

Subsidy or subtraction: how do terrestrial inputs influence consumer production in lakes?

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Abstract

Cross-ecosystem fluxes are ubiquitous in food webs and are generally thought of as subsidies to consumer populations. Yet external or allochthonous inputs may in fact have complex and habitat-specific effects on recipient ecosystems. In lakes, terrestrial inputs of organic carbon contribute to basal resource availability, but can also reduce resource availability via shading effects on phytoplankton and periphyton. Terrestrial inputs might therefore either subsidise or subtract from consumer production. We developed and parameterised a simple model to explore this idea. The model estimates basal resource supply and consumer production given lake-level characteristics including total phosphorus (TP) and dissolved organic carbon (DOC) concentration, and consumer-level characteristics including resource preferences and growth efficiencies. Terrestrial inputs diminished primary production and total basal resource supply at the whole-lake level, except in ultra-oligotrophic systems. However, this system-level generalisation masked complex habitat-specific effects. In the pelagic zone, dissolved and particulate terrestrial carbon inputs were available to zooplankton via several food web pathways. Consequently, zooplankton production usually increased with terrestrial inputs, even as total whole-lake resource availability decreased. In contrast, in the benthic zone the dominant, dissolved portion of the terrestrial carbon load had predominantly negative effects on resource availability via shading of periphyton. Consequently, terrestrial inputs always decreased zoobenthic production except under extreme and unrealistic parameterisations of the model. Appreciating the complex and habitat-specific effects of allochthonous inputs may be essential for resolving the effects of cross-habitat fluxes on consumers in lakes and other food webs.

Keywords: resource subsidy; aquatic; benthic; pelagic; production

Introduction

The classical perception of a lake food web as a unidirectional transfer of carbon, nutrients and energy from phytoplankton to zooplankton to planktivores to piscivores most likely arose from research in marine ecology (Hensen, 1887; Reynolds, 2008). However, this paradigm in aquatic ecology has slowly eroded over the past half-century with growing appreciation for detrital (Lindeman, 1942; Wetzel, 1995), benthic (Vadeboncoeur et al., 2002; Vander Zanden & Vadeboncoeur, 2002), and terrestrial (Jones et al., 1998; Carpenter et al., 2005; Solomon et al., 2011) inputs to pelagic food webs (Reynolds, 2008). Therefore, to evaluate the importance of a particular trophic flow in a modern conceptualisation of a lacustrine food web, a multitude of direct and indirect interactions must be considered from both food web and ecosystem perspectives (Marcarelli et al., 2011). In this review, we attempt to take such a broad overview in order to explore the potential influences of terrestrial carbon on an integrated model of pelagic and benthic lake food webs.

An appreciation for the potential influences of terrestrial carbon on aquatic ecosystems has been a part of aquatic ecology from its beginning, e.g. Birge and Juday's classification of lakes as autotrophic (self-nourished) or allotrophic (nourished in other ways) (Birge & Juday, 1926). The early recognition of terrestrial-aquatic linkages probably arose due to the large magnitude of terrestrial carbon inputs to many aquatic ecosystems and the pervasive impacts terrestrial carbon can have on physical, chemical and biological aspects of lakes (Jones, 1992). The majority of terrestrial carbon enters lakes primarily as dissolved organic carbon (DOC), but also as particulate organic (POC) and dissolved inorganic forms (Dillon & Molot, 1997a; Cole et al., 2006). Terrestrial DOC is chemically complex, but is dominated by humic substances (Jones, 1992). These high molecular weight compounds have a great capacity to attenuate light (Jones, 1992). Reduced light penetration can impose light limitation on primary producers (Carpenter et al., 1998; Karlsson et al., 2009), enhance larval fish survival as a result of reduced UV irradiance (Zagarese & Williamson,

2001), influence the distribution of temperature with depth (Houser, 2006), and indirectly influence anoxia in bottom waters (Numberg, 1995). Finally, terrestrial DOC often carries with it mineral and organic nutrients that can have stimulatory influences on aquatic primary and bacterial production (Lennon & Pfaff, 2005).

In addition to the physical and chemical impacts of terrestrial carbon, aquatic consumers are known to exploit terrestrial carbon as a resource. The high molecular weight and complex chemical structure suggest a biologically unavailable or recalcitrant nature, but evidence for microbial use of terrestrial organic carbon is quite widespread (Tranvik, 1988; Kritzberg et al., 2004; Berggren et al., 2010). For example, the role of terrestrial carbon in enhancing microbial respiration and driving lakes to a net heterotrophic state is well supported (Cole et al., 1994; Lennon, 2004; Cole et al., 2007). In addition, terrestrial resources supported 35 % to 70 % of bacterial production in small northern temperate lakes (Kritzberg et al., 2004). Both zooplankton (12 % to 80 %) and zoobenthos (22 % to 85 %) also appear to incorporate significant levels of terrestrial carbon (Carpenter et al., 2005; Solomon et al., 2008, 2011). Consumer incorporation of terrestrial carbon is hypothesised to occur through consumption of terrestrial-DOC-utilising bacteria and their predators (Jurgens, 1994; Pace & Vaque, 1994; Agasild & Noges, 2005), as well as by direct consumption of terrestrial POC (Cole et al., 2002, 2006; Brett et al., 2009). Although many of these studies were conducted in small, forested lakes in northern central USA, studies conducted in Scandinavia, the United Kingdom and Australia produced comparable results (Bunn & Boon, 1993; Jones et al., 1999; Grey et al., 2001; Ask et al., 2009; Karlsson et al., 2009). A general trend of increased incorporation of terrestrial carbon with increasing measures of terrestrial carbon supply (e.g. light attenuation, water colour, or the colour:chlorophyll *a* ratio) has emerged from these studies (Pace et al., 2007; Weidel et al., 2008; Solomon et al., 2011).

The research described to this point has led many to declare terrestrial carbon as a clear example of a resource subsidy. However, to be considered a resource subsidy, matter or energy must be supplied across ecosystem

boundaries, lack feedbacks for the magnitude of supply (donor-control), and enhance production in the recipient ecosystem (Polis et al., 1997). Although there is little doubt that terrestrial carbon is supplied to aquatic ecosystems in a donor-controlled manner, and is incorporated into the tissues of aquatic consumers, evidence to support claims of widespread aquatic consumer subsidy by terrestrial carbon is largely absent from the literature.

A handful of microcosm experiments have been conducted to evaluate the influence of terrestrial organic carbon supply on consumer growth or production. The most recent example indicated that a diet containing exclusively terrestrial POC results in reduced production of a common aquatic consumer, *Daphnia magna* (Brett et al., 2009). However, if a small amount of algal resource was provided (10–30% of available carbon), *Daphnia* production was comparable to production on a pure algal diet (Brett et al., 2009). This result emphasises that an aquatic consumer's ability to incorporate terrestrial organic matter (t-OM) into biomass does not ensure that terrestrial carbon will act as a subsidy. Few comparable studies have been conducted for lake zoobenthos, but benthic invertebrate use of terrestrial detritus and its bacterial biofilms has been addressed in the literature (e.g. the peanut butter/cracker debate; Cummins, 1974). A commonality between the planktonic and benthic studies is the widespread assertion that terrestrial carbon resources are of a relatively low quality (Tranvik, 1988; Brett et al., 2009; Marcarelli et al., 2011), although this has recently been questioned (Berggren et al., 2010).

The lack of understanding of how the resource-mediated and non-resource-mediated impacts of terrestrial carbon interact to influence lake food webs precludes predictions of whether enhanced terrestrial carbon inputs yield increases or decreases in aquatic consumer production. An improved understanding of the impact of terrestrial carbon on aquatic production is particularly important because terrestrial carbon supply to aquatic ecosystems is increasing (Roulet & Moore, 2006). To begin to address the question of whether terrestrial carbon subsidises lake food webs, we have developed a model of aquatic production that includes multiple avenues for terrestrial carbon influence. Using this model, we sought to explore

the likelihood of terrestrial carbon subsidies to aquatic consumers and identify the key interactions or rates that are likely to determine whether terrestrial carbon acts as a subsidy in its classical definition (Polis et al., 1997). We used the following questions to guide our model simulations:

1. how does basal carbon supply respond to elevated terrestrial carbon supply?
2. how likely are zooplankton or zoobenthos to be subsidised?
3. where are the greatest uncertainties pertaining to terrestrial carbon influences on aquatic secondary production?

Model description

The effects of terrestrial inputs on consumer secondary production in lakes can be conceptualised as being dependent on three primary factors: how terrestrial inputs influence the supply of fixed C from terrestrial and aquatic sources; any preference that a consumer may have for one resource over the other; and the growth efficiency, i.e. the fraction of consumed carbon that is incorporated into new biomass, of the consumer on each of the resources (Marcarelli et al., 2011). We developed a model to explore the interplay of these factors and predict the response of consumer production to changes in terrestrial organic matter loads. Most of the parameter values selected for our model are derived from northern temperate glacial lakes embedded in a forested landscape, including bathymetric information (for the latter, see Appendix Figure 1, available as supplementary material to the electronic version of this paper at <https://www.fba.org.uk/journals/index.php/FRJ/article/view/475>). This does not preclude the application of our model to lakes in other geographic settings, but these alternative applications should be executed with caution. Equations, parameter values, and other details for our calibrated model are available in Tables 1–3. Equation numbers cited in the text refer to Table 1.

The model works in two steps. In the first step, we determine the rate of supply of fixed organic C from each of several sources: phytoplankton primary production, periphyton primary production, terrestrial DOC load, and

Table 1: Equations of the food web productivity model.

	Model Output	Unit	Equation
1	Phytoplankton chlorophyll <i>a</i> maximum	mg m ⁻³	$Chl = 0.41TP_0^{0.87}$
2	phytoplankton productivity	mg C m ⁻³ h ⁻¹	$PP_{\max} = 1.56Chl$
3	maximum periphyton productivity	mg C m ⁻² h ⁻¹	$BP_{\max} = 28.1TP_0^{0.24}$
4	light-attenuation coefficient	m ⁻¹	$K_D = 0.0213 + 0.0177Chl + 0.0514DOC$
5	surface light at time <i>t</i>	μmol m ⁻² s ⁻¹	$I_{0,t} = I_{0,\max} \sin\left(\pi \frac{t}{daylen}\right)$
6	light at depth <i>z</i> and time <i>t</i>	μmol m ⁻² s ⁻¹	$I_{z,t} = I_{0,t} e^{-K_D z}$
7	whole-lake phytoplankton production	mg C m ⁻² d ⁻¹	$TPP = \sum_{z=0}^{z_{\max}} \sum_{sunrise}^{sunset} PP_{\max} \tanh\left(\frac{I_{z,t}}{I_{kp}}\right) (V_z - V_{z-\Delta z}) / A_0$
8	whole-lake periphyton production	mg C m ⁻² d ⁻¹	$TBP = \sum_{z=0}^{z_{\max}} \sum_{sunrise}^{sunset} BP_{\max} \tanh\left(\frac{I_{z,t}}{I_{kb}}\right) (A_{z-\Delta z} - A_z) / A_0$
9	terrestrial DOC load	mg C m ⁻² d ⁻¹	$Q_{DOC} = 1000DOC\tau / 365$
10	terrestrial POC load	mg C m ⁻² d ⁻¹	$Q_{POC} = Q_{DOC}\omega$
11	phytoplankton exudate	mg C m ⁻² d ⁻¹	$TPP_{Bt} = TPP(1 - R_{TPP})\varepsilon$
12	zooplankton-available phytoplankton production	mg C m ⁻² d ⁻¹	$TPP_{Zp} = TPP(1 - R_{TPP})(1 - \varepsilon)$
13	zoobenthos-available periphyton production	mg C m ⁻² d ⁻¹	$TBP_{Zb} = TBP(1 - R_{TBP})$
14	bacteria-available terrestrial DOC	mg C m ⁻² d ⁻¹	$tDOC_{Bt} = Q_{DOC}(1 - \phi)$
15	zooplankton-available terrestrial POC	mg C m ⁻² d ⁻¹	$tPOC_{Zp} = Q_{POC} + Q_{DOC}\phi$
16	bacterial production	mg C m ⁻² d ⁻¹	$P_{Bt} = TPP_{Bt}C_{TPP,Bt}GE_{TPP,Bt} + tDOC_{Bt}C_{tDOC,Bt}GE_{tDOC,Bt}$
17	heterotrophic protist and zooplankton available bacterial production	mg C m ⁻² d ⁻¹	$Bt_{Zp} = Bt_{Pt} = P_{Bt}(1 - m_{Bt}) / 2$
18	heterotrophic protist production	mg C m ⁻² d ⁻¹	$P_{Pt} = Bt_{Pt}GE_{Bt,Pt}$

Table 1 (cont.): Equations of the food web productivity model.

Model Output	Unit	Equation
19 Zooplankton production	mg C m ⁻² d ⁻¹	$P_{Zp} = (TPP_{Zp} + P_{Pt})C_{TPP,Zp}^{GE_{TPP,Zp}} + tPOC_{Zp}C_{tPOC,Zp}^{GE_{tPOC,Zp}} + Bt_{Zp}^{GE_{Bt,Zp}}$
20 Detritus production	mg C m ⁻² d ⁻¹	$P_{Dt} = P_{Zp}S_{Zp} + (TPP_{Zp} + P_{Pt})(1 - C_{TPP,Zp}) + tPOC_{Zp}(1 - C_{tPOC,Zp}) + TBP_{Zb}(1 - C_{TBP,Zb})$
21 Zoobenthos production	mg C m ⁻² d ⁻¹	$P_{Zb} = TBP_{Zb}C_{TBP,Zb}^{GE_{TBP,Zb}} + P_{Dt}C_{Dt,Zb}^{GE_{Dt,Zb}}$

terrestrial POC load (Fig. 1). The key lake characteristics that control basal C supply from these sources are the total phosphorus concentration, the DOC concentration, and the loading rates of terrestrial DOC and POC. Based on these characteristics we calculate whole-lake phytoplankton and periphyton primary production (Eqns 7 & 8), using the model of Vadeboncoeur et al. (2008) with modifications to incorporate the effects of terrestrial DOC loads. Specifically, our modified model accounts for the shading effects of DOC as well as phytoplankton biomass in determining the light climate in the lake (Eqn. 4) and it considers the fertilisation effects of nutrients that enter the lake as part of the terrestrial organic matter load with the assumption that the terrestrial load is 2000:1 C:P by mass (Donald et al, 1993; Dillon & Molot, 1997b; Lennon & Pfaff, 2005). In our model, as in real lakes, both the load and the standing stock of terrestrial DOC are potentially important in determining consumer production. A change in load has a direct effect on the basal C supply to the lake food web, and may also indirectly alter basal C supply because DOC shades within-system or aquatic (autochthonous) primary producers. We considered a range of literature-derived values for the relationship between terrestrial DOC load and DOC concentration, which we call the ‘terrestrial loading index’, τ (Table 2). We defined τ as the ratio of the areal terrestrial DOC loading rate (g C m⁻² year⁻¹) to the measured DOC concentration (g C m⁻³).

Finally, we assumed that lakes with higher DOC inputs also had higher POC inputs (Eqn. 10).

The second step of the model determines rates of consumer secondary production, given the basal resource supply rates determined in the first step as well as the consumption rates, preferences, and growth efficiencies of each consumer (Eqns 16-21). We focused our analysis on the response of generalised insect zoobenthos and cladoceran zooplankton, although the model also includes heterotrophic bacteria and heterotrophic protists as part of the pelagic assemblage (Fig. 1). We assumed that consumer populations used a constant proportion of resource production. We considered two scenarios for preference: either consumers had no preference, or they preferred autochthonous resources to allochthonous resources

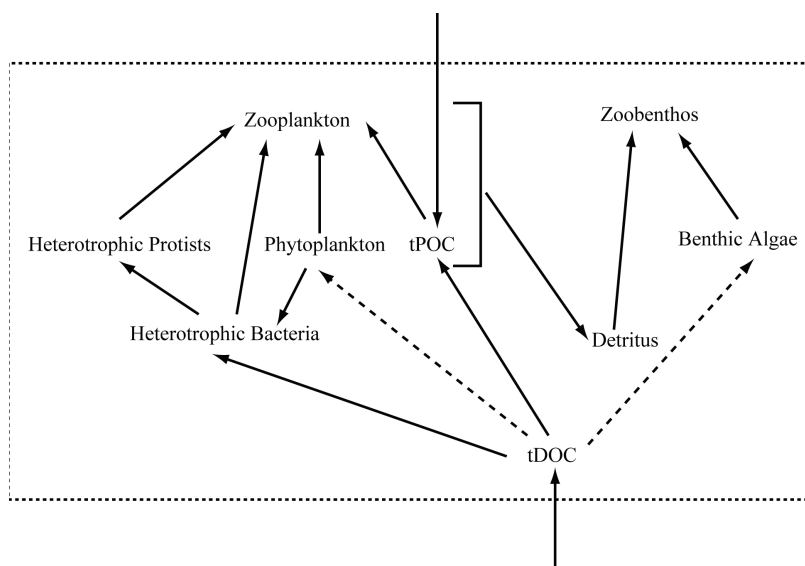


Fig. 1. Box and arrow depiction of the lake food web model, which tracks production (not abundance) of each food web component. Dissolved (tDOC) and particulate (tPOC) terrestrial carbon entered the lake (dashed box) and were incorporated into consumer biomass. Terrestrial inputs also had indirect effects (dashed arrows) on benthic and pelagic primary production, by providing nutrients and by decreasing light availability. For all food web components, unconsumed production is returned to the detrital pool (some arrows not shown).

Table 2. Parameter symbols, values and sources for the food web productivity model.

Parameter	Symbol	Value(s)	Units	Sources
total phosphorus	TP_0	2, 25, 50	$mg\ m^{-3}$	n.a.
dissolved organic carbon	DOC	2-24	$g\ m^{-3}$	n.a.
maximum incident light	$I_{0,max}$	1500	$\mu mol\ photons\ m^{-2}\ s^{-1}$	(Vadeboncoeur et al., 2008)
day length	daylen	15	hr	(Vadeboncoeur et al., 2008)
depth increment	Δd	0.1	m	(Vadeboncoeur et al., 2008)
time increment	Δt	0.25	hr	(Vadeboncoeur et al., 2008)
light intensity at onset of phytoplankton saturation	I_{kp}	180	$\mu mol\ photons\ m^{-2}\ s^{-1}$	(Vadeboncoeur et al., 2008)
light intensity at onset of periphyton saturation	I_{kb}	300	$\mu mol\ photons\ m^{-2}\ s^{-1}$	(Vadeboncoeur et al., 2008)
fraction of phytoplankton and periphyton primary production respired	R_{pp}, R_{bp}	0.3	unitless	(Falkowski et al., 1985; Weger et al., 1989; Turner et al., 1991)
fraction of phytoplankton production exuded as DOC	ϵ	0.13	unitless	(Baines and Pace, 1991)
terrestrial loading index	τ	7-50 [12.5]	$m\ year^{-1}$	(Dillon and Molot, 1997a; Hanson et al., 2004; Cole et al., 2006)
POC:DOC in terrestrial load	ω	0.1-0.3 [0.2]	$(g\ POC)(g\ DOC)^{-1}$	(Carpenter et al., 2005; Cole et al., 2006; Buffam et al., 2010)
DOC flocculation	ϕ	0.005	unitless	(von Wachenfeldt and Tranvik, 2008)
fraction of resource consumed	γ	0-1; See Table 4	unitless	n.a.
consumption of available x by y	$C_{x,y}$	0.5 γ , γ , or 2 γ , with a maximum of 1	unitless	n.a.
growth efficiency of y on x	$GE_{x,y}$	0-1; See Table 3	$(g\ consumer)(g\ consumed)^{-1}$	n.a.
non-grazing bacterial mortality (e.g. viral lysis)	m_B	0.5	unitless	(Fuhrman and Noble, 1995; Fischer and Velimirov, 2002)
zooplankton settling rate	S_{zp}	0.2	unitless	Stoke's Law

at a 4:1 ratio. Bacteria were assumed to have a constant 2:1 preference for autochthonous resources. Growth efficiencies of each consumer on each resource were derived from the literature (Table 3). Unconsumed production of any food web component was returned to the detrital pool.

We calibrated our model to existing production estimates for benthic and pelagic primary producers and consumers in the northern temperate region. First, we reduced the maximum biomass-specific phytoplankton production from the default value of 2.20 in the Vadeboncoeur et al. (2008) model to 1.56 to force pelagic primary production within the range of

observed values for northern temperate lakes (Hanson et al., 2003; Solomon et al., unpublished data). In addition, we tuned the Type I functional response parameters (γ ; effectively, the proportion of available resource consumed) until the range of modeled production for a given consumer in lakes across gradients of TP (2-50 $mg\ m^{-3}$) and DOC (2-24 $g\ m^{-3}$) approximately matched the range commonly observed in the northern temperate landscape (see also Table 4). Calibrated secondary productions agreed well with the upper limit of published production measures, but slightly overestimated production at the bottom of the ranges.

Table 3: Growth efficiencies (GE) for all combinations of food web predators and prey in the productivity model.

Consumer	Resource	Range of GEs	Default GE	Sources
Bacteria	Phytoplankton exudate	0.3-0.8	0.6	(del Giorgio and Cole, 1998)
Bacteria	Terrestrial DOC	0.05-0.75	0.3	(del Giorgio and Cole, 1998)
Heterotrophic Protists	Bacteria	-	0.6	(Fenchel, 1982)
Zooplankton	Bacteria	0.05-0.55	0.4	(Le Borgne, 1982; Muller-Navarra et al., 2000; Brett et al., 2009)
Zooplankton	Phytoplankton	0.05-0.55	0.4	(Le Borgne, 1982; Muller-Navarra et al., 2000; Brett et al., 2009)
Zooplankton	Terrestrial POC	0.05-0.55	0.2	(Le Borgne, 1982; Muller-Navarra et al., 2000; Brett et al., 2009)
Zoobenthos	Periphyton	0.15-0.55	0.35	(Banse and Mosher, 1980)
Zoobenthos	Detritus	0.15-0.55	0.35	(Banse and Mosher, 1980)

Table 4: Range of modeled rates of consumer production, and observed ranges from studies in north temperate lakes.

Food web component	Modeled Range (mg C m ⁻² day ⁻¹)	Observed Range (mg C m ⁻² day ⁻¹)	Citations
Bacteria $\gamma = 0$	23-290	1-1000	(del Giorgio et al., 1997; del Giorgio and Cole, 1998; Fouilland and Mostajir, 2010)
Zooplankton $\gamma = 0.1$	9-162	0.5-160	(Coveney et al., 1977; Andrew, 1983; Strayer and Likens, 1986)
Zoobenthos $\gamma = 0.03$	11-63	0.1-60	(Strayer and Likens, 1986; Babler et al., 2008) and citations therein

Model results

Increased terrestrial inputs generally reduced phytoplankton and periphyton primary production and total basal resource availability (Fig. 2). Only in the lowest productivity system ($TP_0 = 2 \text{ mg m}^{-3}$) did we observe an increase in basal resource supply with elevated DOC; in such an oligotrophic system, the P that enters the lake along with C as part of the terrestrial DOM load has an appreciable fertilisation effect on phytoplankton. At the highest DOC concentration, benthic primary production was on average 40 % of that at the lowest DOC concentration. Pelagic primary production at the highest DOC concentration was approximately half of that at the lowest, with the exception of the fertilisation effect observed in our lowest productivity simulations ($TP_0 = 2 \text{ mg m}^{-3}$). Terrestrial (POC and DOC) contributions to basal resource supply ranged from 2 % (most productive systems with lowest loading) to 53 % (least productive system with highest loading).

Contrasts in access to terrestrial organic matter drove stark differences in the response of zooplankton and zoobenthos production to elevated terrestrial organic matter supply (Fig. 3). Zooplankton production often increased with DOC concentration across the lake productivity (TP) gradient that we considered. Because DOC load has positive effects on resource availability for zooplankton while DOC concentration has negative effects, the net effect depended on τ , the loading rate required to maintain a given concentration. Specifically, increasing DOC increased zooplankton production for any value of τ in the low TP lake, for $\tau > 20$ in the medium TP lake, and for $\tau > 45$ in the high TP lake. Neither the ratio of POC to DOC in the loaded terrestrial carbon nor the rate of DOC flocculation altered these patterns (see Appendix Figs. 2 & 3).

Zoobenthos production did not increase with increasing terrestrial inputs at any lake productivity level, and did not vary in response to changes in τ (Fig. 3). Indeed, only under extreme and unrealistic

parameterisations could we force subsidy of zoobenthos production in our model. Both ecosystem-scale (τ) and organismal parameters had to be manipulated to create a subsidy (Fig. 4). Removal of zoobenthos preference for periphyton and a reduction of zoobenthos growth efficiency when using periphyton to 0.01 resulted in a

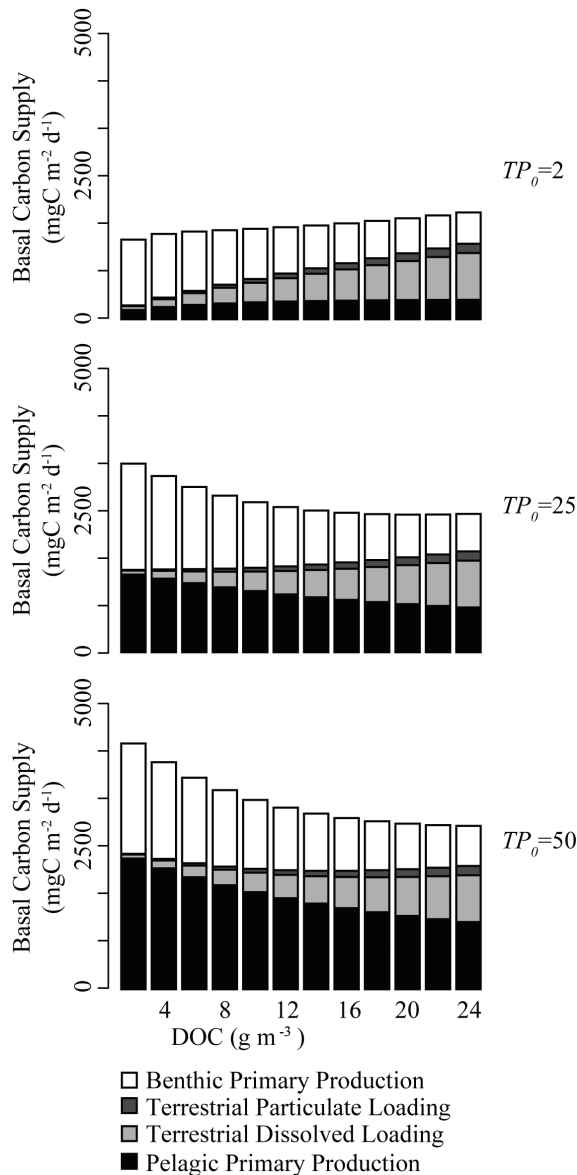


Fig. 2. Basal carbon supply (within-system primary production and terrestrial carbon load) for simulations of our lake productivity model across a gradient of terrestrial inputs (dissolved organic carbon, DOC). Each panel presents results for one level of within-system productivity ($TP_0 = 2, 25, 50 \text{ mg m}^{-3}$).

simulation where zoobenthos production remained nearly constant with greater terrestrial carbon loading (Fig. 4, lower left). To induce subsidised zoobenthos production (Fig. 4, lower right) the above unrealistic parameterisation and a terrestrial loading index (τ) of 100 were required.

In general, organismal-scale parameters had little influence on subsidy of secondary production. Growth efficiency parameters and consumer preferences had only weak effects on the presence or absence of subsidies for zooplankton and zoobenthos (Fig. 4 and Appendix Figs. 4–6). Growth efficiencies had strong impacts on the magnitude of consumer production at a given DOC concentration,

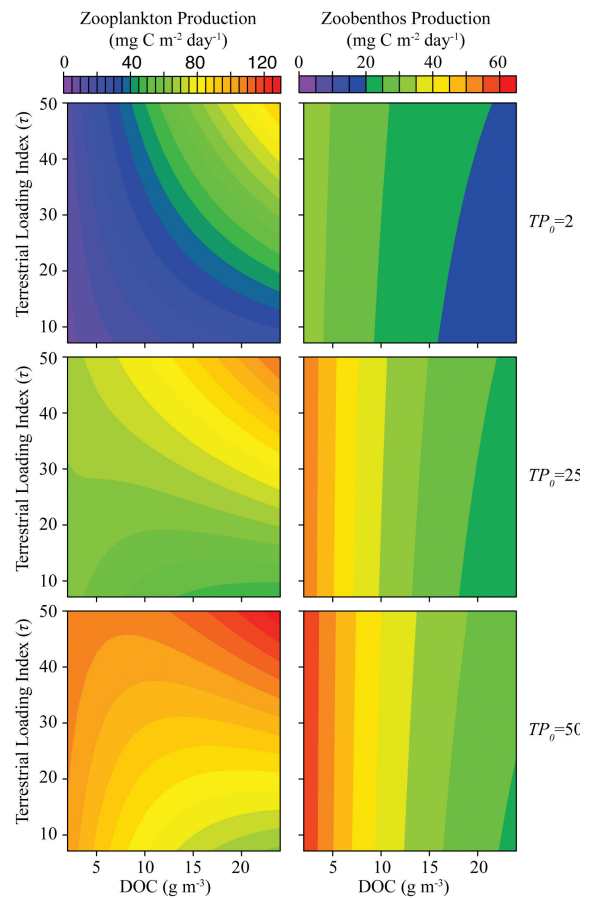


Fig. 3. Zooplankton (left column) and zoobenthos (right column) production in our model simulations. Within system primary productivity varies with panel rows ($TP_0 = 2, 25, 50 \text{ mg m}^{-3}$). Each panel presents consumer production at combinations of dissolved organic carbon (DOC) concentrations and values of the terrestrial loading index parameter (τ) in our model. τ represents how much DOC load is required to achieve a given steady-state DOC concentration.

but again, rarely influenced the qualitative response of consumer productivity to terrestrial carbon enrichment.

Discussion

The first goal of our modeling effort was to determine whether elevated terrestrial carbon loading would increase or decrease the total basal resource supply, regardless of source or quality. The flux of terrestrial DOC and POC directly acts to increase basal resources, but important indirect mechanisms were also included in our model. Our simulations suggest that, except in the most oligotrophic systems, the negative influence of DOC shading on autochthonous primary production exceeds the positive effects of DOC on resource availability via direct supply of fixed C and potential fertilisation of autochthonous production (Fig. 2). A recent survey of fifteen Swedish lakes lends empirical support for our basal carbon findings. Ask et al. (2009) explored the relationship between lake DOC concentration and aquatic energy mobilisation (pelagic, benthic, and whole-lake). These researchers defined energy mobilisation as the combination of primary production and terrestrial-supported bacterial production, a measure that should be strongly and positively correlated with our simulated basal carbon supply. They found a significant decrease in whole-lake energy mobilisation along a gradient of increasing DOC. In addition, DOC negatively influenced benthic energy mobilisation, but pelagic energy mobilisation had a weak positive correlation with lake DOC concentration. These findings qualitatively agree with our model results.

We found that an increase in basal carbon resources with increasing terrestrial organic carbon supply provided the potential for subsidy of zooplankton. For zoobenthos, in contrast, our modeling suggests that subsidy by terrestrial inputs is unlikely; we could induce a subsidy for zoobenthos only under extreme parameterisations. This contrast occurred because terrestrial carbon inputs were more accessible to zooplankton than to zoobenthos. The dominant, dissolved portion of the terrestrial load is accessible to zooplankton via the microbial loop, and the particulate portion is accessible via direct consumption.

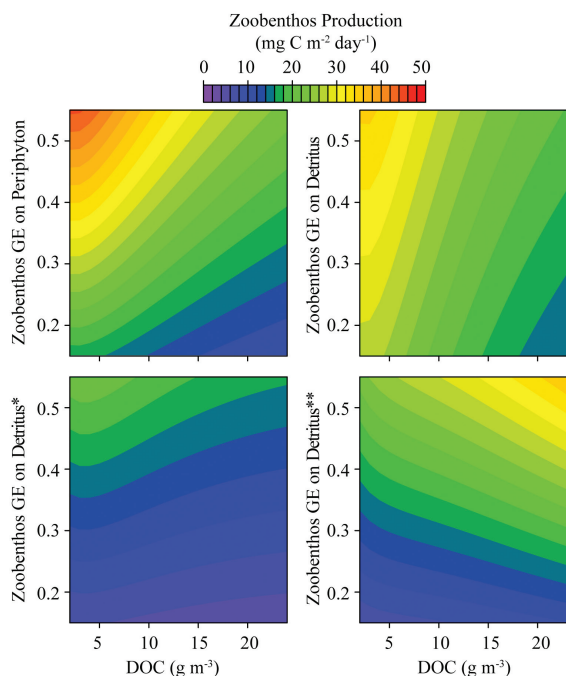


Fig. 4. Zoobenthos production as a function of dissolved organic carbon (DOC) concentrations and zoobenthos growth efficiencies, in low productivity lake ($TP_0 = 2 \text{ mg m}^{-3}$). Results in the lower two panels come from simulations with non-default parameterisations: *Zoobenthos use of periphyton was not extremely inefficient ($GE_{\text{TBp,Zb}} = 0.01$) and zoobenthos had no preference for periphyton. **Zoobenthos use of periphyton was extremely inefficient ($GE_{\text{TBp,Zb}} = 0.01$), zoobenthos had no preference for periphyton, and the terrestrial loading index (τ) was 100, where τ represents how much DOC load is required to achieve a given steady-state DOC concentration.

While both forms of terrestrial C are also available to zoobenthos, the link to the dominant dissolved portion of the DOC load is mediated by flocculation of DOC, and this flux appears to be too small to significantly enhance resource availability for zoobenthos (see Appendix Fig. 3). Our prediction of a net negative effect of terrestrial C inputs on benthic secondary production at the whole-lake level matches results from a recent survey of 12 Swedish lakes (Karlsson et al., 2009), and may be a general feature of natural systems. Nonetheless, different patterns might be observed at a finer spatial grain; for instance, the whole-lake POC:DOC loading ratios that we used might not accurately reflect the loading of these resources in nearshore littoral areas, where inputs of leaves and other terrestrial POC can be quite high (Preston et al., 2008). Terrestrial inputs could

perhaps have a net positive effect on nearshore zoobenthos despite having a net negative effect on zoobenthos at the whole-lake level. Additionally, our predictions for zoobenthos could be wrong if in fact zoobenthos prefer detritus over periphyton as a resource. Further modeling and experimental work is needed to resolve these questions.

Variation across a DOC gradient in the extent to which terrestrial inputs subsidise consumers is not necessarily correlated with variation in the extent to which consumers utilise terrestrial inputs across that gradient. Previous research using stable isotope tracers has demonstrated that zoobenthos and zooplankton ingest and assimilate organic matter of terrestrial origin, and that their reliance on terrestrial OM is higher in lakes with higher DOC concentrations (Karlsson et al. 2003, Carpenter et al. 2005, Solomon et al. 2011). This same pattern occurs in our model, because utilisation is driven by resource supply (given fixed functional response and preference parameters). Yet consumer production may increase or decrease across the same gradient of terrestrial inputs, depending on the relative quality or supply of different resources (Fig. 2). Recent laboratory experiments with zooplankton make a similar point about the distinction between resource utilisation and subsidy (Brett et al. 2009). Understanding the utilisation-subsidy relationship in a field setting remains an important challenge for food web research.

The apparent contrast in the respective abilities of zooplankton and zoobenthos to access terrestrial carbon emphasises the major findings of a recent resource subsidy meta-analysis. Marczak et al. (2007) identified the “ratio of subsidy resources to equivalent resources in the recipient habitat” as an important predictor of consumer response to potential subsidies. The invocation of “equivalent resources” is directly applicable to the contrast in the likelihood of zooplankton and zoobenthos exploiting terrestrial DOC and POC in our model. In addition, lake total phosphorus (TP), which determines pelagic phytoplankton and benthic algae production, was an important determinant of the presence or absence of a zooplankton subsidy in our model. These results highlight the agreement between simulations produced by our model and general ecological theory (Polis et al., 1997; Marczak et

al., 2007), which predicts resource subsidies where subsidy supply is high relative to within system resource production.

The importance of the terrestrial loading index (τ) in our model is matched by our uncertainty about this parameter. We estimated τ from the relationship between lake DOC concentrations and annual areal loading of terrestrial DOC, based on two modeling studies (Hanson et al., 2004; Cole et al., 2006) and a lake survey (Dillon & Molot, 1997a). Better constraining the relationship between terrestrial carbon load and lake DOC concentration for a variety of systems would enable development of more robust ecosystem models and enhance our understanding of the role of fresh waters in the global carbon cycle.

In conclusion, we explored, through a simple modeling exercise, the potential for terrestrial inputs of organic matter to subsidise the production of aquatic consumers. Our findings suggest that, except in very oligotrophic systems, the negative influence of terrestrial DOC on within-system primary production via shading generally exceeds any increase in fixed C supplied by terrestrial DOC and POC inputs. Zooplankton may nonetheless be subsidised by terrestrial inputs, while the relative unavailability of terrestrial carbon to zoobenthos means that this component is unlikely to be subsidised. We believe our model captures the qualitative responses of aquatic food webs to elevated terrestrial carbon supply, but uncertainty in essentially all of the parameters in the model preclude any quantitative predictions. Further theoretical work, alongside empirical surveys and experimental studies, is required to allow improved predictions of aquatic ecosystem responses to increases in terrestrial carbon loading.

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