhibit the entire range of energetic linkages between food chains based on attached and planktonic algae.

The heavy energetic reliance of fishes on carbon fixed by periphyton begs the question of why most lake food web studies focus on phytoplankton-based carbon. Hecky and Hesslein (1995) postulate that ecologists either consistently underestimate periphyton productivity or that periphyton is more efficiently transferred up food chains. Although these possibilities are not mutually exclusive, evidence is accumulating that periphyton production is an often overlooked component of whole-lake primary production that can dominate whole-lake metabolism in oligotrophic lakes (Westlake and others 1980; Havens and others 2001; Vadeboncoeur and others 2001; Vadeboncoeur and Steinman 2002; Wetzel 1964). Relative periphyton contributions diminish with increased nutrient loading to the water column due to light limitation imposed by high phytoplankton concentrations (Jeppesen and others 1990; Hansson 1992; Scheffer and others 1993; Vadeboncoeur and others 2001), and phytoplankton is the dominant algal production source in eutrophic lakes (Vadeboncoeur and others 2003) (Figure 3). Furthermore, the expression of 4<sup>th</sup> trophic level top-down control varies unimodally over eutrophication gradients and is most common in mesotrophic lakes (Jeppesen and others 2003) suggesting underlying connections between patterns of energy production and trophic control.

Based on this evidence of cross-habitat energy linkages, we hypothesize that variable contributions of periphyton to whole-lake primary production combined with the dual reliance of fish on littoral and pelagic carbon provide a mechanism for the variation in the ability of piscivores to exert fourth level top-down control in lakes. Specifically, we used 4-trophic-level consumer-resource models to understand how linked benthic and pelagic food chains simultaneously influence the strength and stability of top-down control. Here, strength refers to the biomass of a consumer relative to the bio-

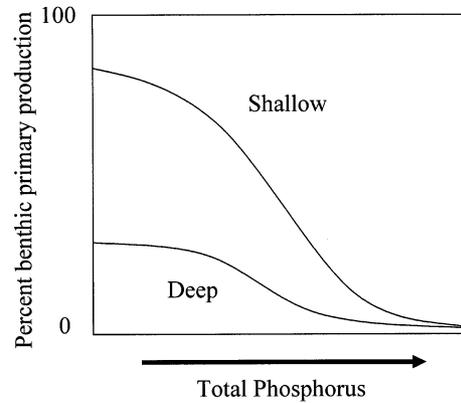


**Figure 2.** Stable isotope data demonstrating that many fish are multi-chain omnivores exploiting food chains based on attached littoral algae and phytoplankton. Data sources: ○ Experimental Lakes Area Lakes, Canada (Hecky and Hesslein 1995); ● Lake Memphremagog, Canada (Y. Vadeboncoeur, unpublished data); □ Lake Tahoe, US (Vander Zanden and others 2003); ▲ Lake Baikal, Russia (Yoshii 1999; Yoshii and others 1999); △ Lake Malawi, Africa (Hecky and Hesslein 1995). Fish were assigned functional feeding groups based on literature description of their feeding habits and prey derived from Scott and Crossman (1973) and Froese and Pauly (2002). Littoral and pelagic  $^{13}\text{C}$  endpoints were derived from primary consumers collected from multiple depths (if available) or primary producers.

mass of its resource. The more inverted the biomass pyramid, the stronger the top-down control. Stability refers to the capacity for a system to consistently express a given strength of control. In an unstable system, biomass pyramids shift among multiple possible configurations. The models are based on 4-trophic-level food webs linked at the top by piscivore predation. We examine the model output in the context of the extensive literature on whole-lake food web manipulations and piscivore dominance in lakes.

### MODELING ENERGY FLOW AND DYNAMIC CONTROL IN LAKES: LINEAR VERSUS LINKED FOOD CHAINS

A basic understanding of food chain theory can be derived from the two species Rosenzweig-MacArthur consumer-resource model (Rosenzweig 1971) (System 1 in Table 1). The “paradox of enrichment” is the classic example of the interaction between stability and trophic control in food chains. Rosenzweig (1971) pointed out that, for a broad suite of models, increases in resource carrying



**Figure 3.** Patterns in the distribution of primary production across eutrophication gradients in lakes: Whole-lake primary production becomes increasingly dominated by phytoplankton as lakes become more eutrophic and larger (redrawn from Vadeboncoeur and others 2003).

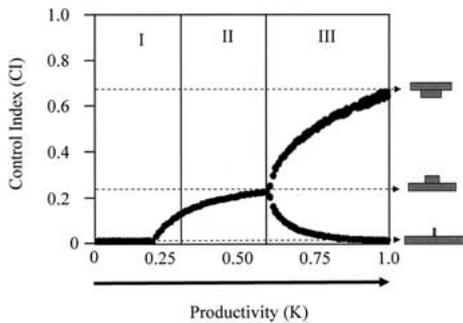
capacity ( $K$ ) (that is, productivity) impaired the stability of consumer-resource interactions. It is often not appreciated that increases in  $K$  in linear food chains also simultaneously modify the strength of top-down control such that increased productivity is associated with both decreased stability and the potential for the system to exhibit much stronger top-down trophic control on the resource.

To demonstrate this, we increased  $K$  and tracked the strength of top-down trophic control for each value of  $K$  by using the simple control index ( $\text{CI} = C_2 / (R_1 + C_2)$ ). Here, values of  $\text{CI}$  near 0 indicate that the zooplankton consumer density ( $C_2$ ) is low relative to its algal resource ( $R_1$ ), and the pyramid is “Eltonian” in shape. Conversely,  $\text{CI}$  values near 1 occur when consumer density is high relative to the resource and the biomass pyramid is inverted. We tracked maximum and minimum values for the  $\text{CI}$  index after 1000 time units at each productivity level,  $K$ . A stable outcome generates a single value for the control index, whereas a system that does not reach a single stable outcome generates multiple local minima and maxima for a given  $K$  (Figure 4). Increasing  $K$  generates unstable dynamics in which the system switches between relatively high and low control indices. Notably, when top-down control is expressed in this unstable region, it is stronger (higher  $\text{CI}$ ) than in the stable, lower productivity regions (Figure 4). Thus, the potential for strong top-down control is accompanied by a concomitant reduction in stability: strong top-down control is transitory and followed by periods of bottom up control (low  $\text{CI}$ 's). A corollary of this result is that strong top-down

**Table 1.** Consumer-resource Models

Model	Equation
System 1	$\frac{dZ}{dt} = ea_{Z,P} \frac{ZA_P}{A_P+b_{Z,P}} - d_{Z,P}Z$
System 2	$\frac{dA_P}{dt} = r_P A_P \left(1 - \frac{A_P}{K}\right) - a_{Z,P} \frac{ZA_P}{A_P+b_{Z,P}}$
Pelagic	$\frac{dA_P}{dt} = r_P A_P \left(1 - \frac{A_P}{K_T \rho}\right) - a_{Z,P} \frac{ZA_P}{A_P+b_{Z,P}}$
	$\frac{dZ}{dt} = ea_{Z,P} \frac{ZA_P}{A_P+b_{Z,P}} - d_{Z,P}Z - a_{P,P} \frac{P_P Z}{Z+b_{P,P}}$
	$\frac{dP_P}{dt} = ea_{P,P} \frac{P_P Z}{Z+b_{P,P}} - d_{P,P} P_P - a_{F,P} \delta \frac{FP_P}{P_P+b_{F,A}}$
	$\frac{dF}{dt} = e \left( \delta a_{F,P} \frac{P_P F}{P_P+b_{F,A}} + (1-\delta) a_{F,L} \frac{P_L F}{P_L+b_{F,A}} \right) - d_{F,A} F$
Littoral	$\frac{dA_L}{dt} = r_L A_L \left(1 - \frac{A_L}{K_T(1-\rho)}\right) - a_{I,L} \frac{IA_L}{A_L+b_{I,L}}$
	$\frac{dI}{dt} = ea_{I,L} \frac{IA_L}{A_L+b_{I,L}} - d_{I,L} I - a_{P,L} \frac{P_L I}{I+b_{P,L}}$
	$\frac{dP_L}{dt} = ea_{P,L} \frac{P_L I}{I+b_{P,L}} - d_{P,L} P_L - a_{F,L} (1-\delta) \frac{FP_L}{P_L+b_{F,A}}$

All are extensions of the classical Rosenzweig-MacArthur model and System 2 is a modification of the model used by McCann and others (1998) and Post and others (2000). Definitions of terms are given in Table 2. Parameter values are given in appropriate figure legends.



**Figure 4.** Bifurcation diagram for a simple 2-species consumer-resource model (see System 1 in Table 1). Data points were generated by following local maxima and minima in  $C_2$  and then calculating the control index, CI ( $CI = C_2 / (C_2 + R_1)$ ), for each maxima and minima across a gradient in resource productivity ( $K$ ). Top-down control increases and becomes less stable with increasing productivity. The pyramids all have the same amounts of biomass, but biomass is distributed to correspond to actual control indices. Gridlines point to the biomass pyramids associated with values of corresponding control indices. Parameters are as follows:  $r = 0.20$ ;  $K = 1.0$ ;  $e = 0.80$ ;  $a = 2.5$ ;  $b_Z = 0.20$ ; and  $d = 1.0$ .

control in simple linear food chains is inherently unstable.

The instability associated with top-down control would seem to make trophic cascades unlikely and begs the question: when we observe strong and persistent top-down control in ecosystems, what underlying biological mechanisms enable this control? To specifically explore whether coupled

food chains enable persistent, strong, top-down control in lakes, we modified the consumer-resource models to reflect recent evidence that both periphyton and phytoplankton energy pathways are exploited by top predators in lakes. At the coarsest level, the degree of coupling between energy pathways will be driven by factors that determine the magnitude of production in each habitat. Lake size will determine the relative distribution of pelagic and littoral habitats, whereas nutrient concentrations will determine habitat-specific primary productivity (Vadeboncoeur and others 2003). As nutrient concentrations increase, whole-lake metabolism can switch from predominantly littoral periphyton production in well-lit oligotrophic lakes to almost exclusively pelagic production in turbid eutrophic lakes. Based on these patterns, we constructed a theoretical model in which increases in phytoplankton productivity were offset by decreases in periphyton productivity over a eutrophication gradient. The 4-trophic-level model coupling littoral and pelagic pathways through a mobile top predator (Table 1, Table 2) is based on that of McCann and others (1998) and is an extension of linked food chain models developed for lake and soil food webs (Post and others 2000).

To model the redistribution of productivity across a eutrophication gradient, we varied the carrying capacities of the pelagic ( $K_P$ ) and littoral-benthic ( $K_L$ ) pathways (where  $K_T = K_L + K_P$ ). Thus, relative inputs from the focal food chain (in this case phytoplankton) varies from 0–1. For simplicity, we held  $K_T$

**Table 2.** Trophic Level Designations and Parameter Definitions for the Consumer-Resource Models (Table 1)

Symbol	Definition
Trophic group	
$A_P$	Pelagic primary producer
$Z$	Zooplankton (pelagic)
$P_P$	Pelagic predator (planktivore)
$F$	Generalist predator (fish)
$A_L$	Littoral primary producer
$I$	Littoral invertebrate
$P_L$	Littoral predator
Parameter	
$r_i$	Per capita rate of increase for habitat type $i$ (P = pelagic; L = littoral)
$K$	Carrying capacity of the lake
$e$	Conversion efficiency of resource biomass into consumer biomass
$\rho$	Proportion of productivity in pelagic food chain
$a_{i,j}$	Attack rate of species $i$ which is in habitat $j$ (P = pelagic; L = littoral; A = all)
$d_{i,j}$	Biomass loss rate of species $i$ in habitat $j$ (P = pelagic; L = littoral; A = all)
$b_{i,j}$	Half saturation rate of species $i$ in habitat $j$ (P = pelagic; L = littoral; A = all)
$\delta$	Consumer preference

constant in the models presented here because the outcomes were not qualitatively different than when we allow increases in phytoplankton ( $K_P$ ) to simultaneously drive increases in total ecosystem productivity ( $K_T$ ). Furthermore, the redistribution of primary production from littoral-benthic ( $K_L \gg K_P$ ) to pelagic ( $K_P = K_T$ ) can occur over a narrow phosphorus range without dramatic changes in total primary production (Vadeboncoeur and others 2003). We constructed a linked food chain model that is similar to Post and others (2000) except that rather than exploring predator preference, the model allows for productivity to be shunted up the different food chains in different proportions. Top predators forage on food relative to its availability in each chain, which is determined by the relative primary productivity in the littoral and pelagic food chain. This enabled us to investigate how differential productivity influences stability and strength of trophic control. We assumed that littoral primary and secondary consumers are slightly less vulnerable to predation than consumers in the pelagic pathway due to habitat complexity (Diehl 1988). Note, though, that the qualitative results that follow are not sensitive to this assumption.

It is important to remember several points when placing the model presented here in more familiar models of eutrophication: 1) the phosphorus concentration at which  $K_P = K_T$  is a function of lake size and shape; 2) The condition of  $K_P = K_T$  is true for a broad suite of eutrophic and hypereutrophic lakes in which  $K_T$  is a positive function of phosphorus; and 3) The model outcomes represent food web structures for different lakes with a given initial ratio of  $K_P:K_T$ . They are not meant to describe within-lake feedbacks on the distribution of primary producer biomass addressed by the models of Scheffer and others (1993). Finally, the models were parameterized to explore the range of possible outcomes of linked food chains. They are not meant to predict the actual degree of trophic control in real lakes with a given ratio of benthic to pelagic primary productivity. Therefore, we discuss the model outcomes in general terms for unproductive (oligotrophic), moderately productive (mesotrophic) and highly productive (eutrophic) pelagic production pathways.

To track the strength of top-down control in the 4 trophic level food chain and qualitatively estimate the shape of the resulting biomass pyramid, we extended the two trophic level control index (CI) to the following trophic control index (TCI):

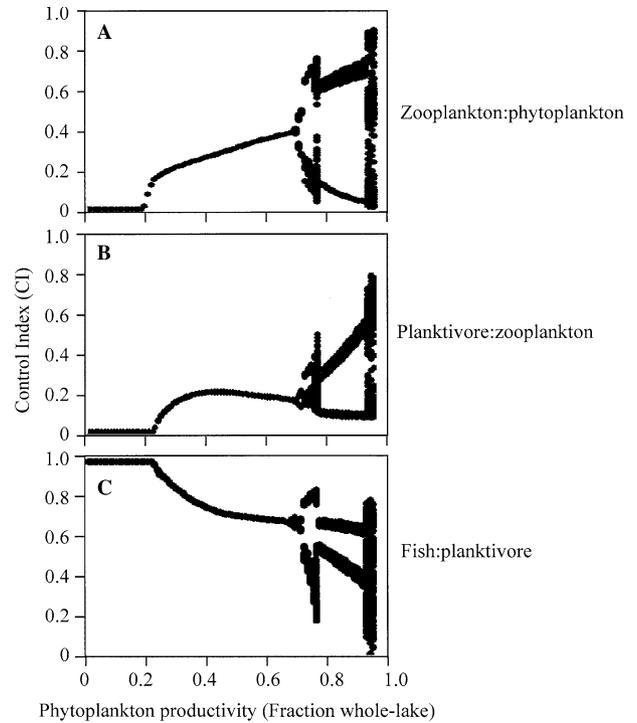
$$\begin{aligned} \text{TCI} &= \left( \frac{C_4}{C_3 + C_4} \right) \left( \frac{C_2}{C_2 + R_1} \right) \left( \frac{C_2}{C_3 + C_2} \right) \\ &= \text{CI}_{4,3} \text{CI}_{2,1} \text{CI}_{2,3} \end{aligned}$$

where  $R_1$  is the basal resource on the first trophic level,  $C_i$  is the consumer on trophic level  $i$  and  $\text{CI}_{i,j}$  measures the control index of trophic level  $i$  relative to  $j$ . The third element in the equation is the inverse of a control index and quantifies the biomass of trophic level 2 relative to trophic level 3. Thus, the index captures the dynamics of a true trophic cascade in which trophic levels should be alternately controlled by and released from predation across trophic levels. Notably, if a biomass pyramid is dumbbell shaped with the fourth and second trophic levels strongly suppressing their respective resources, then all three elements in the equation approach 1 and the index itself approaches 1. Conversely, when a system exhibits strong top-down control by the penultimate predator (third trophic level top-down control) the index approaches 0. Eltonian shaped biomass pyramids also generate low values of TCI relative to systems that exhibit any top down control. The trophic control index equals 0.125 in systems in which biomass is equally distributed among all trophic levels. Although incapable of distinguishing

among all the possible combinations of biomass pyramid shapes, the TCI enables a continuous quantitative comparison of the strength of fourth level trophic control. To aid interpretation of our results we include schematic representations of biomass pyramids in our figures.

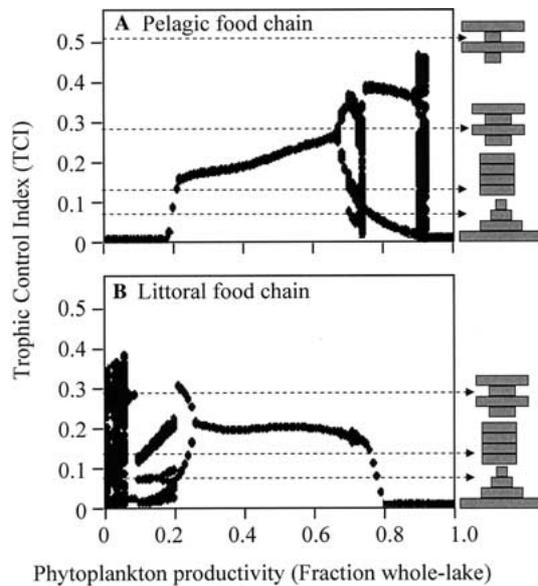
In oligotrophic lakes, the individual CI's depict bottom up control of the first two trophic levels (Figures. 5A, 5B). However, the planktivore simultaneously experiences extremely strong top-down control by the piscivore that is subsisting on littoral resources (Figure 5c). In moderately productive lakes, top-down control on phytoplankton increases with increasing phytoplankton productivity. Finally, when phytoplankton dominates whole-lake primary productivity, all trophic levels exhibit oscillations between top-down and bottom-up control. Figure 6 shows the resulting maximum and minimum TCI's for the pelagic and littoral consumer-resource interactions across the eutrophication gradient. The region in which the two food chains co-dominate is characterized by more bounded dynamics with reduced oscillations in both food chains. This stabilizing effect of coupling occurs readily and is not qualitatively dependent on parameter values. When all of the production is shunted up the planktonic pathway alone (far right region of Figure 6A), the dynamics are unstable switching between very strong fourth trophic level cascades and extremely low TCI's that are characteristic of strong third trophic level top down control. We can also compare coupled (Figure 6A) and uncoupled (Figure 7) pelagic food chains, each with the same gradient of phytoplankton productivity. Critically, the stable region of the coupled model (Figure 6A) is expressed over a broader range of productivity and is characterized by stronger top-down control (higher TCI) than in the single food chain model (Figure 7). Thus, coupled food chains in which phytoplankton and periphyton pathways co-dominate can generate stronger, more persistent top down control relative to a single phytoplankton-based food chain.

Interestingly, very strong top-down suppression can appear at the piscivore-planktivore link in the pelagic chain in oligotrophic systems (for example, Figure 5C). This situation arises for two reasons: 1) the generalist piscivore is supported largely by the littoral chain driving a strong top-down potential on the planktivore, and; 2) the pelagic chain is simultaneously experiencing lower production levels in oligotrophic lakes (that is, bottom-up effect). These two effects allow predators capable of sustaining significant biomass from the littoral chain to further suppress an already limited pelagic



**Figure 5.** Individual control indices (CI) for System 2 model output for trophic control on the pelagic food chain. The x-axis represents the fraction of whole-lake primary production contributed by phytoplankton. **A)** Zooplankton control on phytoplankton; **B)** planktivore control on zooplankton; **C)** generalist predator control on planktivore. Strong top-down control of the piscivore on the planktivore occurs in oligotrophic lakes because the top predator is supplied by the littoral pathway and is, to some extent, de-coupled from pelagic production. Parameters and definitions are in Tables 1 and 2. Parameters are as follows:  $r_p = 1.0$ ;  $r_L = 0.8$ ;  $K_T = 1.0$  (divided between chains according to percentage);  $e = 0.80$ ;  $a_{z,p} = 1.550$ ;  $b_{z,p} = 0.20$ ;  $d_{z,p} = 0.60$ ;  $a_{p,p} = 1.35$ ;  $b_{p,p} = 0.20$ ;  $d_{p,p} = 0.150$ ;  $a_{l,l} = 1.45$ ;  $b_{l,l} = 0.20$ ;  $d_{l,l} = 0.60$ ;  $a_{p,l} = 1.25$ ;  $b_{p,l} = 0.20$ ;  $d_{p,l} = 0.15$ ;  $a_{f,a} = 1.05$ ;  $a_{f,l} = 1.00$ ;  $b_{f,a} = 0.20$ ;  $d_{f,a} = 0.1$  and  $\delta = 0.50$ .

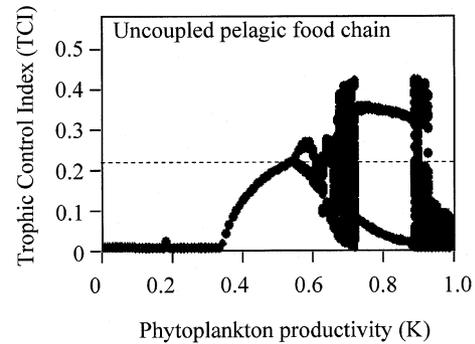
chain. However, the overall TCI approaches zero because strong bottom-up control (low CI) exerted on zooplankton by low phytoplankton productivity dominates the index. A similar strong suppression on the penultimate trophic level can theoretically act on the third trophic level of the littoral chain in eutrophic lakes. These results highlight that within a food chain, bottom-up (phytoplankton-zooplankton) and top-down forces both play significant roles at the low productivity end of the continuum while top-down forces gain ascendancy as overall productivity increases. A final characteristic of the model outcome is that littoral



**Figure 6.** Trophic control index (TCI) for the pelagic (**A**) and littoral (**B**) 4-trophic-level food chains generated by the System 2 food web model (see Table 1). The trophic control index (TCI) is accompanied by biomass pyramid drawings to aid interpretation of the results. The pyramids all have the same amounts of biomass, but biomass is distributed to correspond to actual control indices. Gridlines for the y-axis point to the biomass pyramids associated with particular values of trophic control indices. Note that increasing the coupling between the two habitats (that is, moving towards the center of the graph) increases the stability of the pelagic food chain, allowing strong, stable top-down control in mesotrophic lakes. Parameters are as for Fig. 5.

dynamics are less stable in oligotrophic lakes where the single littoral food chain dominates. Similarly, the pelagic food chain is less stable in very eutrophic lakes where a phytoplankton-based food chain dominates.

The model suggests that multi-chain omnivores have the potential to produce persistent pelagic trophic cascades when classical single chain cascades are less stable and more variable in magnitude. This result is analogous to others showing that external subsidies (Polis and Strong 1996; Huxel and McCann 1998), single-chain omnivory (McCann and Hastings 1997) and prey preference (Post and others 2000) can stabilize trophic dynamics. Clearly, the model ignores a number of important phenomena that may mediate this pattern: inedible algae can dominate in eutrophic lakes, predation usually has a more pronounced effect on zooplankton size than biomass, and single chain omnivory can shorten food chain length. Nonetheless, the results highlight a mechanism



**Figure 7.** Dynamics of the 4-trophic-level pelagic food chain in the absence of a linked littoral food chain. Pelagic food chain is parameterized as for Figure 5 with productivity increasing from 0 to 1.0. When compared with Figure 6A, the single food chain model shows a narrower range of top-down control, less stability over the productivity gradient, and a lower maximal TCI. Dotted line indicates maximum TCI before unstable dynamics occur and corresponds to 0.22 as compared with 0.28 in the coupled chain (Figure 6A).

facilitating persistent, strong fourth trophic level top-down control in moderately productive lakes (Jeppesen and others 1990; Carpenter and Kitchell 1993; Jeppesen and others 1997; Jeppesen and others 1998; Scheffer 1998; Carpenter and others 2001). It would be informative to expand on the basic models presented here to unfold some of these complex interactions. For instance, when we incorporated a parameter in the model to reduce visibility for predators under eutrophic conditions, the model tended to exhibit strong trophic control by the third trophic level (planktivores) in hypereutrophic lakes. Although the qualitative outcome of the model was not sensitive to parameter values, it would also be informative to perform a complete bifurcation analysis of this model. Such analyses would augment the general result presented here: stable food web outcomes exhibit higher TCI's and thus stronger trophic control in linked as opposed to single food chain scenarios.

## DISCUSSION

Models such as the one presented above allow the exploration of potential mechanisms that stabilize and mediate the strength of top down control in different focal food chains. However, interpreting the model's outcome in terms of observed patterns can be complicated by the diverse mechanisms affecting food web structure in nature. If a model predicts that a given structure is unstable, then that structure may be rare in complex natural systems

with other stable attractors. Nevertheless, many elements of the model are consistent with patterns in lakes. The model was constructed on the assumption that top predators are dependent on littoral algal based food chains in oligotrophic lakes, but that this pathway is eroded as eutrophication increases and phytoplankton becomes the dominant energy pathway in lakes. Benthic macroinvertebrates shift from feeding primarily on littoral algae to exploiting phytoplankton detritus as lakes become more eutrophic (Vadeboncoeur and others 2003) which is strong evidence of a change in energy flow associated with eutrophication. Stable isotopes (Figure 2) and diet analysis demonstrate significant energy flow from the littoral-benthic organisms to top piscivores in both North American and northern European lakes (Persson and others 1991; Jacobsen and others 2002; Vander Zanden and Vadeboncoeur 2002). Together, these patterns are consistent with the assumptions underlying the structure of the models.

A characteristic of the model outcome is that food chain coupling by piscivores generates trophic cascades in both littoral and pelagic habitats. Although strong trophic cascades develop in benthic habitats (Shurin and others 2002), littoral trophic cascades have received far less attention than their pelagic counterparts in lakes (Martin and others 1992; Brönmark 1994). However, predation by piscivores such as bass and salmonids, has been shown to reduce abundance and biomass of large littoral zoobenthos in lakes (Blumenshine and others 2000; Knapp and others 2001) and this predation effect can cascade to primary producers (Brönmark 1994).

In contrast to the paucity of experiments in littoral zones, the potential for piscivores to induce trophic cascades to the level of phytoplankton is clear from experimental evidence (Hansson and others 1998; Carpenter and others 2001; Lathrop and others 2002). However, the frequently demonstrated capacity for large-scale fish manipulations to generate trophic cascades does not mean that these trophic structures persist. Variation in the expression of top-down control across eutrophication gradients has been the subject of intense debate and analysis (McQueen and others 1986). Fertilization experiments in North American lakes demonstrate that trophic cascades can be stable across a wide range of  $P$  input rates and that the strength of trophic control increases with increasing fertilization (Carpenter and others 2001), a result analogous to the mid-region of Figure 6. In contrast, biomanipulation of fishes as a water quality management tool in Europe is often

unstable above a phosphorus loading threshold (Hansson and others 1998). Highly eutrophic lakes do not repeatedly oscillate between planktivore and piscivore dominance as shown in the model (Figure 6A), rather they exhibit strong, stable third level trophic control (Jeppesen and others 1990; Jeppesen and others 2000), and are extremely resistant to mitigation techniques (Scheffer and others 1993). These apparently contrasting experimental results can be resolved by comparing trophic structures in lakes over as extensive a eutrophication gradient as possible (Jeppesen and others 2003). In an analysis of 466 lakes, Jeppesen and others (2003), found that fourth level trophic control, as evidenced by high representation by daphnia in the zooplankton, was most common in the mid-phosphorus range.

The model we present demonstrates that linked periphyton and phytoplankton-based food chains provide a plausible mechanism to strengthen fourth level trophic control by piscivores in mesotrophic lakes where periphyton and phytoplankton co-dominate. These linkages are degraded as whole-lake metabolism becomes dominated by phytoplankton and shifts to a single food chain structure. Although the stabilizing effects of littoral pathways are expected to be weaker in very large lakes, analogous stabilizing pathways may develop because fish exploit profundal zoobenthos that are supported by phytoplankton detritus (Yoshi and others 1999) or if energy is more efficiently transferred through littoral, as opposed to pelagic, trophic links (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002).

We have argued that the multi-chain omnivory based on multiple primary producers enables strong trophic control in lakes. The multi-chain omnivory of fish, and the reciprocal relationships between benthic and pelagic primary producers challenge the generalization that lakes have fundamentally simple and homogeneous trophic structures (Chase 2000; Power 2000). The mechanism we invoke for the stabilization of trophic control – generalist foragers coupling food chains – is unlikely to be exclusive to lake ecosystems. The complexity of energy pathways within and among ecosystems makes it difficult to generalize about the importance of top-down control, but does not diminish its relevance (Strong 1992; Polis and Strong 1996; Persson 1999). There is evidence of strong trophic control in diverse ecosystems, even if these are sometimes limited to a subset of species (Pace and others 1999; Persson 1999; Schmitz and others 2000; Terborgh and others 2001). Omnivory tends to prevent all organisms within trophic levels

from acting in synchrony, but can intensify the effect of select predators and stabilize their dynamics (Fagan 1997; Roemer and others 2002). The models presented here suggest that multi-chain omnivory has stabilizing effects similar to those of single-chain omnivory (McCann and Hastings 1997; Polis and others 2000) although they achieve this stabilization in different ways. Although single-chain omnivory necessarily lowers the trophic position of the top predator (by eating into the penultimate trophic level), multi-chain omnivory allows the extension of food chains by bridging ecosystem or habitat boundaries.

Intense episodes of cyclical predation caused by motile predators (Shiomoto 1997; Estes and others 1998; Roemer and others 2002) or prey (Nakano and Murakami 2001) crossing ecosystem boundaries is likely to have a different effect on ecosystem structure and function than persistent, "home grown" predation that has to be produced and maintained by a single habitat or ecosystem. Many large mobile predators have been annihilated from terrestrial ecosystems, and over-fishing in the oceans is lowering the overall trophic position of fish (Pauly and others 1998; Pace and others 1999). If multi-chain omnivores impose strong but temporally variable trophic control over multiple ecosystems, then the consequences of their elimination may be profound over large spatial scales. At smaller spatial scales, multi-chain predators may be influential in maintaining habitat mosaics within ecosystems by exerting strong control on preferred food chains. The potential for multi-chain omnivores to couple discrete and often distant food chains, habitats, and ecosystems challenges ecologists to bridge spatial and disciplinary boundaries (Lundberg and Moberg 2003) when assessing the dynamics of top-down control in specific ecological systems.

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