LETTER

Response of plankton to nutrients, planktivory and terrestrial organic matter: a model analysis of whole-lake experiments

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Abstract

Terrestrial organic matter can be assimilated by aquatic consumers but implications for biomass and production are unresolved. An ecosystem model was fit to estimate effects of phosphorus (P) load, planktivory, and supply rate of terrestrial particulate organic carbon (TPOC) on phytoplankton and zooplankton in five whole-lake experiments. Phytoplankton biomass increased with P load and planktivory and decreased with TPOC supply rate. Zooplankton biomass increased with P load and responded weakly to planktivory and TPOC supply rate. Zooplankton allochthony (proportion of carbon from terrestrial sources) decreased with P load and planktivory and increased with TPOC supply rate. Lakes with low allochthony (< 0.3) had wide ranges of phytoplankton and zooplankton biomass and production, depending on P load and planktivory. Lakes with high allochthony (> 0.3) had low biomass and production of both phytoplankton and zooplankton. In summary, terrestrial OC inhibits primary production and is a relatively low-quality food source for zooplankton.

INTRODUCTION

External inputs strongly affect ecosystems. Cross-boundary flows are routinely considered in perspectives of ecosystem (Weathers *et al*. 2013) and landscape (Turner *et al*. 2001) ecology. Meta-ecosystem research is now merging biogeochemical mass balances with concepts of metapopulation persistence and community food webs (Massol *et al*. 2011). External inputs of organic matter and nutrients interact with food web structure in complex ways (Leroux & Loreau 2008; Rosemond *et al*. 2015). Such interactions appear to be critical for understanding change in ecosystems.

Nutrient supply limits primary and secondary production but this limitation is modified by the food web structure and light availability in aquatic ecosystems. Phosphorus and nitrogen loading from external and internal sources are principal drivers that determine variation in productivity and biomass (Schindler 1977, 2012; Elser *et al*. 2009). However, trophic cascades arising from top predators also affect grazers and their capacity to control primary producers (Carpenter *et al*. 1985; Power 1992). In the case of lakes, predation may substantially diminish or eliminate large-bodied zooplankton – reducing grazing and thereby enhancing phytoplankton. Manipulations of planktivory and nutrient loading indicate that shifts in grazing pressure can result in substantially different levels of primary production and phytoplankton biomass at the same level of nutrient loading (Jeppesen *et al*. 1997; Carpenter *et al*. 2001).

The combined effects of nutrients and planktivory may be further influenced by terrestrial organic matter inputs to lakes. Dissolved terrestrial organic matter absorbs light, limiting irradiance at depth, and influencing photosynthesis (Carpenter *et al*. 1998). For example, in a survey of Norwegian lakes,

daily primary production per unit light input was negatively related to dissolved organic carbon (DOC) and positively related to total phosphorus (Thrane *et al*. 2014). This outcome reflects the importance of variation in light absorbing dissolved organic matter which in non-eutrophic lakes is largely of terrestrial origin (Wilkinson *et al*. 2013b). Terrestrial organic matter is also assimilated directly or indirectly by many aquatic consumers and a terrestrial signal is widespread in zooplankton, benthic invertebrates, and fishes (Cole 2013). The use of terrestrial organic matter, referred to as allochthony, is distinct from the use of organic matter arising from internal primary production (autochthony). This use of terrestrial organic matter potentially acts as a subsidy for consumers.

Recent research provides mixed results on the importance of terrestrial organic matter as a subsidy. In a large Canadian lake, fish growth in stream–lake deltas increased in relation with forest cover (Tanentzap *et al*. 2014). The higher growth was correlated with greater zooplankton and bacterial biomass, suggesting terrestrial organic matter acted as a subsidy. Kelly *et al*. (2013) measured zooplankton allochthony and production among lakes that varied in DOC. While zooplankton was 30–50% allochthonous, production of zooplankton was inversely related to light extinction which was primarily correlated with differences in concentrations of light-absorbing dissolved organic matter. Kelly *et al*. (2013) concluded that zooplankton is not subsidised (meaning production is not enhanced) by terrestrial organic matter, because of limitations on zooplankton habitat and food quality associated with allochthonous materials. Thus, while a variety of studies document that zooplankton biomass is derived in part from terrestrial organic matter (Karlsson *et al*. 2012; Cole 2013; Wilkinson *et al*. 2013a), the negative effects of terrestrial

organic matter on zooplankton production may offset any benefits of terrestrial material as a true subsidy to growth (Jones *et al.* 2012; Solomon *et al.* 2015).

Here we investigate the positive and negative effects of terrestrial organic matter on plankton production and biomass in relation to variations in other drivers – phosphorus and planktivory. Using data from five whole-ecosystem ^{13}C-additions in lakes of varying trophic status (described below), we calibrated a plankton dynamics model for each experiment. We then compared the equilibrium responses of the model along three gradients: phosphorus load, planktivory and terrestrial organic carbon supply. For the ensemble of lakes studied, we tested the importance of the three factors in determining phytoplankton and zooplankton production and biomass. We also analysed patterns of zooplankton allochthony relative to primary and secondary production across the three gradients.

METHODS

Study sites and field data

Data were obtained during five whole-lake isotope addition experiments in four small north temperate lakes (Carpenter *et al.* 2005; Pace *et al.* 2007; Coloso *et al.* 2008). The lakes are deep and strongly stratified during summer, with narrow littoral zones. Characteristics of the lakes encompass a range of conditions including clear water oligotrophic (Crampton Lake), moderately colored mesotrophic (Peter and Paul Lakes) and highly colored dystrophic Tuesday Lake.

Each whole-lake experiment took place for 14–16 weeks during summer stratification. The plankton dynamics model requires time series of zooplankton biomass, chlorophyll, DOC, primary production, and the allochthonous and autochthonous portions of particulate organic carbon (POC) and zooplankton (Table 1). Limnological profiles were measured weekly for 14 weeks of the summer stratified season. Primary production was computed from automated measurements of dissolved oxygen and temperature made every 5 min during the same 14-week period. Over the time frame of these experiments we assumed that changes in fish biomass were negligible

and therefore the model (below) addresses dynamics for phytoplankton, zooplankton and terrestrial particulate organic carbon (TPOC).

In order to label autochthonous primary production and follow that label through the food web, $H^{13}CO_3$ was added continuously to the epilimnia of the lakes. Zooplankton consume phytoplankton and TPOC, but only the phytoplankton are enriched in ^{13}C from the added $H^{13}CO_3$. In one of the experiments (Peter Lake, 2002) inorganic nitrogen and phosphorus were also added continuously to enhance primary production. Phosphorus loads to the study lakes were low (< 0.3 mg P m^{-2} day^{-1}) except in the case of the enrichment of Peter Lake in 2002 (Table 1). Several models were employed to calculate the allochthonous proportions of POC pools and zooplankton (ϕ_{POC} and ϕ_{Zoop} in Table 2). For consistency, we used allochthony estimates from multivariate autoregressions fitted by both Carpenter *et al.* (2005) (for Peter, Paul and Tuesday lakes in 2001 and 2002) and Pace *et al.* (2007) (for Crampton lake in 2005). Additional data in Table 1 provide context on lake conditions including mean mixed layer depth and mean concentrations of: POC, DOC, chlorophyll *a*, zooplankton biomass, and TPOC for the lake-years of ^{13}C addition.

Model

We built a dynamic model to study the responses of phytoplankton, TPOC and zooplankton to phosphorus load, planktivory, and supply of TPOC to zooplankton (Fig. 1). The four state variables of the model are biomasses (g C m^{-2}) of phytoplankton, detritus derived from phytoplankton, TPOC and zooplankton. Symbols and units are explained in Table 2. Phytoplankton (A) dynamics follow

$$\frac{dA}{dt} = NPP - s_A A - Q_{AZ} \tag{1}$$

NPP is net primary production. Losses are sinking and other non-predatory losses with rate coefficient s_A and grazing Q_{AZ} via a type II functional response (see below).

Dynamics of TPOC (T) available to zooplankton are determined by supply rate I_T, sedimentation mineralisation and

Table 1 Input values used in the models. The five lake experiments are identified in the columns by lake name and year. The parameter values are means for each lake and year. z_T is the depth of the thermocline. DOC, POC and Chl are the concentrations of dissolved and particulate organic C and chlorophyll-*a* in the epilimnion. Z is depth-integrated zooplankton biomass. The proportions of total POC and zooplankton of terrestrial origin are ϕ_{POC} and ϕ_{Zoop} respectively. TPOC is the concentration of POC of terrestrial origin in the epilimnion of each lake. Data for Peter, Paul and Tuesday lakes (2001 and 2002) are from Carpenter *et al.* 2005; Data for Crampton Lake (2005) are from Pace *et al.* 2007 and Coloso *et al.* 2008.

Parameter	Units	Paul 2001	Peter 2001	Peter 2002	Tuesday 2002	Crampton 2005
z_T	m	3.5	3.6	3.1	2.6	4.1
DOC	mg L^{-1}	3.64	4.51	5.80	8.40	3.66
POC	mg L^{-1}	0.43	0.41	1.82	0.92	0.60
Chl	μg L^{-1}	4.2	3.6	50.7	6.8	3.1
P Load	mg P m^{-2} day^{-1}	0.3	0.3	3.4	0.3	0.3
GPP	mg C m^{-2} day^{-1}	521	376	1254	515	472
Z	g C m^{-2}	0.53	1.06	2.06	0.13	0.9
ϕ_{POC}	fraction	0.38	0.47	0.1	0.57	0.12
ϕ_{Zoop}	fraction	0.36	0.41	0.08	0.49	0.08
TPOC	mg L^{-1}	0.16	0.19	0.18	0.52	0.07

Symbol	Explanation	Units	Equation
A	Phytoplankton biomass	g C m^{-2}	1
a	Attack rate for grazing	m^2 g^{-1} day^{-1}	10
C	Dissolved organic carbon (DOC) concentration	g C m^{-3}	5
C : Chl	Carbon to Chlorophyll ratio of phytoplankton	g : g	7
cF	Maximum planktivory	g C m^{-2} day^{-1}	19
Chl	Chlorophyll concentration	mg m^{-3}	6
D	Detritus derived from phytoplankton	g C m^{-2}	3
g_{AZ}	Growth efficiency from phytoplankton	dimensionless	4
g_{DZ}	Growth efficiency from phytoplankton detritus	dimensionless	4
GPP	Gross Primary Production	g C m^{-2} day^{-1}	5
g_{TZ}	Growth efficiency from TPOC	dimensionless	4
h	Handling time for grazing	d g g^{-1}	10
h_F	Half saturation coefficient for planktivory	g C m^{-2}	19
I_0	Surface irradiance	μE m^{-2} s^{-1}	5
I_T	Supply rate of TPOC to zooplankton	g C m^{-2} day^{-1}	2
k_0	Light extinction coefficient for pure water	m^{-1}	6
k_{DOC}	Light extinction by DOC	m^2 g^{-1}	6
k_{grow}	Effect of irradiance on growth	m^2 s μE^{-1}	8
k_{inhib}	Photo inhibition of growth	m^2 s μE^{-1}	8
k_P	Half-saturation for P effect on GPP	mg P m^{-2} day^{-1}	5
k_{phyto}	Light extinction by chlorophyll	m^2 mg^{-1}	6
L_P	Phosphorus input rate (load)	mg P m^{-2} day^{-1}	5
m_Z	Non-predatory mortality of zooplankton	day^{-1}	4
NPP	Net Primary Production	g C m^{-2} day^{-1}	1
p_A	Egestion coefficient of phytoplankton	dimensionless	3
p_D	Egestion coefficient of detritus	dimensionless	3
POC	Particulate organic carbon (POC) concentration	g m^{-3}	7
p_T	Egestion coefficient of TPOC	dimensionless	2
Q_{AZ}	Grazing of phytoplankton	g C m^{-2} day^{-1}	1
Q_{DZ}	Ingestion of phytoplankton detritus	g C m^{-2} day^{-1}	3
Q_{TZ}	Grazing of TPOC	g C m^{-2} day^{-1}	2
Q_{ZF}	Planktivory of zooplankton	g C m^{-2} day^{-1}	4
r	Maximum GPP coefficient	day^{-1}	5
s_A	Sinking coefficient of phytoplankton	day^{-1}	1
s_D	Sinking coefficient of detritus	day^{-1}	3
s_T	Sinking coefficient of TPOC	day^{-1}	2
T	Terrestrial particulate organic carbon (TPOC)	g C m^{-2}	2
Z	Zooplankton biomass	g C m^{-2}	4
z	Depth	m	6
z_T	Thermocline depth	m	8
γ	Function for irradiance effect on GPP	dimensionless	5
κ	Normalisation coefficient for γ	dimensionless	8
ϕ_{POC}	Allochthony of POC	proportion	7
ϕ_Z	Allochthony of zooplankton	proportion	16

washout with rate coefficient s_T, and consumption by zooplankton:

$$\frac{dT}{dt} = I_T - s_T T - Q_{TZ} + p_T Q_{TZ} \tag{2}$$

The last term is egestion of TPOC that was consumed by zooplankton. The egestion coefficient is p_T ($0 \leq p_T < 1$). Note that supply rate of TPOC to zooplankton includes every process that could contribute terrestrial OC to the seston available to zooplankton. These include influx from the atmosphere and watershed, resuspension, flux of particles from the littoral zone, assimilation of terrestrial OC by bacteria, and flocculation of DOC (von Wachenfeldt & Tranvik 2008).

Egestion by zooplankton also adds phytoplankton detritus to the water. This detritus is a small component of the carbon flows but it cannot be neglected for mass balance and therefore we include it in the model. Dynamics of detritus derived from egested phytoplankton, D, follow

$$\frac{dD}{dt} = p_A Q_{AZ} - s_D D - Q_{DZ} + p_D Q_{DZ} \tag{3}$$

Here the egestion coefficient is p_A for fresh algae and p_D for algae that were previously consumed. Egestion coefficients must be zero or greater, and less than one. The sinking rate coefficient is s_D.
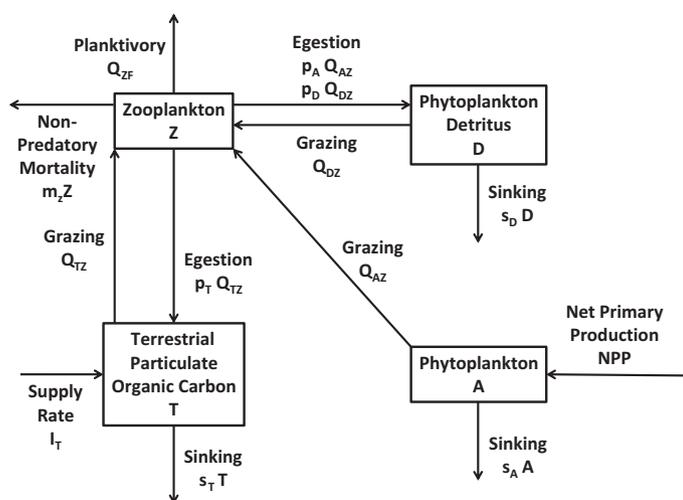
Figure 1 Carbon flows in the model (eqns 1–4).

Zooplankton (Z) dynamics involve growth by eating phytoplankton, TPOC, and algal detritus and losses due to non-predatory mortality and planktivory:

$$\frac{dZ}{dt} = g_{AZ}Q_{AZ} + g_{TZ}Q_{TZ} + g_{DZ}Q_{DZ} - m_ZZ - Q_{ZF} \quad (4)$$

Growth efficiencies on phytoplankton, TPOC and detritus derived from phytoplankton are g_{AZ}, g_{TZ} and g_{DZ} respectively. The non-predatory loss rate coefficient is m_Z and the predation flux from zooplankton to fish (planktivory) is Q_{ZF}. Collectively, eqns 1–4 are a complete mass balance for POC and zooplankton in the epilimnion of an experimental lake.

Parameter estimates

For each whole-lake experiment, we calibrated the model so that its stable equilibrium matched the summer mean observations for each of the five lake experiments. Parameter estimates were obtained from three sources. Some parameters were measured directly in each whole-lake experiment (Table 1). Other parameters were taken from the literature and these are presented below. The remaining parameters were estimated by mass balance for steady-state solutions of the model. This section presents the values obtained from the literature and explains the process for computing mass-balance estimates. The mass-balance values obtained for each whole-lake experiment are presented in Results.

Phytoplankton
We assumed that NPP was $0.7 \times$ GPP where GPP is measured gross primary production for a full 24-h period including when it is dark (Raven & Beardall 1981; Cole *et al.* 1992). We modelled the effects of phosphorus load and irradiance on GPP using the equations of Follows *et al.* (2007). GPP depends on P load rate L_P and irradiance I, which is subject to shading by phytoplankton and DOC (C) through the function $\gamma(I_0, A, C)$

$$GPP = r\left(\frac{L_P}{k_P + L_P}\right)\gamma(I_0, A, C)A \quad (5)$$

We calibrated the growth parameter r to match observed GPP (measured as cited above) after estimating the other parameters of eqn 5. We set the half-saturation response to P load, k_P, at 2 mg m^{-2} day^{-1} which is near the median P load of our whole-lake experiments used to measure P effects on phytoplankton (Carpenter *et al.* 2001).

Irradiance at depth z in the epilimnion is

$$I(z, I_0, A, C) = I_0 e^{-z(k_0 + k_{DOC}C + k_{phyto}Chl)} \quad (6)$$

The light extinction coefficients due to water, DOC and phytoplankton are k_0, k_{DOC} and k_{phyto} which were measured as 0.0213 m^{-1}, 0.0514 m^2 g^{-1} DOC and 0.0177 m^2 mg^{-1} Chl a respectively (Carpenter *et al.* 1998). We converted phytoplankton biomass in g C to chlorophyll in mg using the carbon to chlorophyll ratio (C : Chl) estimated as

$$C : Chl = (1 - \phi_{POC})POC/Chl \quad (7)$$

where ϕ_{POC} is the measured allochthony of POC and Chl is measured chlorophyll *a* concentration (Table 1).

We set surface irradiance I_0= 600 µE m^{-2} s^{-1} which is the median summer value for Peter Lake. All of the lakes are within 5 km of Peter Lake and have similar surface irradiance. Adjusted for light and shading and integrated from the surface to the thermocline depth z_T, $\gamma(I_0, A, C)$ is computed as

$$\gamma(I_0, A, C) = \int_0^{z_T} \frac{1}{\kappa}\left[\left(1 - e^{-k_{grow}I(z,I_0,A,C)}\right)e^{-k_{inhib}I(z,I_0,A,C)}\right]dz$$
$$\kappa \equiv \frac{k_{grow} + k_{inhib}}{k_{grow}}\exp\left(\frac{-k_{inhib}}{k_{grow}}\ln\left(\frac{k_{inhib}}{k_{grow} + k_{inhib}}\right)\right) \quad (8)$$

(Follows *et al.* 2007). The light response parameters k_{grow} and k_{inhib} were measured as 0.0194 and 0.00065, respectively, from photosynthesis-irradiance curves fitted to data from the North Temperate Lakes Long Term Ecological Research site (http://lter.limnology.wisc.edu/data). z_T was computed from regressions of z_T vs. DOC for these whole lake experiments ($z_T = 4.53 - 0.182 \times$ DOC; residual standard error = 0.346 m with 56 d.f.; $R^2 = 0.681$).

The instantaneous loss rate of particles from a turbulent layer of thickness z in meters is $-v/z$ where v is sinking rate in m day^{-1} (Reynolds 1984). Sinking rates measured for living phytoplankton range from ~ 0.1 to 1 m day^{-1}. We assumed that sinking was the major nonpredatory loss of phytoplankton. We estimated the phytoplankton sinking coefficient s_A as $0.3/Z_T$.

Given NPP and sinking losses, we estimated the flux of phytoplankton carbon to zooplankton Q_{AZ} by solving eqn 1 at steady state

$$Q_{AZ} = NPP - s_A A \quad (9)$$

Zooplankton consumption of phytoplankton
Grazing flux to zooplankton follows a Type 2 functional response which depends on attack rate a and handling time h. Using the flux from phytoplankton to zooplankton as an example,

$$Q_{AZ} = \frac{aAZ}{1 + ahA} \quad (10)$$

We set handling time h = 0.005 day (g zooplankton C) (g Algal C)$^{-1}$ which is a typical value for *Daphnia* (Chow-

Fraser & Sprules 1992). Given h, we solve eqn 10 for each whole-lake experiment to estimate a (in m^2 (g zooplankton C)$^{-1}$ day^{-1}) as

$$a = \frac{Q_{AZ}}{AZ - hAQ_{AZ}} \quad (11)$$

Phytoplankton detritus
Phytoplankton detritus may be re-ingested by zooplankton. The flux of phytoplankton detritus to zooplankton follows

$$Q_{DZ} = \frac{aDZ}{1 + ahD} \quad (12)$$

We substituted eqn 12 for Q_{DZ} in eqn 3 and solved at steady state to obtain a quadratic equation in D

$$0 = p_A Q_{AZ} + [p_A Q_{AZ} ah - s_D - (1 - p_D)aZ]D - s_D ahD^2 \quad (13)$$

Equation 13 has one positive root which is the steady state value of D. We estimated the sinking loss rate of D as $s_D = 0.5/z_T$. We set the proportion of ingested phytoplankton that was egested by zooplankton, pA, to 0.3 and assumed $p_A = p_D$. We assumed that the attack rate and handling time for phytoplankton also applied to detritus.

Terrestrial particulate organic carbon
Consumption of TPOC by zooplankton follows

$$Q_{TZ} = \frac{aTZ}{1 + ahT} \quad (14)$$

We assumed that the attack rate and handling time for phytoplankton also applied to TPOC. We estimated the sinking loss of TPOC as $0.1/z_T$ (Reynolds 1984). With these assumptions combining eqns 2 and 14 at steady state, the supply rate of TPOC available to zooplankton (I_T) is calculated as

$$I_T = s_T T + (1 - p_T)Q_{TZ} \quad (15)$$

Zooplankton growth efficiencies
Growth efficiencies of zooplankton can be estimated using the definition of allochthony for zooplankton

$$\phi_Z = \frac{g_{TZ}Q_{TZ}}{g_{AZ}Q_{AZ} + g_{DZ}Q_{DZ} + g_{TZ}Q_{TZ}} \quad (16)$$

where g_{AZ}, g_{DZ} and g_{TZ} are the growth efficiency of zooplankton consuming phytoplankton, detritus derived from phytoplankton, and TPOC respectively. We assumed $g_{AZ} = 0.25$ and $g_{DZ} = 0.1$ (Straile 1997) to solve for g_{TZ} as

$$g_{TZ} = \frac{\phi_Z(g_{AZ}Q_{AZ} + g_{DZ}Q_{DZ})}{(1 - \phi_Z)Q_{TZ}} \quad (17)$$

Zooplankton losses
At steady state, eqn 3 can be solved for the flux of zooplankton carbon to planktivores

$$Q_{ZF} = g_{AZ}Q_{AZ} + g_{DZ}Q_{DZ} + g_{TZ}Q_{TZ} - m_Z Z \quad (18)$$

We assumed that the non-predatory mortality coefficient $m_Z = 0.04$ day^{-1}. All other terms on the right side of the equation were estimated above.

The functional response for consumption of zooplankton by fish planktivores is often modelled as

$$Q_{ZF} = \frac{cFZ^2}{h_F^2 + Z^2} \quad (19)$$

(Chow-Fraser & Sprules 1992; Scheffer *et al.* 2000; Carpenter 2003). We set $h_F = 1.4Z$ where Z is the mean observed biomass of zooplankton in a given whole-lake experiment (Carpenter 2003). With this assumption we can solve for the total flux of zooplankton biomass to fish, represented by the predation coefficient c multiplied by fish biomass F for the whole-lake experiment

$$cF = \frac{Q_{ZF}(h_F^2 + Z^2)}{Z^2} \quad (20)$$

Equations 1–4, together with the input values from Table 1 and parameter estimates described above, form a complete organic carbon balance model for POC (derived from both phytoplankton and terrestrial sources) and zooplankton in each experimental lake. At steady state, the model has no residual error. It exactly matches the mean conditions observed during each whole-lake experiment.

Analysis of driver gradients

For each whole-lake experiment, we computed equilibria of the calibrated model along gradients of phosphorus load, planktivory and TPOC supply. For computation of light extinction, these calculations assumed that the DOC : POC ratio of each lake remained constant. At each point along the gradients, we determined the stability of the equilibrium by computing the dominant eigenvalue of the Jacobian matrix. For each gradient (phosphorus load, planktivory or TPOC supply), we present only the portion of the gradient with stable equilibria.

Computations were performed in R 3.1.1 using standard packages (R Development Team 2012). Stability analyses were computed with the numDeriv() package. A sample program is downloadable from https://github.com/SRCarpen/ATZ_Cascade/.

RESULTS

Several rate coefficients and ratios were fit by the model and in some cases these can be evaluated relative to expectations and patterns (Table 3). For example, the carbon to chlorophyll ratio (g : g) was lowest, as expected, in the fertilised lake and approximately twofold higher in the other lakes with the exception of Crampton Lake. Sedimentation rates of TPOC were similar among lakes. The attack rate by zooplankton was highest in Tuesday Lake, which was dominated by small-bodied grazers, and about 50-fold lower in the enriched year for Peter Lake. The maximum planktivory rate ranged from about 100 g C m^{-2} day^{-1} in Tuesday Lake where planktivorous minnows dominated the fish community to 0.135 g C m^{-2} day^{-1} for 2002 in Peter Lake. Half-saturation coefficients for planktivory were relatively uniform among lakes.

Table 3 Parameters estimated by mass balance and their units for each of the five experiments

Parameters	Units	Paul	Peter 01	Peter 02	Tuesday	Crampton
C : Chl	Ratio, g : g	62.7	61.1	32.4	58.05	170.4
TPOC Sedimentation Coefficient	day^{-1}	0.0286	0.0278	0.0323	0.0385	0.0244
Attack rate coefficient for grazing	m^2 (mg zooplankton C)$^{-1}$ day^{-1}	0.59	0.24	0.0369	1.904	0.892
Zooplankton Mortality Coefficient	day^{-1}	0.223	0.0833	0.052	0.986	0.0535
Planktivory Half Saturation coefficient	g C m^{-2}	4.90	5.04	4.34	3.64	5.74
Planktivory Maximum rate coefficient	g C m^{-2} day^{-1}	8.48	1.088	0.135	100.44	0.508

Sensitivities of the four model outputs that were not directly measured (cF, D^*, g_{TZ}, I_T) to 1% increases in the ten parameters that were estimated from the literature (g_{AZ}, g_{DZ}, h, h_F, p_A, p_D, p_T, s_A, s_D, s_T) are presented in Table S1. Most sensitivities were small. The planktivory flux increases 1.16% with a 1% increase in the growth efficiency of zooplankton feeding on phytoplankton, and nearly 2% with a 1% increase in the half saturation coefficient for planktivory. A 1% increase in the egestion of phytoplankton by zooplankton leads to a 1% increase in the standing stock of phytoplankton detritus.

Equilibrium phytoplankton biomass was the largest pool of particulate organic matter in model results for all the lakes except the Peter 2001 case where zooplankton biomass exceeded phytoplankton (Fig. 2a). Phytoplankton biomass was more than twice as large as zooplankton biomass when Peter Lake was fertilised (Peter 2002 case). Detrital phytoplankton was a relatively small pool in all cases because phytoplankton was mainly consumed or sank. Zooplankton biomass was lowest in Tuesday Lake and about 2× larger in fertilised Peter Lake (Fig. 2a).

Net primary production exceeded the TPOC supply rate available for zooplankton in all cases (Fig. 2b). In this model

TPOC supply rate includes all processes by which terrestrial organic carbon can become available to zooplankton, including TPOC input but also bacterial production, flocculation, and resuspension of previous deposited TPOC from sediments. TPOC consumption sometimes exceeded the supply rate because TPOC could be egested and re-ingested by zooplankton (eqn 2). Phytoplankton was the largest source of carbon for zooplankton, except in Tuesday Lake. Detrital phytoplankton was a minor source of organic carbon for zooplankton. Planktivory was an important fate of zooplankton and was highest in the most oligotrophic lake (Crampton) and lowest in the most eutrophic lake (Peter 2002).

Ecosystem responses to gradients of P load, planktivory and TPOC supply rate to zooplankton were calculated for each experiment (Fig. 3). Phytoplankton biomass increased with P load (Fig. 3a) and planktivory (Fig. 3b) consistent with whole-lake experiments on trophic cascades (Carpenter et al. 2001). Differences among lakes were due in part to differences in zooplankton community composition. Phytoplankton biomass showed little response to TPOC supply rate when it was below 0.1 g m^{-2} day^{-1} (Fig. 3c). At higher TPOC supply rates, however, phytoplankton biomass declined steeply. This decline was due to increased shading by DOC associated with high TPOC supply rates.

Zooplankton biomass also increased with P load (Fig. 3d) as shown by other studies of eutrophication and zooplankton biomass (Pace 1986; Carpenter et al. 1991, 2001). Planktivory, in contrast, had little effect on zooplankton biomass (Fig. 3e). Previous studies have shown that planktivory changes zooplankton community composition and the mean size of zooplankton, with no change in the biomass (Carpenter & Kitchell 1993; Carpenter et al. 2001). TPOC supply rate had positive but small effects on zooplankton biomass (Fig. 3f).

The standing stock of TPOC declined with P load (Fig. 3g). With increasing P load, zooplankton biomass increased (Fig. 3d) along with grazing of both phytoplankton and TPOC. Thus, TPOC standing stock declined because P load increased phytoplankton biomass, zooplankton biomass and grazing. Planktivory, in contrast, had little effect on the standing stock of TPOC (Fig. 3h) because planktivory had little effect on zooplankton biomass (Fig. 3e). The standing stock of TPOC increased steeply with TPOC supply rate (Fig. 3i).

The allochthony of zooplankton decreased with P load (Fig. 3j). With increasing P load, more phytoplankton and less TPOC were available to zooplankton, leading to lower allochthony. Allochthony also decreased with increasing planktivory (Fig. 3k), primarily because planktivory increased phytoplankton biomass available to zooplankton (Fig. 3b).
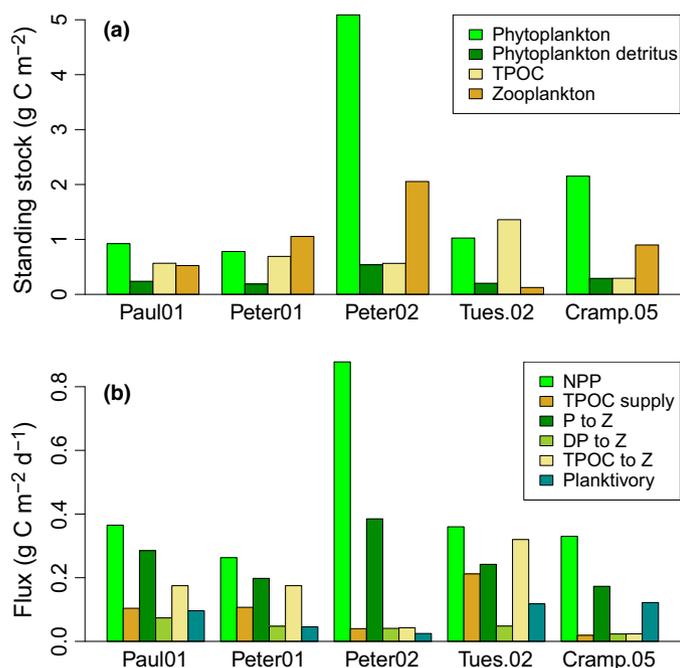
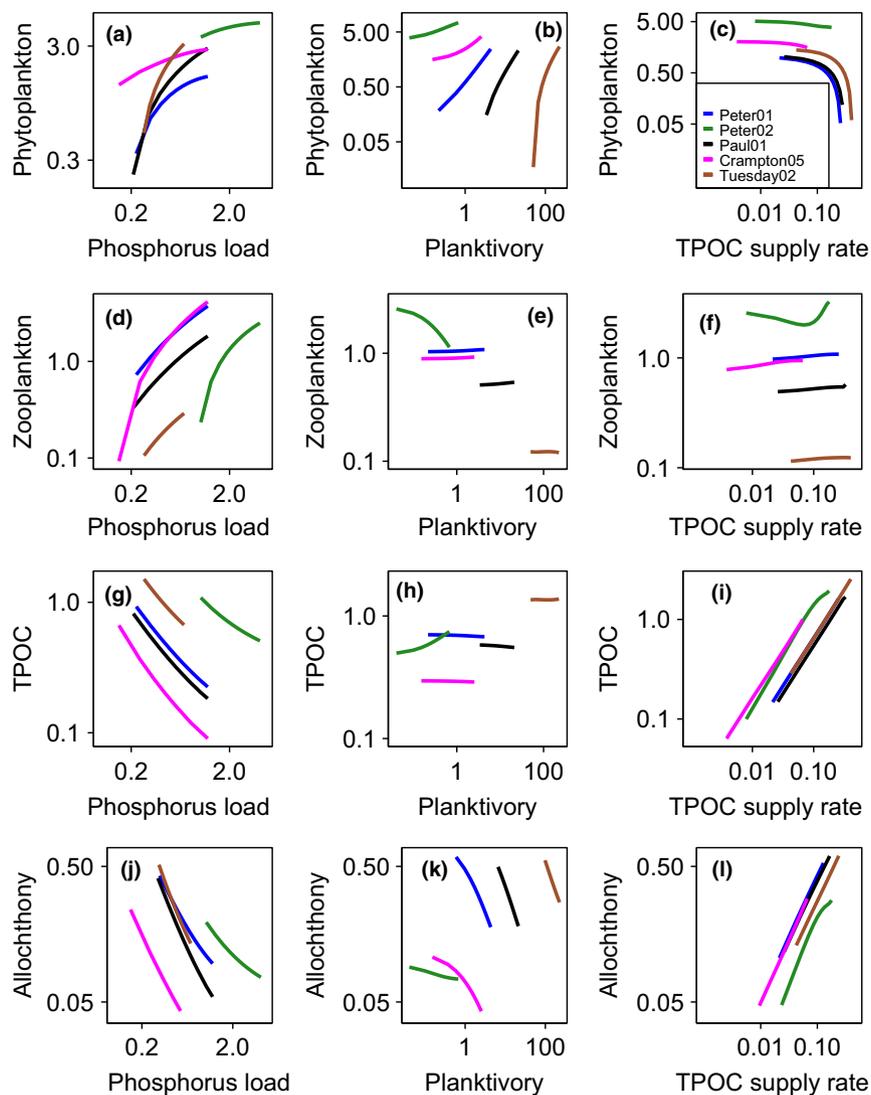**Figure 2** Standing stocks (a) and fluxes (b) estimated by the model at steady state.

Figure 3 Ecosystem responses to gradients of P load, planktivory and terrestrial particulate organic carbon (TPOC) supply rate. Each panel shows stable equilibria for each of the five whole-lake experiments. Columns show effects of the three drivers, P load (mg P m^{-2} day^{-1}), planktivory (cF, the maximum planktivory rate, in g C m^{-2} day^{-1}), and TPOC supply rate (g C m^{-2} day^{-1}). Rows show responses of four ecosystem variables, phytoplankton biomass (g C m^{-2}), zooplankton biomass (g C m^{-2}), TPOC (g C m^{-2}) and allochthony (proportion of zooplankton growth that is terrestrial carbon).

Conversely, zooplankton allochthony increased with TPOC supply rate (Fig. 3l) because greater amounts of TPOC were available to zooplankton (Fig. 3i).

When allochthony was less than ~ 0.3 (i.e. 30% of zooplankton C derived from terrestrial sources), phytoplankton and zooplankton biomass and production spanned a wide range, depending primarily on P load and planktivory (Fig. 4). When allochthony was greater than about 0.3, phytoplankton and zooplankton biomass and production were relatively low. Thus, when zooplankton use a high percentage of terrestrially derived organic carbon, phytoplankton biomass and production were low and zooplankton did not achieve high biomass or secondary production.

DISCUSSION

Lake pelagic ecosystems are known to be affected by P load and trophic cascades, and the interactions of these factors with terrestrial organic matter inputs are still uncertain. This paper exposes some of the responses of lakes to TPOC supply in the context of P load and trophic cascades. Phytoplankton responses to TPOC supply rates were weak when TPOC supply rate is less than 0.1 g m^{-2} day^{-1}, but became steeply negative at higher rates of TPOC supply. Conversely, when phytoplankton biomass was high due to high P load or planktivory, TPOC standing stock was low as a consequence of increased grazing. This pattern is analogous to apparent competition in food webs (Holt 1977). TPOC supply rate had a small positive effect on zooplankton biomass. The allochthony of zooplankton was inversely related to P load, because high P load was directly related to the biomass of phytoplankton available for consumption by zooplankton. Allochthony of zooplankton was inversely related to planktivory because planktivory was directly related to phytoplankton biomass. Thus there was a notable effect of trophic cascades on allochthony of zooplankton.
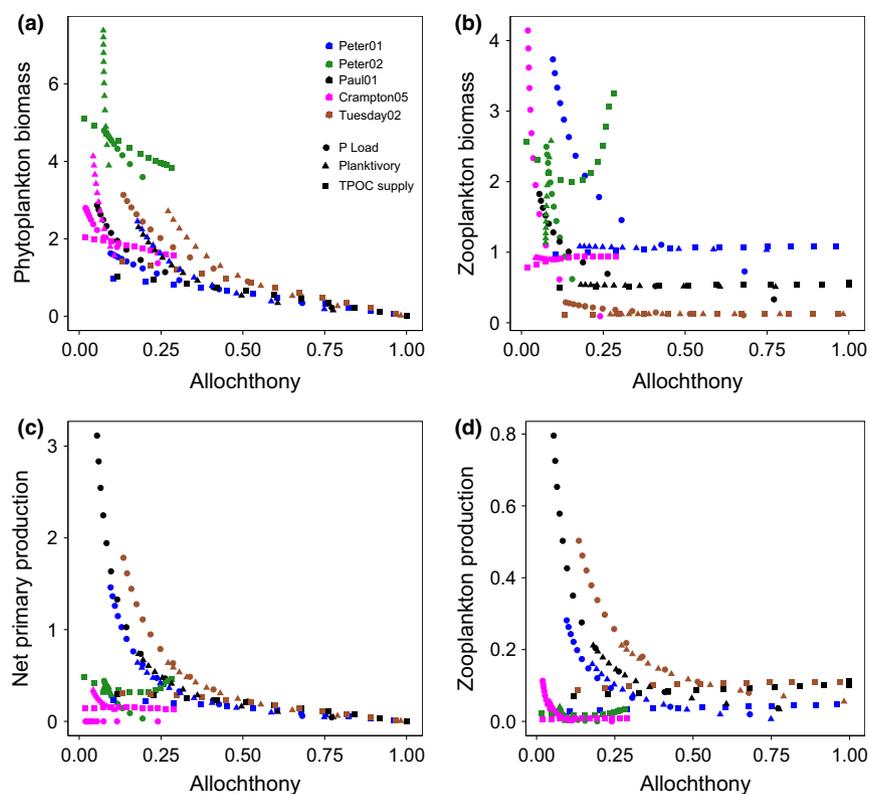
Figure 4 Phytoplankton biomass (a, g C m^{-2}), Zooplankton biomass (b, g C m^{-2}), Net primary production (c, g C m^{-2} day^{-1}) and Secondary production of zooplankton (d, g C m^{-2} day^{-1}) vs. allochthony (proportion of zooplankton growth from terrestrial carbon sources). Symbol shape indicates the driver gradient: circle P load, triangle Planktivory, square terrestrial particulate organic carbon (TPOC) supply rate. Colour code for whole-lake experiments is the same as Fig. 2.

When allochthony of zooplankton was less than ~ 0.3, phytoplankton and zooplankton biomass or production spanned a wide range of values, depending on P load and planktivory. Allochthony above 0.3 was associated with low zooplankton biomass and production, low phytoplankton biomass and production, and high TPOC concentrations and supply rates. This pattern suggests that TPOC is a low quality food source consistent with lab (Brett *et al.* 2009; Taipale *et al.* 2013) and field (Kelly *et al.* 2013) studies. In our study, high allochthony was never associated with high biomass or production of phytoplankton. If phytoplankton were abundant, they would be consumed and zooplankton allochthony would therefore decrease.

Based on patterns of Fig. 4, we expected that lakes with high allochthony of zooplankton would have relatively high concentrations of TPOC. This pattern was corroborated by an independent data set in which the allochthony of zooplankton and POC in 40 lakes was estimated using ambient stable isotopes (δ^2H) rather than added ^{13}C (Wilkinson *et al.* 2013a,b). We split the data into two groups, those lakes with zooplankton allochthony > 0.3 (high allochthony, $n = 15$ lakes) and those with zooplankton allochthony < 0.3 (low allochthony; $n = 25$ lakes). Lakes with high zooplankton allochthony had much higher TPOC concentrations (mean 1.55 mg L^{-1}, SE 0.35) than lakes with low zooplankton allochthony (mean = 0.37 mg L^{-1}, SE 0.11).

Batt *et al.* (2012, 2015) provide data that allow another independent test of model predictions using unmanipulated stable isotopes of C, H and N. Ward Lake was experimentally darkened using an inert dye, resulting in a two-fold decrease in chlorophyll concentration and an increase in allochthony of particulate organic matter from 0.33 to 0.53. Responses of the zooplankton to this manipulation support the model in several ways: allochthony of *Chaoborus* increased, and biomass of *Chaoborus* and the dominant copepod *Skistodiaptomus oregonensis* declined. However, the autochthony of *S. oregonensis* was high (> 0.85) both before and after the manipulation despite the decline in chlorophyll, suggesting feeding specialisation of this calanoid copepod (Batt *et al.* 2015).

Kelly *et al.* (2013) studied 10 lakes in the same region of our study along a gradient of TPOC concentration. They found that zooplankton production was inversely related to zooplankton allochthony, with considerable variability. In Swedish boreal lakes, Karlsson *et al.* (2015) observed a similar pattern in TPOC loading and fish allochthony among lakes. While consumer allochthony increased with increasing DOC, fish biomass was suppressed at high allochthony. The patterns in these two studies are consistent with Fig. 4, and with the pattern hypothesised by Jones *et al.* (2012).

The model, like all ecosystem models, is a simplification of complex interactions built for a specific purpose. In this case, the goal is to better integrate TPOC supply with the P

load and trophic cascade paradigms for lake pelagic ecosystems. The model includes functional relationships (GPP equations, functional responses) that are used in a wide array of other lake ecosystem models, and it accurately reproduces the seasonal mean conditions observed in the experimental lakes. For quantities that are not directly measured, such as C : Chl ratios, TPOC supply rates, attack rates and planktivory rates, the model generates plausible estimates from mass balance. The model is dynamically stable over a range of drivers (P load, planktivory, TPOC supply rate) and this enables us to understand responses to these varying drivers. On the other hand, the model is not stable over an unlimited range of these drivers, as has been shown for other meta-ecosystem models (Marleau *et al.* 2010). Thus, it is not possible to use a particular set of parameter estimates to analyse the full range of drivers known from the world's lakes. The model employs lake-specific estimates of the quantities in Table 1, and these estimates require a substantial field program of measurements. Thus, the model may not be readily applied to lakes beyond the scope of our data. Nonetheless, the model does provide useful insights into the diverse conditions seen in these five whole-lake experiments.

All lakes receive terrestrial inputs of POC and DOC that may be converted into TPOC by flocculation or bacterial growth. This TPOC can be incorporated into food webs. The relative contribution of TPOC to zooplankton biomass depends on phytoplankton biomass, which is in turn affected by P load and planktivory. Moreover, the allochthony of zooplankton is related to potential biomass and production. When allochthony is high, zooplankton biomass and production are constrained to relatively low values. When allochthony is low, zooplankton biomass and production are subject to wide variations due to P load and trophic cascades. Thus, the TPOC supply has strong and significant interactions with phosphorus and food web processes.

Our findings add to a growing body of literature which shows that cross-boundary material flows alter ecosystem processes in diverse ways that affect production, nutrient cycling and trophic interactions (Loreau 2010; Cole 2013; Rosemond *et al.* 2015). At the same time, spatial flows of abiotic materials and organisms can affect source-sink dynamics of rare populations (Gravel *et al.* 2010), stability of food webs (Marleau *et al.* 2010), and strength of trophic cascades (Leroux & Loreau 2008). Further study of organic matter inputs and their interactions with nutrients and food webs seems likely to lead to a deeper understanding of ecosystem dynamics in a landscape context.

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AUTHORSHIP

SRC, JCC, MLP designed the study; SRC performed the analyses; all authors gathered data, interpreted results and wrote the paper.

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SUPPORTING INFORMATION