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Bottom-up and top-down effects in food chains depend on functional dependence: an explicit framework

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Abstract

Observed stock changes in perturbed ecosystems sometimes, but not always, are smaller than predicted by the trophic cascade hypothesis. These varying outcomes can be explained by (1) using detailed analysis of trophic-level interactions within the standard energy-based linear food-chain model, or (2) invoking web models and/or non-energy interactions between organisms. Previously I developed an analytic approach for the linear chain for a press-type perturbation and applied it to ratio-dependent functional relationships. Here I extend the linear chain analysis to a more general functional relationship which allows independent variation of prey dependence and intra-level interference. I find that different combinations of prey dependence and interference lead to large or small cascading effects. Generally, large top-down effects require weak interference, while large bottom-up effects require both weak interference and strong prey dependence.

Keywords: Trophic cascade; Top-down; Bottom-up; Food chain; Ratio dependent; Prey dependent; Predator dependent

1. Introduction

An ecosystem is said to exhibit a trophic cascade (TC) when perturbing the stock of a higher trophic level results in observable changes in the stocks of lower trophic levels. The mirror image, i.e. consequences of perturbing a lower trophic level, is called the bottom-up effect. The trophic cascade is often seen experimentally, but often it is not. Many reasons for its absence derive from various manifestations of food webs rather than linear chains, but it is not necessary to abandon chains to explain a wide range of observations. A typical result is that the effect of perturbing a high trophic level becomes undetectable two trophic levels down the chain. In Herendeen (1995) I argued, using an analytical model and simulations, that for a press perturbation, this diminution is to be expected for ratio-dependent predator–prey relationships. In this paper I extend chain analysis for a press perturbation to incorporate variable prey dependence and interference in each trophic level. Response to a periodic perturbation will be covered in a subsequent article (Herendeen, in preparation).

I will show that this approach predicts large or small TCs depending on the degree of prey dependence and intralevel interference. The paper is organized as follows.

Section 2: Background on trophic cascades seen and not seen.

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Section 3: General analytical approach for a press-perturbed food chain.
Section 4: Response of a 3-level food chain to a press perturbation.
Section 5: Obtaining large top-down and small bottom-up effects.
Section 6: Conclusions.

2. Background: trophic cascades seen and not seen

The trophic cascade hypothesis has often been criticized because the observed effects are smaller than one hopes for (Diana et al., 1991; Baca and Drenner, 1995; Carter and Rypstra, 1995; Brett and Goldman, 1996, 1997; Brönmark and Weisner, 1996; Mullersolger et al., 1997; Mikola and Setälä, 1998; Bertolo et al., 2000). That is, the change in the stock of one trophic level is less than expected, often to the point of undetectability, when the stock of another trophic level is changed. Because of early claims that the trophic cascade would be a powerful management tool (e.g. to control aquatic vegetation by manipulating fish populations), this has led to a number of criticisms (DeMelo et al., 1992). These include:

Conceptual:

1. Real ecosystems are webs, not chains as the TC assumes (Hill and Lodge, 1995; Polis and Strong, 1996; Polis et al., 2000). Recent work has shown the strength of several mechanisms that work against the TC, for example, omnivory (Nyström et al., 1996; Charlebois and Lamberti, 1996; Strong, 1999), and nutrient loops (Carpenter et al., 1992; Findlay et al., 1994; Vanni and Layne, 1997; Vanni et al., 1997; Perez-Fuentetaja et al., 1996). Polis (1999) argued that chain-like dynamics is much more likely (for trophic levels as distinct from individual species) in aquatic than in terrestrial systems.
2. Even with chain structure, shifts in the strength and functional dependence of predation, as well as non-energy behavioral interactions, change the quantitative interactions of trophic levels and lead to responses not predicted by the simple (time independent) relations assumed in the TC (Balciunas and Lawler, 1995; Chase, 1996; Moran et al., 1996; Schmitz et al., 2000; Beckerman et al., 1997; Pace et al., 1998; Turchin et al., 2000). Specific issues are refuges, prey-dependent instead of ratio-dependent predation (one example being Lotka–Volterra dynamics, which tends to produce oscillations), and intratrophic level interference (Rosenheim et al., 1993; McCann et al., 1998).

Experimental:

Experiments are inadequately defined and executed regarding temporal behavior:

(a) The time profile of the perturbation and the expected response is ambiguous: is the perturbation a pulse, a press (a step function that persists indefinitely), or periodic, such as a sinusoid in time (Blaustein et al., 1995; Leibold et al., 1997)? If top-down and bottom-up perturbations are used simultaneously, is there clear delineation between the two (Diana et al., 1991)?
(b) Experiments are not run long enough (often for good and practical reasons) for transient effects to damp out (Leibold et al., 1997; Persson, 1997; Pace et al., 1998; Polis et al., 2000).

With all these objections there is still an argument for chain-like trophic effects. Hairston and Hairston (1997) claim that even though omnivory is more likely in terrestrial than in aquatic systems, trophic-level dynamics is still often observed. This harkens back to Hairston et al.'s (1960) three-level "green world" hypothesis.

In addition, the size of the sought-after TC effect has often not been carefully predicted. Implicitly, one is seeking effects in distant trophic levels of a magnitude comparable with the perturbed level. For example, halving the biomass of piscivorous fish is casually expected to produce roughly a doubling or halving of stocks in other trophic levels. While effects of this magnitude are sometimes seen (Marquis and Whelan, 1994; Wootton, 1995; Chase, 1996; Moran et al., 1996; Moran and Hurd, 1998; Estes et al., 1998; Nicholls, 1999; Schmitz et al., 2000), the mechanism of the TC does not require them.

It is not necessary to invoke the above conceptual criticisms and abandon a time-independent linear chain model to explain finding small or no TC effects. In Herendeen (1995) I showed analytically, with simulation corroboration, that for ratio-dependent predation, the strength of the TC can fall off rapidly down the chain. Combining this result with the experimental criticism above, we then have the possibility that researchers are often looking for too-large effects in too-quick experiments, and, not surprisingly, often not finding them.

In Herendeen (1995) I investigated the case in which an one level in a chain is perturbed (via a positive or negative step function change in cropping or in light level) so that the level eventually settles down to a fractional stock change of 1 unit (arbitrarily chosen). This is the experiment envisioned, if not explicitly articulated or achieved, by many researchers. I found that with ratio-dependent predation, the fractional stock change diminishes down the trophic chain, but is approximately the same up the trophic chain. The method allowed perturbing several levels simultaneously, which covers experiments combining simultaneous top-down and bottom-up manipulations such as reported by McCarty (1997) and Carpenter et al. (1996). One early hope was that manipulating top carnivores in eutrophicated lakes would cascade to control algal blooms, but the latter authors concluded that "… the potential for increasing eutrophication [of a lake system] by P[hosphorus] input exceeds the potential for controlling eutrophication by food web manipulation" (i.e. bottom-up manipulation is more effective than top-down).

3. General analytical approach for a press-perturbed food chain

Assume a food chain of k trophic levels, as shown in Fig. 1. (Table 1 contains definitions of all symbols.)

For each level i, the general, steady state biomass energy conservation equation is:

$$\mathrm{INPUT}_i = \mathrm{METMORT}_i + \mathrm{CROPPING}_i + \mathrm{INPUT}_{i+1} \tag{1}$$

where INPUT_i is the energy flow into level i resulting from preying upon level $i-1$, $\mathrm{METMORT}_i$ is the energy flow out of level i resulting from metabolism and non-predation mortality, $\mathrm{CROPPING}_i$ is the energy flow out of level i resulting from cropping (if negative, it represents stocking), INPUT_{i+1} is the energy flow out of level i resulting from predation by level $i+1$, S_i is the energy stock in level i.

METMORT is assumed to be proportional to stock (i.e. $\mathrm{METMORT}_i = \mu_i S_i$). $B_i(S_i, S_{i-1})$ is the input per unit stock of level i, where B_i depends nonlinearly on the stocks of predator and prey. For the lowest trophic level the "prey" is light and nutrients, which I call RESOURCE. I will consider three types of press perturbation:

1. Changes in CROPPING.
2. Changes in RESOURCE.
3. Changes in $B_i(S_i, S_{i-1})$, i.e. in functional dependence.

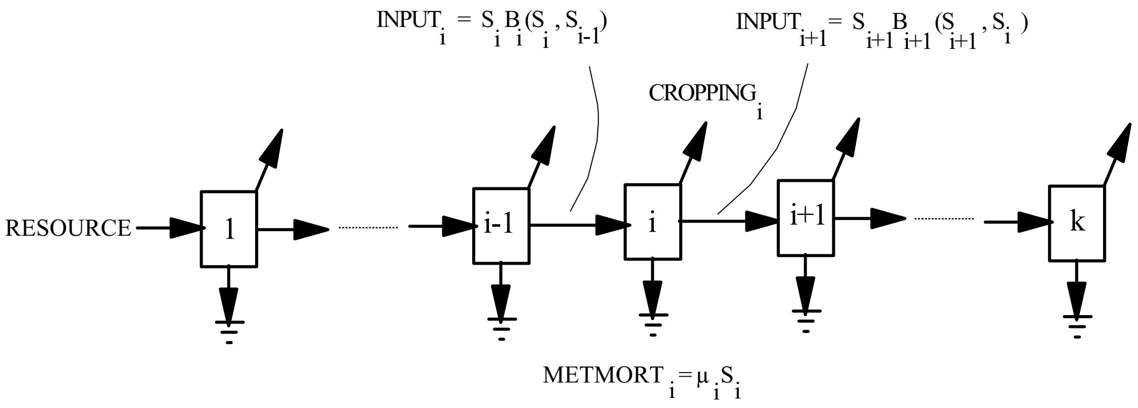

Fig. 1. Food chain. The arrows are biomass energy flows, plus metabolic heat loss and non-predation mortality in METMORT. Trophic level increases to the right.

Table 1
Symbols used

Symbol	Description	Units
$\underline{\underline{A}}$	Matrix of L, M, N	Energy time^{-1} energy^{-1}
b_i	Time-dependent parameter in B_i	Dimensionless
B_i	Feeding input (per unit stock) to level i as function of S_i and S_{i-1}	Energy time^{-1} energy^{-1}
c_i	Parameter in B_i	Dimensionless
CROPPING$_i$	Exogenous removal from level i (negative for stocking)	Energy time^{-1}
fbu$_i$	δ_i/δ_{i-1} (for bottom-up effect)	Dimensionless
ftd$_i$	δ_i/δ_{i+1} (for top-down effect)	Dimensionless
INPUT$_i$	Feeding input to level i	Energy time^{-1}
k	Number of trophic levels in food chain	Dimensionless
L_i, M_i, N_i	Coefficients characterizing relationship between δ_i; function of initial flows and of prey and interference derivatives	Energy time^{-1}
METMORT$_i$	Metabolic and non-predation loss from level i	Energy time^{-1}
$\underline{P}$	Most general perturbation vector	Energy time^{-1} energy^{-1}
q_i	Parameter expressing degree of prey dependence	Dimensionless
r_i	Parameter expressing degree of interference	Dimensionless
Prey derivative$_i$	$\dfrac{\partial B_i}{\partial S_{i-1}}\dfrac{S_{i-1}}{B_i} = q_i\left(\dfrac{c_i}{c_i+1}\right)$	Dimensionless
Interference derivative$_i$	$\dfrac{\partial B_i}{\partial S_i}\dfrac{S_i}{B_i} = -r_i\left(\dfrac{c_i}{c_i+1}\right)$	Dimensionless
RESOURCE$_i$	Resource (light or nutrient) level; affects level 1 only	Vary, depending on particular resource (e.g. light intensity, nutrient concentration)
S_i	Stock of level i	Energy
α_I	Relative abundance of level i's prey	Dimensionless
δ_I	$\Delta S_i/S_i$ (ΔS_i = change in S_i)	Dimensionless
μ_i	METMORT$_i$/S_i (assumed constant)	Energy time^{-1} energy^{-1}

I assume that the perturbations are small enough to induce relatively small changes in stocks, ΔS_i, from the original steady state. Then a linear (Taylor series expansion) approximation can be used for the change of the B_i, yielding equations relating the stock changes in all compartments. (In spite of this restriction, in Section 5 we will see that this approach predicts well the behavior of simulations of nonlinear models undergoing large changes.) With perturbations, Eq. (1) becomes:

$$\Delta\mathrm{INPUT}_i = \Delta\mathrm{METMORT}_i + \Delta\mathrm{CROPPING}_i + \Delta\mathrm{INPUT}_{i+1} \qquad (2)$$

$\Delta\mathrm{METMORT}_i = \mu_i \Delta S_i$ by assumption, and

$$\Delta\mathrm{INPUT}_i = \Delta(S_i B_i) \approx \Delta S_i B_i + S_i \times \left(\frac{\partial B_i}{\partial S_i}\Delta S_i + \frac{\partial B_i}{\partial S_{i-1}}\Delta S_{i-1} + \frac{\partial B_i}{\partial b_i}\Delta b_i\right) \qquad (3)$$

The ΔS_i are the dependent variables, driven by exogenous changes in CROPPING, RESOURCE, and $B_i(S_i, S_{i-1})$. I have assumed that B_i has the form $b_i f_i(S_i, S_{i-1})$, where b_i is a (potentially time-dependent) parameter and f_i is a nonlinear function of S_i and S_{i-1}. As an example, b_i could increase if snow cover makes it easier for wolves to take moose (Post et al., 1999).

As shown in Herendeen (1995), manipulating Eqs. (3) and (4) then gives for each compartment:

$$L_i\frac{\Delta S_{i-1}}{S_{i-1}} + M_i\frac{\Delta S_i}{S_i} + N_i\frac{\Delta S_{i+1}}{S_{i+1}} = L_i\frac{\Delta\mathrm{RESOURCE}}{\mathrm{RESOURCE}} + \Delta\mathrm{CROPPING}_i - \mathrm{INPUT}_i\frac{\Delta b_i}{b_i} + \mathrm{INPUT}_{i+1}\frac{\Delta b_{i+1}}{b_{i+1}} \qquad (4)$$

where

$$
\begin{aligned}
L_i &\equiv \mathrm{INPUT}_i \frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} \\
M_i &\equiv \mathrm{INPUT}_i \left(1 + \frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i}\right) \\
&\quad - \mathrm{INPUT}_{i+1} \frac{\partial B_{i+1}}{\partial S_i} \frac{S_i}{B_{i+1}} - \mathrm{METMORT}_i \\
N_i &\equiv -\mathrm{INPUT}_{i+1} \left(1 + \frac{\partial B_{i+1}}{\partial S_{i+1}} \frac{S_{i+1}}{B_{i+1}}\right)
\end{aligned}
\tag{5}
$$

Because initial and end states are steady states, Eq. (4) contains only the original flows but not the stocks. The dynamic transition between steady states would be described by a time-dependent version of Eq. (4) which contains both initial stocks and flows (Herendeen, in preparation).

Let us streamline the notation by defining $\delta_i = \Delta S_i/S_i$. Then Eq. (4) for $i = 1, \ldots, k$ can be written in matrix form as:

$$\underline{\underline{A}}\underline{\delta} = \underline{P} \tag{6}$$

where

$$
\underline{\underline{A}} = \begin{bmatrix}
M_1 & N_1 & 0 & \cdot & 0 & 0 & 0 \\
L_2 & M_2 & M_2 & \cdot & 0 & 0 & 0 \\
0 & L_3 & M_3 & \cdot & 0 & 0 & 0 \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
0 & 0 & 0 & \cdot & M_{k-2} & N_{k-2} & 0 \\
0 & 0 & 0 & \cdot & L_{k-1} & M_{k-1} & N_{k-1} \\
0 & 0 & 0 & \cdot & 0 & L_k & M_k
\end{bmatrix}
\quad \text{and} \quad
\underline{\delta} = \begin{bmatrix}
\delta_1 \\ \delta_2 \\ \delta_3 \\ \cdot \\ \delta_{k-2} \\ \delta_{k-1} \\ \delta_k
\end{bmatrix}
$$

All quantities in Eq. (5), including the derivatives, are evaluated at the original steady state. The derivative in L_i is level i's feeding sensitivity to abundance of its prey and is never negative; therefore $L_i \geq 0$. The derivative in N_i is level $i+1$'s feeding sensitivity to its own abundance, the degree of interference. It is almost never positive, but usually greater than -1. Therefore usually $N_i < 0$. M_i is a function of both interference in level i and prey dependence in level $i+1$. It is usually negative but can have any value. The levels at each end of the chain are special cases. For trophic level 1, $L_1 \Delta S_0/S_0$ is interpreted as resulting from a perturbation to RESOURCE. Also, while perturbing RESOURCE must, and perturbing CROPPING can, directly affect only one level, changing one b_i must directly affect two levels, the predator (level i) and the prey (level $i-1$).

The k equations of the form of Eq. (4) are solved simultaneously for the fractional stock changes $\Delta S_i/S_i$.

and $\underline{P}$, the perturbation vector, contains the terms on the right hand side of Eq. (4). The solution to Eq. (6) is:

$$\underline{\delta} = \underline{\underline{A}}^{-1}\underline{P} \tag{7}$$

$\underline{\underline{A}}$ is related to the community matrix used in analyzing the generalized Lotka–Volterra equations by Case (2000) and Bender et al. (1984). The method is also discussed by van den Berg (1998).

4. Response of a 3-level system to a press perturbation

This method can be applied to a system with any number of trophic levels. For a 3-level system:

$$
\underline{\underline{A}} = \begin{bmatrix}
M_1 & N_1 & 0 \\
L_2 & M_2 & N_2 \\
0 & L_3 & M_3
\end{bmatrix}
$$

$\det \underline{\underline{A}} = M_1 M_2 M_3 - L_3 N_2 M_1 - L_2 N_1 M_3$, and

$$
\underline{\underline{A}}^{-1} = \frac{1}{\det \underline{\underline{A}}} \begin{bmatrix}
M_2 M_3 - L_3 N_2 & -M_3 N_1 & N_1 N_2 \\
-L_2 M_3 & M_1 M_3 & -M_1 N_2 \\
L_2 L_3 & -L_3 M_1 & M_1 M_2 - L_2 N_1
\end{bmatrix}
\tag{8}
$$

For a bottom-up perturbation, $\underline{P}$ is proportional to $\begin{pmatrix}1\\0\\0\end{pmatrix}$; for a top-down perturbation, to $\begin{pmatrix}0\\0\\1\end{pmatrix}$.

As in Herendeen (1995), define the bottom-up factor $\text{fbu}_i = \delta_i/\delta_{i-1,}$ and the top-down factor $\text{ftd}_i = \delta_i/\delta_{i+1}$. Then from Eqs. (7) and (8):

$$\begin{array}{ll}
\text{Action: Perturb level 1} & \text{Action: Perturb level 3} \\
- & \text{ftd}_1 = \dfrac{\delta_1}{\delta_2} = -\dfrac{N_1}{M_1} \\
\text{fbu}_2 = \dfrac{\delta_2}{\delta_1} = -\dfrac{L_2M_3}{M_2M_3 - L_3N_2} & \text{ftd}_2 = \dfrac{\delta_2}{\delta_3} = -\dfrac{M_1N_2}{M_1M_2 - L_2N_1} \\
\text{fbu}_3 = \dfrac{\delta_3}{\delta_2} = -\dfrac{L_3}{M_3} & -
\end{array} \tag{9}$$

Eqs. (7) and (8) show that the δ_i depend on all the L_i, M_i, and N_i, not just those in level i or the adjacent level; this is truly a coupled system. Even the fbu and ftd (for which $\det \underline{\underline{A}}$ cancels out) can have such indirect dependence; for example, ftd_1 depends on c_2, r_2, c_3, and q_3. The results in Eq. (9) were analyzed for ratio-dependent predation in Herendeen (1995). In the next section I use other functional dependences.

5. Obtaining large or small top-down and bottom-up effects

I will use a general predator–prey relationship in which prey dependence and predator interference can be varied independently. Let

$$B_i = \frac{\text{INPUT}_i}{S_i} = \frac{\text{INPUT}_{i,0}}{S_{i,0}}\left[\frac{b_i(c_i+1)\alpha_i}{(c_i+\alpha_i)}\right] \quad \text{where}$$

$$\alpha_i \equiv \text{“abundance”} \equiv \frac{(\text{S}_{i-1}/S_{i-i,0})^q}{(S_i/S_{i,0})^r} \tag{10}$$

Eq. (10) is a Holling Type 2 functional relationship with respect to prey abundance. The subscript “0” refers to the initial steady state, where α_i and $b_i = 1$; hence the bracketed term $= 1$. c_i, q_i, and r_i are parameters. The c_i, are always non-negative. q_i, and r_i are usually non-negative, though negativity is possible (consider cooperation between predators). If $q_i = 0$, level i is totally insensitive to abundance of prey. If $r_i = 0$, level i is totally free of interference between individuals. $q_i = r_i = 1$ defines ratio dependence. For finite c_i, consumption saturates for infinite abundance. For $c_i \to \infty$, consumption is linear in abundance; Lotka–Volterra, and pure donor and recipient control forms occur for particular values of q and r. (A recent discussion of ratio, prey, and predator dependence is Vucetich et al., 2002.) For $c_i \to 0$, recipient control is the only possibility. (Limiting cases for Eq. (10) are detailed in Table 2.) At the initial steady state:

$$\begin{aligned}
\text{prey derivative}_i &\equiv \frac{\partial B_i}{\partial S_{i-1}}\frac{S_{i-1}}{B_i} = q_i\left(\frac{c_i}{c_i+1}\right) \\
\text{interference derivative}_i &\equiv \frac{\partial B_i}{\partial S_i}\frac{S_i}{B_i} = -r_i\left(\frac{c_i}{c_i+1}\right)
\end{aligned} \tag{11}$$

These derivatives go into the L, M, and N. For the three level system, fbu_3 (Eq. (9)) is proportional to L_3, and hence proportional to q_3. If $q_3 = 0$, there is no bottom-up effect of level 2 on level 3. Analogously, ftd_1 is proportional to N_1 and hence to $(1-r_2c_2/(c_2+1))$; it is affected by r_2, but not as strongly as fbu_3 is affected by q_3. If $r_2 = 0$, i.e. no interference in level 2, the top-down effect of level 2 on level 1 is maximized. This is reasonable; if level 2 had strong interference, then (say) increasing its stock would result in less consumption per individual, and hence a lesser change of impact on level 1 as compared with no interference, when the consumption per individual would not be affected.

Eq. (9) shows that both ftd_1 and fbu_3 are strongly affected by M_1 and M_3, respectively. Eq. (5) shows that M_i is affected by the interference derivative term for level i and the prey derivative term for level $i+1$. These would have equal influences on M_i only if level i had an ecological efficiency of 50%. With a more typical efficiency of 10%, M_i is dominated by the interference derivative. M_i can approach zero, corresponding to low interference and resulting in a large top-down

Table 2
Algebraic form of the functional form (Eq. (10)) for various limiting values of the parameters c, q, and r

q_i	r_i	Finite c_i		$c_i \to \infty$	
		$\mathrm{INPUT}_i/S_i = B_i$	$\mathrm{INPUT}_i = B_iS_i$	$\mathrm{INPUT}_i/S_i = B_i$	$\mathrm{INPUT}_i = B_iS_i$
Ratio dependence					
1	1	$B_{i,0}\dfrac{(c_i+1)((S_{i-1}/S_{i-1,0})/(S_i/S_{i,0}))}{c_i+((S_{i-1}/S_{i-1,0})/(S_i/S_{i,0}))}$ (nonlinear ratio dependence)	$B_{i,0}S_i\dfrac{(c_i+1)((S_{i-1}/S_{i-1,0})/(S_i/S_{i,0}))}{c_i+((S_{i-1}/S_{i-1,0})/(S_i/S_{i,0}))}$	$B_{i,0}\dfrac{(S_{i-1}/S_{i-1,0})}{(S_i/S_{i,0})}$ (linear ratio dependence)	$B_{i,0}\dfrac{(S_{i-1}/S_{i-1,0})}{(1/S_{i,0})}$ (linear prey dependence = donor control)
Prey dependence					
1	0	$B_{i,0}\dfrac{(c_i+1)(S_{i-1}/S_{i-1,0})}{c_i+(S_{i-1}/S_{i-1,0})}$ (nonlinear prey dependence)	$B_{i,0}S_i\dfrac{(c_i+1)(S_{i-1}/S_{i-1,0})}{c_i+\ (S_{i-1}/S_{i-1,0})}$	$B_{i,0}\left(\dfrac{S_{i-1}}{S_{i-1,0}}\right)$ (linear prey dependence = donor control)	$B_{i,0}S_i\left(\dfrac{S_{i-1}}{S_{i-1,0}}\right)$ (Lotka–Volterra)
Interference (predator) dependence					
0	1	$B_{i,0}\dfrac{(c_i+1)(1/(S_i/S_{i,0}))}{c_i+(1/(S_i/S_{i,0}))}$ (nonlinear predator dependence)	$B_{i,0}S_i\dfrac{(c_i+1)(1/(S_i/S_{i,0}))}{c_i+(1/(S_i/S_{i,0}))}$ (nonlinear predator dependence)	$B_{i,0}\dfrac{1}{(S_i/S_{i,0})}$ (nonlinear predator dependence)	$B_{i,0}\dfrac{1}{(1/S_{i,0})}$ (constant)
No prey- or interference (predator) dependence					
0	0	$B_{i,0}$ (constant)	$B_{i,0}S_i$ (linear predator dependence = recipient control)	$B_{i,0}$ (constant)	$B_{i,0}S_i$ (linear predator dependence = recipient control)

Subscript “0” refers to the original steady state. Many of the cases have standard names, which are listed. There is some ambiguity about whether the terms apply to INPUT/S or INPUT, so both are given.

Table 3
Sensitivity of top-down and bottom-up effects to changes in parameters

Assuming increase in	Resulting change in magnitude of $\text{fbu}_i = \delta_i/\delta_{i-1}$	Resulting change in magnitude of $\text{ftd}_i = \delta_i/\delta_{i+1}$
c_i	Small+	Moderate−
c_{i+1}	Small+	Moderate−
q_i	*Large+*	Small−
q_{i+1}	Moderate−	Moderate−
r_i	*Large−*	*Large−*
r_{i+1}	Moderate+	*Large−*

Reference conditions: all c, q, $r = 1$; all ecological efficiencies = 10%. Increase in q signifies increased prey dependence; increase in r signifies increased interference. Strongest influences are in italics.

effect. Table 3 summarizes the effect of parameter changes.

All of these conclusions are based on a linear approximation. Simulation of a nonlinear model will allow checking of validity and applicability.

I now compare the analytical results above with results of simulating a perturbed hypothetical three-compartment food chain illustrated at steady state in Fig. 2 and having the functional relationships of Eq. (10). The simulation is performed using the software Stella 3.0.7 (High Performance Systems, Hanover, NH). The following relationships connect the stocks (units = energy) and the flows (units = energy/time).

METMORT (metabolic loss and non-predation mortality):

$$\text{METMORT}_i = \mu_i S_i \quad \text{with}$$
$$\mu_i = 30.0,\ 4.5,\ \text{and}\ 9/7\ (\text{time unit})^{-1},$$
$$\text{respectively for}\ i = 1, \ldots, 3.$$

INPUT:

$$\frac{\text{INPUT}_{i,0}}{S_{i,0}} = \frac{100}{3},\ 5.0,\ \text{and}\ 10/7\ (\text{time unit})^{-1},\ \text{respectively}.$$

$$\text{Level 1}: \alpha_1(\text{“abundance”}) = \left(\frac{\text{RESOURCE}}{\text{RESOURCE}_0}\right) \Big/ \left(\frac{S_1}{S_{1,0}}\right).$$

$$\text{Levels 2 and 3}: \alpha_i = \frac{(S_{i-1}/S_{i-1,0})}{(S_i/S_{i,0})}.$$

Figs. 3–6 show the simulation results for a press perturbation (bottom up: increased light, or top down: changed cropping of level 3) for four combinations of c_i, q_i, and r_i. Detailed quantitative results are given in Table 4. Discussion of the four cases follows.

Case 1. Nonlinear ratio-dependent predation in all levels (Fig. 3).

In Fig. 3a, a doubling of the light level produces roughly a doubling in stock in all levels. (This would be exactly true for an uncropped ratio-dependent system.) On the other hand, increasing the cropping of level 3 produces fractional stock changes that decrease

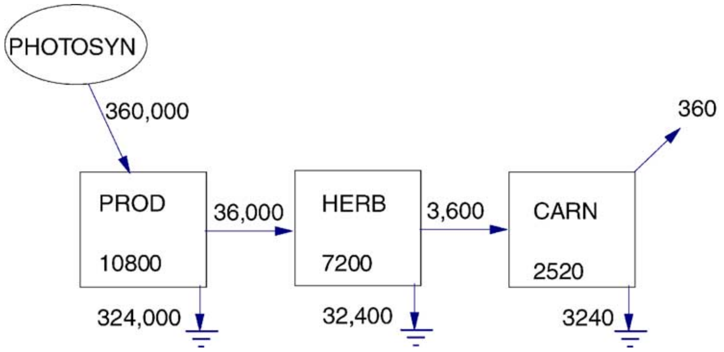

Fig. 2. A hypothetical 3-level food chain at initial steady state. Numbers in compartments are stocks (units = cal). Other numbers are flows (units = cal/year).

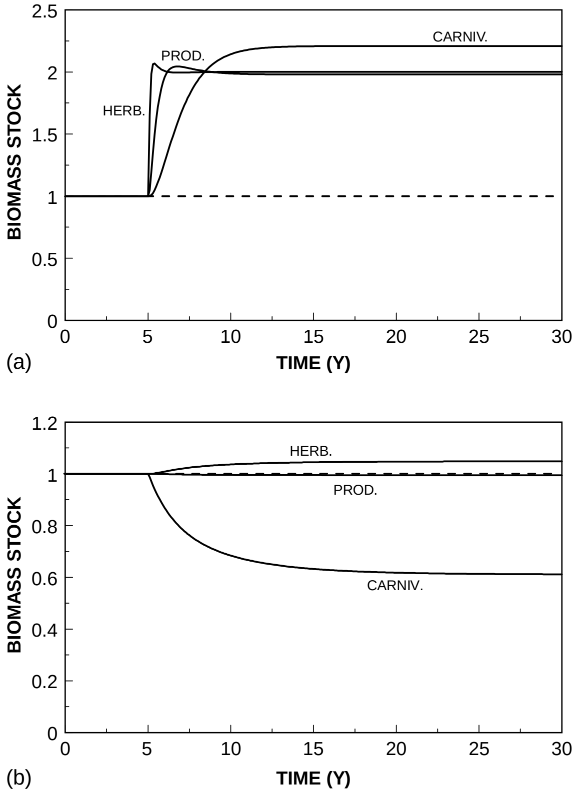

Fig. 3. Case 1. Response of biomass stocks in system in Fig. 2 to press perturbation at time = 5 years. All levels have ratio dependence (values for *c*, *q*, and *r* are given in Table 4). (a) Bottom up: light is doubled; (b) top down: cropping of level 3 (carnivores) increases from 360 to 800 cal/year. All stocks are normalized to initial value of one.

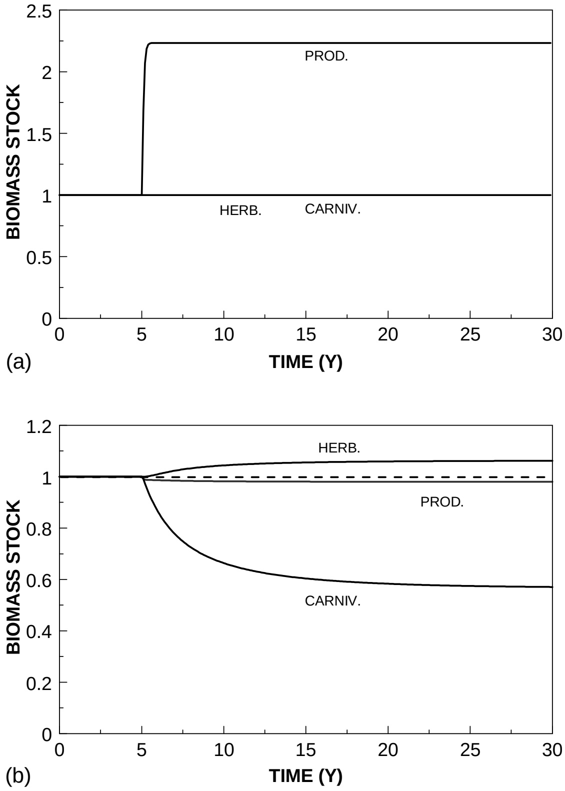

Fig. 4. Case 2. Response of biomass stocks in system in Fig. 2 to press perturbation at time = 5 years. “Green world” scenario. As in Case 1 except that herbivores have zero prey dependence on producers (values for *c*, *q*, and *r* are given in Table 4). (a) Bottom up: light is doubled; (b) top down: cropping of level 3 (carnivores) increases from 360 to 800 cal/year.

by roughly a factor of ten for each level down the chain (Fig. 3b). In Herendeen (1995) these patterns were noted for a ratio-dependent system and proposed as a reason that top-down effects often are not observed. Table 4 indicates excellent agreement for fbu (within 2%) and good agreement for ftd (within 20%) between calculation and simulation, even though stocks change by large amounts (+121 to −39%).

Case 2. “Green world” hypothesis of Hairston et al. (1960) (Fig. 4).

Here level 2, herbivores, has $q = 0$, making it insensitive to the abundance of producers. Indeed, the bottom-up perturbation stops at level 2, as shown in Fig. 4a. The top-down effect is approximately the same as for Case 1, i.e. rapid diminution (Fig. 4b). Agreement between calculation and simulation is good (within 20%) for ftd, even while stocks change by up to 38%.

Case 3. “Green world” plus increased c_1 and low interference in producers and herbivores (Fig. 5).

As in Case 2, the bottom-up response (Fig. 5a) stops at level 2. However, top-down effects are now large: ftd is approximately −1 for levels 1 and 2. This is therefore a system that exhibits weak bottom-up and strong top-down effects, the opposite of Case 1. ftd (Fig. 4b) shows good (within 28%) agreement between calculation and simulation for a maximum stock change of 26%.

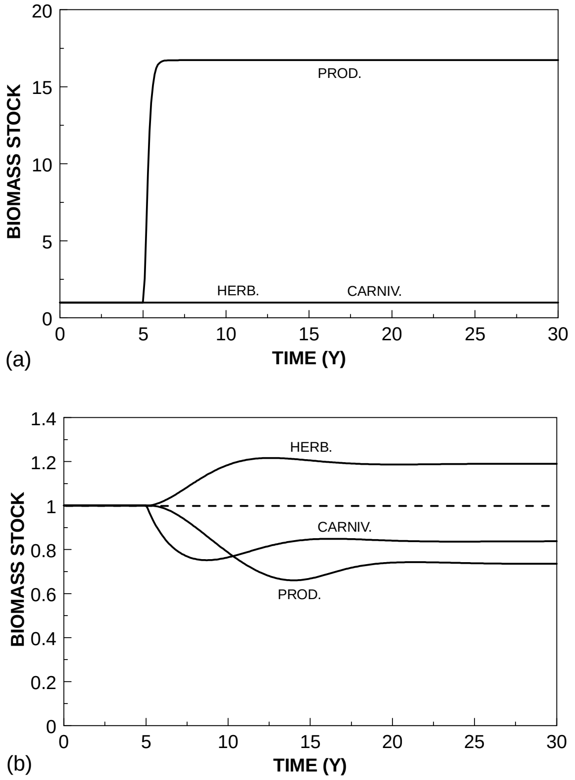

Fig. 5. Case 3. Response of biomass stocks in system in Fig. 2 to press perturbation at time = 5 years. "Green world" (Case 2) plus increased c_1 and decreased interference in producers and herbivores (values for c, q, and r are given in Table 4). (a) Bottom up: light is doubled; (b) top down: cropping of level 3 (carnivores) increases from 360 to 825 cal/year.

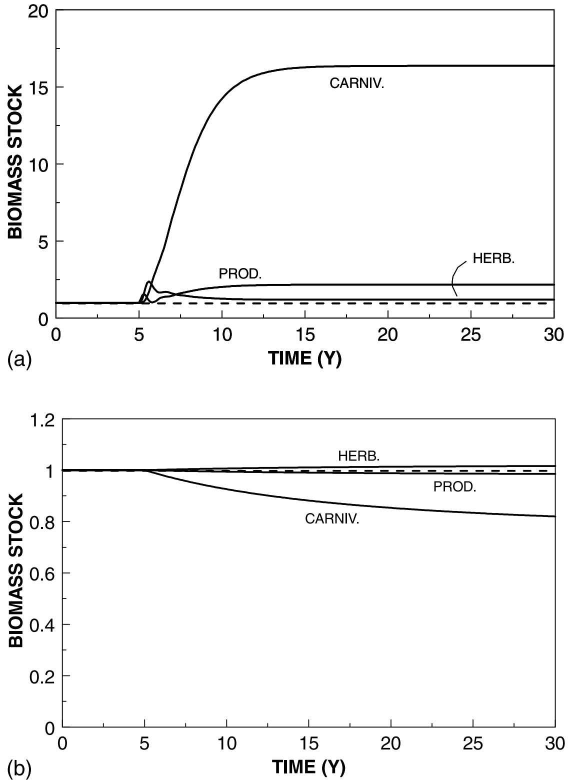

Fig. 6. Case 4. Response of biomass stocks in system in Fig. 2 to press perturbation at time = 5 years. All levels are approximately Lotka–Volterra (values for c, q, and r are given in Table 4). (a) Bottom up: light is increased by 10%; (b) top down: cropping of level 3 (carnivores) increases from 360 to 410 cal/year.

Case 4. All levels have approximately Lotka–Volterra dependence (Fig. 6).

Stock changes for the bottom-up perturbation (Fig. 6a) approximate δ_1:δ_2:δ_3 = 1:0:10 (for ecological efficiencies of 10%) as noted in Herendeen (1995) and described qualitatively by Oksanen et al. (1981). In this case the bottom-up effect is large but occurs only for every other level. Top-down response (Fig. 6b) shows δ_1:δ_2:δ_3 =∼ 10:1:1, again giving alternate small and large ftd. ftd shows excellent (within 3%) agreement between simulation and calculation. For fbu agreement is poorer, but still satisfactory given the 16-fold change in level 3.

The four cases can be summarized thus:

Case 1: Ratio dependent. Large bottom-up effect, rapidly diminishing top-down effect.
Case 2. "Green world". Zero bottom-up effect, rapidly diminishing top-down effect.
Case 3. "Green world" plus increased c_1. Zero bottom-up effect, large top-down effect.
Case 4. Lotka–Volterra. Mixed top-down and bottom-up effect.

One can ask if this system can be designed to show both large bottom-up and top-down effects. I believe it cannot; the combinations of c, q, and r that predict that outcome from Eq. (9) also result in an unstable initial steady state. A perturbation drives it to expand without limit or diminish to extinction in one or more

Table 4

Comparison of simulation and calculation for predicting stock changes under bottom-up or top-down press perturbation

Level	c	q	r	BOTTOM UP					TOP DOWN				
				Perturbation	Simulated		Calculated		Perturbation	Simulated		Calculated	
					δ	fbu	δ	fbu		δ	ftd	δ	ftd
Case 1. All levels are nonlinear, ratio dependent													
1	1	1	1	Light is doubled	+1.002	–	+1.002	–	Cropping of level 3 is increased	−0.0052	−0.108	−0.00299	−0.111
2	1	1	1		+0.980	+0.978	+0.978	+0.976	from 360 to 800	+0.0486	−**0.125**	+0.0269	−**0.0989**
3	1	1	1		+1.210	+1.23	+1.222	+1.25		−0.389	–	−0.272	–
Case 2. "Green world": as in Case 1 but herbivores have zero prey dependence on producers													
1	1	1	1	Light is doubled	+1.234	–	+1.250	–	Cropping of level 3 is increased	−0.00646	−0.1223	−0.003726	−0.1250
2	1	0	1		0	0	0	0	from 360 to 800	+0.05283	−**0.1397**	+0.02981	−**0.1111**
3	1	1	1		0	0	0	0		−0.3782	–	−0.2683	–
Case 3. "Green world" plus increased c_1 and low interference in producers and herbivores													
1	1.72	1	0.3	Light is doubled	+15.70	–	+7.05	–	Cropping of level 3 is increased	−0.2646	−1.394	−0.1440	−1.003
2	1	0	0.2		0	0	0	0	from 360 to 825	+0.1898	−**1.170**	+0.1435	−**1.000**
3	1	1	1		0	0	0	0		−0.1662	–	−0.1435	–
Case 4. All levels are approximately Lotka–Volterra													
1	1E6	1	0.1	Light is increased by 10%	+1.084	–	+1.000	–	Cropping of level 3 is increased	−0.01824	−0.894	−0.0125	−0.900
2	1E6	1	0.1		+0.1983	+*0.183*	+1.11E−6	+*1.00E−6*	from 360 to 410	+0.02040	−0.0923	+0.0139	−0.0900
3	1E6	1	0.1		+15.37	+*77.5*	+11.11	+*1.00E7*		−0.2211	–	−0.1543	–

$\delta_i \equiv$ (change in stock of level i)/(original stock in level i). For fbu and ftd, normal values have $<$10% difference between calculation and simulation; bold values, $<$25%; and italic values, >25%. In Case 4, $r = 0.1$ instead of 0.0 to prevent the simulation from crashing. Transient response is discussed in Herendeen (in preparation).

levels. Dynamic issues are addressed in Herendeen (in preparation).

6. Conclusions

In spite of valid concerns about web structure, a linear chain model is useful and successful in interpreting and explaining the widely varying strengths of observed trophic cascades under press perturbation:

1. The method for analyzing a press perturbation in Herendeen (1995) has been extended from ratio-dependent predation to incorporate functional relationships which vary among levels and for which the degree of prey dependence and interference can be varied independently. This results in a wide range of predicted bottom-up and top-down effects.
2. Top-down and bottom-up effects depend strongly on interference within the "target" level. Additionally, the bottom-up effect depends strongly on prey dependence of the target level.
3. The analysis of press perturbations to a food chain, though based on a linear approach, is shown by simulations of a nonlinear model to be useful for interpreting large changes.

The approach presented here is a rather extreme effort in the direction of using an analytical method for the linear chain, i.e. an idealization of an idealization. One suspects that in the future, incorporating nonlinearities and web structure will result in less analytical tractability and increased reliance on simulation. How far to pursue quantitatively predicting trophic cascade effects will also depend strongly on the feasibility and precision of whole-ecosystem experiments.

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References

Baca, R., Drenner, R., 1995. Do the effects of piscivorus largemouth bass cascade to the plankton. Hydrobiologia 316, 139–151.

Balciunas, D., Lawler, S.P., 1995. Effects of basal resources, predation, and alternative prey in microcosm food chains. Ecology 76, 1327–1336.

Beckerman, A., Uriarte, M., Schmitz, O.J., 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proc. Natl. Acad. Sci. U.S.A. 94, 10735–10738.

Bender, E., Case, T., Gilpin, M., 1984. Perturbation experiments in community ecology. Ecology 65, 1–13.

Bertolo, A., Lacroix, G., Lescher-Moutoue, F., Cardinal-Legrand, C., 2000. Plankton dynamics in planktivore- and piscivore-dominated mesocosms. Arch. Hydrobiol. 147, 327–349.

Blaustein, L., Kotler, B.P., Ward, D., 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. Ecol. Entomol. 20, 311–318.

Brett, M., Goldman, C., 1996. A meta-analysis of the freshwater trophic cascade. Proc. Natl. Acad. Sci. U.S.A. 93, 7723–7726.

Brett, M., Goldman, C., 1997. Consumer versus resource control in freshwater pelagic food webs. Science 275, 384–386.

Brönmark, C., Weisner, S., 1996. Decoupling of cascading trophic interactions in a freshwater, benthic food chain. Oecologia 108, 534–541.

Carpenter, S., Kraft, C., Wright, R., Soranno, P., Hodgson, J., 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. Am. Nat. 140, 781–798.

Carpenter, S.R., Kitchell, J.F., Cottingham, K.L., Schindler, D.E., Christensen, D.L., Post, D.M., Voichick, N., 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole lake experiments. Ecology 77, 725–735.

Carter, P.E., Rypstra, A.L., 1995. Top-down effects in soybean agroecosystems: spider density affects herbivore damage. Oikos 72, 433–439.

Case, T., 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press, pp. 345–367.

Charlebois, P., Lamberti, G., 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. J. North Am. Benthol. Soc. 15, 551–563.

Chase, J., 1996. Abiotic controls of trophic cascades in a simple grassland food chain. Oikos 77, 495–506.

DeMelo, R., France, R., McQueen, D., 1992. Biomanipulation: hit or myth? Limnol. Oceanogr. 37, 192–207.

Diana, J.S., Dettweiler, D.J., Lin, C.K., 1991. Effect of Nile tilapia (*Oreochromis niloticus*) on the ecosystem of aquaculture ponds, and its significance to the trophic cascade hypothesis. Can. J. Fisheries Aquat. Sci. 48, 183–190.

Estes, J., Tinker, M., Williams, T., Doak, D., 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282, 473–476.

Findlay, D., Kasian, S., Hendzel, L., Regehr, G., Schindler, E., Shearer, J., 1994. Biomanipulation of lake 221 in the experimental lakes area (ELA): effects on phytoplankton and nutrients. Can. J. Fisheries Aquat. Sci. 51, 2794–2807.

Hairston Jr., N., Hairston Sr., N., 1997. Does food web complexity eliminate trophic-level dynamics? Am. Nat. 149, 1001–1007.

Hairston, N., Smith, F., Slobodkin, L., 1960. Community structure, population control, and competition. Am. Nat. 94, 421–425.

Herendeen, R., 1995. A unified quantitative approach to bottom-up:top-down and trophic cascade hypotheses. J. Theor. Biol. 176, 13–26.

Herendeen, R., in preparation. Dynamic Trophic Cascade.

Hill, A.M., Lodge, D.M., 1995. Multi-trophic-level impact of sublethal interactions between bass and omnivorous crayfish. J. North Am. Benthol. Soc. 14, 306–314.

Leibold, M., Chase, J., Shurin, J., Downing, A., 1997. Species turnover and the regulation of trophic structure. Annu. Rev. Ecol. Syst. 28, 67–494.

Marquis, R., Whelan, C., 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75, 2007–2014.

McCann, K., Hastings, A., Strong, D., 1998. Trophic cascades and trophic trickles in pelagic food webs. Proc. R. Soc. Lond. Ser. B. Biol. Sci. 265, 205–209.

McCarty, J.P., 1997. Aquatic community characteristics influence the foraging patterns of three swallows. Condor 99, 210–213.

Mikola, J., Setälä, H., 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. Ecology 79, 153–164.

Moran, M.D., Hurd, L.E., 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. Oecologia 113, 126–132.

Moran, M., Rooney, T., Hurd, L., 1996. Top-down cascade from a bitrophic predator in an old-field community. Ecology 77, 2219–2227.

Mullersolger, A., Brett, M., Luecke, C., Elser, J., Goldman, C., 1997. The effects of planktivorous fish (golden shiners) on the ciliate community of a mesotrophic lake. J. Plankton Res. 19, 1815–1828.

Nicholls, K., 1999. Evidence for a trophic cascade effect on north-shore western lake Erie phytoplankton prior to the zebra mussel invasion. J. Great Lakes Res. 25, 942–949.

Nyström, P., Brönmark, C., Graneli, W., 1996. Patterns in benthic food webs: a role for omnivorous crayfish? Freshwater Biol. 36, 631–646.

Oksanen, L., Fretwell, S., Arruda, J., Nielema, P., 1981. Exploitation of ecosystems in gradients of primary productivity. Am. Nat. 118, 240–261.

Pace, M.L., Cole, J.J., Carpenter, S.R., 1998. Trophic cascades and compensation: differential responses of microzooplankton in whole-lake experiments. Ecology 79, 138–152.

Perez-Fuentetaja, A., McQueen, D., Ramcharan, C., 1996. Predator-induced bottom-up effects in oligotrophic systems. Hydrobiologia 317, 163–176.

Persson, A., 1997. Effects of fish predation and excretion on the configuration of aquatic food webs. Oikos 79, 137–146.

Polis, G., 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86, 3–15.

Polis, G., Strong, D., 1996. Food web complexity and community dynamics. Am. Nat. 147, 813–846.

Polis, G., Sears, A., Huxel, G., Strong, D., Maron, J., 2000. When is a trophic cascade a trophic cascade? Tree 15, 473–475.

Post, E., Peterson, R., Stenseth, N., McLaren, B., 1999. Ecosystem consequences of wolf behavioural responses to climate. Nature 401, 905–907.

Rosenheim, J., Wilhoit, L., Armer, C., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96, 439–449.

Schmitz, O., Hamback, P., Beckerman, A., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am. Nat. 155, 141–153.

Strong, D., 1999. Predator control in terrestrial ecosystems: the underground food chain of bush lupine. In: Olff, H., Brown, V., Drent, R. (Eds.), Herbivores: Between Plants and Predators. pp. 577–602.

Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T., Henttonen, H., 2000. Are lemmings prey or predators? Nature 405, 562–565.

van den Berg, H., 1998. Propagation of permanent perturbations in food chains and food webs. Ecol. Model. 107, 225–236.

Vanni, M., Layne, C., 1997. Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. Ecology 78, 21–40.

Vanni, M., Layne, C., Arnott, S., 1997. “Top-down” trophic interactions in lakes: effects of fish on nutrient dynamics. Ecology 78, 1–20.

Vucetich, J., Peterson, R., Schaeffer, C., 2002. The effect of prey and predator densities on wolf predation. Ecology 83, 3003–3013.

Wootton, J., 1995. Effects of birds on sea urchins and algae: a lower-intertidal trophic cascade. Ecoscience 2, 321–328.