

Food-web structure and planktonic predator–prey relationships in two eutrophic European lakes: Stability constraints on carbon fluxes

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Abstract

The food webs in two eutrophic European lakes were analyzed with respect to their stability characteristics. The food web during the summer in Lake Nesjøvatn (Norway) appeared to be stable; its response time to small perturbations was ~12 d. In Lake Kastoria (Greece), the summer food web was almost neutrally stable, with a response time of ~160 d. The major difference in the two systems was the species composition of the phytoplankton community, which was dominated by unicellular cryptophytes in Lake Nesjøvatn and by toxic filamentous and colonial cyanobacteria in Lake Kastoria. The macrozooplankton in both lakes showed a distinct inclination toward carnivory versus herbivory, and the heterotrophic flagellates showed a preference for small phytoplankton versus heterotrophic bacteria as a food source. The requirement for stability of the food webs constrains the grazing rates of predators to values substantially less than those that would maximize the energy flux through the system. This is especially true when a predator preferentially consumes one of several prey species.

The factors that regulate the composition of biological communities and the flow of fixed carbon within and through them have been the subject of debate for many years. Lotka (1922) argued that natural selection tends to structure biological communities in a way that maximizes the energy flux through the system, “so far as compatible with the constraints to which the system is subject” (p. 148). Odum (1983, p. 6) expanded on Lotka’s ideas and concluded that “theories and corollaries derived from the maximum power principle explain much about the structure and processes of systems.” Using a different approach, May (1974) and Steele (1974) reasoned that biological communities could persist only if they were stable to perturbations associated with natural variations in environmental forcing functions. They therefore reasoned that, at least to some extent, the composition of biological communities and the flow of energy through and within them must reflect a requirement for resiliency, i.e., the ability to return to an equilibrium configuration within a reasonably short time following a perturbation. Cropp and Gabric (2002) examined the implications of these theories in the case of a simple linear food chain and concluded that, at least in that case, the requirements for resiliency and the implications of the goal functions associated with Odum’s work were consistent with similar distributions of biomass and energy flux. In more complex systems, the application of Odum’s ideas in determining ecosystem behavior has met with mixed success. Månsson and McGlade (1993), for example, pointed out that the flows of carbon in six marine ecosystems studied by Baird et al. (1991) “were contrary to what Odum has suggested, in that the aggregate amount of cycling was an indication

not of maturity but rather of the type of dynamics and levels of stress.” On the other hand, Cropp and Gabric (2002) observed that in some cases the thermodynamic approaches advocated by Odum have met with considerable success in estimating parameters to describe real ecosystems (e.g., Jorgensen and Straskraba 2000).

In his seminal paper, Lotka (1922) was careful to qualify his conclusions about energy flux with the caveat that system behavior would be subject to constraints. Indeed, it seems unlikely that a single principle or law could explain all aspects of the distribution of biomass and patterns of energy flux within biological communities. Nevertheless, principles and laws may be used to significantly constrain the range of possibilities. As noted by Patten (1993), “The admissibility of virtually any system configuration, within given physical and resource constraints, does not mean the processes of ecosystem organization are lawless. The challenge is to find the laws” (p. 602).

Through a painstaking analysis of numerous food webs, Pimm (1982) and Pimm et al. (1991) have in fact been able to identify a number of patterns that seem to characterize natural food webs. Although the components of most of the food webs they examined were species rather than functional groups of organisms, several of the patterns they identified are of direct relevance to the analysis of food webs based on functional groups (Fasham et al. 1999; Rivkin et al. 1996; Laws et al. 2000). They found, for example, that the average number of trophic levels is three or four and that the resilience of food chains to perturbations is negatively correlated with food-chain length. Furthermore, although there are distinct pathways of energy flow at the primary consumer level of detritus and grazing food chains, those pathways tend to merge at the secondary consumer level and higher (Pimm 1982).

In this paper, I have applied the argument that biological communities are stable to at least small perturbations (Pimm 1982) in order to explore the implications of this

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constraint on pelagic microbial community behavior in two limnetic systems where substantial information exists on biomass and/or energy flow. The approach taken is similar to that used by Laws et al. (2000). In both cases, I use organic carbon within functional groups of organisms as a measure of biomass, and the interactions between functional groups are quantified in terms of carbon fluxes.

Lake Nesjøvatn

Lake Nesjøvatn is a eutrophic lake in central Norway, and its pelagic microbial community was studied by Vadstein and colleagues (Vadstein et al. 1988, 1989, 1993) during the period April–October 1981. Vadstein et al. (1988) documented the physical and chemical characteristics of the lake. The phytoplankton population appears to be phosphorus limited during the ice-free period, in part due to competition with heterotrophic bacteria, which account for 80% of the phosphorus uptake during the summer (Vadstein et al. 1993). The euphotic zone food-web model I employed is taken directly from Vadstein et al. (see fig. 6 in Vadstein et al. 1989) and is consistent with the patterns noted by Pimm (1982). The microbial community consists of four functional groups: phytoplankton (X_1), heterotrophic bacteria (X_2), flagellates (X_3), and zooplankton (X_4). The zooplankton feed on phytoplankton, heterotrophic bacteria, and flagellates. The flagellates feed exclusively on heterotrophic bacteria (Fig. 1). Equations describing the dynamics of the carbon in the four functional groups and dissolved organic carbon (DOC) (X_5) are as follows:

$$\frac{dX_1}{dt} = q_1 A_1 f_1 X_1 - A_4 X_4 f_4 \frac{\rho_1 X_1}{\rho_1 X_1 + \rho_2 X_2 + \rho_3 X_3} - M_1 X_1 \quad (1)$$

$$\frac{dX_2}{dt} = q_2 A_2 f_2 X_2 - A_4 X_4 f_4 \frac{\rho_2 X_2}{\rho_1 X_1 + \rho_2 X_2 + \rho_3 X_3} - A_3 f_3 X_3 - M_2 X_2 \quad (2)$$

$$\frac{dX_3}{dt} = q_3 A_3 f_3 X_3 - A_4 X_4 f_4 \frac{\rho_3 X_3}{\rho_1 X_1 + \rho_2 X_2 + \rho_3 X_3} - M_3 X_3 \quad (3)$$

$$\frac{dX_4}{dt} = q_4 A_4 f_4 X_4 - M_4 X_4 \quad (4)$$

$$\frac{dX_5}{dt} = s_1 A_1 f_1 X_1 + s_3 A_3 f_3 X_3 + s_4 A_4 f_4 X_4 - A_2 f_2 X_2 + M_2 X_2 + M_3 X_3 \quad (5)$$

Table 1 provides a definition of all parameters in Eqs. 1–5 and the values assigned to those parameters. Carbon not converted to biomass or excreted as DOC was assumed to be lost to respiration or sedimentation. The temperature of the lake was assumed to be 16°C (Vadstein et al. 1988).

Most of the parameters in Eqs. 1–5 were constrained by information provided in fig. 6 of Vadstein et al. (1989) but five were not. I assumed the maximum growth rates of the phytoplankton ($q_1 A_1$), heterotrophic bacteria ($q_2 A_2$), and flagellates ($q_3 A_3$) to be 0.68 d⁻¹ (Eppley 1972), 1.2 d⁻¹ (Hobbie and Cole 1984; White et al. 1991), and 5.75 d⁻¹ (Fenchel and Finlay 1983), respectively, at 16°C. The maximum growth rate of the zooplankton ($q_4 A_4$) was varied to explore the stability characteristics of the system at steady state. Vadstein et al. (1989) reported the concentration of detrital carbon (dissolved + particulate) in the lake as ~8,000 mg m⁻³. It is unclear how much of the detrital carbon was dissolved, and typically more than 85% of the dissolved organic carbon (DOC) is refractory (Tranvik 1988; Søndergaard and Borch 1992). Søndergaard et al. (1995), for example, found that 5–9% of the DOC in a eutrophic lake in Denmark was labile. I assumed the concentration of labile DOC in Lake Nesjøvatn to be 250 mg m⁻³, which is about 3% of the sum of particulate and dissolved organic carbon (~8,000 mg m⁻³) in the lake.

The resilience of the steady-state solutions to Eqs. 1–5 is determined by the eigenvalues of the community matrix (May 1974). The elements of the community matrix are the partial derivatives of the right-hand sides of Eqs. 1–5 with respect to the state variables evaluated at the equilibrium point, and for purposes of evaluating the community matrix, an explicit representation of the dimensionless relative growth rates f_2 , f_3 , and f_4 is needed. I assumed

$$f_2 = 1 - \frac{P_2}{X_5} \quad (6)$$

$$f_3 = 1 - \frac{P_3}{X_2} \quad (7)$$

$$f_4 = 1 - \frac{P_4}{X_1 + X_2 + X_3} \quad (8)$$

In Eqs. 6–8, P_2 , P_3 , and P_4 are constants representing the concentrations of substrate or prey below which uptake or grazing by the heterotrophic bacteria, flagellates, and zooplankton, respectively, ceases. The existence of these thresholds helps to stabilize the system (Steele 1974). In this carbon-based model, I did not include the concentration of phosphate as one of the state variables for purposes of examining the resilience of the system to perturbations. In effect, this amounts to assuming that f_1 is constant. While this is undoubtedly not strictly true, data summarized by Vadstein et al. (1988, see their fig. 1) indicate that the concentration of soluble reactive phosphorus (SRP) was drawn down from 70 mg m⁻³ in April to less than 5 mg m⁻³ from the middle of May through the middle of September. The uniformly low SRP concentration during this four-month period suggests that uptake by the phytoplankton and heterotrophic bacteria did an effective job of maintaining the SRP concentration near its equilibrium value. A phosphorus-based model of the same food web, but including phosphate as a state variable, produces similar results to the carbon-based model (vide infra).

Table 1. Parameter values for Lake Nesjøvatn model.

Variable	Definition		Unit
A_1	Maximum carbon uptake rate by phytoplankton per unit phytoplankton carbon	$0.68/q_1$	d^{-1}
A_2	Maximum carbon uptake rate by heterotrophic bacteria per unit heterotrophic bacterial carbon	$1.2/q_2$	d^{-1}
A_3	Maximum carbon consumption by heterotrophic flagellates per unit heterotrophic flagellate carbon	$5.75/q_3$	d^{-1}
A_4	Maximum carbon consumption by zooplankton per unit zooplankton carbon	1.57–11	d^{-1}
f_1	Phytoplankton carbon uptake as a fraction of A_1 due to nutrient and/or light limitation	$(163/1,230)(1/A_1) = 0.14$	dimensionless
f_2	Heterotrophic bacterial carbon uptake as a fraction of A_2 due to substrate limitation	$(71/74)(1/A_2) = 0.48$	dimensionless
f_3	Heterotrophic flagellate carbon uptake as a fraction of A_3 due to prey limitation	$(18/3)(1/A_3) = 0.406$	dimensionless
f_4	Zooplankton carbon uptake as a fraction of A_4 due to prey limitation	$(101/136)(1/A_4)$	dimensionless
M_1	Fractional rate of loss of phytoplankton biomass to sinking	26/1,230	d^{-1}
M_2	Fractional rate of loss of bacterial biomass to death	21/74	d^{-1}
M_3	Fractional rate of loss of flagellate biomass to death	6/3	d^{-1}
M_4	Fractional rate of loss of zooplankton biomass to sinking	43/136	d^{-1}
q_1	Fraction of fixed carbon converted to living biomass by phytoplankton	118/163	dimensionless
q_2	Gross growth efficiency of heterotrophic bacteria	43/71	dimensionless
q_3	Gross growth efficiency of heterotrophic flagellates	7/18	dimensionless
q_4	Gross growth efficiency of zooplankton	43/101	dimensionless
ρ_1	Grazing preference of zooplankton for phytoplankton	1	dimensionless
ρ_2	Grazing preference of zooplankton for heterotrophic bacteria versus phytoplankton	$(4/92)(1,230/74) = 0.72$	dimensionless
ρ_3	Grazing preference of zooplankton for heterotrophic flagellates versus phytoplankton	$(5/92)(1,230/3) = 22.3$	dimensionless
s_1	Fraction of fixed carbon excreted by phytoplankton	10/163	dimensionless
s_3	Fraction of consumed carbon excreted by flagellates	6/18	dimensionless
s_4	Fraction of consumed carbon excreted by zooplankton	32/101	dimensionless
X_1	Phytoplankton carbon	1,230	$mg\ C\ m^{-3}$
X_2	Heterotrophic bacterial carbon	74	$mg\ C\ m^{-3}$
X_3	Heterotrophic flagellate carbon	3	$mg\ C\ m^{-3}$
X_4	Zooplankton carbon	136	$mg\ C\ m^{-3}$
X_5	Labile dissolved organic carbon	250	$mg\ C\ m^{-3}$

Lake Kastoria

Lake Kastoria is a highly eutrophic lake that lies adjacent to the town of Kastoria in western Macedonia, Greece. Moustaka-Gouni et al. (2006) provided a good description of the physical and chemical characteristics of the lake. The plankton population during the ice-free period can be broadly classified into six functional groups: small phytoplankton (X_{1S}), large phytoplankton (X_{1L}), bacteria (X_2), flagellates (X_3), ciliates (X_4), and macrozooplankton (X_5). Most of the phytoplankton biomass falls into the large (microplankton) category. The lake has a history of toxic cyanobacterial blooms involving, among others, *Cylindrospermopsis raciborskii*, *Microcystis aeruginosa*, and *Aphanizomenon* spp. (Moustaka-Gouni et al. 2006).

Table 1 of Moustaka-Gouni et al. (2006) provides information on the carbon biomass in the six functional groups as a function of time from November 1998 to October 1999. I focus here on the summer of 1999, during which temperatures in the lake were relatively constant (21–26°C) and the biomasses of the functional groups were

relatively stable. I assume a food web (Fig. 2) similar to the models described by Rivkin et al. (1996), Fasham et al. (1999), and Laws et al. (2000). All three models include a microbial loop in which bacteria take up labile DOC (X_7) and are consumed by flagellates and microzooplankton, which in turn are grazed by ciliates and mesozooplankton. In all three models, the flagellates and microzooplankton consume both heterotrophic bacteria and small phytoplankton, and large zooplankton consume large phytoplankton as well as the top trophic level in the microbial loop. In addition, the model includes particulate detrital carbon (X_8) and a carnivorous predator (X_6), which grazes on the macrozooplankton (Fig. 2). Equations describing the carbon dynamics in the six functional groups, labile dissolved organic carbon, and particulate detrital carbon are as follows:

$$\frac{dX_{1S}}{dt} = q_{1S}A_{1S}f_{1S}X_{1S} - A_3X_3f_3\frac{\rho_{1S}X_{1S}}{\rho_{1S}X_{1S} + \rho_2X_2} \quad (9)$$

$$\frac{dX_{1L}}{dt} = q_{1L}A_{1L}f_{1L}X_{1L} - A_5X_5f_5\frac{\rho_{1L}X_{1L}}{\rho_{1L}X_{1L} + \rho_4X_4} \quad (10)$$

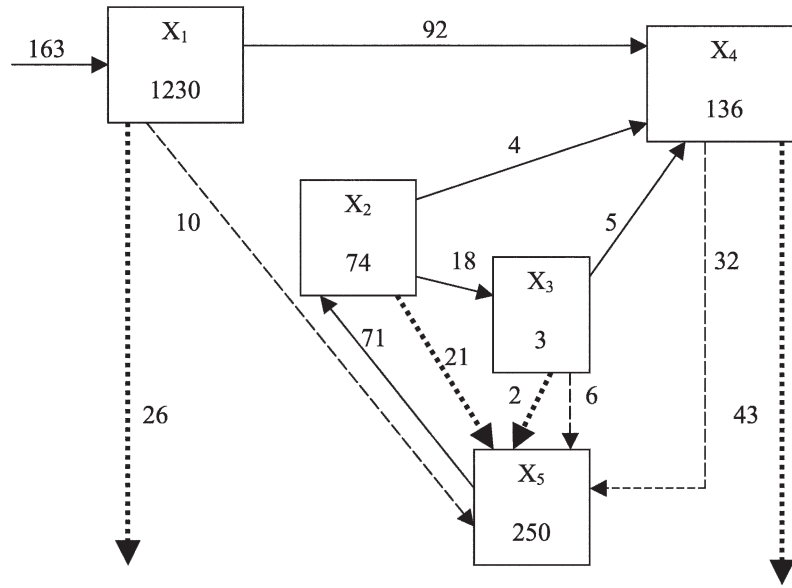


Fig. 1. Lake Nesjøvatn food web. Numbers in boxes indicate biomasses (mg C m⁻³). Arrows indicate fluxes (mg C m⁻³ d⁻¹). Solid arrows are grazing or uptake. Dotted arrows are death or sinking. Dashed arrows are excretion.

$$\frac{dX_2}{dt} = q_2 A_2 f_2 X_2 - A_3 X_3 f_3 \frac{\rho_2 X_2}{\rho_{1S} X_{1S} + \rho_2 X_2} \quad (11)$$

$$\rho_4 q_{1L} A_{1L} f_{1L} = \rho_{1L} q_4 A_4 f_4 \quad (20)$$

and hence

$$\frac{dX_3}{dt} = q_3 A_3 f_3 X_3 - A_4 X_4 f_4 \quad (12)$$

$$X_4 + \frac{\rho_{1L}}{\rho_4} X_{1L} = \frac{A_5 f_5}{A_4 f_4 q_4} X_5 \quad (21)$$

$$\frac{dX_4}{dt} = q_4 A_4 f_4 X_4 - A_5 X_5 f_5 \frac{\rho_4 X_4}{\rho_{1L} X_{1L} + \rho_4 X_4} \quad (13)$$

Setting Eqs. 12 and 14 equal to zero gives

$$\frac{X_4}{X_3} = \frac{q_3 A_3 f_3}{A_4 f_4} \quad (22)$$

$$\frac{dX_5}{dt} = q_5 A_5 f_5 X_5 - A_6 X_6 f_6 \quad (14)$$

and

$$\frac{X_6}{X_5} = \frac{q_5 A_5 f_5}{A_6 f_6} \quad (23)$$

$$\frac{dX_6}{dt} = q_6 A_6 f_6 X_6 - M X_6 \quad (15)$$

Setting Eq. 16 equal to zero and combining it with Eqs. 18, 19, and 22 gives

$$\begin{aligned} \frac{dX_7}{dt} = & s_{1S} A_{1S} f_{1S} X_{1S} + s_3 A_3 f_3 X_3 \\ & + s_4 A_4 f_4 X_4 - A_2 f_2 X_2 \end{aligned} \quad (16)$$

$$\frac{\rho_{1S}}{\rho_2} = \frac{X_2}{X_{1S}} \left(\frac{1 - q_2 (s_3 - q_3 s_4)}{q_2 [s_3 + q_3 s_4 + (s_{1S}/q_{1S})]} \right) \quad (24)$$

$$\begin{aligned} \frac{dX_8}{dt} = & s_{1L} A_{1L} f_{1L} X_{1L} + s_5 A_5 f_5 X_5 \\ & + s_6 A_6 f_6 X_6 + M X_6 - D X_8 \end{aligned} \quad (17)$$

Finally, setting Eq. 17 equal to zero gives

$$\begin{aligned} D X_8 = & s_{1L} A_{1L} f_{1L} X_{1L} + s_5 A_5 f_5 X_5 \\ & + s_6 A_6 f_6 X_6 + M X_6 \end{aligned} \quad (25)$$

If Eqs. 9 and 11 both equal zero, it follows that

$$\rho_2 q_{1S} A_{1S} f_{1S} = \rho_{1S} q_2 A_2 f_2 \quad (18)$$

and hence

$$X_2 + \frac{\rho_{1S}}{\rho_2} X_{1S} = \frac{A_3 f_3}{A_2 f_2 q_2} X_3 \quad (19)$$

If Eqs. 10 and 13 both equal zero, it follows that

Equations 18–25 provide eight constraint equations that must be satisfied for the system to be at steady state. Values of the state variables X_{1S} , X_{1L} , X_2 , X_3 , X_4 , and X_5 were taken from Table 1 of Moustake-Gouni et al. (2006). Gross growth efficiencies (q values) were taken from Table 2 of Laws et al. (2000), with the exception of the heterotrophic bacterial efficiency, which was taken from Rivkin and Legendre (2001) assuming a temperature of 23.5°C. I

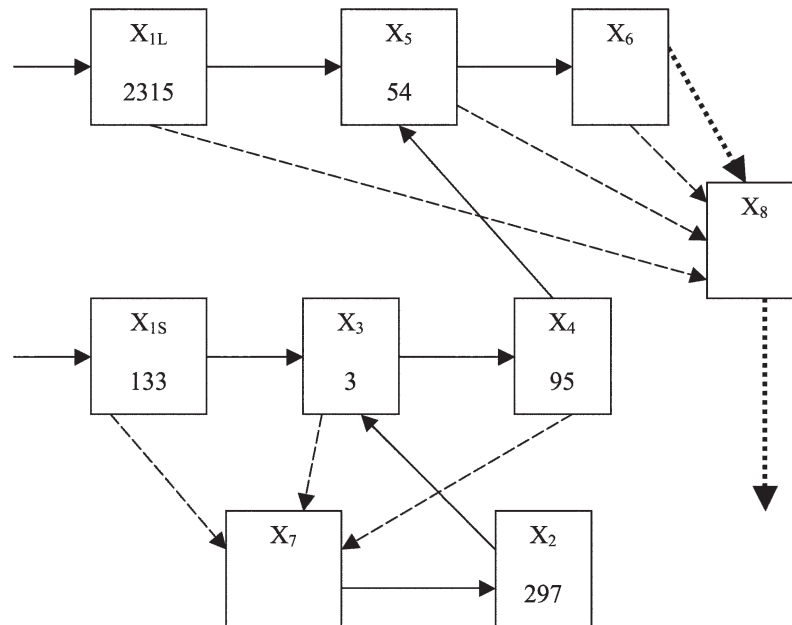


Fig. 2. Lake Kastoria food web. Numbers in boxes indicate biomasses (mg C m⁻³). Arrows indicate fluxes (mg C m⁻³ d⁻¹). Solid arrows are grazing or uptake. Dotted arrows are death or sinking. Dashed arrows are excretion.

assumed that carbon not converted to biomass by the heterotrophic bacteria was respired. The respiration rates for the other functional groups were taken from Table 2 of Laws et al. (2000). I assumed that the fraction of ingested carbon not converted to biomass or respired was excreted, where the carbon excreted by X_{1S}, X₃, and X₄ contributed to the labile dissolved organic carbon pool, and the carbon excreted by X_{1L}, X₅, and X₆ contributed to the particulate detrital carbon pool. The maximum growth rates of the functional groups were calculated using the equations in Table 2 evaluated at a temperature of 23.5°C. These equations are consistent with the maximum growth rates assigned to the corresponding functional groups in the Lake Nesjøvatn model at 16°C. The eight constraint equations were used to assign values to f_{1S} , f_{1L} , f_3 , f_4 , f_5 , X_6 , DX_8 , and $\rho_{1S}:\rho_2$. It was not necessary to specify values for D (fractional loss rate of detrital carbon to sinking) and X_8 separately, since they appear only as the product DX_8 in Eq. 25, and the steady-state solutions to the other equations are independent of D and X_8 . The remaining parameters, f_2 , f_6 , and $\rho_4:\rho_{1L}$, and the equilibrium value of X_7 were varied to produce a steady state with maximum resiliency to perturbations. I discovered that the most stable configuration of the system was independent of the value assigned to X_7 over the range 1–1,000 mg C m⁻³. Although the value of the labile DOC concentration is unknown, it almost certainly is within this range (vide supra). The stability of the system is therefore a function of the values assigned to f_2 , f_6 , and $\rho_4:\rho_{1L}$. Phytoplankton production was assumed to be light limited, which is consistent with the composition of the phytoplankton community during the summer months (Reynolds et al. 2002). For the heterotrophic community, and for purposes of exploring the

resiliency of the equilibrium solution, I assumed

$$f_2 = 1 - \frac{P_2}{X_7} \quad (26)$$

$$f_3 = 1 - \frac{P_3}{X_{1S} + X_2} \quad (27)$$

$$f_4 = 1 - \frac{P_4}{X_3} \quad (28)$$

$$f_5 = 1 - \frac{P_5}{X_{1L} + X_4} \quad (29)$$

$$f_6 = 1 - \frac{P_6}{X_5} \quad (30)$$

where P_2 , P_3 , P_4 , P_5 , and P_6 are constants with a meaning similar to the analogous constants in Eqs. 6–8.

Methods

Elements of the community matrix for Lake Nesjøvatn and Lake Kastoria were calculated by analytical differentiation of the right-hand sides of Eqs. 1–5 and 9–17, respectively, with the right-hand sides of Eqs. 6–8 and 26–30, respectively, substituted for the corresponding f values in the equations. All derivatives were evaluated at the equilibrium point, i.e., with the values of the state variables chosen to make the right-hand sides of Eqs. 1–5 and 9–17 equal zero. The analytical expressions for the derivatives were checked by finite differencing.

Results

Lake Nesjøvatn—The Lake Nesjøvatn model is most stable when the maximum growth rate of the zooplankton is $\sim 1.6 \text{ d}^{-1}$ (Fig. 3A). The model is nevertheless stable and predicts steady-state biomasses and fluxes identical to those shown in Fig. 1 as long as the maximum growth rate of the zooplankton is within the range 0.67 to 4.7 d^{-1} .

Lake Kastoria—The Lake Kastoria model is most stable when $\rho_4 : \rho_{1L} = 38.7$ and f_2 and f_6 are 0.0026 and 0.20, respectively. Given the equilibrium concentrations of biomass in Table 2, $\rho_{1S} : \rho_2$ is constrained by Eq. 24 to equal 19.4. The equilibrium is stable for positive values of f_2 less than ~ 0.0031 (Fig. 3B) and for positive values of f_6 less than ~ 0.5 (Fig. 3C). The resilience of the system is, however, almost independent of f_6 for values of f_6 between roughly 0.05 and 0.4. The system is stable over a wide range of $\rho_4 : \rho_{1L}$ values, from ~ 6 to more than 500 (Fig. 3D).

Discussion

In their discussion of experiments related to the stability of plant communities in a lawn, Roxburgh and Wilson (2000*a,b*) commented, “In using community matrix theory to predict stability in the real world, four assumptions must be met: (1) equilibrium, (2) small perturbations, (3) instantaneous perturbations, and (4) spatial homogeneity” (Roxburgh and Wilson 2000*a*, p. 397). “Application of community matrix theory requires that the community is at equilibrium, or the definition of stability is meaningless. ... All natural communities violate the strict equilibrium assumption required by the theory, invalidating application to any community” (Roxburgh and Wilson 2000*b*, p. 413). “Difficulties in its practical application, and more importantly, the restrictive assumptions on which the theory is based, will limit its relevance to most natural systems. These results call into question the generality of a large volume of theoretical studies based on these methods” (Roxburgh and Wilson 2000*b*, p. 409).

Taken together, these comments certainly question the validity of my analysis of the Lake Nesjøvatn and Lake Kastoria food webs. Is community matrix theory really so irrelevant? Roxburgh and Wilson (2000*b*) estimated the elements of the community matrix for the plants in the Otago University Botany lawn by studying the interactions between 7 of the 23 vascular plant species recorded in the undisturbed lawn. The experiments involved two-way mixtures of the seven species. Thus, only 2 of the 23 species in the undisturbed lawn were included in any one of their two-way experiments. They concluded, “Eigenvalue analysis of the estimated community matrix predicted instability of the mixture, with a maximum eigenvalue $R(\lambda)_{\max} = 0.019$. This suggests that the Botany lawn is unstable” (Roxburgh and Wilson 2000*b*). This was a provocative conclusion, given that the lawn had “already persisted for 30 years” (Roxburgh and Wilson 2000*b*). They also carried out perturbation experiments. During the shade perturbation, “The vegetation was completely shaded for six weeks” (Roxburgh and Wilson 2000*a*, p.

413). In their herbicide perturbation, a herbicide was “applied in sufficient quantity to saturate the foliage of all species within the plot. The manufacturer advises that the herbicide remains active in the soil for only three to six weeks, and a greenhouse experiment confirmed this” (Roxburgh and Wilson 2000*a*, p. 413).

Since the elements of the community matrix are by definition partial derivatives evaluated with all state variables at their equilibrium values, it is not difficult to imagine how an experiment involving only 2 of 23 species (i.e., with 21 of the 23 state variables set equal to zero) might give a misleading estimate of an element in the community matrix. I am inclined to feel that evaluating the elements of the community matrix empirically for a community of many species is a difficult task, nor is it easy to carry out meaningful perturbation experiments that satisfy the small and instantaneous criteria.

The approach I have used here is very different. The use of an analytical model to describe the population dynamics of the state variables in the community eliminates the need to carry out small and instantaneous perturbation experiments. The requirement to carry out such experiments is, however, replaced by the requirement that the model give a realistic representation of the interactions between the state variables in the model. Furthermore, there must be some way to determine the parameters in the model and to estimate the equilibrium values of the state variables.

Given the Lake Nesjøvatn and Lake Kastoria data sets, I had to assume that the average values of the state variables were satisfactory estimates of the equilibrium values. In order to get a quantitative sense of the variability in the mean values, I examined the temporal (summer months) and spatial (six stations) variability of three components of the Lake Kastoria food web studied by Moustaka-Gouni et al. (2006), total phytoplankton, nanophytoplankton, and rotifers. Information on the temporal and spatial variability of the carbon biomass in these three groups may be found in figs. 5B, 5H, and 8B, respectively, of Moustaka-Gouni et al. (2006). I used the ratio of the standard error of the mean to the mean as a measure of variability. When averaged for the three groups, this statistic was 14% as a measure of temporal variability and 18% as a measure of spatial variability. I carried out a similar analysis for the time series of phytoplankton and bacterial biomass in Lake Nesjøvatn reported by Vadstein et al. (1989, figs. 3B and 3D, respectively). The ratio of the standard error of the mean to the mean was 22% and 15% for phytoplankton and bacterial carbon, respectively. Assuming that the biomass estimates made by Moustaka-Gouni et al. (2004) and Vadstein et al. (1989) are unbiased estimates of the equilibrium values of the state variables, this analysis suggests that my estimates of the equilibrium values of the state variables are probably accurate to $\pm 15\text{--}20\%$. I feel that this degree of uncertainty does not preclude application of community matrix theory to these two lakes.

Another general concern relates to the fact that I quantified all fluxes and biomasses in terms of carbon. This choice reflects a desire to examine the ideas of Lotka (1922) and Odum (1983), which are based on energetic arguments, and carbon is a useful proxy for energy. The choice also

Table 2. Parameter values for Lake Kastoria model during the time when the bacterial : autotrophic biomass ratio was less than 0.5 (Moustaka-Gouni et al. 2006, Table 1). All equations were evaluated at $T = 23.5^\circ\text{C}$.

Variable	Definition	Value	Units
A_{1S}	Maximum carbon uptake rate by small phytoplankton per unit small phytoplankton carbon	$\frac{1.2}{q_1} e^{0.0633(T-25)}$	d^{-1}
A_{1L}	Maximum carbon uptake rate by large phytoplankton per unit large phytoplankton carbon	$\frac{1.2}{q_{1L}} e^{0.0633(T-25)}$	d^{-1}
A_2	Maximum carbon uptake rate by heterotrophic bacteria per unit heterotrophic bacterial carbon	$\frac{3}{q_2} e^{0.1(T-25)}$	d^{-1}
A_3	Maximum carbon consumption by heterotrophic flagellates per unit heterotrophic flagellate carbon	$\frac{24}{q_3 \sqrt{10}} 2^{(T-20)/10}$	d^{-1}
A_4	Maximum carbon consumption by heterotrophic ciliates per unit heterotrophic ciliate carbon	$\frac{24}{10q_4} 2^{(T-20)/10}$	d^{-1}
A_5	Maximum carbon consumption by macrozooplankton per unit macrozooplankton carbon	$0.5e^{0.1(T-25)}$	d^{-1}
A_6	Maximum carbon consumption by carnivore per unit carnivore carbon	$0.5e^{0.1(T-25)}$	d^{-1}
f_{1S}	Small phytoplankton carbon uptake as a fraction of A_{1S} due to nutrient and/or light limitation	$\frac{\rho_{1S} q_2 A_2 f_2}{\rho_2 q_{1S} A_{1S}}$	dimensionless
f_{1L}	Large phytoplankton carbon uptake as a fraction of A_{1L} due to nutrient and/or light limitation	$\frac{\rho_{1L} q_4 A_4 f_4}{\rho_4 q_{1L} A_{1L}}$	dimensionless
f_2	Heterotrophic bacterial carbon uptake as a fraction of A_2 due to substrate limitation	0.0005–0.0032	dimensionless
f_3	Heterotrophic flagellate carbon uptake as a fraction of A_3 due to prey limitation	$\left(X_2 + \frac{\rho_{1S}}{\rho_2} X_{1S} \right) \frac{A_2 f_2 q_2}{A_3 X_3} = 0.22$	dimensionless
f_4	Ciliate carbon uptake as a fraction of A_4 due to prey limitation	$\frac{q_3 A_3 f_3 X_3}{A_4 X_4} = 0.0076$	dimensionless
f_5	Macrozooplankton carbon uptake as a fraction of A_5 due to prey limitation	$\left(X_4 + \frac{\rho_{1L}}{\rho_4} X_{1L} \right) \frac{A_4 f_4 q_4}{A_5 X_5} = 0.15$	dimensionless
f_6	Carnivore carbon uptake as a fraction of A_6 due to prey limitation	0.04–0.7	dimensionless
M	Mortality rate of carnivores	$q_6 A_6 f_6$	d^{-1}
q_{1S}	Fraction of fixed carbon converted to living biomass by small phytoplankton	0.7	dimensionless
q_{1L}	Fraction of fixed carbon converted to living biomass by large phytoplankton	0.7	dimensionless
q_2	Gross growth efficiency of heterotrophic bacteria	$0.374 - 0.0104T$	dimensionless
q_3	Gross growth efficiency of heterotrophic flagellates	5/18	dimensionless
q_4	Gross growth efficiency of zooplankton	43/101	dimensionless
$\rho_{1S} : \rho_2$	Grazing preference of flagellates for small phytoplankton relative to heterotrophic bacteria	$\frac{X_2}{X_{1S}} \left(\frac{1 - q_2(s_3 - q_3 s_4)}{q_2(s_3 + q_3 s_4 + (s_{1S}/q_{1S}))} \right) = 19.4$	dimensionless
$\rho_4 : \rho_{1L}$	Grazing preference of macrozooplankton for ciliates relative to large phytoplankton	6–500	dimensionless
r_2	Fraction of consumed carbon respired by bacteria	$1 - q_2$	dimensionless
r_3	Fraction of consumed carbon respired by flagellates	0.3	dimensionless
r_4	Fraction of consumed carbon respired by ciliates	0.3	dimensionless
r_5	Fraction of consumed carbon respired by macrozooplankton	0.3	dimensionless
r_6	Fraction of consumed carbon respired by carnivore	0.5	dimensionless
s_{1S}	Fraction of fixed carbon excreted by small phytoplankton	$1 - q_{1S}$	dimensionless
s_{1L}	Fraction of fixed carbon excreted by large phytoplankton	$1 - q_{1L}$	dimensionless
s_3	Fraction of consumed carbon excreted by flagellates	$1 - q_3 - r_3$	dimensionless
s_4	Fraction of consumed carbon excreted by ciliates	$1 - q_4 - r_4$	dimensionless
s_5	Fraction of consumed carbon excreted by macrozooplankton	$1 - q_5 - r_5$	dimensionless
s_6	Fraction of consumed carbon excreted by carnivores	$1 - q_6 - r_6$	dimensionless

Table 2. Continued.

Variable	Definition	Value	Units
X_{1S}	Small phytoplankton carbon	123	mg C m ⁻³
X_{1L}	Large phytoplankton carbon	2,315	mg C m ⁻³
X_2	Heterotrophic bacterial carbon	297	mg C m ⁻³
X_3	Heterotrophic flagellate carbon	3	mg C m ⁻³
X_4	Ciliate carbon	95	mg C m ⁻³
X_5	Macrozooplankton carbon	54	mg C m ⁻³
X_6	Carnivore carbon	6–500	mg C m ⁻³
X_7	Labile dissolved organic carbon	1–1,000	mg C m ⁻³
DX_8	Loss rate of particulate detrital carbon to sinking	$s_{1L}A_{1L}f_{1L}X_{1L} + s_5A_5f_5X_5 + s_6A_6f_6X_6 + MX_6$	mg C m ⁻³ d ⁻¹

reflects the databases in Moustaka-Gouni et al. (2006) and Vadstein et al. (1989). Vadstein et al. (1988), however, argued that the phytoplankton and possibly bacteria in Lake Nesjøvatn were phosphorus (P) limited during most of the ice-free period. This raises the question of whether other components of the Lake Nesjøvatn food web may have been P limited and, by extension, whether nutrient limitation in general might invalidate the calculation of community matrix elements using carbon as a metric.

To address this concern, I developed an alternative model of the Lake Nesjøvatn food web using phosphorus as the metric of biomass (Fig. 4). X_0 is here the concentration of phosphate. In accord with the results of Vadstein et al. (1988), I assumed that the P:C ratios in the phytoplankton and heterotrophic bacteria were 0.0051 and 0.089 by weight, respectively, and that the heterotrophic bacteria took up four times as much phosphate as the

phytoplankton. I assumed that the P:C ratio in the flagellates followed Redfield (0.024 by weight). Organic matter exiting a box in the model was assumed to have the same P:C ratio as the organic matter in the source box. The P:C ratios in the zooplankton (X_4) and dissolved organic matter (X_5) were constrained by mass balance considerations and the requirement that the growth rates of the functional groups be independent of whether carbon or phosphorus was used as the metric of biomass. To ensure steady state, I required that the external loading rate (L) of phosphate equal the loss of particulate P to sinking. The forms of the equations describing the dynamics of the phytoplankton, heterotrophic bacteria, flagellates, and zooplankton (Eqs. 1, 2, 3, and 4) are unchanged in the phosphorus representation. The equations describing the dynamics of phosphate and dissolved organic phosphorus (X_0 and X_5) in the phosphorus-limited model are

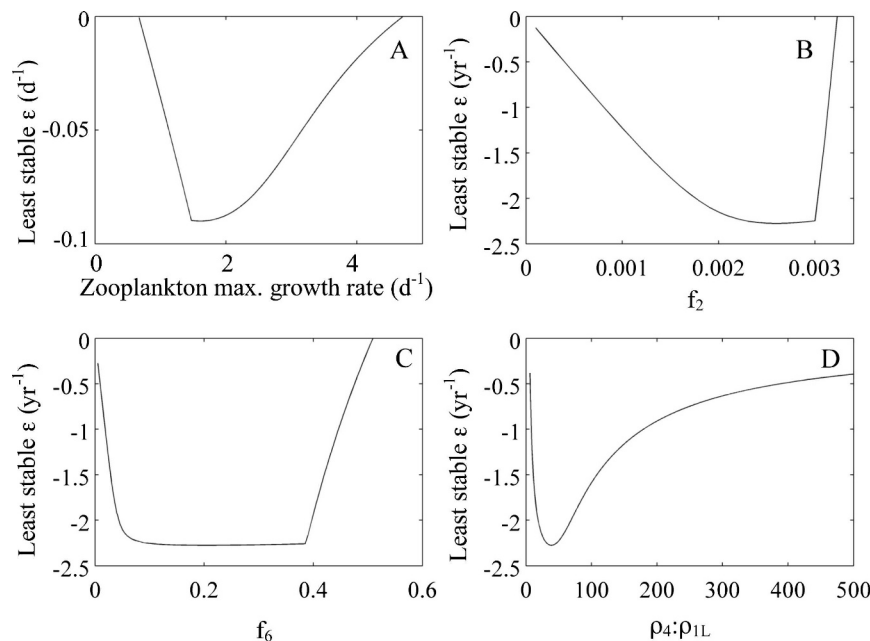


Fig. 3. Least-stable eigenvalue of community matrix for (A) Lake Nesjøvatn food web as function of the maximum growth rate of the zooplankton, and Lake Kastoria food web as a function of (B) the relative growth rate of the heterotrophic bacteria, (C) the relative growth rate of the carnivores, and (D) the ratio $\rho_4 : \rho_{1L}$. Note that in panel A, the eigenvalue has units of d^{-1} , while in panels B–D, the units are yr^{-1} .

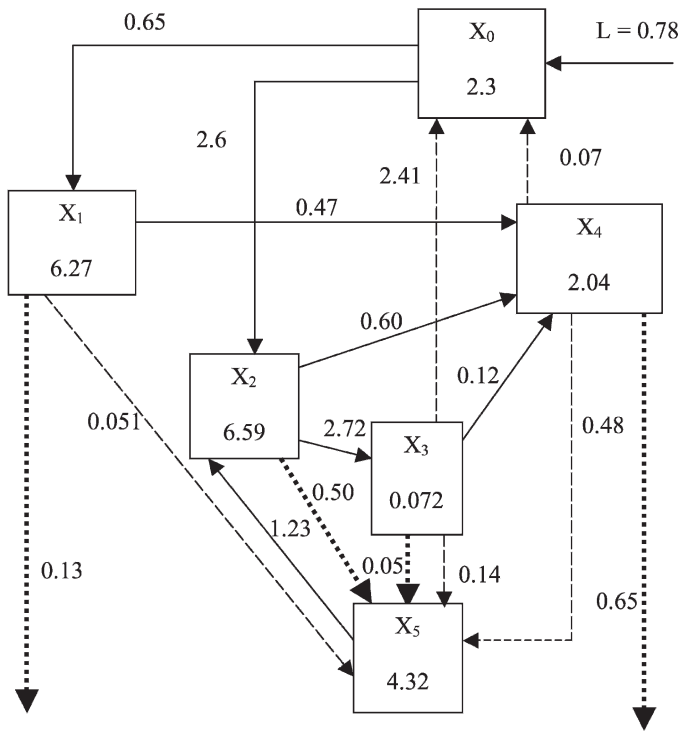


Fig. 4. Phosphorus-limited Lake Nesjøvatn food web. Numbers in boxes indicate biomasses (mg P m^{-3}). Arrows indicate fluxes ($\text{mg P m}^{-3} \text{d}^{-1}$). Solid arrows are grazing or uptake. Dotted arrows are death or sinking. Dashed arrows are excretion.

as follows:

$$\frac{dX_0}{dt} = L + r_3 A_3 f_3 X_3 + r_4 A_4 f_4 X_4 - A_1 f_1 X_1 - A_2 f_2 X_2 \frac{\rho_0 X_0}{\rho_0 X_0 + \rho_5 X_5} \quad (31)$$

$$\frac{dX_5}{dt} = s_1 A_1 f_1 X_1 + s_3 A_3 f_3 X_3 + s_4 A_4 f_4 X_4 - A_2 f_2 X_2 \frac{\rho_5 X_5}{\rho_0 X_0 + \rho_5 X_5} + M_2 X_2 + M_3 X_3 \quad (32)$$

The function f_1 is defined by the equation

$$f_1 = 1 - \frac{P_1}{X_0} \quad (33)$$

Here P_1 is the concentration of phosphate below which phytoplankton uptake ceases. I assumed that $P_1 = 2 \text{ mg m}^{-3}$, which is consistent with the low phosphate concentrations ($<5 \text{ mg m}^{-3}$) reported by Vadstein et al. (1988) during the ice-free period. The heterotrophic bacteria obtain phosphorus from two sources, phosphate (X_0) and dissolved organic phosphorus (X_5), and accordingly

$$f_2 = 1 - \frac{P_2}{X_0 + X_5} \quad (34)$$

The model results indicate that $P_2 = 3.5 \text{ mg m}^{-3}$. The

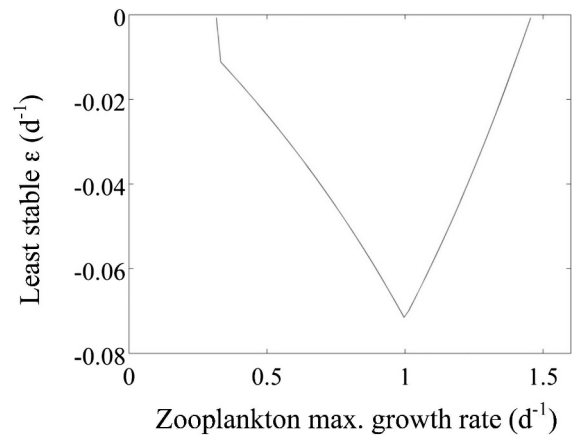


Fig. 5. Least-stable eigenvalue of community matrix for P-limited model of Lake Nesjøvatn food web as function of the maximum growth rate of the zooplankton.

parameters r_3 and r_4 represent the fraction of consumed phosphorus that is respired by the flagellates and zooplankton, respectively, and must satisfy the mass-balance equations $r_3 + s_3 + q_3 = 1$ and $r_4 + s_4 + q_4 = 1$. The parameters ρ_0 and ρ_5 reflect the preference of the heterotrophic bacteria for phosphate or dissolved organic phosphorus (DOP) as a phosphorus source.

Figure 5 is the analog of Fig. 3A for the phosphate-limited model. The model is stable as long as the maximum growth rate of the zooplankton lies between 0.32 and 1.45 d^{-1} . Thus, both the carbon-limited and phosphorus-limited food webs are stable as long as the maximum growth rate of the zooplankton lies in the range 0.67 to 1.45 d^{-1} .

Lake Nesjøvatn—The fact that all biomasses and fluxes are quantified in fig. 6 of Vadstein et al. (1989) imposes many constraints on the values of parameters in the model food web (Fig. 1). Although the maximum uptake or grazing rates of the functional groups cannot be determined from the biomass and flux information, lower bounds can clearly be set. For example, the maximum grazing rate of the flagellates must be at least $18/3 = 6 \text{ d}^{-1}$. Information provided by Fenchel and Finlay (1983) indicates that at 20°C, small flagellates can grow as rapidly as 7.6 d^{-1} . Assuming a Q_{10} of 2 (Fenchel and Finlay 1983), this translates to a maximum growth rate of 5.75 d^{-1} at 16°C (Table 1). Assuming a gross growth efficiency of 7/18 (Fig. 1), the implied grazing rate is 14.8 d^{-1} . Hence, $f_3 = 6/14.8 = 0.405$.

The maximum growth rate of the zooplankton is difficult to specify, since identified species account for only 35% and 41% of the grazing on phytoplankton and bacteria, respectively, in the euphotic zone (Vadstein et al. 1989, their Table 3). *Daphnia pulex*, which accounted for about 10% of the documented grazing on phytoplankton, has a growth rate of only 0.236 d^{-1} at 25°C (Stark et al. 2004). Assuming a Q_{10} of 2, its growth rate at 16°C would be only 0.126 d^{-1} . The observed growth rate of the zooplankton ($A_4 f_4 q_4$) is $43/136 = 0.32 \text{ d}^{-1}$. Clearly, organisms capable of growing substantially faster than *D. pulex* must have made

substantial contributions to the zooplankton in Lake Nesjøvatn. In a typical microbial loop, ciliates account for much of the grazing on flagellates (Pomeroy 1974; Azam et al. 1983), and based on growth rate data summarized by Fenchel and Finlay (1983) and assuming a Q_{10} of 2 (Laws et al. 2000), the maximum growth rate of ciliates at 16°C could easily lie within the range 0.67 to 1.45 d⁻¹, i.e., where stability of the food web is implied by this analysis.

Lake Kastoria—One striking feature of the Lake Kastoria results is the low growth rates of the large phytoplankton and heterotrophic bacteria, 0.0006 d⁻¹ and 0.0067 d⁻¹, respectively. Both functional groups appear to have been in virtually stationary phase. The selectivity of the predators indicates that the macrozooplankton much preferred ciliates to large phytoplankton ($\rho_4 : \rho_{1L} = 38.7$) and that the flagellates much preferred small phytoplankton to heterotrophic bacteria ($\rho_{1S} : \rho_2 = 19.4$). The rejection of toxic filamentous and colonial cyanobacteria by herbivorous predators is well established (e.g., Edmondson and Litt 1982) and therefore comes as no surprise. Within the context of the steady-state model, the preference of the macrozooplankton for ciliates is required to ensure grazing control of the ciliate population. If the macrozooplankton grazed indiscriminately, most of the prey they consumed would be large phytoplankton, and there would be inadequate top-down control of the ciliate population.

The lack of predator control on the heterotrophic bacterial population in Lake Kastoria is probably due to several factors, one of which is certainly the large ratio (99) of heterotrophic bacterial carbon to heterotrophic nanoflagellate carbon ($X_2 : X_3$). The unusually large size of the heterotrophic bacterial community relative to the biomass of heterotrophic nanoflagellates during the summer of 1999 appears to reflect events that occurred earlier in the year. The biomass of large phytoplankton declined by roughly a factor of 50 in response to flushing of the lake at an average rate of $\sim 0.1\%$ d⁻¹ during roughly a six-week period in March and April 1999 (see fig. 2 in Moustaka-Gouni et al. 2006). A fiftyfold decline in biomass over a period of 42 d implies a loss rate of 0.093 d⁻¹, 93 times the average flushing rate. The phytoplankton population just prior to the initiation of flushing was completely dominated by the filamentous nitrogen-fixing cyanobacterium *Limnothrix redekei*, which is known to be sensitive to flushing (Reynolds et al. 2002). The population of *L. redekei* appears to have been uniformly distributed throughout the water column (see fig. 5D in Moustaka-Gouni et al. 2006). The implication is that the flushing process triggered a net loss of *L. redekei* roughly 92 times the loss associated with physical flushing. Roughly order-of-magnitude increases in ammonium and total dissolved phosphorus concentrations coincident with the decrease in *L. redekei* and a subsequent order-of-magnitude increase in the concentration of heterotrophic bacterial carbon (see figs. 4C, 4F, and 7B in Moustaka-Gouni et al. 2006) suggest that flushing of the lake triggered a massive die-off of *L. redekei*, the demise of which triggered a tenfold increase in

the concentration of heterotrophic bacteria. This set the stage for the blooms of toxic cyanobacteria that occurred during the summer and the unusual distribution of biomass within the microbial loop.

The minimal grazing control of heterotrophic bacteria by heterotrophic flagellates also reflects the distinct preference of the heterotrophic flagellate community for small phytoplankton versus heterotrophic bacteria as a food source. This preference is probably due to the larger size of the nanophytoplankton (2–20 μm longest dimension). The average carbon content of the heterotrophic bacteria, 50 fg cell⁻¹ (see fig. 7B in Moustaka-Gouni et al. 2006), and the assumed conversion factor of 120 fg μm^{-3} are consistent with a spherical cell with a diameter of 0.93 μm . Stability of the steady state in fact requires that the heterotrophic flagellates graze preferentially on small phytoplankton. If they grazed indiscriminately, most of the prey they consumed would be heterotrophic bacteria, and there would be inadequate top-down control of the small phytoplankton.

Synthesis

Although there are noteworthy differences in the Lake Nesjøvatn and Lake Kastoria food webs, several important similarities emerge from this analysis. First, the zooplankton in both cases showed a distinct inclination toward carnivory versus herbivory, the result being high concentrations of autotrophic microplankton carbon, 1.2 g m⁻³ in the case of Lake Nesjøvatn and 2.3 g m⁻³ in the case of Lake Kastoria. Second, there is a suggestion that the flagellates in both lakes showed a distinct preference for small phytoplankton versus heterotrophic bacteria as a food source. This is apparent from the low biomass of small phytoplankton in Lake Kastoria, the absence (or at least absence of any mention) of small phytoplankton in Lake Nesjøvatn, and the $\rho_{1S} : \rho_2$ ratio of 19.4 for the flagellates in Lake Kastoria. Third, the ratios of phytoplankton carbon to heterotrophic bacterial carbon in the two lakes were comparable, 16.6 and 8.2 in the cases of Lake Nesjøvatn and Lake Kastoria, respectively. In both cases, the heterotrophic bacterial community responded positively to the collapse of spring phytoplankton blooms, in the case of Lake Nesjøvatn involving *M. aeruginosa* (see fig. 3 in Vadstein et al. 1989) and in the case of Lake Kastoria, *L. redekei* (vide supra). Fourth, relative growth rates, i.e., average growth rates expressed as a fraction of maximum growth rates, were in all cases less than 0.5. This fact and the existence of feeding thresholds lend stability to the model food webs in the two lakes (Steele 1974). Bottom-up control vanishes as relative growth rates approach 1.0.

One very obvious difference between the two food webs was the effect of grazing on the populations of phytoplankton and heterotrophic bacteria. In the case of Lake Nesjøvatn, “Grazing was an important removal process for both groups of organisms” (Vadstein et al. 1989, p. 847). A balance between growth and grazing losses requires that the relative growth rate of the heterotrophic bacteria in Lake Nesjøvatn be 0.48 d⁻¹, the largest relative growth rate of any functional group, and 75% of the primary production

in the lake was removed by grazing (Vadstein et al. 1989, p. 852). A balance between photosynthesis and grazing requires that the phytoplankton in Lake Nesjøvatn and the small phytoplankton in Lake Kastoria grow at comparable relative rates, 0.14 and 0.12, respectively, but as noted, the heterotrophic bacteria and large phytoplankton in Lake Kastoria were in virtually stationary phase. The difference in grazing on the phytoplankton in the two lakes appears to reflect difference in the species composition of their autotrophic communities. The large phytoplankton community in Lake Kastoria was dominated during the summer months by toxic filamentous and colonial cyanobacteria, which were evidently ignored or avoided by potential grazers. The summer phytoplankton community in Lake Nesjøvatn consisted mainly of unicellular cryptophytes, in particular *Cryptomonas erosa*, *C. marssonii*, and *Rhodomonas lacustris* (Vadstein et al. 1989), and these accounted for more than 90% of the carbon consumed by the zooplankton in the lake. As noted, the fact that grazing by flagellates had minimal effect on the heterotrophic bacterial community in Lake Kastoria probably reflects the following factors: (1) the large size of the heterotrophic bacterial community due to the release of dissolved organic carbon associated with the flushing-induced die-off of a *L. redekei* bloom in March/April, and (2) the preference of the flagellates for nanophytoplankton as a food source.

One dramatic difference in the two food webs is their resilience to perturbations. The most stable configuration of the Lake Nesjøvatn food web is associated with a response time of $\sim 1/0.08 = 12.5$ d. The eigenvector corresponding to this response time is almost entirely (92%) a simultaneous perturbation to the concentrations of heterotrophic bacteria and labile DOC. The relatively sluggish response of the system to this perturbation reflects the fact that the heterotrophic bacteria are already growing at almost half their maximum rate and that the assumed concentration of labile DOC is more than three times the concentration of heterotrophic bacterial carbon. In the phosphorus-based model, the concentrations of heterotrophic bacteria and DOP are comparable, and the perturbation associated with the most sluggish response is a simultaneous change in the concentrations of phytoplankton, zooplankton, and heterotrophic bacteria. The response time of the Lake Kastoria food web is much longer, $1/2.26 = 0.44$ yr = 161 d. The perturbation (eigenvector) associated with this very long recovery time is a simultaneous change in the concentrations of the large phytoplankton and ciliates, both of which are grazed by the macrozooplankton. It is because of the sensitivity of the system to this perturbation that the most stable configuration of the system is virtually independent of the value assumed for the labile DOC. Given perturbations of the magnitude and frequency that are likely to occur in temperate lakes, it seems fair to say that the Lake Kastoria food web lacks adequate resilience to be considered stable sensu May (1974). The relative constancy of the phytoplankton carbon (CV [coefficient of variation]= 40%) and heterotrophic bacterial carbon (CV = 17%) during the summer of 1999 in the lake might therefore be more

accurately described as a no-change condition rather than a dynamic equilibrium (Leitão et al. 2003).

With a little calculus, and using the models of the Lake Nesjøvatn and Lake Kastoria food webs, it is straightforward to show how the stability considerations of May (1974) and Steele (1974) constrain the implications of the energy flux ideas of Lotka (1922) and Odum (1983) in these systems. Maximizing the flux of energy through a food web would be consistent with very large concentrations of prey and predators and all functional groups turning over at maximum rates. Clearly, this is not what we see in the cases of the Lake Nesjøvatn and Lake Kastoria food webs, nor is it true in general, but why not?

To begin to understand why not, we consider the differential equation describing the rate of change of functional group X :

$$\frac{dX}{dt} = \mu X - fg \quad (35)$$

Here μ is the growth rate of X , and g is the rate at which X is grazed in the limit of large X . The dimensions of μ and g are inverse time and biomass per unit time, respectively. The function f is dimensionless and lies in the range 0 to 1. It expresses the extent to which the actual grazing rate, fg , is limited by the concentration of prey. In order to facilitate community matrix analysis, it is convenient to write Eq. 35 in the form

$$\frac{dX}{dt} = \left(\mu - \frac{fg}{X} \right) X \quad (36)$$

Differentiating the right-hand side of Eq. 36 with respect to X and evaluating the derivative at the equilibrium point (where $\mu = fg/X$) gives the diagonal element of the community matrix,

$$-X \frac{d}{dX} \left(\frac{fg}{X} \right) = g \left(\frac{f}{X} - \frac{df}{dX} \right) \quad (37)$$

which must be evaluated at the equilibrium value of X , X_{eq} . A necessary condition for the model food web to be qualitatively stable is that all diagonal elements of the community matrix be less than or equal to zero (May 1974, p. 71). This condition will be satisfied if $df/dX > f/X$, i.e., if the rate of change of f at X_{eq} is greater than the slope of a straight line drawn from the origin to the point (X_{eq}, f) .

In the model used here, $f = 1 - P/X$, where P is a constant, and the diagonal element of the community matrix becomes

$$\frac{g}{X_{eq}^2} \left(1 - \frac{2P}{X_{eq}} \right) = \frac{g}{X_{eq}^2} (2f_{eq} - 1) \quad (38)$$

where $f_{eq} = 1 - P/X_{eq}$ is the relative growth rate of the predator when the system is at equilibrium. The right-hand side of Eq. 38 will be negative (i.e., the model will be qualitatively stable) only if $f_{eq} \leq 0.5$. Furthermore, since the sum of the eigenvalues of the community matrix is equal to the sum of its diagonal elements, the real parts of the eigenvalues can all be negative only if the sum of the

diagonal elements is negative. This explains the tendency of the f values in Tables 1–2 to be less than 0.5.

One obvious implication of Eq. 37 is that the rate of change of the grazing rate per unit of prey biomass, fg/X , must be positive at the equilibrium point if the system is to be qualitatively stable. The grazing rate per unit prey biomass reaches a maximum when $d/dX(fg/X) = 0$. This is somewhat analogous to the maximum sustainable yield in a simple fisheries management model (Laws 1993). Regardless of the form of the mathematical expression describing the relationship between grazing rate per unit biomass and prey concentration, if $d/dX(fg/X) = 0$ for all state variables X , then all the prey in a food web are being grazed at the maximum rate, and all diagonal elements of the community matrix will be zero. Under these conditions, the system will at best be neutrally stable, but more likely unstable. Thus, the requirement for stability constrains grazing rates to be less than those associated with maximizing the rate of prey removal, a lesson evidenced by the collapse of numerous poorly regulated commercial fish stocks.

The conclusion is similar when a predator preys on multiple prey. Equation 3, for example, has the form

$$\frac{dX}{dt} = \left(\mu_X - g \times \left(1 - \frac{P}{X + Y + Z} \right) \frac{\rho_1}{\rho_1 X + \rho_2 Y + \rho_3 Z} \right) X \quad (39)$$

The partial derivative of the right-hand side of Eq. 39 is negative only if

$$f < \frac{1}{\left(1 + \frac{\rho_1(X + Y + Z)}{\rho_1 X + \rho_2 Y + \rho_3 Z} \right)} \quad (40)$$

where

$$f = 1 - \frac{P}{X + Y + Z} \quad (41)$$

If ρ_1 is greater than both ρ_2 and ρ_3 , this clearly implies that $f < 0.5$. Since $(\rho_1 X + \rho_2 Y + \rho_3 Z)/(X + Y + Z)$ is just a biomass-weighted average of the ρ values, if preferential grazing on X substantially reduces its biomass relative to Y and Z , Eq. 40 may require that f be very much smaller than 0.5 in order to ensure qualitative stability of the food web. Furthermore, in order for all three prey species (X , Y , and Z) to be in equilibrium, it will be necessary that

$$\rho_2 \rho_3 \mu_X = \rho_1 \rho_3 \mu_Y = \rho_1 \rho_2 \mu_Z \quad (42)$$

If ρ_1 is greater than both ρ_2 and ρ_3 , the growth rates of Y and Z will clearly be less than the growth rate of X , and we have just seen that the relative growth rate of X must be less than 0.5 if the equilibrium is to be qualitatively stable. Equation 20 is the counterpart of Eq. 42 in the case of the Lake Kastoria food web and requires that f_{1L} be only $\sim 7\%$ of f_4 . Finally, as noted by May (1974) and Pimm (1982), merely requiring that the real parts of all eigenvalues of the community matrix be negative may be insufficient to ensure stability in a randomly fluctuating environment. Instead,

“The eigenvalues must lie to the left of the imaginary axis by an amount measured roughly by the degree of environmental variance” (May 1974, p. 112). Since the diagonal elements of the community matrix are positively correlated with the relative growth rates of the functional groups in the food web (e.g., Eq. 38), the implication is that relative growth rates must be even smaller to ensure food-web stability in a stochastic environment.

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