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LETTER

Macrophyte refuges, prey behaviour and trophic interactions: consequences for lake water clarity

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Abstract

Macrophytes may enhance grazing on phytoplankton by providing a refuge for zooplankton against fish predation. Loss of macrophytes can trigger sudden degradation of water clarity (regime shift) in lakes. However, the presence of piscivores may drive planktivorous fish to take refuge amongst littoral macrophytes. To address the possibility of regime shifts, I here constructed an empirically based model that combined population dynamics of organisms with game theory for optimal habitat selection, taking into consideration the trophic structure, lake size and eutrophication. The model showed that macrophytes generally acted as a refuge for zooplankton, rather than for fish. The model predicted that regime shifts were more likely in small, shallow lakes and that the presence of macrophytes raised the possibility of regime shifts. The present study demonstrated that the fast dynamics of animal behaviour could lead to regime shifts, in connection with slower variables such as nutrient loading.

Keywords

Eutrophication, game theory, lake morphometry, macrophytes, regime shift, trophic structure.

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INTRODUCTION

There is increasing evidence of sudden, drastic changes in ecosystem states due to multiple, locally stable equilibria (Scheffer *et al.* 2001). These changes are often termed regime shifts. Lakes have provided good model systems for the study of regime shifts because of their island-like characteristics and suitability for whole-ecosystem experiments (Carpenter 2003). Regime shifts in lakes, the shift from a clear-water state with sparse phytoplankton to a turbid one with algal blooms, are suggested to occur in relation to macrophytes (Scheffer 1998). Macrophytes occupy the littoral zone of lakes, so macrophyte-related regime shifts should depend on the ratio of littoral to pelagic area. Macrophytes can reduce phosphorus recycling from lake sediments (hereafter the 'nutrient-control role'), and this role of macrophytes depends on lake morphometry and is related to regime shifts (Genkai-Kato & Carpenter 2005).

In addition to the nutrient-control role, it is suggested that macrophytes provide a refuge for zooplankton against fish predation (Burks *et al.* 2002). Thus a lake with abundant macrophytes accompanied by zooplankton maintains high grazing pressure on phytoplankton, so that a clear-water state is maintained (hereafter the 'grazing-control role'). Many existing models have contributed to the concepts and qualitative prediction of regime shifts (e.g. Scheffer 1999), but so far minimal models have not provided a clear quantitative prediction of the grazer-control role of macrophytes in regime shifts.

The actual ecological relationships between prey, predators and refuges in nature complicate the simple game theory outlined above. Macrophytes can also be viewed as a refuge for small planktivorous fish against large piscivorous fish (Persson 1991). The macrophyte habitat with abundant planktivorous fish may not be a safe place for zooplankton, which negates the grazing-control role. Therefore, a model that puts predators into behavioural predator–prey interactions competing for macrophyte refuge is needed (Lima 2002).

Hugie & Dill (1994) prepared a foundation for a game theoretic approach to habitat selection by predators and prey. However, this model has limitations in its application to evaluation of regime shifts in the case of nutrient enrichment in lakes. It assumed that lake productivity was held constant that predator and prey populations were at a constant density, and that the risk of predation in a habitat was independent of the predator density. van Baalen & Sabelis (1993) dealt with changing productivity and

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dynamically variable populations of predators and prey. As the resource (phytoplankton) dynamics was not involved in the model of van Baalen and Sabelis, it was still difficult to apply to the prediction of regime shifts in water clarity. Neither model included the higher trophic level (i.e. piscivores). Here I constructed a new model dealing with population dynamics of zooplankton and fish including game theory for habitat selection between littoral and pelagic habitats. Then I addressed the following two questions: 'which organism, zooplankton or planktivorous fish, uses macrophytes more intensively as a refuge against predation?' and can habitat selection drive a lake ecosystem to a regime shift, taking into consideration the trophic structure, lake size and eutrophication?'.

ANALYTICAL MODEL

The model in this paper consists of dynamics on two different time scales: behavioural dynamics of zooplankton and planktivorous fish and population dynamics of phytoplankton. The behavioural dynamics is faster than the population dynamics.

Zooplankton and planktivorous fish are free to choose their habitat, pelagic ($i = 1$) or littoral ($i = 2$) areas, to maximize their fitness. In the following, fish refer to planktivorous fish and piscivores refer to piscivorous fish. Macrophytes are present only in the littoral area where zooplankton and fish can utilize them as a refuge against predation by fish and piscivores respectively. The basic model is composed of the dynamics of the total zooplankton abundance (Z) and total fish abundance (F) in a lake (symbols and notation are explained in Table 1):

$$\frac{\mathrm{d}Z}{\mathrm{d}t} = \sum^{i} s_i \left[q_i \sigma m g(A) - b_i - \varphi_i(A) \frac{\beta_i F}{s_i} \right] \frac{\alpha_i Z}{s_i}, \tag{1a}$$

$$\frac{\mathrm{d}F}{\mathrm{d}t} = \sum^{i} s_i \left[e \varphi_i(A) \frac{\alpha_i Z}{s_i} - c_i - \psi_i(A) - d_i \frac{\beta_i F}{s_i} \right] \frac{\beta_i F}{s_i}. \tag{1b}$$

I used the areal ratio of littoral (with area s_2) to pelagic (s_1) habitat to represent a variety of lake sizes. I assumed that larger lakes have a lower s_2/s_1 ratio because they have more

Table 1 State variables, parameters and their units as used in the model

Symbol	Meaning	Units	Value	Source
State variables				
A	Algal density	mg m^{-3}		
F	Fish abundance	ind		
f	Fish density	ind m^{-3}		
Z	Zooplankton abundance	ind		
z	Zooplankton density	ind m^{-3}		
Functions				
g	Per capita grazing rate of zooplankton	mg ind^{-1} day^{-1}	eqn 6	
φ	Fish attack rate	m^3 ind^{-1} day^{-1}	0.5*, eqn 7a†	Persson *et al.* (1998)*
ψ	Piscivore attack rate	day^{-1}	0.03*, eqn 7b†	Luecke *et al.* (1992)*
Parameters				
a	Zooplankton filtering rate	m^3 ind^{-1} day^{-1}	4×10^{-5}	Grover (1995)
b	Zooplankton natural death rate	day^{-1}	0.1*†	Vanni *et al.* (1992)
c	Fish natural death rate	day^{-1}	0.006*†	Luecke *et al.* (1992)*†
d	Fish density-dependent death rate	m^3 ind^{-1} day^{-1}	0*, 0.0025†	Schriver *et al.* (1995)†
e	Conversion rate of zooplankton to fish	ind$_F$ ind$_Z^{-1}$	10^{-5}	Mylius *et al.* (2001)
h	Handling time for algae	ind days µg^{-1}	5.1	Grover (1995)
K	Algal-carrying capacity	mg m^{-3}	0.1–100	
k	Half-saturation constant for fish attack rate	mg m^{-3}	11	Canfield *et al.* (1984)
l	Half-saturation constant for piscivore attack rate	mg m^{-3}	31	Priyadarshana *et al.* (2001)
m	Conversion rate of chlorophyll to zooplankton	ind µg^{-1}	5	Muck & Lampert (1984) and Reynolds (1984)
q	Zooplankton impact coefficient	Dimensionless	1*, 0.5†	
r	Maximum growth rate of algae	day^{-1}	0.9	Vanni *et al.* (1992)
s	Habitat area	m^2	1–10 000*, 100†	
α	Distribution strategy of zooplankton	Dimensionless		Equation 4a
β	Distribution strategy of fish	Dimensionless		Equation 4b
σ	Assimilability of algae	Dimensionless	0.65	Vanni *et al.* (1992)

*†The value and source in the pelagic and littoral habitats respectively.

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pelagic area. Strictly speaking, the lake size included area, depth and other morphometric characteristics. The aim of this study was to elucidate the effect of macrophytes in terms of a horizontal refuge for zooplankton on regime shifts. A large lake usually has a deep layer (i.e. hypolimnion), which has the potential to be a vertical refuge for zooplankton (Iwasa 1982). Inclusion of depth will lead to a two-dimensional refuge model, which requires a substantial alteration of the present model. This alteration is beyond the primary scope of this study. I assumed here a water column with depth of a unit length (1 m) in the upper mixing layer (epilimnion). I dealt with only horizontal distribution and migration of zooplankton and fish within the water column.

The habitat selection by zooplankton and fish results in their distributions. Thus the zooplankton (or fish) abundances in the pelagic and littoral habitats are given by $\alpha_1 Z$ and $\alpha_2 Z$ (or $\beta_1 F$ and $\beta_2 F$), respectively, where $\alpha_1 + \alpha_2 = 1$ (or $\beta_1 + \beta_2 = 1$). For convenience, I also used a new notation z_i and f_i to express densities of zooplankton and fish, respectively, within the water column of 1-m deep (i.e. $z_i = \alpha_i Z/s_i$ and $f_i = \beta_i F/s_i$). In this study, I assumed that the distributions of zooplankton and fish reflect their behavioural habitat choice, rather than their genetic properties, and that no individual zooplankton or fish can gain by moving to another habitat (i.e. ideal free distribution, Fretwell & Lucas 1970). Under the assumption of the ideal free distribution, there is no difference in behavioural fitness measured as the per capita growth rate between habitats. Thus the optimal behaviors for zooplankton and fish are characterized by α_i* and β_i* such that

$$\left[q_i \sigma m g(A) - b_i - \frac{\varphi_i(A)\beta_i^* F}{s_i}\right]\alpha_i^* = C_Z \tag{2a}$$

$$\left[\frac{e\varphi_i(A)\alpha_i^* Z}{s_i} - c_i - \psi_i(A) - \frac{d_i \beta_i^* F}{s_i}\right]\beta_i^* = C_F, \tag{2b}$$

for all i, where C_Z and C_F are constants. At equilibrium ($Z = \bar{Z}$, $F = \bar{F}$), the right-hand sides of eqn 1 are zero (i.e. $\mathrm{d}\bar{Z}/\mathrm{d}t = 0$ and $\mathrm{d}\bar{F}/\mathrm{d}t = 0$). With the optimal distributions at equilibrium, $C_Z = C_F = 0$. Then, eqn 2 leads to the solution for the equilibrium abundances and optimal distributions for zooplankton and fish:

$$\bar{Z} = \frac{1}{e}\sum^{i}\left\{\frac{c_i + \psi_i(A)}{\varphi_i(A)} + \frac{[q_i \sigma m g(A) - b_i]d_i}{[\varphi_i(A)]^2}\right\}s_i, \tag{3a}$$

$$\bar{F} = \sum^{i}\frac{q_i \sigma m g(A) - b_i}{\varphi_i(A)}s_i \tag{3b}$$

and

$$\alpha_i^* = \left\{\frac{c_i + \psi_i(A)}{\varphi_i(A)} + \frac{[q_i \sigma m g(A) - b_i]d_i}{[\varphi_i(A)]^2}\right\}s_i \Big/ \sum^{j}\left\{\frac{c_j + \psi_j(A)}{\varphi_j(A)} + \frac{[q_j \sigma m g(A) - b_j]d_j}{[\varphi_j(A)]^2}\right\}s_j, \tag{4a}$$

$$\beta_i^* = \frac{q_i \sigma m g(A) - b_i}{\varphi_i(A)}s_i \Big/ \sum^{j}\frac{q_j \sigma m g(A) - b_j}{\varphi_j(A)}s_j. \tag{4b}$$

The solution given by eqns 3 and 4 are globally stable equilibrium if $\bar{Z}$ and $\bar{F}$ are positive (Appendix S1; see also Křivan & Sirot 2002 and Cressman *et al.* 2004 for population and distribution dynamics of systems with two species in a two-habitat environment).

EFFECT OF EUTROPHICATION ON WATER CLARITY

To see if refuge effect of macrophytes for zooplankton results in a drastic transition in water clarity with eutrophication, I additionally dealt with the dynamics of algal density (A) in the pelagic habitat. Here I assumed that the behavioural dynamics regarding habitat choice by zooplankton and fish are faster than the population dynamics of algae, and that the algal density depends on the dynamics of zooplankton (symbols and notation are explained in Table 1):

$$\frac{\mathrm{d}A}{\mathrm{d}t} = r\left(1 - \frac{A}{K}\right)A - \frac{q_1\alpha_1^*\bar{Z} + q_2\alpha_2^*\bar{Z}}{s_1}g(A). \tag{5}$$

The effect of nutrient loading and index for water clarity in the lake are represented by the algal-carrying capacity (K) and the algal density determined by eqn 5 respectively. The algal-carrying capacity and density are measured in chlorophyll units in the present study.

I assumed that zooplankton follow the optimal distribution in the daytime, while at night organisms are free from predation risk and, therefore, littoral zooplankton can graze on phytoplankton in the pelagic habitat (Timms & Moss 1984). This discrimination in grazing impact between pelagic and littoral zooplankton is reflected in q_i. Per capita grazing rate of zooplankton [g (mg ind^{-1} day^{-1})] is a saturating function of algal density (symbols and notation are explained in Table 1):

$$g(A) = \frac{aA}{1 + haA}. \tag{6}$$

EFFECTS OF MACROPHYTE AND/OR PISCIVORE PRESENCE ON WATER CLARITY

The dynamics of algal density in response to nutrient loading depends on the distributions of zooplankton and

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fish. Comparison of the algal density at equilibrium given by eqn 5 is carried out among four cases with regard to the presence or absence of macrophytes and/or piscivores: macrophytes and piscivores are present (MP), macrophytes only (M), piscivores only (P) and none of these is present (N). The effects of the presence of macrophytes and/or piscivores were incorporated into the model as follows.

I assumed that there is competition for light between phytoplankton and macrophytes. Phytoplankton are usually superior competitors for light because macrophytes grow on lake sediments. Thus it is likely that abundant phytoplankton reduce macrophyte abundance through reduction in light availability, resulting in increased predator success. In this model, attack rates of predators on prey in the littoral habitat increase with algal density, but in a saturating manner. Thus far, relationships between phytoplankton abundance, macrophyte abundance and refuge effects of macrophytes on predator attack rates have not been well documented to describe a relationship as an empirically based model. For this reason, the attack rates in the pelagic habitat (φ_1 and ψ_1) are set at constants assuming that the present model does not deal with dense algal blooms with chlorophyll concentration > 100 mg m^{-3}, which could cause decreases in attack rates of predators; on the other hand, the attack rates in the littoral habitat (φ_2 and ψ_2) are assumed to follow the relationship with algal density:

$$\varphi_2(A) = \frac{A}{A+k}\varphi_1, \tag{7a}$$

$$\psi_2(A) = \frac{A}{A+l}\psi_1, \tag{7b}$$

where k and l are half-saturation constants. The attack rates in the littoral habitat of fish and piscivores on zooplankton (φ_2) and fish (ψ_2), respectively, increase and asymptotically approach their pelagic values (φ_1 and ψ_1) with increasing algal density. I assume that when algal density is extremely low ($A \sim 0$) and therefore water is clear, macrophytes are too abundant for predators to attack their prey in the littoral habitat (i.e. $\varphi_2 = \psi_2 = 0$ when $A = 0$). In the absence of macrophytes, the attack rates in the littoral habitat are at the same level as the pelagic habitat (i.e. $\varphi_1 = \varphi_2$ and $\psi_1 = \psi_2$). The effect of piscivores is represented in the attack rate of piscivores on fish such that $\psi_i > 0$ in the presence of piscivores, and $\psi_1 = \psi_2 = 0$ in the absence of piscivores ($i = 1, 2$).

NUMERICAL ANALYSES

Parameterization

Here, I used empirically based, realistic parameter values to analyse optimal distributions of zooplankton and fish and made practical predictions on the possibility of regime shifts in lakes. Because the basic model, eqn 1, has quite a few parameters, it is difficult to show general dynamics of the model analytically using general parameter values. Instead, I conducted sensitivity analyses later to test the generality of the model results by varying parameter values in the model. The parameter values estimated from empirical studies and used for the model analyses are summarized in Table 1.

I used the averaged value of nanoplankton and cyanobacteria reported by Vanni *et al.* (1992) for the maximum growth rate of algae (r) to represent the phytoplankton community with mixed algal species. I followed the estimation by Grover (1995) for the parameters in eqn 6: grazing rate of zooplankton (a) and handling time for phytoplankton (b). I used $\sigma = 0.65$ for assimilability of algae for *Daphnia* (Vanni *et al.* 1992). The conversion rate of unit chlorophyll into one individual zooplankton, m, was calculated based on the carbon content of a 1.75-mm *Daphnia* (10.1 μg C) reported by Muck & Lampert (1984) and assuming the relationship 1 μg chl = 50 μg C (Reynolds 1984). The coefficient q_i is related to the grazing impact of zooplankton on phytoplankton inhabiting the pelagic habitat. I used $q_2 = 0.5$ for the relative impact of littoral zooplankton to pelagic zooplankton assuming that the littoral zooplankton graze on phytoplankton inhabiting the pelagic habitat only at night, while the pelagic zooplankton graze all day long ($q_1 = 1$). The natural death rate of zooplankton was set at $b_i = 0.1$ (Vanni *et al.* 1992).

The conversion rate of one individual zooplankton to one individual fish (e) was estimated at 10^{-5} according to Mylius *et al.* (2001). The attack rate of fish on zooplankton in the pelagic habitat ($\varphi_1 = 0.5$) was used based on the perch–zooplankton system in Persson *et al.* (1998). I substituted the lower value of fish mortality to piscivores reported by Luecke *et al.* (1992) for the natural death rate of fish ($c_i = 0.006$). I used the higher value of fish mortality to piscivores by Luecke *et al.* (1992) for the attack rate of piscivores on fish in the pelagic habitat ($\psi_1 = 0.03$). The value for d is one of the most difficult parameters to estimate. I assumed that the density-dependent death term ($d\beta^2F^2/s^2$) was comparable with the density-independent death term ($c\beta F/s$) at moderate fish density of catch per unit effort (CPUE) = 6 reported by Schriver *et al.* (1995). Given that the report was based on enclosures with 0.5-m depth, the density corresponded to 2.4 ind m^{-3}. Setting $\beta F/s = 2.4$, I obtained $d_2 = 0.0025$ in the littoral habitat; I set $d_1 = 0$ in the pelagic habitat.

Parameter estimation for k in eqn 7a was based on the report by Schriver *et al.* (1995) that the macrophyte effect as a refuge for zooplankton was effective when the percentage of the lake volume infested with macrophytes (PVI) exceeded 15–20%. Using the data on the relationship between chlorophyll a and PVI of Canfield *et al.* (1984),

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Table 2 Effects of changing one of model parameters on the relative increases or decreases in z_2^*/z_1^* and f_2^*/f_1^*, and the critical littoral : pelagic areal ratio (s_2/s_1) below which no regime shift occurred with any value of K

Parameter (default value)	Value	z_2^*/z_1^*†	f_2^*/f_1^*†	s_2/s_1 value for regime shift
$b_{1,2}$ (0.1)	0.01	++	++	0.26
	0.25	−−−	−−−	8.3
$c_{1,2}$ (0.006)	0.0012	−−	0	10.9
	0.03	+++	0	0.16
d_2 (0.0025)	0.0015	−	0	2.3
	0.015	+	0	3.6
k (11)	9.9	−	−	3.1
l (31)	19	+	0	2.6
	77	−	0	3.1
φ_1 (0.5)	0.1	+	0	< 0.01
	2.5	−	0	7.0
ψ_1 (0.03)	0.006	+++	0	4.3
	0.15	−−−	0	< 0.01

†The relative increases (+) or decreases (−) in z_2^*/z_1^* (or f_2^*/f_1^*) are expressed as the z_2^*/z_1^* (or f_2^*/f_1^*) at $A = 2.5$ (or $A = 4.5$ for fish) with the changed parameter values divided by its original z_2^*/z_1^* (or f_2^*/f_1^*) with the default parameter values. +++, > 2; ++, 1.2–2; +, 1–1.2; 0, 1 (no change); −, 0.8–1; −−, 0.5–0.8; −−−, < 0.5.

Table 2), the half-saturation constant k was assumed to be the chlorophyll a concentration averaged over the lakes with PVI > 15% (11 mg m^{-3}). To obtain the parameter value for l in eqn 7b, I referred to the compiled data on foraging behaviour of fish in artificial vegetation (Priyadarshana *et al.* 2001, Table 1). They reported that captures of zooplankton by fish and of fish by piscivores dropped significantly on average at macrophyte densities ≥1750 and 625 (stems m^{-2}) respectively. Because of a negative relationship between chlorophyll concentration and macrophyte density, half-saturation constants for predator attack rate in units of chlorophyll concentration (i.e. k and l) were assumed to be related to the critical macrophyte densities reported by Priyadarshana *et al.* (2001) (i.e. 1750 and 625 stems m^{-2}) such that $1/k : 1/l = 1750 : 625$ where $k = 11$.

In this study, the ratio of littoral area to pelagic area (s_2/s_1) was used to represent various lake sizes, based on the assumption that a larger lake had a smaller proportion of littoral habitat. I fixed the littoral area s_2 at a constant value (100 m^2), while the pelagic area s_1 was left variable to represent a variety of littoral : pelagic ratios.

Optimal distributions

The optimal distributions of zooplankton ($z_i^* = \alpha_i^* \bar{Z}/s_i$) and fish ($f_i^* = \beta_i^* \bar{F}/s_i$) in density are shown in Fig. 1.

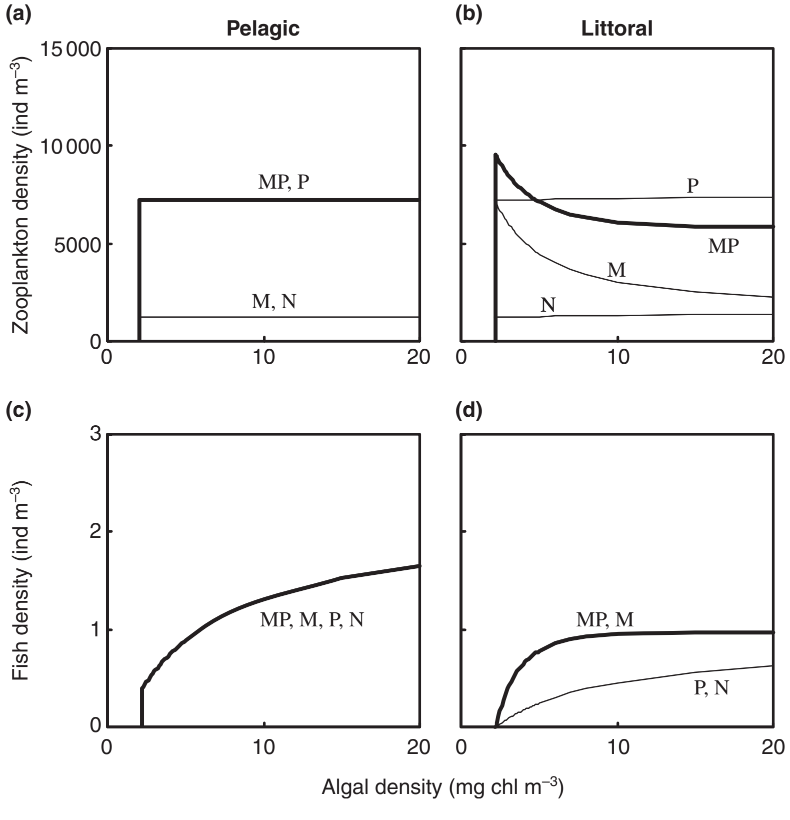

Figure 1 Equilibrium densities of zooplankton and fish under their optimal distributions plotted against algal density. Top (a, b) and bottom (c, d) panels represent zooplankton and fish abundances respectively. Left (a, c) and right (b, d) panels represent populations in the pelagic and littoral habitats respectively. MP represents a lake in which both macrophytes and piscivores are present; M, only macrophytes are present; P, only piscivores are present; N, macrophytes and piscivores are absent.

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Combining eqns 3 and 4, it is obvious that the densities of zooplankton (z_i^*) and fish (f_i^*) do not depend on habitat area, s_1 or s_2. Neither zooplankton nor fish could invade into the system with low algal densities ($A < 2$), because production was too low to sustain the populations. The pelagic zooplankton density differed depending only on the presence or absence of piscivores (Fig. 1a). The pelagic density shown in Fig. 1a was independent of algal density because of the assumption that there was no density-dependent death of fish in the pelagic habitat ($d_1 = 0$), although the density ($\alpha_1^* \bar{Z} / s_1$ given by eqns 3a and 4a) increases with algal density in general when d_1 takes a positive value. Positive d_1 might be the case for small lakes where the area of the pelagic habitat is limited. The littoral zooplankton density decreased with algal density in the presence of macrophytes (Fig. 1b). The density hardly varied with algal density in the absence of macrophytes, because of the constant attack rates of fish (φ_2) and piscivores (ψ_2) in the littoral habitat. Fish densities increased with algal density and saturated at high algal densities in both habitats (Fig. 1c,d). The pelagic fish density was independent of the presence or absence of macrophytes or piscivores; the littoral fish density differed depending on the presence or absence of macrophytes.

The relative density of zooplankton in the littoral habitat to that in the pelagic habitat decreased with algal density in the presence of macrophytes, whereas in the absence of macrophytes it took values close to 1 (Fig. 2a). The relative density of fish in the littoral habitat increased with algal density for $A < 4.5$ and then decreased in the presence of macrophytes, whereas it monotonically increased with algal density in the absence of macrophytes (Fig. 2b). The fish density in the littoral habitat was always lower than that in the pelagic habitat (i.e. $f_2^*/f_1^* < 1$). Here, I introduced an aggregation index

$$\theta_Z = \frac{z_2^*/z_1^*}{f_2^*/f_1^*} = \frac{z_2^*/f_2^*}{z_1^*/f_1^*}$$

to examine whether zooplankton or fish use the littoral habitat more intensively as a refuge against predation. This index is the relative density of littoral population to pelagic one with regard to zooplankton, compared to that with regard to fish. $\theta_Z > 1$ indicates that the relative use of the macrophyte refuge by zooplankton is more intensive than that by fish. In all cases, zooplankton tended to use macrophytes as a refuge more than fish (i.e. $\theta_Z > 1$, Fig. 2c). The cascading effect of piscivores resulted in lower utilization of the macrophyte refuge by zooplankton in the presence of piscivores (i.e. cases P and MP). In the presence of both macrophytes and piscivores (case MP), the relative zooplankton aggregation index took a minimum value at $A = 7$.

Water clarity

Numerical simulations were conducted to obtain the algal density at equilibrium and determine whether or not a regime shift occurred in a lake with a given littoral : pelagic ratio (s_2/s_1). The presence or absence of a regime shift depends on the number of equilibria of algal density. The simulations had a nested structure with regard to iterations of algal density value (A), carrying capacity (K) and pelagic area (s_1). The equilibrium algal density (i.e. $dA/dt = 0$) was calculated numerically by checking the arithmetic sign (i.e. +, > 0 or −, < 0) of the right-hand side of eqn 5, with A values increasing from $A = 0.1$ to a given carrying capacity K, for a given pelagic area (s_1). The increments of A were

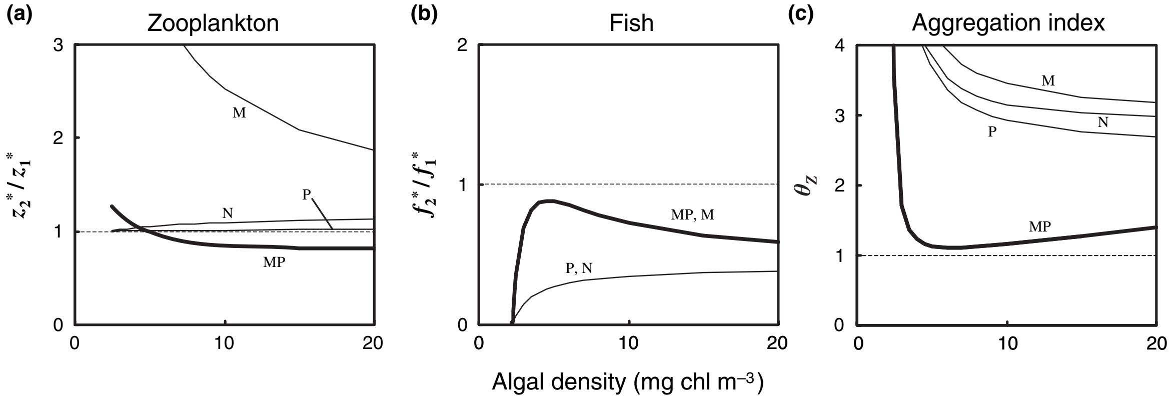

Figure 2 Relative density of littoral population to pelagic population under the condition of optimal distribution. (a) Zooplankton, (b) fish, (c) aggregation index $\theta_Z = \frac{z_2^*/z_1^*}{f_2^*/f_1^*} = \frac{z_2^*/f_2^*}{z_1^*/f_1^*}$ of zooplankton in the littoral habitat plotted against algal density. Letters next to curves are explained in Fig. 1. Broken lines at $\theta_Z = 1$ indicate even distribution, above which zooplankton aggregate in the littoral habitat more than fish.

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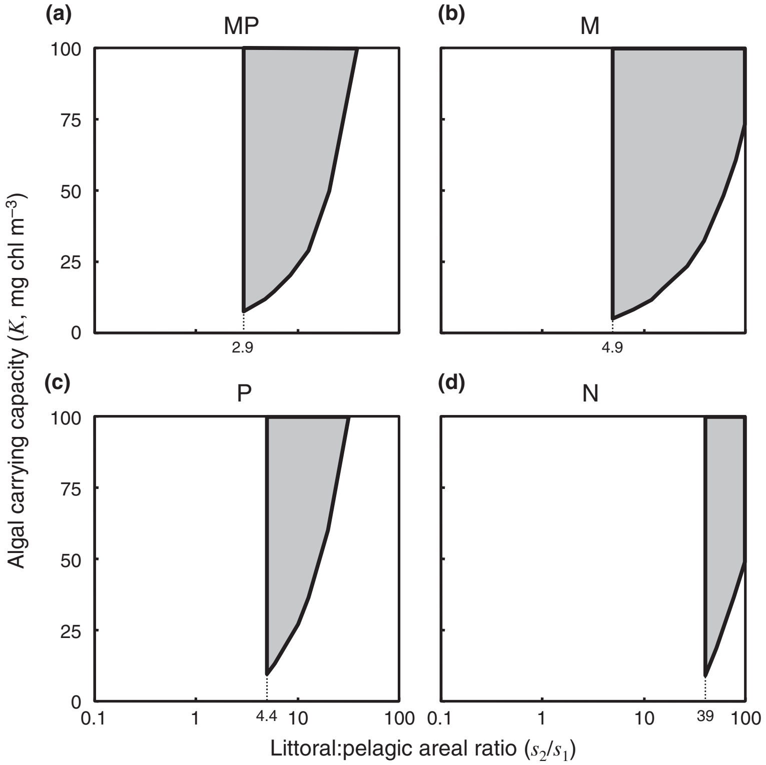

Figure 3 Regions where regime shifts were predicted to occur (*shaded area*) plotted in the phase space of algal-carrying capacity (K) and littoral : pelagic areal ratio (s_2/s_1). Higher s_2/s_1 ratios imply smaller lakes and vice versa. (a) Macrophytes and piscivores are present, (b) macrophytes only, (c) piscivores only, (d) none of these are present. The critical s_2/s_1 ratios below which no regime shift occurred with any value of K were also indicated on the horizontal axis.

conducted on the $\log_{10}$ scale such that the A value at $(i + 1)$th iteration was given by $A(i + 1) = 10^{\mathrm{LA}(i) + 0.005}$ where LA(i) is the power to produce the value A at ith iteration and I used 0.005 for the increments [i.e. $A(0) = 0.1$, $A(i) = 10^{\mathrm{LA}(i)}$, and $\mathrm{LA}(i + 1) = \mathrm{LA}(i) + 0.005$]. An equilibrium value of A was attained for each case in which the new A value changed the arithmetic sign of the right-hand side of eqn 5 (i.e. either $+ \rightarrow -$ or $- \rightarrow +$). This iteration was repeated as long as $A < K$. For a given K value, this iteration yielded either a single stable equilibrium (the arithmetic sign changed once), or three equilibria (the arithmetic sign changed three times). In the case of multiple equilibria, one equilibrium had low algal density, the other high algal density, with the unstable equilibrium in between. Regime shifts were thus related to instability of population dynamics of eqn 5. To model the effect of eutrophication in a lake with a given pelagic area (s_1), the K value was also increased from 0.1 to 1000 with the same protocol as A with regard to increments (0.02 was used for the increments on the $\log_{10}$ scale). I determined whether multiple equilibria were obtained in the entire iteration with regard to K. I defined that a regime shift did (or not) occur in the lake with a given s_1 when multiple equilibria were (or not) obtained. The s_1 value was also varied between 1 and 10 000 with increments of 0.01 on the $\log_{10}$ scale to model a variety of lake size in terms of the littoral : pelagic areal ratio.

Shown in Fig. 3 is the region where three equilibria were obtained and hence regime shifts were predicted to occur, plotted in the space of algal-carrying capacity (K) and littoral : pelagic areal ratio (s_2/s_1). In all cases, there was a critical s_2/s_1 ratio below which no regime shift occurred with any value of K. Above the critical littoral : pelagic ratio, there was a critical K value above which regime shifts occurred. A lower s_2/s_1 ratio corresponds to a lake with a wider pelagic area. The model revealed that the critical s_2/s_1 ratio was 2.9 in the presence of both macrophytes and piscivores (Fig. 3a). The critical littoral : pelagic ratio was much lower in the presence of macrophytes ($s_2/s_1 = 4.9$, Fig. 3b) or piscivores ($s_2/s_1 = 4.4$, Fig. 3c) than in their absence ($s_2/s_1 = 39$, Fig. 3d). Although lakes with higher littoral proportions were more vulnerable to regime shifts, the critical carrying capacity to cause a regime shift was considerably high ($K > 100$) in the presence of piscivores (Fig. 3a,c).

Sensitivity analyses of the model outcomes

Sensitivity analyses were performed by calculating the relative increase or decrease in z_2^*/z_1^* and f_2^*/f_1^* and by calculating the critical s_2/s_1 ratio below which no regime shift occurred with any value of K in the presence of macrophytes and piscivores, in response to changes in the value of each of parameters used in the model. I focused on the changes in density, not abundance, because abundance depends on habitat area and the relative use of habitats by organisms can be better represented by their density distributions (e.g. Figs 1 and 2). I selected the following parameters for sensitivity analyses: zooplankton natural death rate (b), fish natural death rate (c), density-dependent death rate of fish in the littoral habitat (d_2), half-saturation constants for fish attack rate (k) and piscivore attack rate (l), and attack rates of fish and piscivores on zooplankton and fish, respectively, in the pelagic habitat (φ_1 and ψ_1). The zooplankton natural death rate was varied between 0.01 and 0.25 according to Scavia *et al.* (1988) and Grover (1995). The variation range, 0.0015–0.015, for d_2 was used, corresponding to low fish abundance (CPUE = 1) and high fish abundance (CPUE = 10) based on Schriver *et al.* (1995). As Schriver *et al.* (1995) reported that macrophyte refuge was effective with PVI > 15–20%, I conducted sensitivity analysis with $k = 9.9$ being the chlorophyll *a* concentration averaged over the lakes with PVI > 20% listed in Canfield *et al.* (1984), Table 2). Priyadarshana *et al.* (2001) pointed out that the critical densities of macrophytes at which predation efficiency significantly dropped in a largemouth bass–bluegill combination were 250–1000 (stems m^{-2}) based on Savino & Stein (1989). These macrophyte densities with $k = 11$ corresponded to $19 \le l \le 77$ and this range was used for the sensitivity analysis for l. The φ_1 value was varied over a fivefold range based on Mylius *et al.* (2001), Fig. 3). I used the same range (i.e. fivefold) for the other parameters, c and ψ_1.

The zooplankton density was sensitive to all parameter changes, while the fish density was less sensitive to altered parameter values (Table 2). Among these parameter changes, the natural death rate of zooplankton (b) had remarkable influences on the relative use of the littoral habitat by zooplankton and fish. The natural death rate of fish (c) and piscivore attack rate on fish (ψ_1) had strong influences on the zooplankton density. The maximum relative increase value (2.36) in z_2^*/z_1^* was obtained when ψ_1 was 0.006. When the natural death rate of zooplankton (b) was set at the highest value 0.25, the zooplankton and fish populations could not invade the system with $A < 18$. The minimum algal density at which zooplankton and fish populations could invade increased with increasing b. The aggregation index θ_Z was not sensitive to many parameter changes in that zooplankton used macrophytes as a refuge more than fish (i.e. $\theta_Z > 1$). However, the index θ_Z as a function of A (as shown in Fig. 2c) could take its minimum value slightly lower than 1 when the parameter b or c was lowered or ψ_i was raised. Among the parameter changes, fish attack rate on zooplankton (φ_1) and piscivore attack rate on fish (ψ_1) had remarkable influences on the possibility of regime shifts (Table 2). A regime shift occurred at any s_2/s_1 ratio investigated when $\varphi_1 < 0.15$ or $\psi_1 > 0.13$.

I set the s_2 value at 100 m^2, while s_1 was varied in these simulations. As the grazing term of zooplankton on algae (second term on the right-hand side of eqn 5) can be rewritten as a function of s_2/s_1 using eqns 3a and 4a, the generality of the model outcome with regard to water clarity illustrated in Fig. 3 held with the assumption $s_2 = 100$ when the outcome was described in terms of the littoral : pelagic ratios.

DISCUSSION

In this article, I have reported on the study of the behavioural habitat selection by two species in a two-habitat environment, following an ideal free distribution approach (Fretwell & Lucas 1970). This approach has been recently developed in models dealing with behavioural dynamics and population dynamics simultaneously (Křivan 1997; Křivan & Sirot 2002; Cressman *et al.* 2004). The ideal free distribution has been demonstrated in animal populations (Milinski 1988) and its basic idea is useful for predictions of animal behaviors (Kacelnik *et al.* 1992).

My model examined, using game theory, the interaction between zooplankton and fish for macrophyte refuge in lakes with macrophytes and piscivores. Previous studies have repeatedly shown that productivity influenced the distribution of predators (fish), while the distribution of prey (zooplankton) was independent of productivity (e.g. Iwasa 1982; Hugie & Dill 1994). van Baalen & Sabelis (1993) showed that the distributions of predators and prey in a habitat increased with productivity of the habitat, but the predators displayed stronger aggregation in more productive habitat than the prey. My model including macrophytes and piscivores revealed more complex interaction effects of productivity and risk of predation on the distributions of zooplankton and fish. With macrophytes, zooplankton and fish densities changed with productivity, except for pelagic zooplankton, and their response patterns to productivity were various (Fig. 1). The zooplankton density in the pelagic habitat decreased, while the fish densities in both habitats increased, with productivity. The effect of piscivores was reflected indirectly in the zooplankton density, not directly in the fish density. In lakes, however, pelagic fish densities observed may be variable depending on the presence or absence of macrophytes or piscivores, because fish often form schools (Wootton 1998). The relative density of littoral population to pelagic population tended to decrease with productivity for both zooplankton and fish due to increased predation risk caused by deterioration of macrophyte refuge effect (Fig. 2a,b). Macrophytes generally acted as a refuge for zooplankton (Fig. 2c), which answers the first question raised in the *Introduction*.

Based on the results of game theory, I then addressed the possibility of top-down control of phytoplankton by zooplankton grazers mediated through the effect of macrophytes. Regime shifts in water clarity can occur through effects of macrophytes on nutrients (Genkai-Kato & Carpenter 2005) or zooplankton. The present study answered the second question using a model with empirically based parameters and showed that regime shifts through macrophyte-associated zooplankton were likely, but limited to small, shallow lakes (Fig. 3). Regime shifts were shown to be more likely in the presence of macrophytes (Fig. 3a vs. c, b vs. d). The presence of piscivores raised the critical carrying capacity (*K*) above which regime shifts occurred (Fig. 3a vs. b, c vs. d). Taken together, a regime shift was most likely to occur in macrophyte lakes without piscivores (Fig. 3b).

Regime shifts were more likely in small lakes with higher proportions of littoral area (i.e. higher s_2/s_1 ratios), but the critical carrying capacity (*K*) to cause regime shifts was also considerably high in such lakes (Fig. 3). For example, the critical *K* to cause a regime shift was > 100 μg chl L^{-1} in a lake with macrophytes and piscivores where $s_2/s_1 = 100$ (Fig. 3a). My model revealed that there were critical littoral : pelagic ratios below which no regime shift was caused by an enhancement of algal-carrying capacity (Fig. 3). Lakes of intermediate size (i.e. intermediate littoral : pelagic ratios slightly higher than the critical ratios) were susceptible to regime shifts at lower eutrophication levels of *K*. This implies that a regime shift can be readily induced by nutrient enrichment in such lakes where littoral : pelagic areal ratios are slightly higher than 2.9–4.9 depending on the presence or absence of macrophytes and/or piscivores.

My model dealt with various ratios of littoral to pelagic area to represent a variety of lake sizes. It has important limitations, especially in small, shallow lakes where the littoral proportion is high. The food resources of zooplankton and fish were assumed to come from the pelagic habitat in the present study, but recent works showed that fish communities are considerably subsidized by the littoral production (Vander Zanden & Vadeboncoeur 2002) and that littoral subsidy increases with decreasing trophic status (Vadeboncoeur *et al.* 2002, 2003). These works suggest that subsidy from lake surroundings to the whole ecosystem through the littoral habitat depends on lake size and eutrophication (Carpenter *et al.* 2005). Future research involving my model can include these subsidy effects, which would further elucidate the possibility of regime shifts and population dynamics more precisely in relation to lake size and nutrient loading from the watersheds. In addition, some lakes have sit-and-wait predators such as pike in the littoral habitat. Such predators, which were not addressed by this study, may alter the interactions.

Games for an optimal habitat between predators and prey are widely seen in ecology, not only in aquatic (e.g. zooplankton–juvenile sockeye salmon, Clark & Levy 1988; krill–penguins, Alonzo *et al.* 2003) but also in terrestrial systems (e.g. mountain lion–mule deer, Brown *et al.* 1999). Insights from the games have implications for ecosystem management such as conservation biology and resource control, as well as maintenance of water quality in lakes. My model demonstrated that the fast dynamics of animal behaviours could bring about regime shifts at an ecosystem scale, in connection with the slower variable of nutrient loading.

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REFERENCES

Alonzo, S.H., Switzer, P.V. & Mangel, M. (2003). Ecological games in space and time: the distribution and abundance of antarctic krill and penguins. *Ecology*, 84, 1598–1607.

van Baalen, M. & Sabelis, M.W. (1993). Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *Am. Nat.*, 142, 646–670.

Brown, J.S., Laundré, J.W. & Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.*, 80, 385–399.

Burks, R.L., Lodge, D.M., Jeppesen, E. & Lauridsen, T.L. (2002). Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshw. Biol.*, 47, 343–365.

Canfield, D.E. Jr, Shireman, J.V., Colle, D.E., Haller, W.T., Watkins, C.E. & Maceina, M.J. (1984). Prediction of chlorophyll a concentrations in Florida lakes: importance of aquatic macrophytes. *Can. J. Fish. Aquat. Sci.*, 41, 497–501.

Carpenter, S.R. (2003). *Regime Shifts in Lake Ecosystems: Pattern and Variation*. Volume 15 in the Excellence in Ecology Series. Ecology Institute, Oldendorf/Luhe.

Carpenter, S.R., Cole, J.J., Pace, M.L., Van de Bogert, M., Bade, D.L., Bastviken, D. *et al.* (2005). Ecosystem subsidies: terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. *Ecology*, 86, 2737–2750.

Clark, C.W. & Levy, D.A. (1988). Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.*, 131, 271–290.

Cressman, R., Křivan, V. & Garay, J. (2004). Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *Am. Nat.*, 164, 473–489.

Fretwell, S.D. & Lucas, H.L. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.*, 19, 16–36.

Genkai-Kato, M. & Carpenter, S.R. (2005). Eutrophication due to phosphorus recycling in relation to lake morphometry, temperature, and macrophytes. *Ecology*, 86, 210–219.

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Grover, J.P. (1995). Competition, herbivory, and enrichment: nutrient-based models for edible and inedible plants. *Am. Nat.*, 145, 746–774.

Hugie, D.M. & Dill, L.M. (1994). Fish and game: a game theoretic approach to habitat selection by predators and prey. *J. Fish Biol.*, 45, 151–169.

Iwasa, Y. (1982). Vertical migration of zooplankton: a game between predator and prey. *Am. Nat.*, 120, 171–180.

Kacelnik, A., Krebs, J.R. & Bernstein, C. (1992). The ideal free distribution and predator-prey populations. *Trends Ecol. Evol.*, 7, 50–55.

Křivan, V. (1997). Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. *Am. Nat.*, 149, 164–178.

Křivan, V. & Sirot, E. (2002). Habitat selection by two competing species in a two-habitat environment. *Am. Nat.*, 160, 214–234.

Lima, S.L. (2002). Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.*, 17, 70–75.

Luecke, C., Lunte, C.C., Wright, R.A., Robertson, D. & McLain, A.S. (1992). Impacts of variation in planktivorous fish on abundance of Daphnids: a simulation model of the Lake Mendota food web. In: *Food Web Management: A Case Study of Lake Mendota* (ed. Kitchell, J.F.). Springer-Verlag, New York, pp. 407–425.

Milinski, M. (1988). Games fish play: making decisions as a social forager. *Trends Ecol. Evol.*, 3, 325–330.

Muck, P. & Lampert, W. (1984). An experimental study on the importance of food conditions for the relative abundance of calanoid copepods and cladocerans. *Arch. Hydrobiol. Suppl.*, 66, 157–179.

Mylius, S., Klumpers, K., de Roos, A.M. & Persson, L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.*, 158, 259–276.

Persson, L. (1991). Behavioral response to predators reverses the outcome of competition between prey species. *Behav. Ecol. Sociobiol.*, 28, 101–105.

Persson, L., Leonardsson, K., de Roos, A.M., Gyllenberg, M. & Christensen, B. (1998). Ontogenetic scaling of foraging rate and the dynamics of a size-structured consumer–resource model. *Theor. Popul. Biol.*, 54, 270–293.

Priyadarshana, T., Asaeda, T. & Manatunge, J. (2001). Foraging behaviour of planktivorous fish in artificial vegetation: the effects on swimming and feeding. *Hydrobiologia*, 442, 231–239.

Reynolds, C.S. (1984). *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge.

Savino, J.F. & Stein, R.A. (1989). Behavioural interaction between fish predators and their prey: effects of plant density. *Anim. Behav.*, 37, 311–321.

Scavia, D., Land, G.A. & Kitchell, J.F. (1988). Dynamics of Lake Michigan plankton: a model evaluation of nutrient loading, competition, and predation. *Can. J. Fish. Aquat. Sci.*, 45, 165–177.

Scheffer, M. (1998). *Ecology of Shallow Lakes*. Chapman and Hall, New York.

Scheffer, M. (1999). The effect of aquatic vegetation on turbidity; how important are the filter feeders? *Hydrobiologia*, 408/409, 307–316.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Schriver, P., Bøgestrand, J., Jeppesen, E. & Søndergaard, M. (1995). Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshw. Biol.*, 33, 255–270.

Timms, R.M. & Moss, B. (1984). Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.*, 29, 472–486.

Vadeboncoeur, Y., Vander Zanden, M.J. & Lodge, D.M. (2002). Putting the lake back together: reintegrating benthic pathways into lake food web models. *BioScience*, 52, 44–54.

Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.-H., Christoffersen, K. & Lodge, D.M. (2003). From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnol. Oceanogr.*, 48, 1408–1418.

Vander Zanden, M.J. & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, 83, 2152–2161.

Vanni, M.J., Carpenter, S.R. & Luecke, C. (1992). A simulation model of the interactions among nutrients, phytoplankton, and zooplankton in Lake Mendota. In: *Food Web Management: A Case Study of Lake Mendota* (ed. Kitchell, J.F.). Springer-Verlag, New York, pp. 427–449.

Wootton, R.J. (1998). *Ecology of Teleost Fishes*. Kluwer Academic Publishers, Dordrecht.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Stability of the zooplankton–fish system given in eqn 1.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2006.01000.x

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