

Consumer-mediated recycling and cascading trophic interactions

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Abstract. Cascading trophic interactions mediated by consumers are complex phenomena, which encompass many direct and indirect effects. Nonetheless, most experiments and theory on the topic focus uniquely on the indirect, positive effects of predators on producers via regulation of herbivores. Empirical research in aquatic ecosystems, however, demonstrate that the indirect, positive effects of consumer-mediated recycling on primary producer stocks may be larger than the effects of herbivore regulation, particularly when predators have access to alternative prey. We derive an ecosystem model with both recipient- and donor-controlled trophic relationships to test the conditions of four hypotheses generated from recent empirical work on the role of consumer-mediated recycling in cascading trophic interactions. Our model predicts that predator regulation of herbivores will have larger, positive effects on producers than consumer-mediated recycling in most cases but that consumer-mediated recycling does generally have a positive effect on producer stocks. We demonstrate that herbivore recycling will have larger effects on producer biomass than predator recycling when turnover rates and recycling efficiencies are high and predators prefer local prey. In addition, predictions suggest that consumer-mediated recycling has the largest effects on primary producers when predators prefer allochthonous prey and predator attack rates are high. Finally, our model predicts that consumer-mediated recycling effects may not be largest when external nutrient loading is low. Our model predictions highlight predator and prey feeding relationships, turnover rates, and external nutrient loading rates as key determinants of the strength of cascading trophic interactions. We show that existing hypotheses from specific empirical systems do not occur under all conditions, which further exacerbates the need to consider a broad suite of mechanisms when investigating trophic cascades.

Key words: *biomanipulation; bottom-up; consumer-mediated recycling; ecosystem model; food web; nutrient cycling; recycling; regulation; top-down; trophic cascade.*

INTRODUCTION

Consumer species exert a suite of direct and indirect effects in ecosystems (Carpenter et al. 1985, Northcote 1988). Ecologists are particularly interested in the effects of cascading trophic interactions mediated by top consumers on primary producer stocks and production (Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985). While many recognize that consumers may affect producers through a variety of mechanisms, the majority of research on this relationship focuses on the indirect effect of predator regulation of herbivores on primary producers (Attayde and Hansson 1999, Shurin et al. 2002). The relationship between consumers and producers, however, is more complex and may include additional mechanisms such as nutrient recycling and transport (Vanni 2002), predation of nutrient sources (Maron et al. 2006), omnivory (Polis and Strong 1996), and ecosystem engineering (Jones et al. 1994).

Consumer-mediated recycling, although less studied, is stipulated as a key mechanism driving producer biomass in certain ecosystems (Northcote 1988, Vanni

and Layne 1997, Attayde and Hansson 2001a). It has, however, led to some confusion in the literature because some authors refer to it as a bottom-up process (Northcote 1988) while others call it a top-down process (Glaholt and Vanni 2005). Predators may recycle more nutrient than is provided by external nutrient loading, and highly mobile or migratory consumers such as salmon also may provide significant nutrient flows via excretion, egestion, and death (Northcote 1988, Vanni 2002, Moore et al. 2007). In many streams, fish consumption of detritivores can reduce the amount of detrital breakdown, which provides a novel potential link between predators, resources, and autotrophs (Greig and McIntosh 2006). A predator's direct consumption of nutrient sources also may influence primary production. For example, Maron et al. (2006) demonstrate how an invasive rat caused significant declines in island productivity by preying on seabirds, the main nutrient source to these isolated islands. Finally, many consumer species can affect soil nutrients and the abiotic environment and subsequently primary producers via their engineering activities (Jones et al. 1994).

Some aquatic producer species known as blue-green algae or cyanobacteria can be a nuisance to humans and wildlife because they contain toxins and can become

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abundant, forming floating algal mats on lake surfaces (Hallegraeff 1993). To control the spread of cyanobacteria, strategies to reduce external nutrient loading and/or biomanipulation are used (reviewed in Mehner et al. [2002]). Biomanipulation typically involves adding piscivorous fish to a body of water but it also may involve removing fish with high recycling rates (Findlay et al. 2005). Fish addition treatments follow predictions from cascading trophic interactions; piscivorous fish are added to regulate planktivorous fish populations, allowing large zooplankton to become more abundant. Large zooplankton (e.g., *Daphnia*) more effectively suppress algal abundance and growth than small zooplankton (e.g., Rotifer), therefore preventing algal outbreaks (Northcote 1988, Findlay et al. 2005). This strategy is effective in theory, but in practice, the success rate of biomanipulation is reported to be as low as 20% (DeMelo et al. 1992, but see Mehner et al. 2002). Harmful algal blooms have become a serious global concern (Hallegraeff 1993). Consequently, a better understanding of the multiple effects of consumers on producers is required to improve the success of strategies for reducing harmful cyanobacteria.

Regulation of herbivores and consumer-mediated recycling are two key mechanisms that influence autotrophs in aquatic ecosystems (Carpenter et al. 1985, Vanni and Layne 1997, Vanni 2002). Predator regulation of herbivores has the strongest effect on producer stocks in lentic ecosystems (Shurin et al. 2002). For example, Carpenter and Kitchell (1987) derive an ecosystem model, which predicts that food web interactions explain up to half of the variation in primary production in temperate lakes. The positive indirect effects of the regulation of herbivores also are reported across ecosystems (e.g., Knight et al. 2005), in other aquatic systems (e.g., Greig and McIntosh 2006), and in terrestrial systems (reviewed in Schmitz 2000). Nutrient cycling by consumers may occur within an ecosystem or may include transported nutrients from consumers feeding on allochthonous resources (Vanni 2002). These two processes for consumer-mediated recycling can lead to direct nutrient excretion by fish and indirect modifications to the rates of zooplankton nutrient release (Vanni 2002, Glaholt and Vanni 2005). Recent experiments demonstrate that direct recycling by fish can increase primary producer stocks in aquatic enclosures (Vanni and Layne 1997, Attayde and Hansson 2001a, b), but this depends on the rate of external nutrient loading (Braband et al. 1990, Vanni 2002), the fish species of interest (Braband et al. 1990), and the availability of alternative food sources (Vanni 2002, Glaholt and Vanni 2005). Changes to zooplankton recycling efficiency induced by fish also may increase producer biomass (Vanni and Layne 1997, Attayde and Hansson 2001a, Vanni 2002), but few studies have investigated this mechanism in detail. Aquatic ecologists and limnologists have long recognized that a predator's consumptive and recycling activities interact to influence

autotrophs (reviewed in Northcote 1988, Vanni 2002). Despite this, trophic cascade experiments (see Shurin et al. 2002) and classic food web theory (e.g., Hairston et al. 1960, Oksanen et al. 1981; but see Carpenter et al. [1985] and DeAngelis [1992]) have largely ignored this aspect of cascading trophic interactions. Consequently, we currently lack a quantitative assessment of the relative effects of regulation of herbivores and consumer-mediated recycling on primary producers (Glaholt and Vanni 2005).

Here we theoretically investigate the relative contribution of predator regulation of herbivores and consumer-mediated recycling on primary producers. We use an ecosystem model to evaluate a series of novel hypotheses generated from experiments that test the relative contribution of these mechanisms on producer stocks. The hypotheses are: (1) consumer-mediated recycling has a larger, positive, effect on primary producer stocks than herbivore regulation (Schindler 1992, Attayde and Hansson 2001a, Findlay et al. 2005); (2) herbivore recycling can have larger, positive effects on primary producer biomass than predator recycling (Attayde and Hansson 2001a); (3) consumer recycling has a larger, positive effect on primary producer stocks when predators preferentially feed on allochthonous prey (Glaholt and Vanni 2005); and (4) consumer-mediated recycling has a larger, positive effect on primary producer stocks when external nutrient inputs are low (Braband et al. 1990, Shostell and Bukaveckas 2004). We seek to determine the conditions in which our model outcomes match the above hypotheses from empirical work. Our goal is to understand the conditions that enable these mechanisms to dominate and interact to shape primary producer stocks.

ECOSYSTEM MODEL

We derive nutrient-limited ecosystem models with three biotic modules: primary producers (P), herbivores (H), and predators (C), and one abiotic module, inorganic nutrients (R). All modules describe stocks of a limiting inorganic nutrient with explicit nutrient flows that link them. Each module follows nutrient mass-balance constraints. The ecosystems are open at the basal level through a constant and independent input of inorganic nutrient, I . Biotic modules release nutrients at rates d_k , where k denotes the biotic module, and nutrients are lost from the basal level at a constant rate, l . The rate of stock i nutrient uptake by stock j is described by $f_{ji}(i, j)$, where i is an index for resources (e.g., R, P, H) and j is an index for consumers (e.g., P, H, C). In our analyses, we investigate ecosystems with two extreme forms of feeding interactions: Lotka-Volterra and donor control (Appendix A). Lotka-Volterra is a resource-dependent feeding relationship that obeys the law of mass action and is proportional to both consumer and resource stocks, whereas donor control assumes that consumer density does not affect the amount of

resources consumed (Pimm 2002). Both specific functions may only be valid for a limited number of natural ecosystems but the realistic forms of feeding interactions may be somewhere between these two extremes (Pimm 2002). For models with Lotka-Volterra functions, $f_{ji}(i, j) = a_{ji}ij$ and for models with donor-controlled functions, $f_{ji}(i, j) = a_{ji}i$, where a_{ji} is the consumer attack rate. Consumer uptake of prey stock is converted to consumer stock with efficiency e_{ji} . We assume that primary producers only uptake the nutrients that are required for growth and therefore do not include an efficiency term in their equation. Research in aquatic ecosystems has demonstrated that consumer-mediated recycling can have larger effects on primary producer stocks when consumers have access to alternative food sources (Glaholt and Vanni 2005). We assume that predators are generalist, which can feed on local herbivores and allochthonous prey, which is available at a constant amount, A . For example, many fish species prey on pelagic and benthic prey (Vanni 2002). We use π to describe the preference of the predator for the local prey (i.e., H). A fraction of what is released by each biotic module is lost from the system and the rest, including nutrients not converted to consumer biomass ($1 - e_{ji}$), are recycled within the system with efficiency δ_k . For example, sloppy feeding can result in the recycling of food matter (Vanni 2002). We assume that the predator feeds on the allochthonous prey in a different location than where it recycles nutrients, and therefore, allochthonous prey that is not converted to predator biomass is not recycled in our model. The general ecosystem model is described by the dynamical equations (Fig. 1):

$$\begin{aligned} \frac{dR}{dt} = & I - IR - f_{PR}(R, P) + \delta_P d_P P \\ & + \delta_H [(1 - e_{HP})f_{HP}(P, H) + d_H H] \\ & + \delta_C [(1 - e_{CH})\pi f_{CH}(H, C) + d_C C] \end{aligned} \quad (1)$$

$$\frac{dP}{dt} = f_{PR}(R, P) - d_P P - f_{HP}(P, H) \quad (2)$$

$$\frac{dH}{dt} = e_{HP} f_{HP}(P, H) - d_H H - \pi f_{CH}(H, C) \quad (3)$$

$$\frac{dC}{dt} = \pi e_{CH} f_{CH}(H, C) + (1 - \pi) e_{CA} f_{CA}(A, C) - d_C C. \quad (4)$$

METHODS

We set the time derivatives to zero and solve the above system of equations for the nontrivial equilibrium. We analyze the model with both Lotka-Volterra and donor-controlled trophic functions; the results for models with donor-controlled trophic functions are in Appendix A. P^* is the primary producer stock at equilibrium.

We use simple metrics to quantify the independent and interactive effects of predator regulation of herbi-

vores and consumer-mediated recycling on producer stocks. We assess the independent effect of predator regulation of herbivores in models without recycling ($\delta_k = 0$) and the interactive effect of predator regulation of herbivores and consumer-mediated recycling in models with recycling ($\delta_k > 0$). We quantify the effect of predator regulation of herbivores on primary producer stocks in these models by the log-ratio of equilibrium producer stocks (PTI) in the presence (i.e., a model with four trophic levels; subscript 4) and absence (i.e., a model with three trophic levels; subscript 3) of predators and in the presence (i.e., a model with recycling; subscript δ) and absence (i.e., a model without recycling; no subscript) of recycling. We use the metric subscript NRec (i.e., PTI_{NRec}) for models without recycling and Rec (i.e., PTI_{Rec}) for models with recycling. The predator regulation effect size metrics are: $PTI_{NRec} = \ln(P_4^*/P_3^*)$ and $PTI_{Rec} = \ln(P_{4\delta}^*/P_{3\delta}^*)$. To assess the independent effect of recycling, we use models with recycling ($\delta_k > 0$) and predators present (i.e., a model with four trophic levels). We quantify the effect of recycling on primary producer stocks (PRI) by the log-ratio of equilibrium producer stocks in models with and without recycling: $PRI = \ln(P_{4\delta}^*/P_4^*)$. The PRI includes recycling from both consumer trophic levels and from the primary producers. Higher values of PTI and PRI, respectively, indicate a stronger, positive effect of predator regulation of herbivores and recycling on primary producer stocks. To enable comparison between models with and without recycling, we held the turnover rates (d_k) and conversion efficiencies (e_{ji}) constant for all models and simply changed the proportion of nutrients that are lost from the system as opposed to recycled within the system.

To explore the conditions for hypothesis 1, consumer-mediated recycling has a larger, positive effect on primary producer stocks than herbivore regulation, we compared PTI_{Rec} to PRI to determine the relative effect of these mechanisms on primary producer stocks. We also compared PTI_{Rec} and PTI_{NRec} for a range of external input levels and predator preference (π) to measure the additional effect of recycling on the strength of predator regulation of herbivores. For hypothesis 2, herbivore recycling can have larger, positive effects on primary producer biomass than predator recycling, we assessed the relative contribution of herbivore and predator recycling on P^* by quantifying P^* for increasing herbivore (δ_H) and predator (δ_C) recycling efficiencies. We also investigated the influence of predator preference (π) on the relationship between recycling and producer biomass. To evaluate hypothesis 3, consumer recycling has a larger, positive, effect on primary producer stocks when predators preferentially feed on allochthonous prey, we investigated the interaction between herbivore and predator recycling and predator regulation by quantifying P^* for increasing δ_H or δ_C and predator preference for local prey (π). Predators derive more nutrients from allochthonous

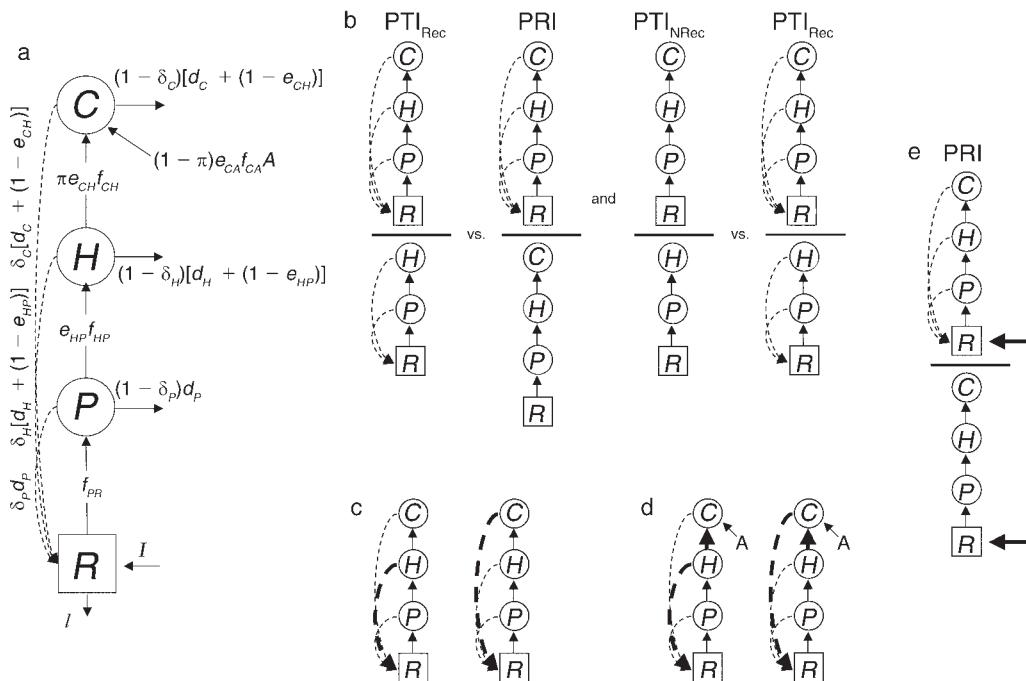


FIG. 1. Conceptual diagram of the general ecosystem model and the methods used to test the four hypotheses. (a) Conceptual model of Eqs. 1–4 as described in *Ecosystem model*. (b) To evaluate hypothesis 1 we compared PTI_{Rec} to PRI and we also compared PTI_{NRec} to PTI_{Rec} . (c) To evaluate hypothesis 2 we quantified P^* for increasing herbivore (δ_H) and predator (δ_C) recycling efficiencies. (d) To evaluate hypothesis 3 we quantified P^* for increasing δ_H or δ_C and predator preference for local prey (π). (e) To evaluate hypothesis 4 we quantified PRI for increasing external input. Circles represent the biotic modules and squares represent the abiotic modules of our ecosystem model. *C*, *H*, *P*, and *R* are predators, herbivores, primary producers, and inorganic nutrient, respectively. Solid vertical lines indicate consumptive relationships between trophic levels and dashed lines indicate recycling from trophic levels. The solid horizontal lines separate the numerator and denominator of the log-ratio metrics and the “vs.” indicates the comparisons made between log-ratio metrics. The thick arrows identify the model treatments (i.e., change of parameter) for hypotheses 2–4. Other variable abbreviations are: PTI_{Rec} , effect size of predator regulation of herbivores on primary producer stocks in models with recycling; PTI_{NRec} , effect size of predator regulation of herbivores on primary producer stocks in models without recycling; PRI , effect size of consumer recycling on primary producer stocks; d_k , nutrient release rate from biotic modules; e_{ji} , consumer conversion efficiency; f_{ji} , consumer functional response; *A*, stock of allochthonous prey; *I*, input of inorganic nutrient; and *l*, rate of nutrient loss from the inorganic nutrient module. PTI and PRI are defined further in *Methods*, and the model parameters are described further in *Ecosystem model*.

prey (*A*) as π decreases. Finally, to test hypothesis 4, consumer-mediated recycling has a larger, positive effect on primary producer stocks when external nutrient inputs are low, we quantified PRI for increasing external input and a range of predator preference levels (Fig. 1).

We show results for specific parameters but we verified the robustness of our results to a range of parameter values. In the results, we indicate when model predictions were sensitive to parameter changes and we provide the full results of our sensitivity analysis in Appendix B. We ran model simulations for a 50% increase and decrease in each a_{ji} , d_k , e_{ji} parameter relative to parameter values used for our figures. In addition, we verified the robustness of the results to when all a_{ji} , d_k , e_{ji} parameters were 50% larger or smaller simultaneously and two mixed scenarios: (1) a_{CH} , d_C , e_{CH} 50% larger and a_{HP} , d_H , e_{HP} 50% smaller and (2) a_{CH} , d_C , e_{CH} 50% smaller and a_{HP} , d_H , e_{HP} 50% larger. These simulations were tested for predator preference

for local ($\pi = 0.75$) or allochthonous ($\pi = 0.25$) prey. Overall, this includes 52 different parameter sets for testing the robustness of the model predictions for each hypothesis. We chose parameter values, however, that enabled the persistence of predators and herbivores because we are interested in the effects of predators and herbivores on primary producers. The stability of simple ecosystem models with Lotka-Volterra and donor-controlled trophic functions has been demonstrated in previous theoretical work (So 1978, Pimm 2002); therefore we do not provide stability analysis here.

RESULTS

The equilibrium stocks of the trophic levels varied with the presence and absence of recycling and predators in our model (Fig. 2a). At equilibrium, producer stocks were largest in models with recycling and predators present and lowest in models without predators. The effect size of predator regulation (PTI) and recycling (PRI) increased with increasing allochthonous prey (*A*)

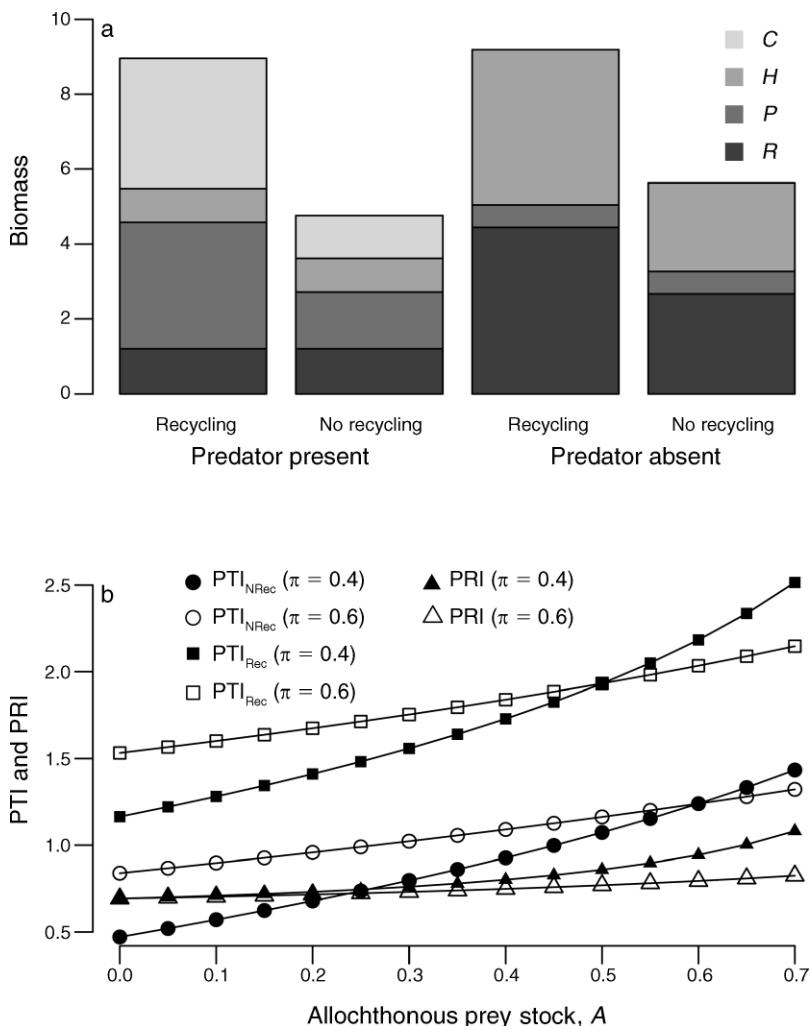


FIG. 2. (a) Biomass distribution (quantity of nutrient per unit area) of all trophic levels for models with and without predators and recycling. Results are for models with predator preference for allochthonous prey ($\pi = 0.4$). (b) Effect size of predator regulation of herbivores on primary producer stocks in models without recycling (PTI_{NRec}), with recycling (PTI_{Rec}), and effect size of consumer recycling on primary producer stocks (PRI) for increasing rate of allochthonous prey (A) and predator preference for local prey ($\pi = 0.6$) or allochthonous prey ($\pi = 0.4$). Other parameter values are $I = 2$, $A = 0.4$, $l = 0.15$, $\delta_k = 0.5$, $d_k = 0.3$, $a_{ij} = 1$, and $e_{ji} = 0.5$. See Fig. 1 for explanations of parameter abbreviations.

input (Fig. 2b). PTI and PRI were both largest at high allochthonous prey inputs ($A = 0.7$) and predator preference for allochthonous prey ($\pi = 0.4$). However, at low allochthonous prey inputs ($A < 0.5$), PTI_{Rec} and PTI_{NRec} were highest when predators preferred local prey ($\pi = 0.6$). The local herbivore does not persist when $A > d_C/e_{CA}a_{CA}(1 - \pi)$.

Hypothesis 1: consumer-mediated recycling has a larger, positive effect on primary producer stocks than herbivore regulation.—For models with Lotka-Volterra and donor-controlled trophic interactions, $PTI_{Rec} > PTI_{NRec}$ for a range of external input values ($I = 1$ to 10 , Fig. 3a and Appendix A: Fig. A2a). At moderate allochthonous prey inputs ($A = 0.4$), the effect of predator regulation is largest when predators prefer local prey ($\pi = 0.75$). For models with Lotka-

trophic interactions $PTI_{Rec} > PRI$ except for models with low external nutrient input rates ($I < 2$; compare Fig. 3a, b), particularly when combined with low attack rates ($a_{CA} = a_{CH} = a_{HP} = a_{PR} = 0.5$) or high nutrient release rates ($d_C = d_H = d_P = 0.45$). PRI increases and PTI decreases with increasing predator preference for allochthonous prey. In donor-controlled models, $PRI > PTI_{Rec}$ (compare Appendix A: Fig. A2a, b).

Hypothesis 2: herbivore recycling can have larger, positive effects on primary producer biomass than predator recycling.—Primary producer stocks increase with increasing predator and herbivore recycling efficiencies (Fig. 4). In donor-controlled models, herbivore recycling had a larger effect on primary producer stocks than predator recycling when recycling efficiencies were high ($\delta > 0.5$; Appendix A: Fig. A3). For Lotka-

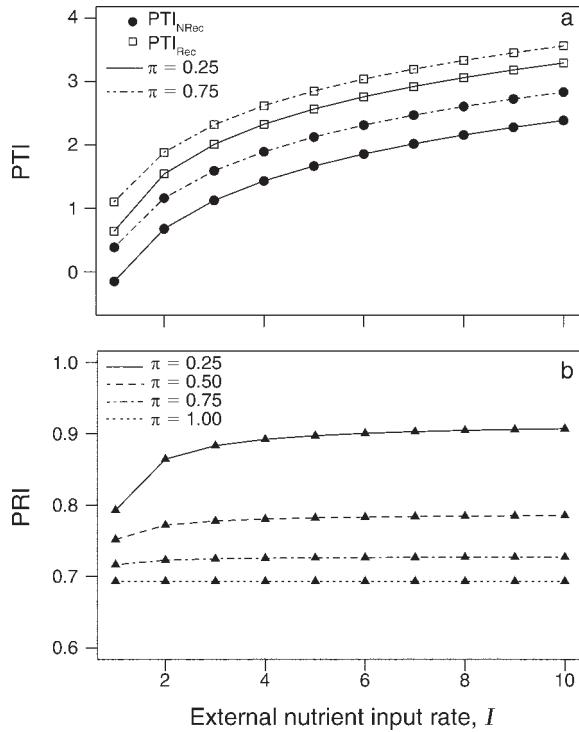


FIG. 3. (a) Effect size of predator regulation of herbivores on primary producer stocks (PTI) with increasing external nutrient loading for models with and without recycling. (b) Effect size of consumer recycling on primary producer stocks (PRI) for increasing external nutrient loading (I). All other parameters are as defined in Fig. 2.

Volterra models, neither predator nor herbivore recycling has a universally larger effect on primary producer stocks (Fig. 4). The specific predictions depend on predator preference for local prey and consumer efficiency and to a lesser extent predator attack rate and turnover rate. For models in which predators prefer allochthonous prey ($\pi = 0.25$), predator recycling usually has a stronger, positive, effect on P^* than herbivore recycling (Fig. 4a). This prediction also occurs for models in which predators prefer local prey ($\pi = 0.75$) and recycling efficiencies are low ($\delta < 0.5$). Conversely, when $\pi = 0.75$ and recycling efficiencies are high ($\delta > 0.5$), herbivore recycling has a stronger, positive effect on P^* than predator recycling (Fig. 4b). This pattern is also observed when $\pi = 0.25$ and recycling is high ($\delta > 0.5$) and consumer efficiency or predator attack are low ($e_{ji} = 0.25$, $a_{CH} = 0.5$) or predator turnover rate is high ($d_C = 0.45$).

Hypothesis 3: consumer recycling has a larger, positive effect on primary producer stocks when predators preferentially feed on allochthonous prey.—For models with Lotka-Volterra feeding relations, increasing herbivore recycling efficiency has a smaller, positive, effect on P^* for lower predator preference for allochthonous prey (i.e., the slope is smaller at high π ; Fig. 5a). P^* decreases with increasing predator preference for allochthonous

prey (i.e., decreasing π). The largest producer stocks occur at high herbivore recycling efficiency and predator preference for local prey ($\pi = 1$). These results are robust for a range of parameter values except when predator attack rates for local and allochthonous prey are high ($a_{Ci} = 1.5$). Under this scenario, P^* peaks at high herbivore recycling efficiency and predator preference for allochthonous prey ($\pi = 0.25$). Increasing predator recycling efficiency has a smaller, positive effect on P^* for lower predator preference for allochthonous prey (Fig. 5b). P^* decreases with increasing predator preference for allochthonous prey (i.e., decreasing π) except when predator recycling is large ($\delta_C > 0.8$). The largest producer stocks occur at high predator recycling efficiency and predator preference for allochthonous prey ($\pi = 0.25$). These results are robust for a range of parameter values except when predator attack rates for local and allochthonous prey are low ($a_{Ci} = 0.5$) or when conversion efficiencies are low ($e_{ji} = 0.25$). Under these scenarios, P^* peaks at high predator recycling efficiency and predator preference for local prey ($\pi = 1$).

Hypothesis 4: consumer-mediated recycling has a larger, positive effect on primary producer stocks when external nutrient inputs are low.—In models with Lotka-Volterra trophic functions, PRI is lowest when external inputs are low (Fig. 3b). The difference between PRI at

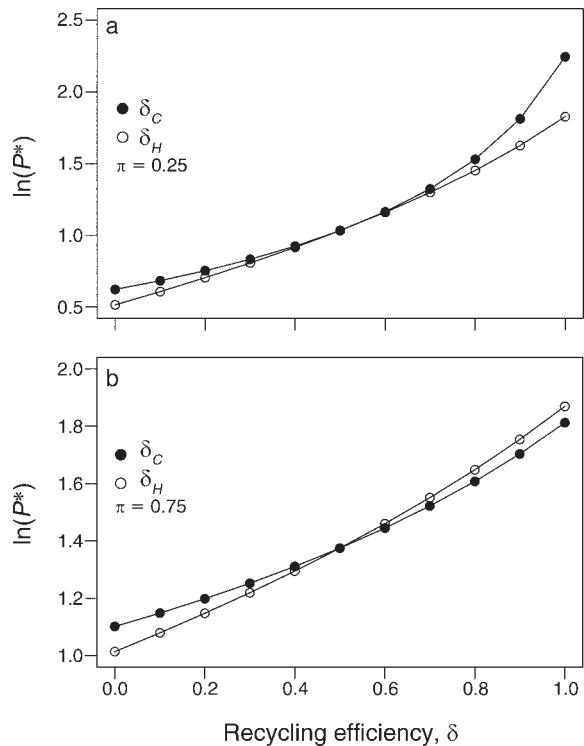


FIG. 4. Primary producer stock at equilibrium (P^*) for increasing predator (δ_C) and herbivore (δ_H) recycling efficiencies for (a) predator preference for allochthonous prey ($\pi = 0.25$) and (b) predator preference for local prey ($\pi = 0.75$). All other parameters are as defined in Fig. 2.

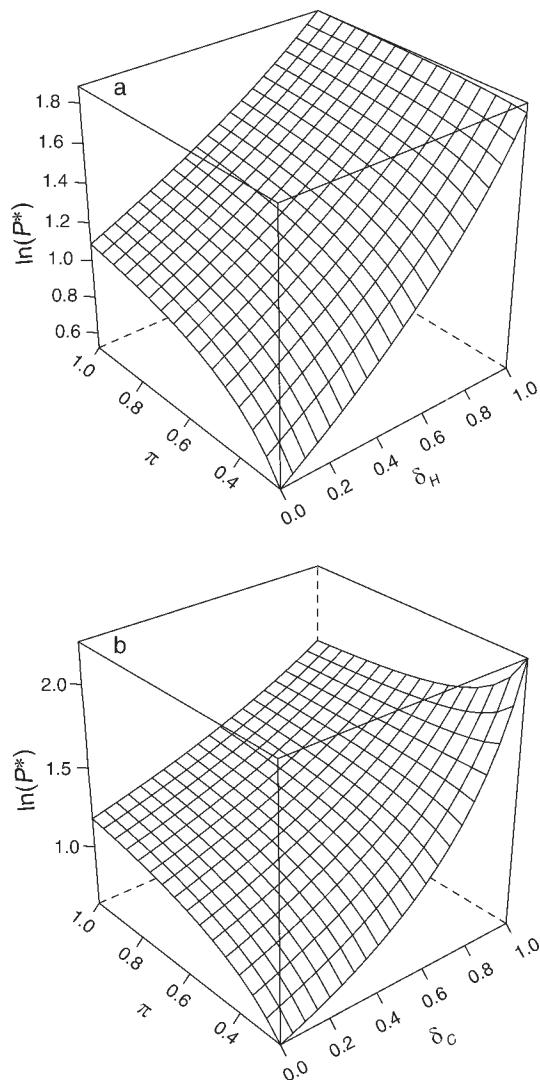


FIG. 5. Primary producer stock at equilibrium (P^*) for (a) increasing herbivore recycling efficiency (δ_H) and predator preference (π) and (b) increasing predator recycling efficiency (δ_C) and π . All other parameters are as defined in Fig. 2.

low inputs and high inputs is smaller when predator preference for local prey increases. When predators uniquely feed on local prey ($\pi = 1$), the effect size of consumer recycling remains unchanged with increasing external nutrient input (Fig. 3b). In models with donor-controlled trophic functions, PRI is largest when external nutrient inputs are low (Appendix A: Fig. A2b).

DISCUSSION

Cascading trophic interactions mediated by consumers are multifaceted phenomena, which integrate aspects of community and ecosystem ecology. The majority of research on the theory of trophic cascades has focused on predator regulation of herbivores, but recent empirical research on consumer-mediated recycling has

provided new insight into the complexity of indirect effects originating from predators. Here we derive an ecosystem model to evaluate some recent hypotheses from empirical research on the relative contribution of consumer regulation of herbivores and consumer-mediated recycling on producers. Our model predictions suggest that ecosystem traits such as feeding relationships, turnover rate, and external nutrient loading rate will influence the relative impact of these mechanisms on producer stocks.

The first hypothesis we examine is that consumer-mediated recycling has a larger, positive effect on primary producer stocks than herbivore regulation (Schindler 1992, Attayde and Hansson 2001a, Findlay et al. 2005). For a wide range of model conditions, our model predictions are in contrast to this hypothesis. Therefore, choosing to focus on the role of predator consumption in trophic cascades, as has been done in most research to date, is a reasonable first step. In a long-term, whole-lake experiment, Sarnelle and Knapp (2005) also observed that regulation of herbivores had a stronger effect on primary producer stocks than consumer-mediated recycling. Both our model predictions and Sarnelle and Knapp's (2005) experiment investigate long-term dynamics, whereas the suite of other experiments that find results that are consistent with this hypothesis are short-term, controlled, laboratory or mesocosm studies (Schindler 1992, Attayde and Hansson 2001a, but see Findlay et al. 2005). Our model predictions are only consistent with this hypothesis when the feeding relationships are described as donor-controlled. Under this scenario, the density of predators does not regulate the growth of prey (Pimm 2002). Poggiale et al. (1998) show the emergence of donor-controlled dynamics in a spatially heterogeneous predator-prey model. This suite of evidence suggests that the spatial and temporal scale of trophic interaction studies plays a key role in determining the relative effect of predator regulation of herbivores and consumer-mediated recycling on primary producers. Other factors such as the external nutrient loading rate and recycling efficiency also may influence the dominant mechanism causing cascading trophic interactions.

The effects of predator regulation and consumer-mediated recycling both increase with increasing allochthonous prey input but high allochthonous prey inputs can lead to the extinction of the local herbivore through apparent competition (Holt and Lawton 1994). At moderate allochthonous prey input, the effect size of consumer-mediated recycling increases whereas the effect size of predator regulation decreases with increasing predator preference for allochthonous prey. These results suggest that consumer-mediated recycling may play a larger role in determining producer stocks when predators feed on local and allochthonous prey (Vanni 2002, Glaholt and Vanni 2005).

We examine the conditions for herbivore recycling to have larger, positive, effects on primary producer

biomass than predator recycling (Attayde and Hansson 2001a). We observe a positive but idiosyncratic response of primary producer stocks to herbivore and predator recycling. The influence of recycling from either trophic level is sensitive to predator preference, attack rate, and turnover rate. At low turnover rate and predator preference for allochthonous prey, high predator recycling has a larger, positive effect on producer stocks than herbivore recycling. In contrast, herbivore recycling has a stronger effect on producer stocks than predator recycling when predators prefer local prey and recycling is high and when turnover rates are high or attack rates are low. When predators preferentially feed on allochthonous prey, the predator stocks may become large as they are able to extract nutrients from two sources and they are decoupled from the dynamics of the local prey (Schindler and Scheuerell 2002). We model recycling as stock dependent; therefore, we expect the stock of recycled nutrients from the predator to be largest when predator stocks are largest. With high turnover, low predator attack rate, or donor-controlled feeding relations, the effect of herbivore recycling on producer stocks is larger because predator regulation is weak under these scenarios. Likewise, Vanni and Layne (1997) hypothesize that the effects of zooplankton recycling on phytoplankton stocks will be greatest when planktivorous fish are regulated by piscivorous fish.

We also find mixed evidence that consumer recycling has a larger, positive effect on primary producer stocks when predators preferentially feed on allochthonous prey (Glaholt and Vanni 2005). Our model demonstrates this outcome for high herbivore recycling efficiency only when predator attack rates are high. However, this outcome prevails under most conditions for models with high predator recycling efficiency. This lends supports to studies, such as Glaholt and Vanni (2005), which demonstrate that consumer nutrient transport may contribute to high producer stocks (Vanni 2002). Although this effect has been mostly documented in aquatic ecosystems, there is evidence of positive effects of nutrient transport on producer stocks in terrestrial ecosystems. For example, Post et al. (1998) showed that geese in New Mexico feed on land but excrete most of their nutrients into their primary roosting wetlands. These spatial subsidies may decouple the predator and local herbivore and lead to larger pools of recycled material and primary producers (Henschel et al. 2001, Leroux and Loreau 2008).

Finally, we observe mixed support for the hypothesis that consumer-mediated recycling has a larger, positive effect on primary producers when external nutrient inputs are low (Braband et al. 1990, Shostell and Bukaveckas 2004). External nutrient inputs are most often temporally variable. For example, aquatic ecosystems in moist biomes may experience low external nutrient loading during the dry season (Shostell and Bukaveckas 2004). At equilibrium, our Lotka-Volterra models are not consistent with this experimental

outcome but donor-controlled models (Appendix A) did predict the largest, positive effect of consumer-mediated recycling when external nutrient inputs were low. In models with low nutrient inputs and Lotka-Volterra feeding relations, consumer stocks will be low, and since we model recycling as stock dependent, the pool of recycled material will be low. Consequently, recycling will have little influence on producer stocks under these conditions. Future models with temporally variable external nutrient inputs may enable us to explore this hypothesis under a broader range of conditions.

We investigate four cases that relate consumer-mediated recycling to higher primary producer stocks but these cases are not mutually exclusive. For example, our results are consistent with Persson (1997), who observed an interactive effect of fish recycling and fish regulation of zooplankton, which enabled higher algal stocks than if each process operated in isolation. What's more, most studies of consumer-mediated recycling do not examine variable external nutrient loading (but see Braband et al. 1990, Shostell and Bukaveckas 2004). Trophic cascade models predict that predator regulation of herbivores will increase with increasing nutrient loading (Attayde and Ripa 2008, Leroux and Loreau 2008); therefore, herbivore regulation, recycling, and nutrient loading should not be investigated in isolation.

A large body of theory on the role of consumers in ecosystems exists (e.g., Oksanen et al. 1981, McCann et al. 2005) but most of this work ignores consumer-mediated recycling (but see DeAngelis 1992, Moore et al. 2004). Despite the strong role of consumer-mediated recycling demonstrated in some recent research in aquatic ecosystems (e.g., Vanni and Layne 1997, Attayde and Hansson 2001a, Shostell and Bukaveckas 2004), we find limited theoretical evidence to show that consumer-mediated recycling is the driving force regulating primary producer stocks. However, our models do predict significant effects of consumer-mediated recycling under some conditions, for example, donor-controlled interactions, low predator attack rates, or low external nutrient loading. This is key because trophic cascade signals may be dampened or strengthened depending on the interaction between predator regulation of herbivores and consumer-mediated recycling. For example, if both processes have strong, opposite effects on producer stocks, then we expect dampened cascades, whereas if both mechanisms contribute positively to producer stocks, we expect stronger cascades. While the inclusion of consumer-mediated recycling adds additional complexity to the investigation of cascading trophic interactions, further investigation of this mechanism is critical, especially given the prominent use of biomanipulation in aquatic ecosystems, which is based on the theory of cascading trophic interactions (Mehner et al. 2002).

Biomanipulation via the addition of piscivore fish is a common management strategy to control harmful algal

outbreaks (reviewed in Mehner et al. 2002). Attayde and Hansson (2001a) argued that the addition of piscivores has the potential to stimulate, rather than suppress, harmful algae through consumer-mediated recycling. For this reason, Mehner et al. (2002) suggest that a biomanipulation strategy that focuses on regulating benthivorous fish could be more successful than one that focuses on regulating planktivorous fish. Cyanobacteria have a competitive advantage under low N:P (Smith 1983), and because recycled nutrients from fish and zooplankton have low N:P, the benefits of an increase in piscivores and subsequent increase in large zooplankton on primary producers may be larger than the negative effects of zooplankton regulation on primary producers. Above we discussed some additional conditions that are most likely to result in confounding effects of piscivore additions and consumer-mediated recycling. These conditions should be assessed prior to the application of biomanipulation, and these strategies should be implemented within an adaptive management framework (Walters 1986).

Consumer-mediated recycling may not only affect producer biomass but also producer species composition or production (Vanni 2002). For example, Attayde and Hanson (1999) demonstrate that fish and zooplankton recycling can have strikingly different effects on the composition of primary producers in an aquatic environment. Our model assumes a single limiting nutrient but recent research suggests that nutrient stoichiometry can set constraints on ecosystem functioning (Sterner and Elser 2002). This may be particularly relevant for designing successful biomanipulation strategies, because the N:P ratio (i.e., quality) of recycled and externally loaded nutrients can influence producer competition in aquatic ecosystems (Smith 1983, Braband et al. 1990, Shostell and Buckavekas 2004). It can be a challenge to design appropriate experiments to address such complex problems but Vanni and Layne (1997) and Attayde and Hansson (2001b) provide examples of elegant experiments that tease apart the relative effects of consumer regulation of herbivores and consumer-mediated recycling. Our model predictions suggest that a particular focus should be on measuring the feeding relationship between predator and multiple prey, the turnover rates of species, and the rate of external nutrient loading.

Conclusion

Cascading trophic interactions mediated by consumers are complex phenomena, which encompass many direct and indirect effects (Carpenter et al. 1985, Vanni 2002). Ecologists classically focus on the indirect effects of predator regulation of herbivores on primary producer stocks, but recent experiments in aquatic ecosystems propose that consumer-mediated recycling may also have a large effect on producer stocks (Schindler 1992, Vanni and Layne 1997, Attayde and

Hansson 2001a, Glaholt and Vanni 2005). Here we synthesize results from a suite of empirical research, which investigate the effects of consumer-mediated recycling in aquatic ecosystems, and we derive an ecosystem model to explore the generality of these empirical outcomes. Overall, our ecosystem model predicts that predator regulation of herbivores will have a larger effect on producer stocks than consumer-mediated recycling; however, consumer-mediated recycling can influence producer biomass in many cases. Future models and experiments under different systems and conditions can serve as useful tools for evaluating the relative contribution of other mechanisms that influence cascading trophic interactions such as predation of nutrient sources (Maron et al. 2006), omnivory (Polis and Strong 1996), and ecosystem engineering (Jones et al. 1994).

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APPENDIX A

Donor control model results (*Ecological Archives* E091-150-A1).

APPENDIX B

Results of sensitivity analysis (*Ecological Archives* E091-150-A2).