

Is pelagic top-down control in lakes augmented by benthic energy pathways?

M. Jake Vander Zanden, Timothy E. Essington, and Yvonne Vadeboncoeur

Abstract: Modern food web studies are typically conducted from a trophic dynamic perspective that focuses on combined roles of top-down and bottom-up forces in regulating food web structure. Recognition of spatial food web subsidies in diverse ecosystems highlights the importance of energy flow as a foundation for understanding trophic dynamics. Here, we consider how different energy flow configurations might affect trophic dynamics in north-temperate lakes. A literature review revealed that littoral piscivores exert top-down control on prey fishes. In contrast, analysis of littoral predator diets indicated extensive omnivory and heavy reliance on zoobenthic prey. We explored this uncoupling between trophic dynamics (piscivores regulate prey fish) and energy flow (zoobenthos in piscivore diets) using a biomass dynamic model. This model compared top-down impacts of a piscivore on prey fishes under two scenarios: consumption of prey fish only and consumption of prey fish plus zoobenthos. The model predicted that elimination of zoobenthivory leads to a 50% reduction in piscivore standing stock and concomitant 2.5-fold increase in prey fish abundance (i.e., zoobenthivory plays a key role in mediating pelagic top-down control). These results highlight the role of benthic–pelagic linkages in regulating trophic dynamics and underscore the value of whole-ecosystem approaches to the study of food webs.

Résumé : Les études modernes des réseaux alimentaires sont menées généralement dans une perspective trophodynamique qui se concentre sur les rôles combinés des forces descendantes et ascendantes dans la régulation de la structure du réseau. La reconnaissance des apports spatiaux dans les réseaux alimentaires des différents écosystèmes met en relief l'importance du flux énergétique comme base de la compréhension de la trophodynamique. Nous examinons ici comment différentes configurations du flux énergétique peuvent affecter la trophodynamique dans les lacs tempérés nordiques. Une revue de la littérature montre que les piscivores littoraux exercent un contrôle descendant sur les poissons proies. En revanche, l'analyse des régimes alimentaires des prédateurs littoraux indique une importante omnivorie et une forte dépendance des proies zoobenthiques. Nous avons analysé cette dissociation entre la trophodynamique (les piscivores contrôlent les poissons proies) et le flux d'énergie (le zoobenthos dans le régime alimentaire des piscivores) à l'aide d'un modèle dynamique de biomasse. Le modèle compare les impacts descendants d'un piscivore sur les poissons proies selon deux scénarios, la consommation de poissons proies seuls et la consommation à la fois de poissons proies et de zoobenthos. Le modèle prédit que l'élimination de la consommation de zoobenthos entraîne une réduction de 50 % de la biomasse des piscivores et une augmentation concomitante de 2,5 fois de l'abondance des poissons proies (c.-à-d., c'est donc dire que la consommation de zoobenthos joue un rôle clé dans la médiation du contrôle descendant pélagique). Ces résultats mettent en lumière le rôle des liens benthiques–pélagiques dans la régulation de la trophodynamique et soulignent la valeur des approches qui englobent tout l'écosystème dans l'étude des réseaux alimentaires.

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Introduction

Modern food web ecology has focused predominantly on interaction strengths (Paine 1992; Berlow et al. 2004) and the importance of top-down (predation) and bottom-up (resources) factors in determining the distribution of biomass at different trophic levels (referred to here as trophic dynamics) (Power 1992; Carpenter et al. 2001; Shurin et al. 2002). The dominance of trophic dynamics in food web ecology (e.g., Paine 1980) has diverted efforts from the elucidation of pathways of energy flow in ecosystems (food web energetics), with the result that important energy and nutrient conduits in food webs may go unrecognized. However, spatial food web subsidies, defined as the movement of organisms, energy, and materials across traditionally defined ecological or habitat boundaries, are energetically important in a wide range of ecosystems (Polis et al. 1997). Recent studies in desert (Polis and Hurd 1996), riparian (Power et al. 2004), marine (Bustamante et al. 1995; Menge 2004), and Arctic coastal (Jefferies 2000; Jefferies et al. 2004) ecosystems demonstrate that cross-habitat energy linkages strongly influence trophic dynamics in the subsidized habitats. The importance of cross-habitat linkages for trophic dynamics and stability is also supported by recent theoretical food web models (Huxel and McCann 1998; Post et al. 2000; Vadeboncoeur et al. 2005).

Lake ecosystems have been an important arena for testing trophic dynamic theory. In particular, lakes have been extensively used for experimental examination of trophic cascades in which changes in predator abundance propagate down the trophic chain to affect primary producer biomass (Carpenter et al. 1985; Pace et al. 1999; Carpenter et al. 2001). Studies of trophic dynamics in lakes are generally based on a conceptual food web model composed of either three or four functional trophic levels: phytoplankton, zooplankton, small-bodied prey fish (planktivores), and sometimes piscivores (Carpenter et al. 1985; Persson et al. 1992; Mittelbach et al. 1995). While this perception of lake food webs as reducible to a simple, linear pelagic food chain may seem overly simplistic, studies of trophic dynamics in lakes are often consistent with a chain-like trophic architecture (Persson et al. 1992; Jeppesen et al. 1997; Carpenter et al. 2001).

In contrast with the above studies of trophic dynamics, research on pathways of energy flow in lakes indicates a high degree of omnivory and reticulate food web structures (Schindler et al. 1996; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). Benthic habitats are often important contributors to whole-lake primary and secondary production (Wetzel 1979; Vadeboncoeur et al. 2002, 2003), and fish are mobile consumers that effectively exploit benthic and pelagic resources, thereby coupling these two habitats (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002; Vanni 2002).

The above descriptions provide two differing views of lake food webs, depending on whether one takes a trophic dynamic or an energy flow perspective (Post 2002). While both perspectives have been informative on their own, the contrast between patterns of energy flow and dynamic control within lakes provides a rich opportunity for exploring linkages between trophic dynamics and energetic linkages (Schindler et al. 1996). Simultaneous consideration of these

two perspectives allows examination of how the strength of benthic–pelagic coupling affects trophic dynamics in lakes.

The goal of this synthesis is to explore the consequences of benthic–pelagic energetic coupling for pelagic top-down control in lakes. Because there are few data or experimental studies that address this question, we review the available evidence for littoral piscivore – prey fish trophic control in North American north-temperate lakes. Second, we synthesize published dietary data to quantify energetic pathways for three bass species that are commonly implicated in top-down control in North American lakes. Finally, we explore the confluence of these two previous sections using a biomass dynamic model in which we perform the experiment of either allowing or prohibiting piscivore consumption of zoobenthos. This modeling exercise allows us to link the results of our two literature syntheses and explore how zoobenthivory is expected to affect top-down control in the pelagic food chain.

Patterns of trophic control

We searched the literature for published studies that examined impacts of littoral piscivorous fishes on prey fish abundance, species richness, and assemblage structure in North American north-temperate lakes. Piscivore species included smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), rock bass (*Ambloplites rupestris*), and northern pike (*Esox lucius*). We included comparative, experimental, and long-term studies. Small-scale enclosure experiments were not included because the physical structure and food web linkages involving piscivorous fishes in natural ecosystem are likely to be disturbed in such studies (Lodge et al. 1998).

Dynamic top-down control is most convincingly demonstrated by the experimental manipulation of top predators. Littoral piscivores, particularly the above bass species, have been widely introduced into lakes well beyond their native range (Lee et al. 1980; Jackson 2002), and such introductions can be viewed as natural experiments. The impacts of these littoral piscivore introductions have been reasonably well studied and provide multiple independent tests of the effects of littoral predators on prey fish populations. We looked for evidence of both direct (predation) and indirect (behavioral) impacts of predators on prey fishes, recognizing that either can have important food web consequences (He and Kitchell 1990). Because we are examining whether littoral piscivore consumption of alternative prey (zoobenthos) increases predation on littoral prey fish, we assessed evidence for predator control at the littoral piscivore – prey fish link rather than full-on trophic cascades. This piscivore – prey fish interaction is a component of a trophic cascade, although even strong piscivore control of prey fish may not cascade down to phytoplankton due to compensatory mechanisms (Liebold 1989; McQueen et al. 1989; Hambright 1994).

We found that the littoral piscivores considered in our review generally have top-down impacts on prey fish abundance, diversity, and assemblage structure in North American north-temperate lakes (Table 1). All 16 of the studies reported a top-down impact of littoral piscivores on either prey fish abundance, diversity, or assemblage structure. Most

Table 1. Summary of published studies examining piscivore impacts on species richness, abundance, and community structure of prey fishes.

Lake or region	Study type ^a	Predator species ^b	No. of lakes	Species richness	Prey abundance	Habitat use or behavior	Assemblage structure	Reference
Adirondack Park, New York, USA	c	SMB, LMB, NP	131	Yes	—	—	Yes	Findlay et al. 2000
East coast, USA	c	SMB, LMB, CP	203	Yes	—	—	Yes	Whittier and Kincaid 1999
East coast, USA	c	SMB, LMB, NP, CP, WP	195	Yes	—	—	Yes	Whittier et al. 1997
Gatineau Park, Quebec, Canada	c	YP, LMB, SMB, NP	37	Yes	—	—	—	Chapleau et al. 1997
Central Ontario, Canada	c	SMB, RB	9	Yes	Yes	—	—	Vander Zanden et al. 1999
Central Ontario, Canada	c	SMB	14	No	Yes	Yes	Yes	MacRae and Jackson 2001
Central Ontario, Canada	c	LMB, SMB, NP	249	—	—	—	Yes	Jackson et al. 1992
Alberta, Canada	c	NP	45	Yes	—	—	Yes	Robinson and Tonn 1989
Northern Wisconsin, USA	c	LMB	18	—	—	—	Yes	Tonn and Magnuson 1982
Central Ontario, Canada	c	LMB, SMB	2	Yes	Yes	—	—	Ramcharan et al. 1995
Northern Wisconsin, USA	c	LMB, SMB, RB, NP	43	Yes	—	—	Yes	Rahel 1984
UNDERC, Michigan, USA	e	NP	1	—	Yes	Yes	Yes	He and Kitchell 1990
UNDERC, Michigan, USA	l, e	LMB	3	—	Yes	—	—	Carpenter et al. 2001
ELA, Lakes 110 and 227, Ontario, Canada	e	NP	2	—	Yes	—	—	Elser et al. 1998
Lake St. George, Ontario, Canada	l, e	NP, LMB	1	—	Yes	—	—	McQueen et al. 1989
Wintergreen Lake, Michigan, USA	l, e	LMB	1	No	Yes	—	—	Mittelbach et al. 1995

Note: —, unable to assess piscivore impact on this variable from the published study; UNDERC, University of Notre Dame Environmental Research Center; ELA, Experimental Lakes Area.

^ac, comparative study; e, experimental manipulation; l, long-term observational study.

^bSMB, smallmouth bass (*Micropterus dolomieu*); LMB, largemouth bass (*Micropterus salmoides*); NP, northern pike (*Esox lucius*); CP, chain pickerel (*Esox niger*); WP, white perch (*Morone americana*); YP, yellow perch (*Perca flavescens*); RB, rock bass (*Ambloplites rupestris*).

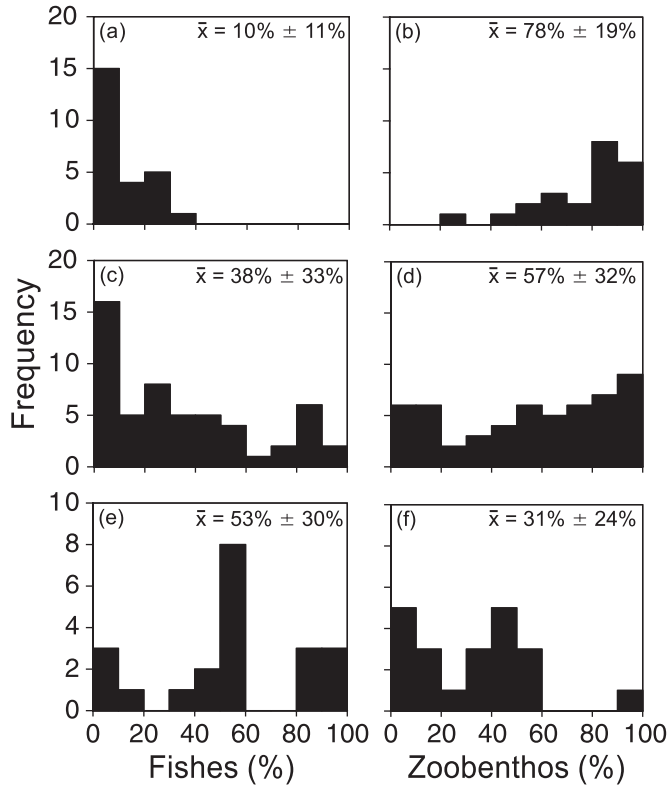
studies reported information on only one or two of these response variables. Eight (50%) of the studies reported impacts of littoral predators on prey fish species richness, eight (50%) indicated impacts on overall prey fish abundance, and nine (56%) reported impacts on prey fish assemblage structure (Table 1). Where littoral piscivores impacted prey fish assemblage structure, soft-rayed fishes such as cyprinids were typically replaced by less edible, spiny-rayed species such as percids and centrarchids. This compensatory response in the prey fish assemblage can dampen the magnitude of trophic control and has been forwarded as a mechanism to explain why the strength of top-down control is dissipated in some food chains (Hambright 1994). Overall, our synthesis indicates that littoral zone predators in north-temperate lakes have great potential to control prey fish abundance and assemblage composition across the wide

range of conditions and lake types included in our literature review.

Patterns of energy flow

In this section, we examine dietary data from a large number of lakes to characterize pathways of energy flow that support production of three representative littoral piscivore species. Quantitative dietary data (expressed as a percentage of total gut content volume or weight) for 57 smallmouth bass populations, 25 rock bass populations, and 21 largemouth bass populations were taken from previous syntheses of the diet data literature (Vander Zanden et al. 1997; Vander Zanden and Vadeboncoeur 2002). The original published studies from which these diet data were extracted varied widely in the degree of taxonomic resolution of diet items.

Fig. 1. Frequency distributions showing the among-population variation in consumption of fishes and zoobenthos (expressed as a percentage of total diet based on gut content studies) for (a and b) rock bass (*Ambloplites rupestris*) ($n = 25$ lakes), (c and d) smallmouth bass (*Micropterus dolomieu*) ($n = 57$ lakes), and (e and f) largemouth bass (*Micropterus salmoides*) ($n = 21$ lakes). Values in the top right corner of each panel are the mean (± 1 SD) percent reliance on fishes or zoobenthos.



Therefore, the prey categories used in this analysis were general prey classes (zoobenthos, zooplankton, and fish) and our data set lacked detailed taxon-specific prey resolution.

A summary of diet data for the three representative littoral piscivores species (smallmouth bass, largemouth bass, and rock bass) indicates a high degree of omnivory and an important dietary role for zoobenthos. Zoobenthos were the dominant prey of rock bass (mean ± 1 SD: 78% \pm 19%) and smallmouth bass (57% \pm 32%). For largemouth bass, fishes and zoobenthos were both important prey items (53% \pm 30% and 31% \pm 24%, respectively). Frequency distributions of the percent contribution of fish and zoobenthos to bass diets also indicated that diets were highly variable among populations of a species (Fig. 1).

For each population, diet breadth was calculated as the number of prey items (from seven potential prey categories: zooplankton, mollusks, crayfish, other nonpredatory zoobenthos, other predatory zoobenthos, detritus, and other prey) that comprised more than 3% of the total gut volume (Vander Zanden et al. 1997). Diet breadth for individual populations ranged from one to six prey items (of the seven possible prey categories). Largemouth bass had the highest diet breadth (mean ± 1 SD: 3.0 \pm 1.1) followed by rock bass (2.7 \pm 1.1) and smallmouth bass (2.4 \pm 1.0).

Synthesis and model description

Our synthesis of bass dietary data corroborates previous studies that report that littoral predators such as bass tend to have diverse and flexible diets (Schindler et al. 1997; Vander Zanden et al. 1997). The littoral predators that we examined are quite reliant on zoobenthos, while consumption of fishes tends to be energetically less important for two of the species. This important role of zoobenthos in the diets of littoral predators (energy flow perspective) contrasts with evidence for strong top-down control of prey fishes by littoral predators (trophic dynamic perspective). In this section, we use a simple model to explore the question of how the presence and magnitude of benthic prey consumption affect predator control of prey fishes. Our model considers the fate and flow of biomass within aggregated biomass pools that represent key ecological groups. In our model, these biomass pools were an idealized piscivore (hereafter referred to as piscivore), zoobenthos, and prey fish. This reliance on a simple model comprising a small number of trophic groups precludes examination of size-structured food web interactions that are common in aquatic systems (Persson and Eklov 1995). However, the model can be parameterized from available empirical data to provide easily interpretable conclusions regarding the role of alternative prey in lake food web dynamics.

The basic model structure is from the simple biomass dynamic models that form the basis of fisheries population biology (Hilborn and Walters 1992) wherein production gains from assimilated consumption are offset by losses via predation and other mortality agents. We assumed that all piscivore production is derived from consumption of fish and zoobenthos, while the production of prey fish and zoobenthos is described by a simple logistic density-dependent function. Feeding linkages between piscivores and their prey are described by a simple functional response model, and all other mortality losses are density independent. Given these structural assumptions, the model equations describing the dynamics of the state variables (P , piscivore biomass; L , prey fish biomass; B , zoobenthos biomass) are

$$(1a) \quad \frac{dP}{dt} = -ZP + AP[C_L(L, B) + C_B(L, B)]$$

$$(1b) \quad \frac{dL}{dt} = (R_{Lmax} - \beta_L L)L - M_{oL}L - C_L(L, B)P$$

$$(1c) \quad \frac{dB}{dt} = (R_{Bmax} - \beta_B B)B - M_{oB}B - C_B(L, B)P$$

where $C_i(L, B)$ is the functional response of the predator to prey type i , Z is the sum of mortality and mass-specific metabolism of the predator, A is assimilation efficiency, R_{imax} is the maximum mass-specific production rate of prey type i , β_i indicates density dependence of R_i (equivalent to r/K in a logistic equation) for prey type i , and M_{oi} is mass losses due to other mortality and metabolism.

We assume that the functional response follows a Holling type II model:

$$(2a) \quad C_L(L, B) = \frac{C_{max} a_L L}{C_{max} + a_L L + a_B B}$$

$$(2b) \quad C_B(L, B) = \frac{C_{\max} a_B B}{C_{\max} + a_L L + a_B B}$$

where a_L and a_B are the attack rates on prey fish and zoobenthos, respectively. This widely used functional response model does not consider reductions in feeding that might accompany prey refuging behavior (e.g., the foraging arena concept). This activity is known to induce predator dependence into the functional response (Abrams and Walters 1996) and to subsequently dampen top-down control (Essington and Hansson 2004). However, the aforementioned literature review indicated that piscivores do indeed exert top-down control of prey fishes, suggesting that the exchange of prey fish between vulnerable and refuge habitats is sufficiently rapid that the above approximation is reasonable. The form of the functional response on zoobenthos does not affect our analyses because our modeling perturbation compared changes in predicted steady state when there was no zoobenthos feeding (attack rate a_B equals zero). Under this condition, the functional response is always equal to zero regardless of the form of the model.

The challenge in deriving parameter estimates for this model lies in the fact that many of the parameters are not directly observable (e.g., attack rates and density-dependent parameters). Our strategy to overcome this challenge was to use available information on feeding rates, steady-state biomasses, production rates, and feeding habits and use this information to find the parameter values that are consistent with this information (Fig. 2). This approach is analogous to that used in other widely adopted model applications (e.g., EcoPath with EcoSim; Walters et al. 2000). The steady-state assumption implicit in our calculations is valid provided that the input data are not collected from lakes whose communities are radically displaced from their steady-state conditions.

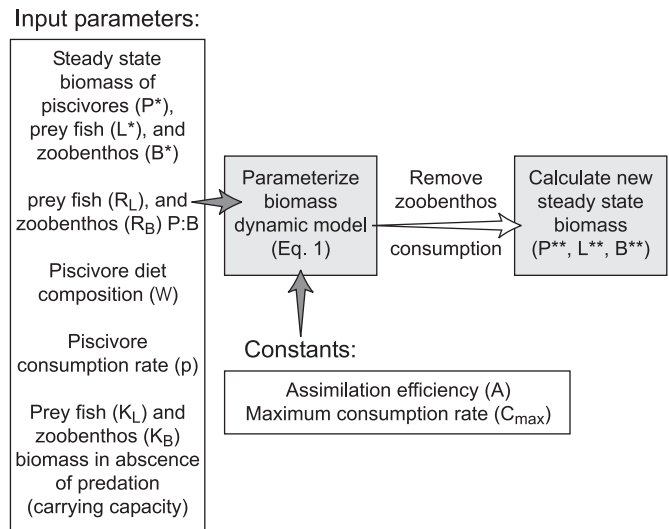
The required input data were (i) steady-state biomasses (P^* , L^* , and B^*), (ii) steady-state net production to biomass ratios of prey fish and zoobenthos (R_L^* and R_B^*), (iii) proportional contribution of prey fish and zoobenthos to piscivore diets (ϕ_L and ϕ_B , respectively) at steady state, (iv) predator consumption rate expressed as a proportion (p) of the maximum consumption rate C_{\max} , and (v) prey biomass in the absence of predation (K_L and K_B) (Fig. 2).

These five sources of input data are sufficient to estimate all parameters in eqs. 1 and 2. At steady state, predator mortality must equal net production, so $Z = ApC_{\max}$. For prey at steady state, production must equal mortality so M_{oi} equals the difference between R_i^* and predation mortality and predation mortality equals $pC_{\max}P^*\phi_i/N_i^*$. When prey are at their carrying capacity (no predation), production ($R_{i\max} - \beta_i K_i$) must equal M_{oi} . Because production minus predation also equals R^* at the specified steady-state biomass, we can therefore solve for $\beta_L = \phi_L p C_{\max} P^* / [L^* (K_L - L^*)]$ and $\beta_B = \phi_B p C_{\max} P^* / [B^* (K_B - B^*)]$. Given these density-dependent parameters, then $R_{i\max} = R_i^* + \beta_i K_i$.

To solve the functional response parameters, we recognize that at the steady-state condition, $p\phi_L = (a_L L^*) / (C_{\max} + a_L L^* + a_B B^*)$ and $p\phi_B = (a_B B^*) / (C_{\max} + a_L L^* + a_B B^*)$. The attack rate coefficients are therefore given by

$$(3a) \quad a_L = \frac{\phi_L p C_{\max}}{L^* (1 - \phi_L p - \phi_B p)}$$

Fig. 2. Modeling approach used to compare the steady-state biomass of prey fish with and without piscivores consumption of zoobenthos. The model was run 1000 times with input parameter values randomly drawn from normal distributions with means shown in Table 2 and a coefficient of variation of 0.3.



$$(3b) \quad a_B = \frac{a_L \phi_B L^*}{\phi_L B^*}$$

We used these parameter estimates to determine the steady-state biomass of piscivores, prey fish, and zoobenthos if there were no benthic energy subsidies to piscivores (Fig. 2). Steady-state biomasses under these conditions (L^{**} , P^{**} , and B^{**}) were determined by setting a_B equal to zero and solving eq. 1. Provided that all state variables are greater than zero (true when $R_{L\max} > \beta_L L^* / \phi_L + M_{oL}$), then the new steady states are

$$(4a) \quad L^{**} = \frac{ZC_{\max}}{Aa_L C_{\max} - Za_L}$$

$$(4b) \quad P^{**} = \frac{(R_{L\max} - \beta_L L^{**} - M_{oL})(C_{\max} + a_L L^{**})}{a_L C_{\max}}$$

$$(4c) \quad B^{**} = K_B$$

When $R_{L\max} < \beta_L L^* / \phi_L + M_{oL}$, predator biomass becomes zero and $L^{**} = K_L$.

Input data

Parameters for the above model were taken from various sources (Table 2). The steady-state biomass values for prey fish, piscivores, and zoobenthos in the presence and absence of piscivores were taken from Ramcharan et al. (1995), who compared the biomasses of these groups in two nearby lakes with contrasting food web structures. The nominal R^* for prey fish was the average value of lake-dwelling cyprinids from Randall and Minns (2000). The R^* for zoobenthos was the mean of published values from Waters (1969) and Barse and Mosher (1980). The nominal value for p (0.4) was taken from Essington et al. (2000), who estimated this parameter for over 400 individual largemouth bass in lakes in northern Wisconsin. The C_{\max} was set to 10-year^{-1} , which is approxi-

Table 2. Model input parameters, description, nominal values, and nominal value source(s) used in the model simulations.

Input parameter	Description	Nominal value	Source(s)
P^*	Steady-state piscivore biomass ($\text{g}\cdot\text{m}^{-2}$)	0.60	Ramcharan et al. 1995
L^*	Steady-state planktivore biomass in presence of piscivores ($\text{g}\cdot\text{m}^{-2}$)	0.38	Ramcharan et al. 1995
B^*	Steady-state zoobenthos biomass in presence of piscivores ($\text{g}\cdot\text{m}^{-2}$)	5.10	Ramcharan et al. 1995
R_L^*	Planktivore net production to biomass ratio at steady state (year^{-1})	2.17	Randall and Minns 2000
R_B^*	Zoobenthos net production to biomass ratio at steady state (year^{-1})	3.80	Banse and Mosher 1980; Waters 1969
p	Proportion of predators' maximum consumption rate	0.30	Essington et al. 2000
Φ_L	Proportion of planktivores in diet	0.45	This study
Φ_B	Proportion of zoobenthos in diet	0.55	This study
K_L	Steady-state planktivore biomass in the absence of piscivores ($\text{g}\cdot\text{m}^{-2}$)	2.00	Ramcharan et al. 1995
K_B	Steady-state zoobenthos biomass in the absence of piscivores ($\text{g}\cdot\text{m}^{-2}$)	7.70	Ramcharan et al. 1995

mately one half the maximum rate for a piscivorous centrarchid at its optimal temperature (Hanson et al. 1997). The 50% reduction therefore reflects realized temperatures likely experienced by piscivores in the north-temperate lakes from which other parameters were derived. The nominal values of ϕ_i of 0.45 for fish and 0.55 for zoobenthos are representative for a generalized littoral predator based on the diet data presented here. We assumed that assimilation efficiency (A) was equal to 0.65, a commonly observed value (Hanson et al. 1997).

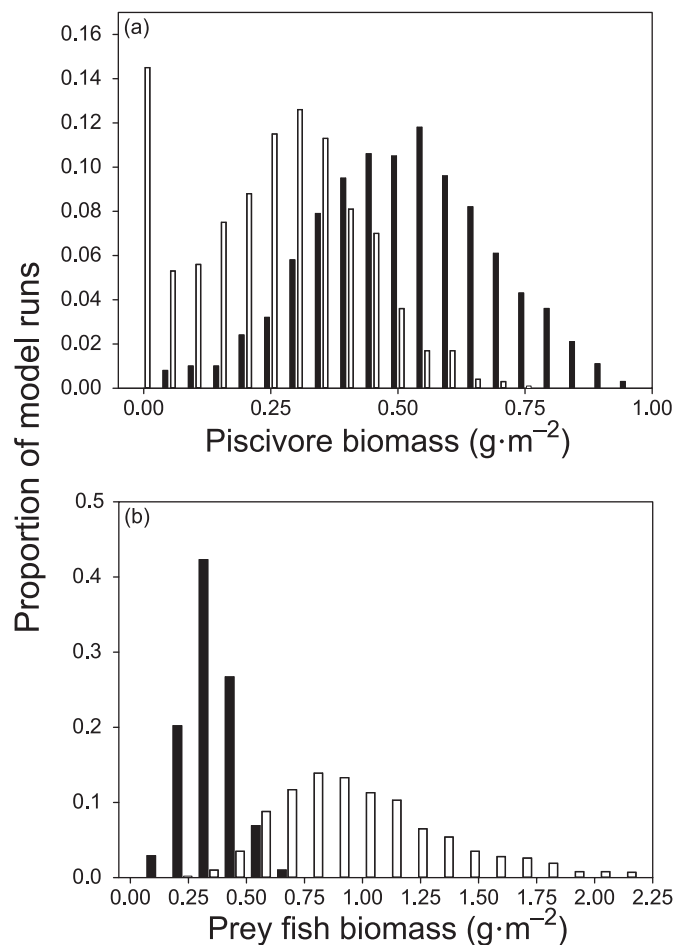
Because these are relatively imprecise parameter estimates, we assumed that each input value (Table 2) followed a normal distribution with a coefficient of variation equal to 30%. We then performed 1000 simulations in which we randomly selected parameter values from these probability distribution functions, solved for the model parameters, and then solved for the new piscivore and prey fish biomasses in the absence of zoobenthivory (P^{**} and L^{**}). Parameter sets that contained biologically implausible parameter values (e.g., negative values) were discarded.

Model results

The modeling results support the notion that zoobenthivory augments the strength of piscivore top-down control of prey fishes. There were sharp reductions in piscivore abundance in the absence of zoobenthivory. Notably, piscivore abundance was zero in the absence of zoobenthivory in 15% of all simulations (Fig. 3a), indicating that prey fish production was insufficient to support a piscivore population. On average, piscivore abundance was 50% less in model runs without benthic feeding (Fig. 3a). These reductions in piscivore populations resulted in marked increases in prey fish biomass (Fig. 3b). The prey fish biomass ratio (prey fish biomass without benthic energy consumption to prey fish biomass with benthic consumption) ranged from 1.06 to 10 and averaged 2.5 (i.e., on average, prey fish biomass was 2.5 times higher when piscivores were denied access to benthic prey).

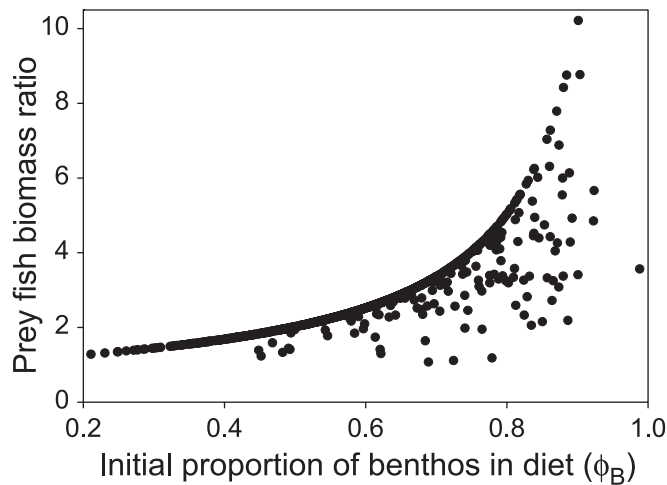
The variation in model results was attributable largely to variation in the baseline contribution of zoobenthos to piscivore diets (Fig. 4). Analytically, the prey fish biomass ratio (the factor by which prey fish biomass increases in response to the loss of the benthic linkage) is equal to the inverse of the input parameter ϕ_B (where ϕ_B is the original

Fig. 3. Frequency distribution showing the proportion of model outcomes resulting in a given steady-state biomass of (a) piscivores and (b) prey fish. Solid bars are for model runs in which piscivores consumed zoobenthos; open bars are for model runs in which piscivores did not consume zoobenthos. Distributions were generated by randomly drawing parameter values from normal distributions with a mean value equal to the nominal values and assuming a coefficient of variation of 0.3 for each parameter.



contribution of benthos to piscivore diets), which is the accelerating upper bound of the prey fish biomass ratio (Fig. 4). However, in some cases, the new piscivore biomass

Fig. 4. Relationship between piscivore zoobenthivory (initial proportion of zoobenthos in the bass diet) and the prey fish biomass ratio (prey fish biomass without benthic energy consumption to prey fish biomass with benthic consumption) from the model output.



was zero when denied access to zoobenthic prey. When this occurred, the prey fish biomass ratio equaled K_L/L^* , and points fell below the upper limit in Fig. 4.

Discussion

What are the dynamic consequences of a top predator deriving energy from multiple or alternative trophic pathways? One possible result is that prey consumption is spread across multiple prey, thereby reducing predation rates on any one prey item (Link 2002). An alternative view is that top-down control can become intensified by consumption of alternative prey, analogous to the idea that food web subsidies are important in driving trophic dynamics (Polis et al. 1997). Our literature syntheses indicated that littoral piscivores exert strong top-down trophic control of prey fish but that zoobenthos are of critical energetic importance to piscivores. In real ecosystems, are these two processes linked such that pelagic top-down control is strengthened in systems dominated by benthic energy flow? Because this question has not been specifically tested, we explored this question using a biomass dynamic model in which we perform the experiment of prohibiting consumption of benthic prey. Our model results indicated that given metabolic, consumption, and production rates typical for these food web components, piscivores are strongly dependent on zoobenthic prey to sustain their production. In the absence of alternative (benthic) energy sources, top-down control of prey fish biomass was substantially weakened.

Like all models, our analysis was a simplification of reality that omitted a considerable amount of biological detail. For example, our model did not consider size-structured interactions (De Roos and Persson 2002) that give rise to ontogenetic diet shifts from zooplanktivory to zoobenthivory to piscivory as individuals outgrow gape limitations (Werner and Gilliam 1984). Our model only considered the dynamics of the component of the piscivore population that regulates prey fish abundance directly. It is possible that ontogenetic

diet shifts even enhance the dynamic importance of zoobenthic energy subsidies. Juvenile bass often compete with the prey fish. If zoobenthic energy pathways act to increase densities of adult bass, which in turn reduce the densities of prey fish, juvenile bass are released from competition. The result is to maintain high bass recruitment rates such that bass population size is limited by resources rather than recruitment (Walters and Kitchell 2001).

A wide range of factors will affect the outcome of piscivore – prey fish interactions. We limited our diet analysis to three common bass species. These littoral piscivores differ greatly in their foraging preferences, efficiency, and habitat use (Scott and Crossman 1973), which should translate into differences in patterns of trophic control of prey fishes. A diversity of fish species is included in our prey fish category. While these fishes are generally considered planktivores and exert top-down control of zooplankton, these fishes also consume a variety of other prey items such as zoobenthos, periphyton, and detritus (Schindler et al. 1993). Prey fish consumption of alternative resources has the opposite effect of subsidies to piscivores and would act to dampen the strength of top-down control (Stein et al. 1995). However, Ramcharan et al. (1995) reported that zoobenthic biomass was higher in a planktivore-dominated systems compared with a piscivore-dominated system, indicating piscivore, rather than prey fish, control of zoobenthos.

Littoral habitat, anthropogenic disturbances, and lake size may also influence benthic–pelagic coupling and piscivore – prey fish dynamics. Macrophytes and fallen trees (course woody habitat) create a refuge for invertebrates and prey fish, decreasing prey vulnerability and potentially reducing the magnitude of top-down control. Lake eutrophication redistributes production from benthic to pelagic habitats (Vadeboncoeur et al. 2003), while invasion of zebra mussels shifts ecosystem production from pelagic to benthic habitats (Strayer et al. 1999). The broader implications of these ecological changes are difficult to predict because the linkages between energy flow and trophic dynamics in lakes are poorly understood. Small lakes have a high perimeter to volume ratio, and we would predict closer coupling between benthic and pelagic energy pathways in a small lake (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). Top-down control of zooplankton is higher in small lakes relative to large lakes, and piscivore biomanipulation is most likely to be successful in small lakes (Drenner and Hambright 1999, 2002; Jeppesen et al. 2003).

Bass and other littoral piscivores have been widely introduced beyond their native range, adversely impacting prey fish populations and threatening fish biodiversity (Whittier and Kincaid 1999; Jackson 2002). Perhaps the highly omnivorous diet of littoral piscivores contributes to their success and sustained impacts on prey fishes. After reducing populations of naïve prey fishes, introduced piscivores sustain high populations by feeding on alternative prey such as zoobenthos, thus preventing prey fish from recovering. A similar mechanism has been proposed in other systems. The brown tree snake (*Boiga irregularis*) devastated bird populations in Guam and was able to sustain high populations by feeding on alternative prey (amphibians and small mammals), thereby preventing bird populations from recovering (Savidge 1987). Other island studies report that exotic pred-

ator (cats and foxes) impacts on native biota are highest where predator populations are sustained by feeding on exotic herbivores such as rabbits and mice (Smith and Quin 1996; Courchamp et al. 1999, 2000).

In an effort to develop tractable conceptual models of ecosystems, ecologists have often invoked the use of simple linear food chain models (Hairston et al. 1960; Oksanen et al. 1981; Hairston and Hairston 1993). In lakes, phytoplankton are often considered the only relevant primary producer, or at best, benthic and pelagic production processes have been treated as separate (Lodge et al. 1998; Vadeboncoeur et al. 2002). This approach neglects the potential role of benthic production and processes at the whole-ecosystem level (Wetzel 1979; Vadeboncoeur et al. 2001, 2002) and the diverse ways in which benthic, pelagic, and riparian habitats can be energetically and dynamically linked (Vanni 1996; Jeppesen et al. 1997; Schindler and Scheuerell 2002).

While we do not explicitly examine trophic cascades in this study, the piscivore – prey fish interactions that we examine are an important component of trophic cascades in lakes. Trophic cascades have most commonly been reported in the pelagic zone of lakes. This has led to the suggestion that trophic cascades are predominantly aquatic phenomena due to the simple, chain-like structure of aquatic food webs (Strong 1992). Trophic cascades may really be more common and more detectable in lakes than in terrestrial systems (Shurin et al. 2002), but aquatic food chains are not particularly simple in structure (Power 2000). In fact, we would suggest the opposite: that lake food webs are reticulate and pelagic trophic cascades in lakes may be bolstered by energetic links to benthic habitats.

Several recent reviews have examined trophic cascades and biomanipulation in lakes (McQueen 1998; Drenner and Hambright 1999, 2002). These studies specifically addressed how fish manipulations such as piscivore additions improve water quality or phytoplankton biomass (Carpenter et al. 1985, 2001). None of these recent reviews specifically examined the impacts of piscivores on prey fish abundances or assemblages, nor did they discuss the role of benthic–pelagic linkages. The general conclusion of these reviews was that fish biomanipulations cascaded down the food chain to affect phytoplankton in some cases and under certain conditions. Small lakes are more likely to exhibit trophic cascades. While it may simply be easier to effectively manipulate small ecosystems, another explanation is that the stronger benthic–pelagic linkages in small lakes intensify trophic interactions and top-down control. If benthic–pelagic linkages play a role in mediating trophic cascades, this knowledge should be useful for predicting the conditions under which lake biomanipulation is likely to be successful.

The idea that top-down control can be subsidized by allochthonous energy inputs has been of recent interest to ecologists (Polis et al. 1997, 2000; Courchamp et al. 2000). Is it appropriate to describe this interaction as a benthic “subsidy” to pelagic trophic dynamics? What is defined as a subsidy clearly depends on the scale at which the system itself is defined (Schindler et al. 1996). From the perspective of lakes as phytoplankton-based food chains, energetic linkages to the zoobenthos may be viewed as a benthic subsidy. This view perpetuates an artificial divide between pelagic and benthic habitats in lakes. We hope to promote a whole-

ecosystem view of lakes in which benthic and pelagic habitats and production are inextricably linked in a reticulate food web (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). In fact, this integrated, holistic view of lake ecosystems has strong historical roots, dating back to Lindeman’s (1942) and Forbes’ (1887) highly integrated depiction of lake food webs. Early fisheries biologists also recognized the energetic importance of benthic secondary production to fish production (Rawson 1930, 1952). This holistic view of lakes has been overshadowed by a predominantly pelagic research focus in the 60 years since Lindeman’s (1942) seminal work, although limnologists are now reexploring benthic–pelagic coupling in lakes and its implications for lake productivity (Vanni and Layne 1997; Vanni 2002) and food web dynamics (Schindler et al. 1996; Schindler and Scheuerell 2002). While we argue for the inseparability of benthic and pelagic habitats in lakes, comparative studies combined with experimental manipulations of energy pathways will ultimately be required to elucidate the interplay between energy flow and trophic dynamics in lakes.

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