

Available online at www.sciencedirect.com



Ecological Modelling 177 (2004) 129-142



www.elsevier.com/locate/ecolmodel

Dynamic trophic cascade

Robert A. Herendeen*

Illinois Natural History Survey, Champaign, IL 61820 USA

Received 23 June 2003; received in revised form 23 December 2003; accepted 5 February 2004

Abstract

In a previous article, I developed, and demonstrated with simulations, an analytical approach for predicting and analyzing effects of press (step-function) perturbations on food chains [Ecol. Model. 171 (2004) 21]. The method allows explicit variation of the functional dependence connecting trophic levels. Here I extend that analysis to perturbations sinusoidal in time. The sinusoid partially bridges the gap between the idealized press-type experiment (which assumes initial and final steady states, but is doubtful experimentally) and a totally dynamic situation (which is daunting analytically but closer to reality). I find that the effect of a sinusoidal perturbation is to multiply the previous press result by a factor that diminishes both up and down the food chain. The factor depends on perturbing frequency approximately as $1/(1 + (\omega \tau_i)^2)^{1/2}$, where τ_i is the characteristic time of affected level *i*. This frequency-dependent diminution is another potential reason why bottom-up and top-down cascade effects are hard to detect.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Trophic cascade; Bottom-up; Top-down; Food chain; Dynamic; Periodic perturbation

1. Introduction

In a food chain, the trophic cascade (TC) refers to the change in the stock of one trophic level when the stock of another trophic level is changed. In Herendeen (2004) I showed that reasonable variation in the functional dependence connecting trophic levels in a food chain yields widely varying bottom-up and top-down outcomes for press-perturbed food chains. In particular, stock changes can be large or vanishingly small depending on parameters reflecting the degree of prey and predator dependence. For example, the same system (i.e., as characterized by the same parameters), can show strong bottom-up effects and weak top-down effects, or with different parameters, can show the opposite. Both of these combinations have been seen experimentally (Carpenter et al., 1996 and Dyer and Letourneau, 1999, respectively).

In this paper, I extend chain analysis to include perturbations sinusoidal in time. Transient and asymptotic oscillatory response are both included. I will show that compared with a press (i.e., a constant perturbation), a sinusoid in time should produce a more severe diminution of effect with increasing trophic distance from the perturbed level.

I investigate a sinusoidal perturbation for two reasons:

- At least one observed trophic cascade (McLaren and Peterson, 1994; Post et al., 1999) is claimed to derive from periodic forcing.
- As discussed in Herendeen (2004), many trophic cascade experiments are dynamic (intentionally or not); therefore dynamic analysis is appropriate. A pure sinusoid is a dynamic perturbation that is

^{*} Tel.: +1-217-244-2137; fax: +1-217-333-6294.

E-mail address: herendee@uiuc.edu (R.A. Herendeen).

 $^{0304\}text{-}3800/\$$ – see front matter © 2004 Elsevier B.V. All rights reserved. doi:10.1016/j.ecolmodel.2004.02.004

tractable analytically. It is a conceptual opposite of the press (step function). With a press, the system starts and ends, hopefully, in steady states. With a sinusoid, the system starts at steady state and ends by oscillating indefinitely.

The paper is organized as follows.

- Section 2. Motivation: a potentially sinusoidal system.
- Section 3. Extending the press analysis to the dynamic regime.
- Section 4. Response of a three-level food chain to a sinusoidal perturbation.
- Section 5. Comparison with simulation results.

Section 6. Conclusions.

2. Motivation: a potentially sinusoidal system

A sinusoidal perturbation is suggested by the wolf-moose-fir tree system in Isle Royale, Michigan. The data of McLaren and Peterson (1994) seemed to show oscillations. The authors' interpretation was that the wolves were oscillating for reasons exogenous to the trophic cascade, and that the moose and fir responded in a lagged fashion. Later Post et al. (1999) presented evidence that this system is driven by winter snow depth: increased depth causes wolves to hunt in larger packs and limits moose's mobility, resulting in higher kill rates. Snow depth is correlated with the North Atlantic Oscillation, a quasi-periodic climatic variation with a period of roughly 50 years.

Another possibility is that a system oscillates naturally because of internal dynamics. Then the TC is problematic to define because there is neither a unique initial state nor a unique perturbation. This was recently suggested for the Ilse Royale system (Post et al., 2002; Vucetich et al., 2002).

From Fig. 1 of Post et al. (1999), I measure the fractional changes in the three stocks as:

Fir:	± 0.57 (period 20 years)
Moose:	± 0.29 (period 21 years)
Wolf:	± 0.40 (period 21 years)

For fir, this is measured as width of annual growth ring, which the authors assume is proportional to that year's fir needle stock. The latter is less than the total fir tree biomass stock. The data are somewhat out of phase, but it appears that the signs of the changes agree with the trophic cascade's prediction of alternating signs in successive levels down the food chain.

3. Extending the press analysis to the dynamic regime

The basic question is how periodic effects propagate through a 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, non-steady-state biomass energy conservation equation is:

$$INPUT_{i} = METMORT_{i} + CROPPING_{i} + INPUT_{i+1} + \frac{dS_{i}}{dt}$$
(1)

where INPUT_i is energy flow into level *i* resulting from preying upon level i - 1, METMORT_i is energy flow out of level *i* resulting from metabolism and non-predation mortality, CROPPING_i is energy flow out of level *i* resulting from cropping (if negative, it represents stocking), INPUT_{i+1} is energy flow out of level *i* resulting from predation by level i + 1, S_i is energy stock in level *i*.

Eq. (1) is identical to that used for press analysis except for the addition of the time derivative. The time independent equation is analyzed in detail in Herendeen (1995, 2004) and will be glossed over here. I will consider three perturbations over time: changes in CROPPING, changes in RESOURCE (light or nutrient), or changes in functional dependence. I assume that the latter is given by $B_i(S_i, S_{i-1}) = b_i$ (function of S_i and S_{i-1}).

With perturbations, Eq. (1) becomes

$$\Delta \text{INPUT}_{i} = \Delta \text{METMORT}_{i} + \Delta \text{CROPPING}_{i} + \Delta \text{INPUT}_{i+1} + \frac{d\Delta S_{i}}{dt}$$
(2)

For small changes

$$L_{i} \frac{\Delta S_{i-1}}{S_{i-1}} + M_{i} \frac{\Delta S_{i}}{S_{i}} + N \frac{\Delta S_{i+1}}{S_{i+1}}$$

= $\Delta \text{CROPPING}_{i} - \text{INPUT}_{i} \frac{\Delta b_{i}}{b_{i}}$
+ $\text{INPUT}_{i+1} \frac{\Delta b_{i+1}}{b_{i+1}} + S_{i} \frac{d\Delta S_{i}/dt}{S_{i}}$ (3)



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

where

$$L_{i} \equiv \text{INPUT}_{i} \frac{\partial B_{i}}{\partial S_{i}} \frac{S_{i-1}}{B_{i}}$$

$$M_{i} \equiv \text{INPUT}_{i} \left(1 + \frac{\partial B_{i}}{\partial S_{i-1}} \frac{S_{i}}{B_{i}}\right)$$

$$- \text{INPUT}_{i+1} \frac{\partial B_{i+1}}{\partial S_{i}} \frac{S_{i}}{B_{i+1}} - \text{METMORT}_{i}$$

$$N_{i} \equiv -\text{INPUT}_{i+1} \left(1 + \frac{\partial B_{i+1}}{\partial S_{i+1}} \frac{S_{i+1}}{B_{i+1}}\right)$$

$$(4)$$

All quantities in Eq. (4) are evaluated at the original steady state. Let us streamline the notation by defining stock-normalized quantities $l_i = L_i/S_i$, $m_i = M_i/S_i$, $n_i = N_i/S_i$, and $\delta_i = S_i/S_i$.

Then Eq. (4) becomes

$$l_{i}\delta_{i-1} + m_{i}\delta_{i} + n_{i}\delta_{i+1} - \frac{d\delta_{i}}{dt}$$

$$= -l_{1}\frac{\Delta \text{RESOURCE}}{\text{RESOURCE}} + \frac{\Delta \text{CROPPING}_{i}}{S_{i}}$$

$$-\frac{\text{INPUT}_{i}}{S_{i}}\frac{\Delta b_{i}}{b_{i}} + \frac{\text{INPUT}_{i+1}}{S_{i}}\frac{\Delta b_{i+1}}{b_{i+1}}$$
(5)

In Eq. (5) all three types of perturbations appear. Level 0 is interpreted as resource, an independent variable. Then $\delta_0 = 0$ and the resource term appears as a perturbation for i = 1.

These equations for i = 1, ..., k can be written in matrix form as

$$\underline{\underline{A\delta}} - \frac{\mathrm{d}\underline{\delta}}{\mathrm{d}t} = \underline{\underline{P}} \tag{6}$$

where $\underline{\underline{A}}$ is a matrix containing the *l*, *m*, and *n*, and $\underline{\delta}$ is a vector of the fractional stock changes. $\underline{\underline{P}}$, the

perturbation vector, contains the terms on the right hand side of Eq. (5). In Herendeen (1995, 2004), \underline{P} was assumed to be time independent

<u>A</u> is related to the community matrix used in analyzing the generalized Lotka–Volterra equations by Bender et al. (1984) and Case (2000, pp. 345–367) The complete solution to Eq. (6) is the sum of the complementary and a particular solution (Spiegel, 1958).

3.1. Complementary solution

$$\underline{\underline{A}}\underline{\delta} - \frac{d\underline{\delta}}{dt} = 0$$
Assume $\underline{\delta} = \underline{\delta}_0 e^{\lambda t}$. Then
$$\underline{A}\underline{\delta} - \lambda \underline{I}\underline{\delta} = 0$$

where $\underline{\underline{I}}$ is the identity matrix. λ is obtained by solving $det(\underline{A} - \lambda \underline{I}) = 0.$

This is a generalized eigenvector problem; λ can have real and imaginary parts, corresponding to exponentials and sinusoids in time. Standard stability analysis requires that the real part of all λ be negative; this assures that the system is at a stable steady state initially, that it "could exist," and implies (but does not assure) that the system will not crash when perturbed. The δ that satisfy Eq. (7) are the eigenvectors of <u>A</u>; they can be complex, the real and imaginary parts indicating the relative phases of the δ_i . Because of the particular form of <u>A</u> here (nearest neighbor interactions), and because typically m_i and n_i are negative and l_i is positive (but not always; see Appendix A), the roots are of the form $\lambda = -|\text{real}|$ or $-|\text{real}| \pm$ imaginary,

(7)

Table 1			
Symbols	and	terms	used

$\begin{array}{ccccc} \underline{A}_{i} & & \text{Matrix of } l, m, n & & \text{Energy time}^{-1} energy^{-1} \\ \underline{b}_{i} & & \text{Time-dependent parameter in } B_{i} & & \text{Dimensionless} \\ B_{i} & & \text{Feeding input (per unit stock) to & & \text{Energy time}^{-1} energy^{-1} \\ evel i a s function of S_{i} and S_{i-1} & & \text{Dimensionless} \\ \hline CROPPING_{i} & & \text{Exogenous removal from level } i & & \text{Energy time}^{-1} \\ \text{Predator dependence (also called & & & \text{INPUT}_{i} is functionally dependent only on S_{i-1} \\ \text{Predator dependence (also called & & & & \text{INPUT}_{i} is functionally dependent only on (S_{i-1}/S_{i}) \\ \hline ba_{i} & & & & & & & & & \\ ba_{i} & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & & \\ ba_{i} & & & & & & & & & & & & & & & & & & &$	Symbol	Description	Units
$ \begin{array}{ccccc} \hline here \\ here \\ \hline here $	<u>A</u> ;	Matrix of <i>l</i> , <i>m</i> , <i>n</i>	Energy time ⁻¹ energy ⁻¹
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\overrightarrow{b_i}$	Time-dependent parameter in B_i	Dimensionless
$\begin{array}{cccc} evel i as function of S_i and S_{i-1} & Dimensionless \\ CROPPING_i & Exogenous removal from level i & Energy time^{-1} \\ Prey dependence (also called & INPUT_i is functionally dependent only on S_{i-1} \\ Predator dependence (also called & INPUT_i is functionally dependent only on S_{i-1}(S_i) \\ Four breator dependence (also called & NPUT_i is functionally dependent only on (S_{i-1}(S_i)) \\ Four breator dependence (also called & NPUT_i is functionally dependent only on (S_{i-1}(S_i)) \\ Four breator dependence (also called & S_i / S_{i-1} (for bottom-up effect) & Dimensionless \\ fdu & S_i / S_{i-1} (for bottom-up effect) & Dimensionless \\ INPUT_i & Feeding input to level i & Energy time^{-1} \\ Identity matrix & Dimensionless \\ j = \sqrt{-1} & Dimensionless \\ I_i, M_i, N_i^a & Coefficients characterizing & Energy time^{-1} energy^{-1} \\ relationship between \delta_i; function of initial flows and of prey and interference derivatives \\ I_i, m_i, n_i^a & I_i = L_i/S_i, etc. & Energy time^{-1} energy^{-1} \\ P & Most general perturbation vector & Energy time^{-1} energy^{-1} \\ P arameter expressing degree of prey dependence Dimensionless \\ Prey derivative_i^a & \frac{\partial B_i}{\partial S_{i-1}} = q_i \left(\frac{c_i}{c_{i+1}}\right) & Dimensionless \\ Prey derivative_i^a & \frac{\partial B_i}{\partial S_{i-1}} = q_i \left(\frac{c_i}{c_{i+1}}\right) & Dimensionless \\ S_i & Stock of level i & Energy time^{-1} energy^{-1} \\ RESOURCE_i & Resource (light or nutrient) level; affects level 1 only vary depending on resource (egi. light intensity, nutrient concentration) \\ S_i & Stock of level i & Energy Dimensionless \\ S_i & Stock of level i & Foregy & Dimensionless \\ S_i & Stock of level i (lept or nutrient) level; affects level 1 only & vary depending on resource (egi. light intensity, nutrient concentration) \\ S_i & Stock of level i & Energy Dimensionless \\ S_i & Stock of level i & Foregy & Dimensionless \\ S_i & Stock of level i (lept nutrient) level; affects level 1 only & targending on resource$	B _i	Feeding input (per unit stock) to	Energy time ⁻¹ energy ⁻¹
c_i Parameter in B_i DimensionlessCROPPINGExogenous removal from level i Energy time ⁻¹ Prey dependenceINPUT _i is functionally dependent only on S_i Energy time ⁻¹ interference dependence)INPUT _i is functionally dependent only on (S_{i-1}/S_i) DimensionlessRatio dependenceINPUT _i is functionally dependent only on (S_{i-1}/S_i) Dimensionlessful _i δ_i/δ_{i-1} (for top-down effect)DimensionlessINPUT _i Feeding input to level i Energy time ⁻¹ $\frac{I}{2}$ Identity matrixDimensionless $j = \sqrt{-1}$ Identity matrixDimensionless k Number of trophic levels in food chainDimensionless k_i Number of trophic levels in food chainDimensionless i_i, m_i, n_i^{β} $l_i = L_i/S_i$, etc.Energy time ⁻¹ P Matabolic and non-predation loss from level i Energy time ⁻¹ P Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_i - 1} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless r_i Constant vectorEnergy time ⁻¹ energy ⁻¹ r_i Resource (light or nutrient) level; affects level 1 onlyvary depending on resource g_i Go farmatter active s_i A_i f_i A_i/δ_i G_i Dimensionless r_i Matrix of normalized eige		level <i>i</i> as function of S_i and S_{i-1}	
CROPPING _i Exogenous removal from level i Energy time ⁻¹ Prey dependence INPUT _i is functionally dependent only on S _i interference dependence (also called INPUT _i is functionally dependent only on S _i interference dependence (also called INPUT _i is functionally dependent only on S _i interference dependence) Ratio dependence interference dependence dependence interference dependence interference dependence dependence dependence interference dependence dependence dependence interference dependence interference dependence dependence interference dependence interference (predator) $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless dependence interference (predator) $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless $\frac{C_i}{C_i}$ dependence interference	Ci	Parameter in B_i	Dimensionless
Prey dependenceINPUT; is functionally dependent only on S_{i-1} Predator dependence (also called interference dependence)INPUT; is functionally dependent only on S_i Ratio dependenceINPUT; is functionally dependent only on (S_{i-1}/S_i) fbu; δ_i/δ_{i-1} (for bottom-up effect)DimensionlessINPUT;Feeding input to level iEnergy time ⁻¹ I_{j} Identity matrixDimensionless $j = \sqrt{-1}$ Identity matrixDimensionlesskNumber of trophic levels in food chainDimensionless L_i, M_i, N_i^a Coefficients characterizing relationship between δ_i ; function of initial flows and of prey and interference derivativesEnergy time ⁻¹ energy ⁻¹ $I_i = L_i/S_i$, etc.Energy time ⁻¹ energy ⁻¹ energy time ⁻¹ Q_i Most general perturbation vectorEnergy time ⁻¹ energy ⁻¹ Q_i Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative _i ^a $\frac{\partial B_i}{\delta_{i}} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless V_{i-1} Relative abundance of level i's preyDimensionless f_i Relative abundance of level i's preyDimensionless f_i Energy time ⁻¹ energy ⁻¹ Energy time ⁻¹ energy ⁻¹ q_i Constant vectorEnergy time ⁻¹ energy ⁻¹ q_i Constant vectorEnergy time ⁻¹ energ	CROPPING _i	Exogenous removal from level <i>i</i>	Energy time ⁻¹
Predator dependence (also called interference dependence) Ratio dependence (INPUT _i is functionally dependent only on S_i interference dependence (INPUT _i is functionally dependent only on (S_{i-1}/S_i) fbu, β_i/δ_{i-1} (for top-down effect) Dimensionless INPUT _i Feeding input to level <i>i</i> Energy time ⁻¹ $\frac{I}{j}$ Identity matrix Dimensionless $I_i = L_i/S_i$ definition of trophic levels in food chain Dimensionless L_i, M_i, N_i^a Coefficients characterizing Energy time ⁻¹ relationship between δ_i ; function of initial flows and of prey and interference derivatives $l_i = l_i/S_i$, etc. Energy time ⁻¹ energy ⁻¹ METMORT _i Metabolic and non-predation loss from level <i>i</i> Energy time ⁻¹ energy ⁻¹ P Most general perturbation vector Energy time ⁻¹ energy ⁻¹ P arameter expressing degree of interference Dimensionless r_i Parameter expressing degree of interference Dimensionless r_i Parameter expressing degree of interference Dimensionless Prey derivative _i ^a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless Interference (predator) $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless β_i Matrix of normalized eigenvectors of \underline{A} Dimensionless β_i Relative abundance of level <i>i'</i> greey Dimensionless β_i Matrix of normalized eigenvectors of \underline{A} Dimensionless $\beta_i = A_i/\delta_i$ (casumed or level <i>i'</i> sprey Dimensionless $\beta_i = A_i (\delta_i for an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ for an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ for an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ for an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ con an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ con an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ con an infinite chain of identical levels Dimensionless \beta_i = A_i (\delta_i \text{ con an infinite chain of identical levels Dimensionless \beta_i$	Prey dependence	INPUT _i is functionally dependent only on S_{i-1}	
Ratio dependenceINPUT _i is functionally dependent only on (S_{i-1}/S_i) fbu _i δ_i/δ_{i-1} (for bottom-up effect)Dimensionlessftd _i δ_i/δ_{i-1} (for to bottom-up effect)DimensionlessINPUT _i Feeding input to level i Energy time ⁻¹ $\frac{I}{2}$ Identity matrixDimensionless $j = \sqrt{-1}$ DimensionlessDimensionlesskNumber of trophic levels in food chainDimensionless l_i , M_i , N_i^{a} Coefficients characterizingEnergy time ⁻¹ relationship between δ_i ; function of initial flows and of prey and interference derivativesEnergy time ⁻¹ energy ⁻¹ $l_i = L_i/S_i$, etc.Energy time ⁻¹ energy time ⁻¹ P Most general perturbation vectorEnergy time ⁻¹ q_i Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) $\frac{\partial B_i}{\partial S_i} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ Dimensionless S_i Stock of level i EnergyEnergy time ⁻¹ energy ⁻¹ q_i Resource (light or nutrient) level; affects level 1 onlyvary depending on resource (cg. light intensity, nutrient concentration) S_i Stock of level i EnergyDimensionless f_i L_i/δ_i ($\Delta S_i = change in S_i$)Dimensionless δ_i Δ_i/δ_i ($\Delta S_i = change in S_i$)Dimensionless	Predator dependence (also called interference dependence)	INPUT _i is functionally dependent only on S_i	
fbu, δ_i/δ_{i-1} (for bottom-up effect) Dimensionless ftd, δ_i/δ_{i+1} (for top-down effect) Dimensionless INPUT _i Feeding input to level i Emergy time ⁻¹ I_{j} Identity matrix Dimensionless j $j = \sqrt{-1}$ Dimensionless k Number of trophic levels in food chain Dimensionless L_i , M_i , N_i^a Coefficients characterizing Energy time ⁻¹ relationship between δ_i ; function of initial flows and of prey and interference derivatives l_i , m_i , n_i^a $l_i = L_i/S_i$, etc. Energy time ⁻¹ energy ⁻¹ METMORT _i Metabolic and non-predation loss from level i Energy time ⁻¹ energy ⁻¹ P_i 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 r_i $\frac{\partial B_{i}}{S_{i-1}} = q_i \left(\frac{c_i}{c_{i+1}} \right)$ Dimensionless Prey derivative _i ^a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}} \right)$ Dimensionless Stock of level i Energy Energy time ⁻¹ energy ⁻¹	Ratio dependence	INPUT _i is functionally dependent only on (S_{i-1}/S_i)	
fid, δ_i / δ_{i+1} (for top-down effect)DimensionlessINPUTiFeeding input to level iEnergy time ⁻¹ I_j Identity matrixDimensionless $j = \sqrt{-1}$ Dimensionless k Number of trophic levels in food chainDimensionless k_i k_i Number of trophic levels in food chainEnergy time ⁻¹ k_i <	fbu _i	δ_i/δ_{i-1} (for bottom-up effect)	Dimensionless
$\begin{array}{llllllllllllllllllllllllllllllllllll$	ftd _i	δ_i/δ_{i+1} (for top-down effect)	Dimensionless
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	INPUT _i	Feeding input to level <i>i</i>	Energy time ⁻¹
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	<u>1</u>	Identity matrix	Dimensionless
kNumber of trophic levels in food chainDimensionless L_i, M_i, N_i^a Coefficients characterizingEnergy time ⁻¹ L_i, M_i, N_i^a relationship between δ_i ; function of initial flows and of prey and interference derivativesEnergy time ⁻¹ energy ⁻¹ l_i, m_i, n_i^a $l_i = L_i/S_i$, etc.Energy time ⁻¹ energy ⁻¹ METMORT_iMetabolic and non-predation loss from level i Energy time ⁻¹ energy ⁻¹ q_i Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative _i ^a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessRESOURCE_iResource (light or nutrient) level; affects level 1 onlyvary depending on resource (eg. light intensity, nutrient concentration) S_i Stock of level i EnergyDimensionless q_i Constant vectorEnergyDimensionless q_i Constant vectorEnergyDimensionless g_i Matrix of normalized eigenvectors of \underline{A} Dimensionless $\beta_i = l_i A_i^i (S_i (\Delta S_i = change in S_i))$ Dimensionless β_i $\Delta_i/S_i (\Delta S_i = change in S_i)$ Dimensionless $i_i = k_i = k$	ī	$j = \sqrt{-1}$	Dimensionless
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	k	Number of trophic levels in food chain	Dimensionless
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	L_i, M_i, N_i^{a}	Coefficients characterizing	Energy time ⁻¹
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		relationship between δ_i ; function	
l_i, m_i, n_i^a interference derivatives $l_i = L_i/S_i$, etc.Energy time ⁻¹ energy ⁻¹ METMORT_iMetabolic and non-predation loss from level i Energy time ⁻¹ P Most general perturbation vectorEnergy time ⁻¹ energy ⁻¹ q_i Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative _i ^a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessRESOURCE_iResource (light or nutrient) level; affects level 1 only vary depending on resource (eg. light intensity, nutrient concentration)Dimensionless S_i Stock of level i EnergyEnergy $\frac{V}{\alpha_i}$ Relative abudance of level i 's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i Δ_S_i/S_i (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level i (=[1/ m_i])Time μ_i METMORT/ S_i (assumed constant)Energy time ⁻¹ energy ⁻¹		of initial flows and of prey and	
$\begin{array}{llllllllllllllllllllllllllllllllllll$		interference derivatives	
METMORTMetabolic and non-predation loss from level i Energy time ⁻¹ P Most general perturbation vectorEnergy time ⁻¹ q_i Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative _i ^a $\frac{\partial B_i}{B_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessRESOURCE_iResource (light or nutrient) level; affects level 1 onlyvary depending on resource (eg. light intensity, nutrient concentration) S_i Stock of level i Energy u Constant vectorEnergy $\frac{Q}{u}$ Constant vectorEnergy $\frac{Q}{u}$ Relative abundance of level i' s preyDimensionless $\delta_i = -i/\delta_i$ for an infinite chain of identical levelsDimensionless δ_i $\Delta_{S_i/S_i} (\Delta_S_i = change in S_i)$ Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ μ_i METMORT _i /S_i (assumed constant)Energy time ⁻¹ energy ⁻¹	l_i, m_i, n_i^{a}	$l_i = L_i/S_i$, etc.	Energy time ⁻¹ energy ⁻¹
$\begin{array}{ccccccc} P & & \mbox{Most general perturbation vector} & & \mbox{Energy time}^{-1} \ energy^{-1} \\ q_i & & \mbox{Parameter expressing degree of prey dependence} & & \mbox{Dimensionless} \\ r_i & & \mbox{Parameter expressing degree of interference} & & \mbox{Dimensionless} \\ \end{array} \\ Prey derivative_i^a & & & \frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}} \right) & & \mbox{Dimensionless} \\ \end{array} \\ \begin{array}{c} \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \begin{array}{c} \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \begin{array}{c} \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \begin{array}{c} \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \begin{array}{c} \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \end{array} \\ \mbox{RESOURCE}_i & & \mbox{Resource (light or nutrient) level; affects level 1 only} & & \mbox{vary depending on resource} \\ & \mbox{(eg. light intensity, nutrient} \\ & \mbox{concentration)} \\ \end{array} \\ \begin{array}{c} S_i & & \mbox{Stock of level } i \\ \mbox{Quantized eigenvectors of } \underline{A} & & \mbox{Dimensionless} \\ \end{array} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \mbox{\beta} & & \mbox{\delta}_{i-1}/\delta_i \text{ for an infinite chain of identical levels} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \mbox{\delta}_i & & \mbox{\Delta}_S/S_i \ (\Delta S_i = change in S_i) & & \mbox{Dimensionless} \\ \mbox{Dimensionless} & & \mbox{Dimensionless} \\ \mbox{A} & & \mbox{Eigenvalue of } \underline{A} & & \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Characteristic time of level } i \ (= 1/m_i) & & \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \\ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \ \mbox{Time}^{-1} \ T$	METMORT _i	Metabolic and non-predation loss from level <i>i</i>	Energy time ⁻¹
q_i Parameter expressing degree of prey dependenceDimensionless r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i ^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative _i ^a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessRESOURCE_iResource (light or nutrient) level; affects level 1 onlyvary depending on resource (eg. light intensity, nutrient concentration) S_i Stock of level iEnergy $\frac{V}{\alpha_i}$ Relative abundance of level i's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ λ METMORT i/S_i (assumed constant)Time μ_i METMORT i/S_i (assumed constant)Energy time ⁻¹ energy ⁻¹	P	Most general perturbation vector	Energy time ⁻¹ energy ⁻¹
r_i Parameter expressing degree of interferenceDimensionlessPrey derivative _i a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative _i a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessRESOURCE_iResource (light or nutrient) level; affects level 1 onlyvary depending on resource (eg. light intensity, nutrient concentration) S_i Stock of level i Energy $\frac{V}{2}$ Matrix of normalized eigenvectors of \underline{A} Dimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless β_i $\Delta_{S_i/S_i} (\Delta_{S_i} = change in S_i)$ Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ α_i METMORT i/S_i (assumed constant)Fnergy time ⁻¹ energy ⁻¹	q_i	Parameter expressing degree of prey dependence	Dimensionless
Prey derivative_i^a $\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessInterference (predator) derivative_i^a $\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$ DimensionlessRESOURCE_iResource (light or nutrient) level; affects level 1 onlyvary depending on resource (eg. light intensity, nutrient concentration) S_i Stock of level i Energy $\frac{U}{V}$ Constant vectorEnergy α_i Relative abundance of level i 's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time^{-1} τ_i METMORT _i /S_i (assumed constant)Energy time^{-1} energy^{-1} μ_i METMORT _i /S_i (assumed constant)Time^{-1}	r_i	Parameter expressing degree of interference	Dimensionless
$ \begin{array}{ll} \text{Interference (predator)} & \frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}} \right) & \text{Dimensionless} \\ \text{RESOURCE}_i & \text{Resource (light or nutrient) level; affects level 1 only} & \text{vary depending on resource} \\ & (eg. light intensity, nutrient \\ & \text{concentration}) \\ \text{S}_i & \text{Stock of level } i & \text{Energy} \\ \underline{y} & \text{Constant vector} & \text{Energy time^{-1} energy^{-1}} \\ \underline{Y} & \text{Matrix of normalized eigenvectors of } \underline{A} & \text{Dimensionless} \\ \beta & \delta_{i-1}/\delta_i \text{ for an infinite chain of identical levels} & \text{Dimensionless} \\ \delta_i & \Delta S_i/S_i (\Delta S_i = \text{change in } S_i) & \text{Dimensionless} \\ \lambda & \text{Eigenvalue of } \underline{A} & \text{Time}^{-1} \\ \tau_i & \text{Characteristic time of level } i (= 1/m_i) & \text{Time} \\ \mu_i & \text{METMORT}_i/S_i (assumed constant) & \text{Energy time}^{-1} energy^{-1} \\ \end{array} $	Prey derivative _i ^a	$\frac{\partial B_i}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_{i+1}}\right)$	Dimensionless
RESOURCEResource (light or nutrient) level; affects level 1 onlyvary depending on resource (eg. light intensity, nutrient concentration) S_i Stock of level i Energy \underline{u} Constant vectorEnergy \underline{V} Matrix of normalized eigenvectors of \underline{A} Dimensionless $\overline{\alpha}_i$ Relative abundance of level i 's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level i (= $ 1/m_i $)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹	Interference (predator) derivative: ^a	$\frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_{i+1}}\right)$	Dimensionless
$\begin{array}{cccc} (eg. light intensity, nutrient concentration) \\ S_i & Stock of level i & Energy \\ \underline{u} & Constant vector & Energy time^{-1} energy^{-1} \\ \underline{V} & Matrix of normalized eigenvectors of \underline{A} & Dimensionless \\ \overline{\alpha}_i & Relative abundance of level i's prey & Dimensionless \\ \beta & \delta_{i-1}/\delta_i \text{ for an infinite chain of identical levels} & Dimensionless \\ \delta_i & \Delta S_i/S_i (\Delta S_i = \text{change in } S_i) & Dimensionless \\ \lambda & Eigenvalue of \underline{A} & Time^{-1} \\ \tau_i & Characteristic time of level i (= 1/m_i) & Time \\ \mu_i & METMORT_i/S_i (assumed constant) & Energy time^{-1} energy^{-1} \\ \omega & Frequency of sinusoidal perturbation & Time^{-1} \end{array}$	RESOURCE	Resource (light or nutrient) level: affects level 1 only	vary depending on resource
S_i Stock of level i Energy \underline{u} Constant vectorEnergy time ⁻¹ energy ⁻¹ \underline{V} Matrix of normalized eigenvectors of \underline{A} Dimensionless $\overline{\alpha_i}$ Relative abundance of level i 's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level i (= 1/m_i)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹			(eg. light intensity, nutrient concentration)
\underline{u} Constant vectorEnergy time ⁻¹ energy ⁻¹ \underline{V} Matrix of normalized eigenvectors of \underline{A} Dimensionless $\overline{\alpha_i}$ Relative abundance of level <i>i</i> 's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless β $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level i (= 1/m_i)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹	Si	Stock of level <i>i</i>	Energy
$\underline{V}_{\overline{\alpha_i}}$ Matrix of normalized eigenvectors of \underline{A} Dimensionless $\overline{\alpha_i}$ Relative abundance of level <i>i</i> 's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level <i>i</i> (= 1/m_i)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹	<u>u</u>	Constant vector	Energy time ⁻¹ energy ⁻¹
$\overline{\alpha_i}$ Relative abundance of level i's preyDimensionless β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level i (= 1/m_i)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹	V	Matrix of normalized eigenvectors of A	Dimensionless
β δ_{i-1}/δ_i for an infinite chain of identical levelsDimensionless δ_i $\Delta S_i/S_i$ (ΔS_i = change in S_i)Dimensionless λ Eigenvalue of \underline{A} Time ⁻¹ τ_i Characteristic time of level i (= 1/m_i)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹	$\overline{\alpha_i}$	Relative abundance of level <i>i</i> 's prey	Dimensionless
$ \begin{array}{ll} \delta_i & \Delta S_i / S_i \ (\Delta S_i = \text{change in } S_i) & \text{Dimensionless} \\ \lambda & \text{Eigenvalue of } \underline{A} & \text{Time}^{-1} \\ \tau_i & \text{Characteristic time of level } i \ (= 1/m_i) & \text{Time} \\ \mu_i & \text{METMORT}_i / S_i \ (\text{assumed constant}) & \text{Energy time}^{-1} \ \text{energy}^{-1} \\ \omega & \text{Frequency of sinusoidal perturbation} & \text{Time}^{-1} \end{array} $	β	δ_{i-1}/δ_i for an infinite chain of identical levels	Dimensionless
λ Eigenvalue of \underline{A} Time^{-1} τ_i Characteristic time of level i (= 1/m _i)Time μ_i METMORT _i /S _i (assumed constant)Energy time^{-1} energy^{-1} ω Frequency of sinusoidal perturbationTime^{-1}	δ_i	$\Delta S_i / S_i$ (ΔS_i = change in S_i)	Dimensionless
τ_i Characteristic time of level i (= 1/m _i)Time μ_i METMORT _i /S _i (assumed constant)Energy time ⁻¹ energy ⁻¹ ω Frequency of sinusoidal perturbationTime ⁻¹	λ	Eigenvalue of <u>A</u>	Time ⁻¹
$ \begin{array}{c} \mu_i \\ \omega \end{array} \qquad \begin{array}{c} \text{METMORT}_i/S_i \text{ (assumed constant)} \\ \text{Frequency of sinusoidal perturbation} \end{array} \qquad \begin{array}{c} \text{Energy time}^{-1} \text{ energy}^{-1} \\ \text{Time}^{-1} \end{array} $	$ au_i$	Characteristic time of level $i = (1/m_i)$	Time
ω Frequency of sinusoidal perturbation Time ⁻¹	μ_i	METMORT _i / S_i (assumed constant)	Energy time ⁻¹ energy ⁻¹
	ω	Frequency of sinusoidal perturbation	Time ⁻¹

^a Quantities are evaluated at initial steady state.

indicating that the solutions are declining exponentials or damped sinusoids. In time these will die out, as can be seen in the graphs in Herendeen (2004) for a press. However, if all the $m_i = 0$, which holds for Lotka–Volterra type predation in an initially uncropped system, at least some of the roots are pure imaginary or have positive real parts, yielding persistent oscillations or an exponential crash. (There is an exception to this statement for k = odd, as described in Table 2.)

Form the matrix $\underline{\underline{V}}$ containing the normalized eigenvectors of $\underline{\underline{A}}$ in each column. $\underline{\underline{A}}$ is diagonalizable; then

$$\underline{\delta} = \underline{V}\hat{\mathbf{e}}^{\lambda t}\underline{V}^{-1}\underline{\delta}_{0c}$$

132

Table 2Aspects of solutions to Eq. (9) for press and sinusoidal perturbations

Functional relationship	Perturbation type			
	Press (step function)	Sinusoidal		
Ratio-dependent predation ($m_i \neq 0$)	Transients can occur but die out. Steady state develops. \underline{A}^{-1} exists and yields the asymmetric results found in Herendeen (1995), e.g., that for bottom-up perturbation, the δ_i are equal in sign and approximately equal in magnitude, while for a top-down perturbation, the δ_i alternate in sign and diminish by approximately an order of magnitude for each additional trophic level up from the perturbed level.	Transients can occur but die out. System oscillates at driving frequency. $(\underline{\underline{A}} - j\omega\underline{\underline{I}})^{-1}$ yields frequency-dependent δ_i . Finite resonances can occur. With increasing frequency, both top-down and bottom-up effects decrease.		
Lotka–Volterra functional dependence, special case of prey-dependent predation ($m_i = 0$)	For all k (=number of trophic levels), transients persist and may mask the steady-state response or lead to crash. If $k = \text{even: } \underline{A}^{-1}$ exists, so a unique steady-state response is possible for an arbitrary perturbation, except for masking by transients. If k = odd: \underline{A}^{-1} does not exist, so a unique steady-state response to an arbitrary perturbation is impossible, with one exception. Because \underline{A} has one root = 0, a press perturbation proportional to the corresponding eigenvector will produce a steady-state response with no oscillations.	A^{-1} always exists. Transients persist and beat against driving frequency, or can lead to a crash. $(\underline{A} - j\omega\underline{I})^{-1}$ gives frequency-dependent δ_i and exhibits unbounded resonances. With increasing frequency, both top-down and bottom-up effects decrease.		

In all cases, the boundary condition is that $\underline{\delta} = 0$ (i.e., system is at steady state) at t = 0.

 $\hat{e}^{\lambda t}$ is a diagonal matrix and $\underline{\delta}_{0c}$ is the initial value of $\underline{\delta}$.

3.2. Particular solution

By the assumption of linearity, a response to perturbations to RESOURCE, CROPPING, and the b_i is a sum of the response to the individual perturbations. For clarity, we look at a single-level perturbation to CROPPING or b_i with sinusoidal time dependence.

3.3. Perturbation to CROPPING

Let us assume a sinusoidal perturbation = $\Delta CROPPING_i / S_i = e^{j\omega t} u$, where u is a constant vector with units of time⁻¹, and $j \equiv \sqrt{-1}$. I use complex notation for conciseness, but it should be understood that it is always the real part that is observed. Then the particular differential equation is

$$\underline{\underline{A}}\underline{\delta} - \frac{\mathrm{d}\underline{\delta}}{\mathrm{d}t} = \mathrm{e}^{j\omega t}\underline{u} \tag{8}$$

To solve, assume $\underline{\delta}_p = \underline{\delta}_{0p} e^{j\omega t}$. Substituting this in Eq. (8) gives

$$\underline{\delta}_{0p} = (\underline{\underline{A}} - j\omega\underline{\underline{I}})^{-1}\underline{\underline{u}}$$

The sum of complementary and particular solutions is

$$\underline{\delta} = \underline{\underline{V}\hat{\mathbf{e}}^{\lambda t} V^{-1} \underline{\delta}_{0c}} + \mathbf{e}^{j\omega t} (\underline{\underline{A}} - j\omega \underline{\underline{I}})^{-1} \underline{\underline{u}}$$

Originally the system is at steady state, so the boundary condition is that $\underline{\delta} = 0$ at t = 0. This dictates the value of $\underline{\delta}_{0c}$ Then the complete solution for a sinusoidal perturbation is

$$\underline{\delta} = (-\underline{\underline{V}\hat{\mathbf{e}}^{\lambda t}}\underline{V}^{-1} + \mathbf{e}^{j\omega t}\underline{\underline{I}})(\underline{\underline{A}} - j\omega\underline{\underline{I}})^{-1}\underline{\underline{u}}$$
(9)

Table 2 gives details about solutions to Eq. (9) for ratio-dependent and Lotka–Volterra predation.

In the limit of the driving frequency, $\omega = 0$, after transients have died out, the steady-state problem to solve is

$$\underline{\delta} = \underline{A}^{-1}\underline{u} \tag{10}$$

The approach was applied to a press perturbation by Bender et al. (1984), and by van den Berg (1998), Schmitz (1997), and Yang and Sykes (1998), and is discussed in Case (2000).

3.4. Perturbation to b_i (e.g., change in wolves' ability to prey on moose)

Following from Eq. (5), a perturbation to b_i must directly affect both levels *i* and i - 1, so the simplest possible perturbation is

$$(\underline{\underline{A}} - j\omega\underline{\underline{I}})^{-1} = \frac{1}{\det(\underline{\underline{A}} - j\omega\underline{\underline{I}})} \begin{pmatrix} (m_2 - j\omega)(m_3 - j\omega) - l_3n_2 \\ -(m_3 - j\omega)l_2 \\ l_2l_3 \end{pmatrix}$$

4. Response of a three-level system to a sinusoidal perturbation

This method can be applied to a system with any number of trophic levels. Later in this section I treat an infinitely long chain, but for clarity I here consider a three-level food chain. For this system,

$$\underline{\underline{A}} = \begin{pmatrix} m_1 & n_1 & 0 \\ l_2 & m_2 & n_2 \\ 0 & l_3 & m_3 \end{pmatrix}$$

The eigenvalues are obtained by solving det($\underline{\underline{A}} - \lambda \underline{\underline{I}} = (m_1 - \lambda)(m_2 - \lambda)(m_3 - \lambda) - (m_1 - \lambda)l_3n_2 - (\overline{\underline{m}}_3 - \lambda)l_2n_1 = 0$, i.e.,

$$\lambda^{3} - (m_{1} + m_{2} + m_{3})\lambda^{2} + (m_{1}m_{2} + m_{2}m_{3} + m_{1}m_{3} - l_{2}n_{1} - l_{3}n_{2})\lambda - (m_{1}m_{2}m_{3} - l_{2}m_{3}n_{1} - l_{3}m_{1}n_{2}) = 0$$

Stability in the usual sense requires that the real parts of all three $\lambda < 0$. By the theory of equations, the sum of the roots is $(m_1 + m_2 + m_3)$, the

product is $(m_1m_2m_3 - l_2m_3n_1 - l_3m_1n_2)$, and the sum of the pairwise products is $(m_1m_2 + m_2m_3 + m_1m_3 - l_2n_1 - l_3n_2)$. Because *l*, *m*, and *n* are real, a necessary and sufficient condition for stability is:

- 1. $(m_1 + m_2 + m_3) < 0$,
- 2. $(m_1m_2 + m_2m_3 + m_1m_3 l_2n_1 l_3n_2) > 0$, and
- 3. $(m_1m_2m_3 l_2m_3n_1 l_3m_1n_2) < 0.$

One can see that a pure Lotka–Volterra system, for which all $m_i = 0$, is unstable. Similarly, ratio dependence, for which typically all $l_i > 0$, $m_i < 0$, and $n_i < 0$ (see Appendix A), yields stability.

Now consider $\omega \neq 0$. det $(\underline{A} - j\omega \underline{I}) = (m_1 - j\omega)(m_2 - j\omega)(m_3 - j\omega) - (m_1 - j\omega)\overline{l_3}n_2 - (m_3 - j\omega)l_2n_1$, and

$$\begin{array}{ccc} -(m_3 - j\omega)n_1 & n_1n_2 \\ (m_1 - j\omega)(m_3 - j\omega) & -(m_1 - j\omega)n_2 \\ -(m_1 - j\omega)l_3 & (m_1 - j\omega)(m_2 - j\omega) - l_2n_1 \end{array} \right)$$
(12)

For example, assume a sinusoidal cropping perturbation applied to the middle level:

$$\underline{P} = \mathrm{e}^{j\omega t} \begin{pmatrix} 0\\1\\0 \end{pmatrix}.$$

The entries in column 2 of Eq. (12) give the relative magnitudes of the after-transient sinusoidal response. As in Herendeen (1995), define the bottom-up factor fbu₃ = δ_3/δ_2 , and the top-down factor ftd₁ = δ_1/δ_2 .

$$fbu_{3} = \frac{\delta_{3}}{\delta_{2}} = -\frac{l_{3}}{(m_{3} - j\omega)},$$
with magnitude = $\left|\frac{l_{3}}{m_{3}}\right| \frac{1}{\sqrt{1 + \omega^{2}/m_{3}^{2}}}$

$$ftd_{1} = \frac{\delta_{1}}{\delta_{2}} = -\frac{n_{1}}{(m_{1} - j\omega)},$$
(13)
with magnitude = $\left|\frac{n_{1}}{m_{1}}\right| \frac{1}{\sqrt{1 + \omega^{2}/m_{3}^{2}}}$

with magnitude =
$$\left|\frac{n_1}{m_1}\right| \frac{1}{\sqrt{1 + \omega^2/m_1^2}}$$

For $\omega = 0$, Eq. (13) reduces to what Herendeen (1995) found for a press perturbation: fbu₃ = $-l_3/m_3$ and ftd₁ = $-n_1/m_1$. This shows the asymmetric nature bottom-up and top-down response to a press. However, as ω increases from 0, both fbu_i and ftd_i are multiplied by the factor $1/\sqrt{1 + (\omega^2/m_i^2)}$. This factor has the same form up as well as down the chain, indicating that frequency dependence causes a diminution of effect above and below the perturbed level. For an infinite ω , this factor is 0, and the influence of the perturbation's effect stops at level *i*.

 $m_i = M_i/S_i$ is a flow divided by a stock and has dimensions of time⁻¹. Let $|m_i| = 1/\tau_i$, where τ_i is the characteristic time of level *i*. Then the diminution factor is

$$\frac{1}{\sqrt{1+(\omega\tau_i)^2}}\tag{14}$$

Here $\tau_i = S_i/M_i$ is defined in metabolic terms: energy stock divided by energy flow. By Eq. (4), however, M_i is not simply INPUT_i, and it can approach 0, resulting in a large τ_i . The details of Eq. (4) must be examined to determine how large τ_i can be, and therefore how likely is a detectable frequency-dependent effect. An extreme example occurs for the top trophic level, for which, if initially uncropped, $INPUT_i =$ METMORT_i, M_i = INPUT_i($\partial B_i / \partial S_i$)(S_i / B_i), and therefore τ_i is inversely proportional to interference in that level. If there is little interference, τ_i can be many times larger than S_i /INPUT_i. To use an extreme example, for a typical affluent adult human, S is roughly 10 kg carbohydrate equivalent, and INPUT 1 kg per day. S/INPUT is then 10 days, but interference between affluent humans for food is essentially 0, giving a nearly infinite τ . On the other hand, perhaps the characteristic time is a reproductive one, with $\tau_i \approx 25$ years for humans. The issue of appropriate τ deserves more study.

By assumption a perturbation to RESOURCE directly affects only level 1 and gives fbus comparable to fbu₃ found above. For a perturbation to b_3 , i.e., to the functional form of predation by level 3 on level 2, we use Eqs. (11) and (12) to obtain

 n_1

In Eq. (15) we see that the top-down effect from level 2 to level 1 is identical to the case where only level 2 was perturbed (Eq. (13)), and ftd₁ vanishes for large ω . On the other hand, fbu₃ does not approach 0 as $\omega \rightarrow \infty$; rather, it approaches $-S_2/S_3$. This is reasonable; the perturbation to b_3 affects both levels 2 and 3 in a reciprocal manner. In Section 5 the predictions of Eqs. (13) and (15) are compared quantitatively with simulation results.

The specific frequency dependence described here for a three-level system also applies to a general k-level system. Besides using matrix inversion, one can also show this by applying the explicit algebraic approach of Herendeen (1995), noting that every equation in that paper can be used here by substituting $M_i - j\omega S_i$ for M_i . For example, we can calculate the ratio of successive δ_i for an infinite chain of identical compartments (identical l, m, n). For levels distant from the perturbation, by translational symmetry we expect the ratio of successive δ_i to be a constant.

Then

$$l\delta_{i-1} + (m - j\omega)\delta_i + n\delta_{i+1} = 0$$

becomes

$$l\beta^2 + (m - j\omega)\beta + n = 0 \tag{16}$$

where $\beta \equiv \delta_{i-1}/\delta_i$, independent of *i*. Solving Eq. (16) gives

$$\beta = \frac{m - j\omega}{2l} \left[-1 \pm \sqrt{1 - \frac{4nl}{(m - j\omega)^2}} \right]$$

Being careful regarding signs when taking the square root and assuming that $nl \ll m^2$, we obtain the limiting cases for fbu and ftd given in Eq. (13).

The asymptotic response to a sinusoidal perturbation, which is steady oscillation, depends on both initial stocks and flows. This contrasts with the asymptotic response to a press, which is a steady state and depends only on the flows. The ratio $l_i:m_i:n_i$ ($=L_i:M_i:N_i$) determines how a press is passed on. Additionally, it is the relative sizes of m_i ($=M_i/S_i=1/\tau_i$) and ω that determines how a sinusoid is passed on. Because

$$ftd_{1} = -\frac{m_{1}}{(m_{1} - j\omega)}$$

$$fbu_{3} = \frac{[(m_{1} - j\omega)l_{3}/S_{2}] + [(m_{1} - j\omega)(m_{2} - j\omega)/S_{3}] - (l_{2}n_{1}/S_{3})}{[(m_{1} - j\omega)(m_{3} - j\omega)/S_{2}] + [(m_{1} - j\omega)n_{2}/S_{3}]}$$
(15)

the τ_i can vary among trophic levels, there is often quantitative asymmetry in the frequency dependence.

5. Comparison with simulation

For this purpose, I use the same functional form as in Herendeen (2004), a Holling Type 2 pattern that shows feeding saturation with infinite prey abundance, with abundance defined in terms of both prey and predator densities.

$$B_i = \frac{\text{INPUT}_i}{S_i} = \frac{\text{INPUT}_{i,0}}{S_{i,0}} \frac{b_i(c_i+1)\alpha_i}{(c_i+\alpha_i)}$$
(17)

where $\alpha_i \equiv$ "abundance" $\equiv (S_{i-1}/S_{i-1,0})^q/(S_i/S_{i,0})^r$

The subscript "0" refers to the initial steady state, where all $\alpha_i = 1$. If $q_i = 0$, level *i* is totally insensitive to abundance of prey. If $r_i = 0$, level *i* is totally insensitive to interference. $q_i = r_i = 1$ defines ratio dependence. For $c \rightarrow \infty$, Lotka–Volterra and pure donor and recipient control forms occur for particular *q* and *r*. For Eq. (17),

prey derivative_i
$$\equiv \frac{\partial Bi}{\partial S_{i-1}} \frac{S_{i-1}}{B_i} = q_i \left(\frac{c_i}{c_i+1}\right)$$

interference derivative_i $\equiv \frac{\partial B_i}{\partial S_i} \frac{S_i}{B_i} = -r_i \left(\frac{c_i}{c_i+1}\right)$
(18)

These derivatives go into the *l*, *m*, and *n*.

Let us look at the three-level food chain of Fig. 2 under two types of sinusoidal perturbation:



Fig. 2. A hypothetical three-level food chain at initial steady state. Numbers in compartments are stocks (unit: energy). Other numbers are flows (unit: energy per week). PROD = producers (level 1), HERB = herbivores (level 2), CARN = carnivores (level 3).

- 1. changed cropping of level 2,
- 2. change in b_3 ,

for two types of functional dependence:

- 1. ratio-dependent predation (all $c_i = q_i = r_i = 1$),
- 2. approximately Lotka–Volterra functional dependence (all $c_i = 1E12$ (approximating), all $q_i = 1$, all $r_i = 0.1$ (approximating \mathcal{D} 0 but assuring stability)).

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); all are determined from Fig. 2.

```
METMORT (metabolic loss and non-predation
mortality):
METMORT<sub>i</sub> = \mu_i S_i, with \mu_i = 30, 4.5, and
```

9/7 per week, respectively for i = 1, ..., 3.

INPUT:

INPUT_i/S_i = INPUT_{i,0}/S_{i,0}(c_i + 1) α_i /(c_i + α_i), with INPUT_{i,0}/S_{i,0} = 100/3, 5, and 10/7 per week. Level 1: α_1 ("abundance") = (1)/(S₁/S_{1,0}). There is no change in resource. Levels 2 and 3: $\alpha_i = (S_{i-1}/S_{i-1,0})/(S_i/S_{i,0})$. Results are shown in Figs. 3–6, as follows.

Ratio-dependent predation

Perturbation to level 2:

- Fig. 3: simulation result for a press perturbation ($\omega = 0$) and sinusoidal cropping perturbations of two frequencies. These frequencies are chosen to demonstrate an increasing effect.
- Fig. 4a: comparison of calculated and simulated results.

Perturbation to b₃:

Fig. 4b: comparison of calculated and simulated results (no simulations are shown).

Approximately Lotka–Volterra functional dependence

Perturbation to level 2:

Fig. 5: simulation result for a press perturbation ($\omega = 0$) and sinusoidal cropping perturbations of two frequencies.

Fig. 6a: comparison of calculated and simulated results.

Perturbation to b₃:

Fig. 6b: comparison of calculated and simulated results (no simulations are shown).



Fig. 3. Ratio dependence (all $c_i = q_i = r_i = 1$): response of three-level food chain of Fig. 2 to perturbation to level 2, herbivores. Amplitude of perturbation is same in all cases. (a) press (step function), (b) sinusoid, $\omega = 1$ per week, (c) sinusoid, $\omega = 2$ per week. $\tau_i = |1/m_i| = 0.066, 0.44, 1.75$ week for levels 1–3.



Fig. 3. (Continued).

5.1. Ratio dependence

Fig. 3a shows that for the press, after transients have died out, levels 2 and 3 have roughly equal fractional stock changes, so $fbu_3 = 1.29$. Level 1 experiences a much smaller fractional stock change, opposite in sign:

ftd₁ = -0.14. Both of these results are expected for ratio dependence (Herendeen, 1995). As the perturbing frequency increases (Fig. 3b and c),after transients have died out, the response of all levels decreases, but more importantly, the response of levels 1 and 3 decreases relative to that of level 2.



Fig. 4. Ratio dependence (all $c_i = q_i = r_i = 1$): comparison of calculated (smooth curve) and simulated (points) $|\text{ftd}_1|$ and $|\text{fbu}_3|$ for sinusoidal perturbation to three-level food chain in Fig. 2. (a) Cropping perturbation to level 2. Note different axes for ftd₁ and fbu₃. (b) Perturbation to b_3 , the strength of the feeding relationship of level 3 on level 2.

Fig. 4a and b show the frequency dependence of $|ftd_1|$ and $|fbu_3|$ calculated from Eqs. (13) and (15) and from the simulations. (I use the absolute values because the sign is ambiguous as phase lags change

for $\omega \neq 0$.) The agreement between theory and simulation is excellent, even though the simulated system is nonlinear and the perturbation was large enough to induce large changes (e.g., $\delta_2 \approx -0.4$). The small



Fig. 5. Approximately Lotka–Volterra functional dependence ($c_i = 1E12$, $q_i = 1$, $r_i = 0.1$): response of three-level food chain of Fig. 2 to perturbation to level 2, herbivores. Amplitude of perturbation is same in all cases. (a) press (step function), (b) sinusoid, $\omega = 1$ per week, (c) sinusoid, $\omega = 2$ per week, $\tau_i = |1/m_i| = 0.3$, 2, 7E12 week for levels 1–3.



Fig. 5. (Continued).

disagreement for $\omega < 4$ per week is due to nonlinearity, as it disappears for a perturbation 1/100th as large as used here. Fig. 4a shows that with a perturbation to level 2, both |ftd₁| and |fbu₁| decrease towards 0 with increasing ω , indicating the qualitative symmetry of the frequency-dependent effect. However, one can see that |fbu₃| diminishes much more rapidly with frequency than does |ftd₁|. This quantitative asymmetry is expected because of the different values for τ_i (0.067, 0.44, and 1.75 week for levels 1–3). These times imply that transients will die out in \approx 5 weeks, which is observed in, e.g., Fig. 3a.

Fig. 4b illustrates the result of perturbing b₃. $|\text{ftd}_1|$ decreases towards zero, but $|\text{fbu}_3|$ approaches a limiting value of 2.86 (= S_3/S_2) for large ω , as predicted by Eq. (15).

5.2. Approximately Lotka–Volterra functional dependence

As mentioned, this deviates from a pure Lotka– Volterra system in that the $r_i = 0.1$, not 0. This is necessary to avoid crash or endless oscillation. In addition, this system is initially cropped, which also violates the "pure" Lotka–Volterra assumption.

Fig. 5a shows that for the press, after transients have died out, levels 1 and 2 have roughly equal fractional

stock changes, both much smaller than the change in level 3. Thus we have $\text{ftd}_1 = -0.89$, and $\text{fbu}_3 = 42$ (Eq. (14) gives 1E13; linearity breaks down for such large changes.). As the perturbing frequency increases from zero to 0.5 per week (Fig. 5b and c), the responses of levels 1 and 2 increase, allowing one to see more clearly that they have approximately the same magnitude, while that of level 3 decreases. As frequency increases further, all decrease.

Fig. 6a and b show the frequency dependence of $|\text{ftd}_1|$ and $|\text{fbu}_3|$ calculated from Eqs. (13) and (15) and from the simulations. The agreement between theory and simulation is excellent, even though the perturbation was large enough to induce large changes (e.g., $\delta_3 \approx -0.3$). Fig. 6a shows that with a perturbation to level 2, both $|\text{ftd}_1|$ and $|\text{fbu}_3|$ decrease towards 0 with increasing ω , again indicating the qualitative symmetry of the frequency-dependent effect. Again, fbu₃ diminishes much more rapidly with increasing frequency than does $|\text{ftd}_1|$ because of the different values for τ_i (0.3, 2.0, and 7E12 (!!) week for levels 1–3).

Fig. 6b illustrates the result of perturbing b₃. $|\text{ftd}_1|$ decreases towards zero. $|\text{fbu}_3|$ decreases from a value of 10.12 for $\omega = 0$, dips to 1.75 for $\omega = 3$ per week and then approaches a limiting value of 2.86 (= S_3/S_2), as predicted by Eq. (15).



Fig. 6. Approximately Lotka–Volterra functional dependence ($c_i = 1E12$, $q_i = 1$, $r_i = 0.1$): comparison of calculated (smooth curve) and simulated (points) |ftd₁| and |fbu₃| for sinusoidal perturbation to three-level food chain in Fig. 2. (a) Cropping perturbation to level 2. Note different axes for ftd₁ and fbu₃. (b) Perturbation to b₃, the strength of the feeding relationship of level 3 on level 2.

6. Conclusions

An analytical method has been developed for interpreting and predicting the effects of period i.e. pertubations on food chains. Its predictions agree well with results from simulation of a model three-level ecosystem. This verifies the hypothesis that, compared with a press, a sinusoidal perturbation produces additional diminution of effect with increasing trophic distance from the perturbed level. This adds to the many possible reasons for the observed varying strength of top-down and bottom-up effects in ecosystems, especially to the absence of top-down effects. A subsequent article will apply the method here and in Herendeen (2004) to experimental results.

Acknowledgements

Many thanks to William Ruesink, Illinois Natural History Survey, for careful reading of an early draft; to I. David Berg, University of Illinois, for mathematical insights; to Ted Case for suggesting sinusoidally perturbing the functional relationships; and to Donald DeAngelis for critical comments.

Appendix A

l, *m*, and *n* (calculated using Eqs. (4) and (18) and Fig. 2) and eigenvalues of $\underline{\underline{A}}$ for the ratio-dependent and approximately Lotka–Volterra cases analyzed here. These are stable. The pure Lotka–Volterra case, which is unstable, is included for comparison

Level	с	\overline{q}	r	l (per week)	m (per week)	n (per week)	$\tau \;(= 1/m_i)$ (week)	Eigenvalues of $\underline{\underline{A}}$ (per week)	Stability under simulation?
Ratio d	lepend	ence							
1	1	1	1	16.67	-15	-1.67	0.067	-0.67, -14.66, -2.49	Stable
2	1	1	1	2.5	-2.25	-0.25	0.444		
3	1	1	1	0.714	-0.57	-0.143	1.25		

Level	С	q	r	l (per week)	m (per week)	n (per week)	$\tau \ (= 1/m_i)$ (week)	Eigenvalues of $\underline{\underline{A}}$ (per week)	Stability under simulation?
Pure Lo	otka–Volt	erra							
1	1E12	1	0	33.33	-3.33E-6	-3.33	3E5	$0.13, 0.007 \pm j4.17$	Unstable
2	1E12	1	0	5	5E-7	-0.5	2E6		
3	1E12	1	0	1.43	0.143	-0.143	7		
Approx	imately 1	Lotka-	-Volter	ra					
1	1E12	1	0.1	33.33	-3.33	-3	0.3	$-0.13, -1.85 \pm j3.66$	Stable
2	1E12	1	0.1	5	-0.5	-0.45	2		
3	1E12	1	0.1	1.43	1.43E-7	-0.143	7E6		

Appendix A (Continued)

References

- Bender, E., Case, T., Gilpin, M., 1984. Perturbation experiments in community ecology. Ecology 65, 1–13.
- 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.
- Case, T., 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press.
- Dyer, L., Letourneau, D., 1999. Relative strengths of top-down and bottom-up forces in a tropical forest community. Oecologia 119, 265–274.
- Herendeen, R., 1995. A unified quantitative approach to bottom-up:top-down and trophic cascade hypotheses. J. Theor. Biol. 176, 13–26.
- Herendeen, R., 2004. Bottom-up and top-down effects in food chains depend on functional dependence: an explicit framework. Ecol. Model. 171, 21–33.

- McLaren, B., Peterson, R., 1994. Wolves, moose, and tree rings on Isle Royale. Science 266, 1555–1558.
- Post, E., Peterson, R., Stenseth, N., McLaren, B., 1999. Ecosystem consequences of wolf behavioural responses to climate. Nature 401, 905–907.
- Post, E., Stenseth, N., Peterson, R., Vucetich, J., et al., 2002. Phase dependence andpopulation cycles in a large-mammal predator-prey system. Ecology 83, 2997–3002.
- Schmitz, O., 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78, 55–68.
- Spiegel, M., 1958. Applied Differential Equations. Prentice-Hall.
- van den Berg, H., 1998. Propagation of permanent perturbations in food chains and food webs. Ecol. Model. 107, 225– 236.
- Vucetich, J., Peterson, R., Schaeffer, C., 2002. The effect of prey and predator densities on wolf predation. Ecology 83, 3003– 3013.
- Yang, M., Sykes, R., 1998. Trophic-dynamic modeling in a shallow eutrophic river ecosystem. Ecol. Model. 105, 129–139.