

LETTER

Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers

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Abstract

Carbon of terrestrial origin often makes up a significant share of consumer biomass in unproductive lake ecosystems. However, the mechanisms for terrestrial support of lake secondary production are largely unclear. By using a modelling approach, we show that terrestrial export of dissolved labile low molecular weight carbon (LMWC) compounds supported 80% (34–95%), 54% (19–90%) and 23% (7–45%) of the secondary production by bacteria, protozoa and metazoa, respectively, in a 7-km² boreal lake (conservative to liberal estimates in brackets). Bacterial growth on LMWC was of similar magnitude as that of primary production (PP), and grazing on bacteria effectively channelled the LMWC carbon to higher trophic levels. We suggest that rapid turnover of forest LMWC pools enables continuous export of fresh photosynthates and other labile metabolites to aquatic systems, and that substantial transfer of LMWC from terrestrial sources to lake consumers can occur within a few days. Sequestration of LMWC of terrestrial origin, thus, helps explain high shares of terrestrial carbon in lake organisms and implies that lake food webs can be closely dependent on recent terrestrial PP.

Keywords

Allochthony, lake secondary production, low molecular weight organic carbon.

Ecology Letters (2010) 13: 870–880

INTRODUCTION

More than 40 years ago Nauwerck (1963) found that phytoplankton production was insufficient for supporting zooplankton secondary production in the mesotrophic lake Erken and suggested additional contributions from allochthonous (terrestrial) sources via bacteria and detritus. In recent years, it has been confirmed that bacterial metabolism in unproductive to moderately productive lakes is subsidized by allochthonous organic carbon (Hessen 1998; Jansson *et al.* 2007; Reynolds 2008) and that the biomass of consumers at higher trophic levels, like zooplankton and fish, to a significant extent (20–80%) consists of allochthonous carbon (Hessen 1998; Karlsson *et al.* 2003; Carpenter *et al.* 2005). Bacterial production (BP) fueled by allochthonous dissolved organic carbon (DOC) (Karlsson *et al.* 2003; Jansson *et al.* 2007) or consumer use of

allochthonous particulate organic carbon (POC) (Hessen 1998; Pace *et al.* 2004; Carpenter *et al.* 2005) are suggested links between terrestrial carbon and lake secondary production. However, it remains to be explained how allochthonous compounds or particles, which are often refractory and used with extremely low growth efficiencies (Kritzberg *et al.* 2005; Brett *et al.* 2009), are able to support large parts of lake secondary production. A possible explanation can be found in new results and novel concepts on the turnover of labile dissolved low molecular weight carbon (LMWC) in forest soils and the microbial consumption of such compounds in aquatic systems.

The forest soil LMWC pool (organic acids, free amino acids and simple carbohydrates) in temperate and boreal areas has recently been shown to have a very short turnover time (1–10 h) due to rapid microbial use of LMWC (van Hees *et al.* 2005; Boddy *et al.* 2008). Soil LMWC input

is, therefore, much larger than previously thought. Besides release from cell lysis and heterotrophic degradation of litter and humus, the input of LMWC to soils is strongly dependent on the flux of LMWC from canopies to roots (Jones 1998; Giesler *et al.* 2007). LMWC compounds serve as bacterial substrates in freshwaters (Rosenstock & Simon 1993; Tranvik & Jørgensen 1995) but their origin, distribution and utilization are poorly documented. A series of recent studies (Berggren *et al.* 2007, 2009; Ågren *et al.* 2008) showed that LMWC was a major driver of BP in boreal streams and lakes receiving drainage from boreal coniferous forests, and that organic acids, amino acids and simple carbohydrates were critical components of this LMWC (Berggren *et al.* 2010). The composition of the aquatic LMWC pool (Berggren *et al.* 2010) was similar to what has been described for temperate and boreal soil systems (Strobel 2001; van Hees *et al.* 2005; Giesler *et al.* 2007), suggesting that the input of LMWC to streams is intimately linked to the soil LMWC pool. Although LMWC only made up between 1 and 8% (mean 3.5%) of the total DOC concentrations in the investigated headwater streams, it supported 15–100% of the bacterial DOC consumption (means: 86% in forest drainage and 16% in mire drainage). Thus, compared to its share of total DOC, LMWC had an unproportionally large impact on aquatic bacterial metabolism (Fig. 1).

High soil turnover rates of LMWC (van Hees *et al.* 2005; Giesler *et al.* 2007), the efficient aquatic bacterial use of LMWC (Berggren *et al.* 2010) and the role of bacteria in aquatic food webs (Jansson *et al.* 2007) lead us to the following hypotheses: (1) that soil pools of LMWC can serve as a significant source for drainage of labile bacterial substrates into aquatic systems, and (2) that uptake of this carbon in bacteria and subsequent grazing on bacteria

contribute substantially to lake secondary production. We tested these hypotheses in boreal ecosystems by first using the literature data to calculate the terrestrial LMWC fluxes and the soil drainage of LMWC in a relatively large boreal catchment (Örträsket catchment). We then modelled LMWC input and the subsequent support of bacterial production (BP_{LMWC}) in Örträsket. Finally, we calculated the transfer of LMWC to higher trophic levels in the lake ecosystem using published data on bacterivory and metazoan contents of terrestrial carbon.

MATERIAL AND METHODS

Study sites

Data of bacterial consumption of LMWC (Berggren *et al.* 2010), used for modelling lake input and fate of LMWC (see below), were collected in headwater streams in the Krycklan catchment (Berggren *et al.* 2007) at the Vindeln Experimental Forests (64°14' N, 19°46' E) in northern Sweden. The streams represented catchments (13–95 ha) with different proportions of the two dominating boreal landscape components, i.e. coniferous forests and wetlands (mires). The forest component of the catchments was dominated by Norway Spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), whereas mires were of ombrotrophic or oligotrophic minerogenic character and dominated by peat forming *Sphagnum* species. A detailed description of the methods used in the Krycklan catchment LMWC bioassays can be found in Appendix S1a.

Calculations of large scale catchment LMWC fluxes and modelling of lake input of LMWC and subsequent effects on lake heterotrophic BP and lake food webs were carried out using a relatively large (area 7.3 km², mean depth 23 m) lake, Örträsket (64°10' N, 18°55' E), and its catchment (area 2210 km²; see map in Figure S1). Despite the high ratio between catchment area and lake area, Örträsket has a theoretical water retention time that is typical for the large number of Swedish boreal lakes, i.e. 2–3 months. The catchment consists of coniferous forests (75%) and mires (20%) of the same types as in the Krycklan catchment and a recent study (Köhler *et al.* 2008) demonstrated a strong agreement in hydrology and DOC export dynamics between the Krycklan and Örträsket catchments. Anthropogenic influences except for forestry are negligible. Örträsket is moderately humic, with DOC concentrations between 8 and 10 mg L⁻¹ which are close to the mean for boreal lakes (Sobek *et al.* 2007). Studies of the lake during the 1990s (Jansson *et al.* 1996; Bergström & Jansson 2000; Meili *et al.* 2000; Jonsson *et al.* 2001; Drakare *et al.* 2003; Bergström 2009) have provided published data on river discharge, BP, grazing on bacteria, phytoplankton primary production

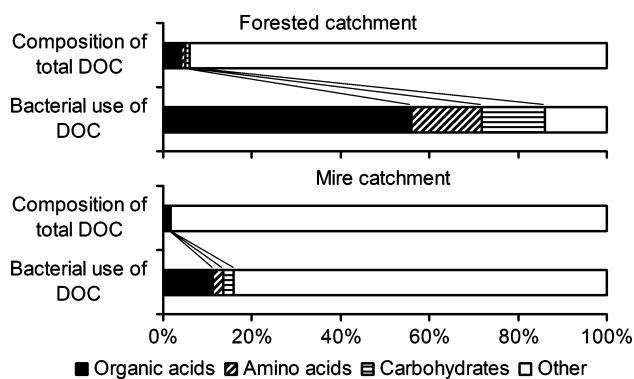


Figure 1 Composition of total dissolved organic carbon (DOC) and bacterial use of different DOC fractions in streams draining forested and mire covered catchments in northern Sweden. Data from Berggren *et al.* (2010).

(PP), allochthonous carbon contents (allochthony) of metazoan zooplankton and biomasses of different components of the planktonic food web.

Monitoring of Örräsket

Örräsket was subject to intensive studies in 1994–1997; especially during the periods from snow melt in spring to the end of summer stratification. We selected 1994, 1995 and 1997 for this study, as these years adequately represented average conditions over a longer period (1987–2006) when discharge and DOC were monitored in the catchment. While the values of discharge and DOC export during snow melt and summer of 1996 were *c.* 2 standard deviations (SD) lower than the 20-year means, values from 1994, 1995 and 1997 showed at most 0.5 SD difference from mean conditions (Figure S2).

Discharge during the ice free seasons was estimated using established relationships between discharge and water levels at the lake outlet (Bergström 2009). In winter, discharge was measured 50 km downstream of the lake at the Torrböle sampling station (see map in Figure S1), which is included in the Swedish national surface water quality monitoring program. We found no systematic differences in mean specific discharge between Örräsket outlet and Torrböle. DOC was measured every second week during the ice free season in the two major inlets of Örräsket, using a Shimadzu TOC 5000 (Kyoto, Japan) (Bergström & Jansson 2000). These inlets drain 96% of the catchment area. Mean inlet DOC concentration was calculated as the catchment area weighted average values from the two inlets. In winter, DOC concentrations were estimated from total organic carbon measured monthly at Torrböle. The POC fraction of total organic carbon (< 5% in surface waters of the Örräsket catchment) was considered negligible (Ivarsson & Jansson 1994). During the whole study period, Örräsket inlet water absorbance at 420 nm was estimated from measurements at Torrböle, performed monthly with a UNICAM 8625 on filtered samples. A comparison with measurements on Örräsket inlet water in 1995 and 1997 (Bergström & Jansson 2000) showed that measurements performed on Örräsket inlet water differed marginally, by 10% on average, from the measurements at Torrböle (see data in Figure S3). Temperature profiles were obtained at each lake sampling date and used to calculate volumes above and below the thermocline depth, defined as the mid-depth of the transect where temperature changes > 1 °C m⁻¹. The BP and PP were measured using modified versions of the H³ leucine and ¹⁴C methods (Jansson *et al.* 1996). Numbers of bacteria, phytoplankton, flagellates, ciliates and metazoan zooplankton were counted on each sampling date and the biomasses were determined (see Appendix S1b).

Modelling of LMWC support of Örräsket bacterial metabolism

Bacterial production based on LMWC (BP_{LMWC}) was calculated by applying a series of equations (eqns 1–7), iteratively for each day in sequence, starting from 1 January 1993. The iteration was initiated 1 year prior to the study period (1994–1997), so that arbitrary start values of lake concentrations of LMWC could be used without affecting model output. To obtain daily values of input variables, linear interpolations between measurements were performed.

The input concentration of LMWC to Örräsket, LMWC_{in} (mg L⁻¹), during any given day was calculated according to eqn 1,

$$\text{LMWC}_{\text{in}} = \text{DOC} \cdot ([-0.57] \cdot a_{420} + 9.06)/100 \quad (1)$$

and based on a negative linear relationship between LMWC (% of DOC) and a_{420} expressed in m⁻¹ (Fig. 2). This relationship (eqn 1, $R^2 = 0.68$, $n = 6$, $P < 0.05$) was obtained by using bioassay data from the three Krycklan streams draining forest, mire and lake catchments, sampled during two different hydrological situations (Berggren *et al.* 2010). The validity of the relationship was tested against data from Jonsson *et al.* (2007b), where LMWC was measured in water drained from a subarctic catchment (inlet to Lake Diktär-Erik) using the same methods as in Berggren *et al.* (2010). The LMWC substrate composition in Jonsson *et al.* (2007b) and Berggren *et al.* (2010) was similar (*c.* 2/3 of total number of detected compounds were found in both studies and in similar concentrations). Excluding non-labile LMWC compounds (*sensu* Berggren *et al.* 2010), the relation between

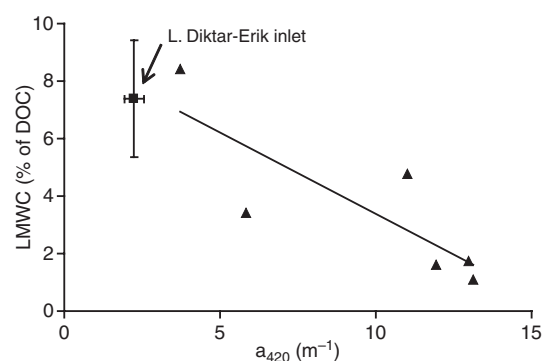


Figure 2 The relationship between low molecular weight organic carbon compounds (% of DOC) and a_{420} ($-0.57 \cdot a_{420} + 9.06$, $R^2 = 0.68$, $n = 6$, $P < 0.05$) in forest, mire and lake catchments sampled in the Krycklan catchment during different stages of the snow melt spring flood of 2007 (triangles). For comparison, the subarctic catchment of Lake Diktär-Erik (Jonsson *et al.* 2007b) in northern Sweden (square) is shown as mean \pm 95% CI of 21 measurements.

LMWC (% of DOC) and a_{420} was the same in the Jonsson *et al.* (2007b) and Berggren *et al.* (2010) data, as suggested by the regression (Fig. 2; eqn 1).

For any given day, it was considered that a certain volume of inflowing water (Vol_{inflow}) mixes with a certain volume of epilimnetic (Vol_{epi} ; above mid-thermocline depth) lake water. During downward dislocation of the thermocline, an additional volume of hypolimnetic water ($Vol_{hypo\ flow}$) mixes into the epilimnion. The volume weighted average LMWC concentrations of the different volumes that mix on a given day were used to calculate the resulting concentration ($LMWC_{epi\ mix}$), according to eqn 2 (days without downwards thermocline dislocation) or eqn 3 (days with downwards thermocline dislocation). $Vol_{hypo\ flow}$ was given from the increase in epilimnetic volume from the previous day.

$$LMWC_{epi\ mix} = \frac{LMWC_{in} \cdot Vol_{inflow} + LMWC_{epi} \cdot Vol_{epi}}{Vol_{inflow} + Vol_{epi}} \quad (2)$$

$$LMWC_{epi\ mix} = \frac{LMWC_{in} \cdot Vol_{inflow} + LMWC_{hypo} \cdot Vol_{hypo\ flow} + LMWC_{epi} \cdot Vol_{epi}}{Vol_{inflow} + Vol_{hypo\ flow} + Vol_{epi}} \quad (3)$$

During a day with upwards thermocline dislocation, the hypolimnetic LMWC concentration ($LMWC_{hypo\ mix}$) resulting from mixing of epilimnetic water ($Vol_{epi\ flow}$) that enters the hypolimnion (Vol_{hypo}) was calculated using eqn 4. During a day without upwards thermocline dislocation, the $LMWC_{hypo\ mix}$ was unaffected by mixing with epilimnetic water (eqn 5). $Vol_{epi\ flow}$ was given from the decrease in epilimnetic volume from the previous day.

$$LMWC_{hypo\ mix} = \frac{LMWC_{epi} \cdot Vol_{epi\ flow} + LMWC_{hypo} \cdot Vol_{hypo}}{Vol_{epi\ flow} + Vol_{hypo}} \quad (4)$$

$$LMWC_{hypo\ mix} = LMWC_{hypo} \quad (5)$$

The bacterial consumption of LMWC from a day (t) to the next day ($t + 1$) was calculated by using the average relative LMWC assimilation rate (AR_{LMWC} ; 8.2% day^{-1}) obtained from the bioassays experiments (Berggren *et al.* 2010). As the consumption rate in these experiments was measured at fixed temperature of 20 °C, a Q_{10} correction of the rate to *in situ* temperatures was performed, assuming Q_{10} of 2.5 (Pomeroy & Wiebe 2001). Thus, $LMWC_{epi}(t + 1)$ and $LMWC_{hypo}(t + 1)$ was calculated as shown by eqns 6 and 7.

$$LMWC_{epi}(t + 1) = LMWC_{epi\ mix}(t) - LMWC_{epi\ mix}(t) \cdot AR_{LMWC} \cdot Q_{10}^{(Temp_{epi} - 20)/10} \quad (6)$$

$$LMWC_{hypo}(t + 1) = LMWC_{hypo\ mix}(t) - LMWC_{hypo\ mix}(t) \cdot AR_{LMWC} \cdot Q_{10}^{(Temp_{hypo} - 20)/10} \quad (7)$$

BP_{LMWC} ($\mu g\ C\ L^{-1}\ day^{-1}$) in the epilimnion of the lake was calculated according to eqn 8. Bacterial growth efficiency (BGE) was set to 0.28, following Berggren *et al.* (2010).

$$BP_{LMWC} = 1000 \cdot BGE \cdot LMWC_{epi} \cdot AR_{LMWC} \cdot Q_{10}^{(Temp_{epi} - 20)/10} \quad (8)$$

Assessing the support for Örträsket food webs during the summer period

A flow scheme was constructed following the fluxes of LMWC from trees to soils, via streams to Örträsket, and further to incorporation into bacteria and bacterivorous grazers. By focusing on processes (and not organism groups), we could separate all fluxes in spite of the high

abundance of mixotrophic plankton in the lake (Bergström 2009). All fluxes in this model were standardized to lake area and expressed as $mg\ C\ m^{-2}\ day^{-1}$.

The flux of LMWC from trees to soils was calculated by scaling the value from Giesler *et al.* (2007) to the Örträsket catchment area. Losses of LMWC from soils to streams were estimated by combining the literature data on total terrestrial organic carbon export from the Örträsket catchment (Algesten *et al.* 2004) with bioassay data from Berggren *et al.* (2010), as described in Appendix S1c. Input of LMWC to Örträsket was calculated as the average daily input during the summer period obtained by multiplying input concentrations (eqn 1) with discharge. Transit times of LMWC from soil discharge to the inlets of Örträsket were estimated by dividing upstream surface water volumes (running waters and small lakes) with total discharge. The volumes of streams and lakes upstream Örträsket were calculated using data from Jonsson *et al.* (2007a).

Average summer season values of BP and PP were obtained from the means of daily values of BP and PP, estimated by linear interpolation between measurements. The average LMWC support for BP was given by the mean of daily BP_{LMWC} model output values (eqn 8). Incorporation of carbon derived from PP into bacteria (BP_{auto}) was calculated following Karlsson *et al.* (2003), assuming that 37% of PP (phytoplankton exudate production and DOC release from zooplankton grazing on phytoplankton) was incorporated into bacteria with an efficiency of 0.26

Table 1 Parameter values used for modelling terrestrial drainage of organic carbon its impact on the food web of Örrträsket

Parameter	Value used	Error range	Source
Bacterial GE on LMWC	0.28	0.23–0.32*	Berggren <i>et al.</i> (2010)
Bacterial GE on phytoplankton exudates	0.26	0.20–0.37†	del Giorgio & Cole (1998)
Bacterial assimilation of ambient LMWC concentrations (AR_{LMWC} ; day^{-1}) at 20 °C	0.08	0.06–0.11†	Berggren <i>et al.</i> (2010)
Q_{10} for bacterial assimilation of LMWC	2.5	2–3‡	Pomeroy & Wiebe (2001)
Flagellate CR ($nL\ individual^{-1}\ h^{-1}$)	1.3§	0.8–1.4†	Bergström (2009)
Ciliate¶ CR ($nL\ individual^{-1}\ h^{-1}$)	105	70–140*	Stabell (1996)
Ciliate** CR ($nL\ individual^{-1}\ h^{-1}$)	30	3–78‡	Simek <i>et al.</i> (1996)
Protist assimilation of TC_{other} ingested (cleared) in the form of POC	0.10	< 0.10††	Sturner & Hessen (1994), Hessen (1998)
Protist GE on bacteria and phytoplankton	0.30	0.20–0.40†	Straile (1997)
GE on assimilated particulate TC_{other}	0.10	< 0.10††	Valiela (1995)
Picoplankton of phytoplankton biomass	0.17	0.12–0.22*	Drakare <i>et al.</i> (2003)
Metazoan GE	0.25	0.15–0.40†	Straile (1997)
Cladocera turnover (day)	14	11–18†	Wetzel (2001)
Copepod turnover (day)	19	12–24†	Wetzel (2001)
Rotifer turnover in summer (day)	8.3	6.7–11.1‡	Straile (1998)
Allochthony of metazoan zooplankton (biomass-weighted summer mean)	0.38	0.32–0.45‡	Calculated from Meili <i>et al.</i> (2000)
POC in relation to DOC	0.05	< 0.05††	Ivarsson & Jansson (1994), A.K. Bergström (unpublished data)
a_{420}	Estimated daily	$\pm 10\%‡‡$	See text and Figure S3
LMWC (% of DOC) estimated from a_{420}	Estimated daily	$\pm 33\%‡‡$	See text and Fig. 2

LMWC, low molecular weight carbon; POC, particulate organic carbon; DOC, dissolved organic carbon; CR, clearance rate; GE, growth efficiency (see also text).

*Standard deviations.

†Quartiles.

‡Range.

§Mean of separate values used for different sampling dates and different groups of flagellates.

¶Bacteria and picophytoplankton grazing ciliates (mainly small oligotrichs).

**Bacteria and phytoplankton (all sizes) grazing ciliates (mainly prostomatids).

††Liberal parameter.

‡‡Average regression residuals as per cent of estimated value.

(del Giorgio & Cole 1998). Support for BP by other carbon sources than terrestrial LMWC or PP was estimated by subtracting BP_{LMWC} and BP_{auto} from the measured total BP.

Heterotrophic protozoan production (by flagellates and ciliates) was calculated by multiplying grazer concentrations ($individuals\ L^{-1}$) with clearance rates (Table 1), food biomasses ($C\ L^{-1}$) and appropriate growth efficiencies (Table 1). Protozoans were also considered to ingest, assimilate and grow directly on allochthonous POC, according to published literature values of POC assimilation and growth efficiency. See Appendix S1d for detailed description of the heterotrophic protozoan production calculations.

Production of metazoan zooplankton was calculated as the sum of cladoceran, copepod and rotifer production, estimated by dividing the biomass of each group (summer means) with literature values of their biomass turnover time

(Table 1). In terms of biomass, the metazooplankton community was dominated by a few species of *Bosmina*, *Cyclops* and *Eudiaptomus* that are not known to preferentially graze on bacteria or POC (Hessen 1998). Reported bacterial clearing rates by *Bosmina* show a narrow range around $10\ \mu L\ individual^{-1}\ L^{-1}\ h^{-1}$ (Vaque *et al.* 1992). Combining this rate and the *Bosmina* numbers in Örrträsket (summer mean of $1\ L^{-1}$) give a total clearance by *Bosmina* two orders of magnitude lower than the clearance by flagellates or ciliates, which is negligible in this study. Daphnids, which have been shown to significantly gain carbon directly from bacteria or POC in other studies (Hessen 1998; Pace *et al.* 2004; Carpenter *et al.* 2005), were absent from Örrträsket (or present in non-significant numbers) on all sampling dates. Therefore, the production of metazooplankton based on terrestrial carbon was assumed to be channelled via ingestion of phagotrophic microorganisms (flagellates and ciliates).

All parameters and estimates used in the modelling of terrestrial export of LMWC and the impact of LMWC and other carbon sources on the food web of Örrträsket are shown in Table 1. Raw data for the most important input variables are shown in Figure S4. A sensitivity analyses was performed by manipulating all parameters within their error ranges (Table 1), in all possible combinations or low or high ends, to assess the maximum error in modelled values of LMWC support of lake secondary production.

RESULTS

The input of LMWC to soils in the Örrträsket catchment was estimated to be in the order of 10^6 kg C day⁻¹ or, standardized to lake area, 10^5 mg C m⁻² day⁻¹. A small portion of this flux (*c.* 552 mg C m⁻² day⁻¹) was exported from soils into streams and lakes of the catchment. The mean input of LMWC to Örrträsket during 1994, 1995 and 1997 was 417 mg C m⁻² day⁻¹ (SD = 65).

Modelled BP_{LMWC} in Örrträsket was in the range of 0.1–10 µg C L⁻¹ day⁻¹ (Fig. 3). The relationship between modelled values of BP_{LMWC} and measured BP (Fig. 3) suggests that LMWC supported *c.* 50–100% of BP, with the highest relative support at low values of BP (< 1 µg C L⁻¹ day⁻¹) occurring mainly during periods of low PP. The LMWC flux model for Örrträsket and its catchment (Fig. 4) showed that input of LMWC to Örrträsket fueled 33.0 mg C m⁻² day⁻¹ (80%) of the total summer season BP in the epilimnion of the lake (mean 1994, 1995 and 1997). Most of the BP (and the BP_{LMWC}) was ingested by flagellates and ciliates, supporting heterotrophic protozoan production. Terrestrial LMWC thereby

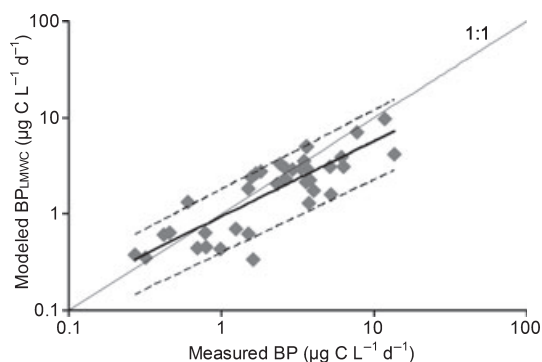


Figure 3 Modelled bacterial production based on terrigenous low molecular weight organic carbon compounds as a function of measured bacterial production ($y = 0.94x^{0.78}$, $R^2 = 0.68$, $n = 37$, $P < 0.001$). Upper ($y = 1.78x^{0.82}$, $R^2 = 0.68$) and lower ($y = 0.39x^{0.76}$, $R^2 = 0.65$) dashed regression lines show the corresponding relationships at maximum and minimum support for BP_{LMWC}, obtained by manipulating all involved parameters and estimates within the error ranges shown in Table 1.

became efficiently integrated into the lake food web. Of the mean total production of heterotrophic protozoans of 20.8 mg C m⁻² day⁻¹ (SD = 5.3), 17.9 mg C m⁻² day⁻¹ (SD = 5.4) was of terrestrial origin and 11.3 mg C m⁻² day⁻¹ (SD = 4.0) was based on BP_{LMWC} (Fig. 4). The importance of BP_{LMWC} was further highlighted by the fact that it corresponded to 72% of the phytoplankton PP in summer (33.0 compared to 45.7 mg C m⁻² day⁻¹) and exceeded PP on an annual basis (17.8 compared to 12.3 mg C m⁻² day⁻¹) assuming no PP under ice.

Mean production of metazoan zooplankton was 6.1 mg C m⁻² day⁻¹ (SD = 1.4) and 38% of this production (range 32–45%) was based on carbon from terrestrial sources. Under the assumption that input of allochthonous organic carbon into metazoan production occurs predominantly via predation on protists, the majority of the metazoan contents of allochthonous carbon originated in LMWC (Fig. 4).

Seasonally, lake LMWC input, BP_{LMWC} and measured BP showed clear couplings to runoff variation (shown in detail for 1997 in Fig. 5 and for all years in Figure S4). High flow episodes (spring flood and summer rain storms) transported large amounts of LMWC to the lake causing peaks in BP_{LMWC} and total BP (Fig. 5b). In 1997 (Fig. 5a) and in the other study years, the metazoan zooplankton biomass was the highest after the BP_{LMWC} peaks, but before the phytoplankton PP peak.

The LMWC support of summer season secondary production by bacteria, protozoa and metazoa was 80, 54, and 23%, respectively, (Fig. 4) and showed similar values in all years (Figure S1). When all sources of error (Table 1) were taken into account, the LMWC pathway still supported a significant share of lake secondary production. The maximum error, obtained by manipulating all parameters and estimates within their error ranges (Table 1), in all possible combinations or low or high ends, gives ranges in LMWC support of modelled secondary production of 34–95% for bacteria, 19–90% for protozoa and 7–45% for metazoa.

DISCUSSION

Our results (Fig. 4) show that terrestrial export of LMWC can be an effective driver of lake secondary production via promotion of BP and subsequent protozoan bacterial grazing. We also demonstrate that this LMWC provides significant support for metazoan zooplankton production which is important since metazoans serve as a bridge between production at lower trophic levels and top fish consumers (Jansson *et al.* 2007).

Input to the soil pool of LMWC potentially includes exudates from roots and microorganisms, degradation products of dead plant material and release of carbon from

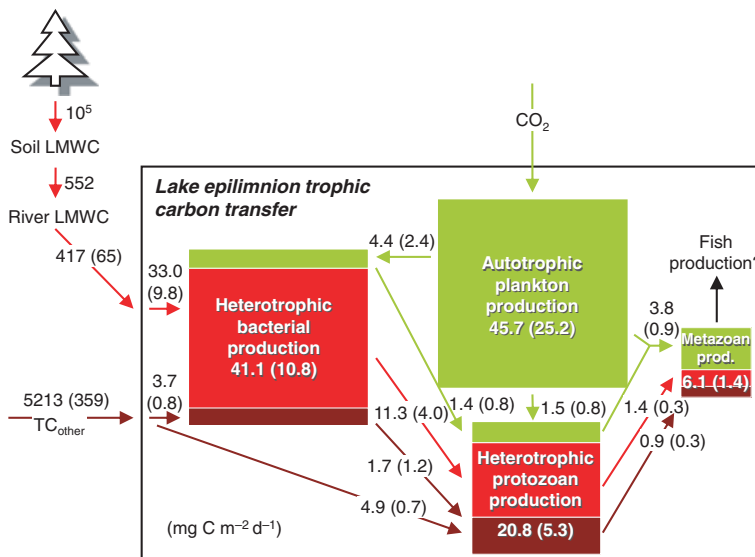


Figure 4 Mean daily summer fluxes of organic carbon (standardized to lake area) to and within the epilimnion of Örrträsket in northern Sweden. All fluxes are shown in mg C m⁻² day⁻¹, as mean values based on data from 1994, 1995 and 1997, with between-year standard deviations in brackets (see values for each year in Table S1). Fluxes within the epilimnion represent net uptake of carbon and boxes represent processes of production. It is assumed that the proportions of carbon of different origin (LMWC, TC_{other} and phytoplankton) in one box represent the proportions of carbon transfer to the next box. LMWC: low molecular weight organic carbon of terrestrial origin. TC_{other} : organic carbon of terrestrial origin minus LMWC.

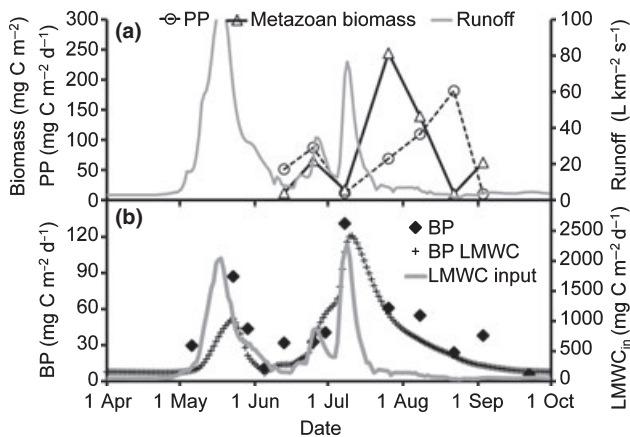


Figure 5 Temporal patterns in measured and modelled processes in Örrträsket in the summer season of 1997. (a) Primary production (PP), metazoan biomass and runoff. (b) Measured bacterial production (BP), modelled LMWC support of BP (BP_{LMWC}) and modelled lake LMWC input. All variables are standardized to lake area (m²) except for catchment runoff which is standardized to catchment area (km²).

lysis of microorganisms during thawing of soil frost (Giesler *et al.* 2007), but little is known about the relative importance of different input pathways (Jones 1998). Strong arguments for the importance of a direct link from tree photosynthesis through roots and mycorrhizal fungi were offered by studies in boreal coniferous forests (Högberg *et al.* 2001, 2008) and the flux from canopies to roots has been estimated to be sufficient to renew the soil pool of LMWC *c.* 5 times per day (Giesler *et al.* 2007). This turnover is similar to the estimate of 1–10 h turnover time for boreal forests (van Hees *et al.* 2005). It is, therefore, possible that rapid allocation of tree

photosynthates can be a dominant input to soil LMWC during the vegetation period.

The carbon flux model for Örrträsket and its catchment (Fig. 4) suggested that a large part of the LMWC release from the catchment (*c.* 3/4) reached the lake. A previous study showed that significant amounts of labile allochthonous DOC were consumed in upstream lakes of the Örrträsket catchment (Berggren *et al.* 2009), and the large share of LMWC reaching Örrträsket is, therefore, likely explained by the fact that there are few and small lakes in the catchment upstream of Örrträsket (Jonsson *et al.* 2007a). Support for the assumption that our model for calculating LMWC input to Örrträsket did account for upstream consumption of LMWC was given by applying eqn 1 on the data in Berggren *et al.* (2009). This exercise suggested that LMWC concentrations could be reduced by half from the inlets to the outlets of small upstream lakes in the catchment of Örrträsket. Thus, we conclude that eqn 1 generated values that represented the actual input of LMWC to Örrträsket, after that some of it had been consumed in upstream ecosystems.

A potential source of LMWC in aquatic systems is production of LMWC compounds via photochemical processes (Bertilsson & Tranvik 1998). However, increased BP_{LMWC} during high flow (Fig. 5) shows that the LMWC input was clearly driven by hydrology and not related to light. Depletion of LMWC during river transport (Fig. 4) also argues against photochemical production of LMWC within upstream aquatic systems as an overriding source for Örrträsket. Moreover, photodegradation has shown to be of little quantitative importance in Örrträsket (Jonsson *et al.* 2001) and other humic lakes (Moran & Covert 2003). We, therefore, suggest that the occurrence of labile LMWC in surface waters is mainly a result of export of dissolved fresh

photosynthates and other labile metabolites from discharge areas of vegetation-soil systems.

The rapid turnover of the soil pool of LMWC suggests that soil LMWC which enters aquatic systems is of very recent origin (< 1 day). The time from entrance into streams to input in downstream lakes varies depending on whether lakes receive water from headwater streams (days) or from upstream areas containing other lakes (weeks–months). Örrträsket is (as most boreal lakes) a mix of these two categories. The average transit time of the surface water entering the lake during 1994, 1995 and 1997 (upstream water volume divided by discharge) was 2 weeks during major snow melt and rain events and 3–4 months on annual basis. However, more than one-third of the catchment drained into flow paths that reached Örrträsket without lake passages in only 3–5 days during average summer flow. In the lake, LMWC substrates were consumed rapidly, indicated by the measured BP which generally peaked 1–7 days after LMWC input pulses (Fig. 5; Figure S4). Moreover, 10% of the LMWC that was incorporated into bacterial biomass at a given moment could be exploited by protozoa in as little as 24 h, suggested by the protozoan grazing rates. Collectively, these results suggest that the time for significant transit of LMWC from the soil LMWC pool to incorporation in lake consumers can be less than weeks for many boreal lakes. Consequently, terrestrial LMWC export and the subsequent aquatic LMWC consumption form a close link between terrestrial PP and lake secondary production.

An important aspect is to what extent LMWC and its metabolism in lakes are able to meet the demand for terrestrial organic carbon in metazoan zooplankton relative to other possible sources. This question is not trivial since direct metazoan consumption of POC can form a quantitative important entry of terrestrial carbon into metazoans (Hessen 1998; Pace *et al.* 2004). However, the metazoan community (*Bosmina* and copepods) of Örrträsket was dominated by species which are not efficient detrital POC or bacteria feeders. We, therefore, assumed that the metazoans relied on food from the protozoan and phytoplankton communities for their carbon nutrition. The critical question is then whether metazoan use of heterotrophic protozoan production can be sufficient to explain their content of terrestrial carbon. Approximately 38% of the mean summer season metazoan body carbon content was of terrestrial origin in Örrträsket (Table 1) and according to Fig. 4 the metazoans had a net uptake of 2.3 mg terrestrial C m⁻² day⁻¹ to sustain this share. A metazoan growth efficiency of 0.25 (Straille 1997) then implies that the metazoans must have consumed about 9.2 mg terrestrial C m⁻² day⁻¹. This gross consumption could, according to our calculation (Fig. 4), be met by assuming metazoan grazing on protozoans since the

protozoans in our model had a net incorporation of 17.9 kg terrestrial C day⁻¹. Moreover, Fig. 4 shows that the majority (63%) of the estimated metazoan uptake of terrestrial carbon via grazing on protozoans came from LMWC incorporated in protozoans via grazing on bacteria.

Our results demonstrates that direct consumption of allochthonous POC or bacterial particles by metazooplankton (Brett *et al.* 2009), although common among many species (Hessen 1998) and highly important in some ecosystems (Pace *et al.* 2004), is not necessarily needed for building up large shares of terrigenous carbon in metazoan biomass. In the case of Örrträsket and many other humic systems, a dominating part of PP is performed by mixotrophic species of flagellates and ciliates, who are also responsible for most of the grazing on bacteria. This means that metazooplankton may have limited possibilities to feed on any organism without incorporating significant amounts of terrestrial carbon via the DOC (LMWC)–bacteria–protozoan pathway.

The sum of all summer season planktonic secondary production by bacteria, protozoa and metazoa was to *c.* 2/3 supported by LMWC in all study years (61% in 1994, 72% in 1995 and 69% in 1997; error range 27–92%). Thus, the mobilization of terrestrial LMWC for use in the pelagic food web made up a most significant base for the overall lake secondary production. The estimated values of this support indicate that LMWC mobilized in this respect was more important than PP. The efficient incorporation and transfer of LMWC in the lake food web depended on the fact that LMWC can be used by bacteria with a high growth efficiency (Table 1; Berggren *et al.* 2010) similar to growth on autochthonous carbon (del Giorgio & Cole 1998).

In conclusion, we demonstrate a rapid transition of terrestrial LMWC to lake secondary producers, possibly mediated by root exudation, drainage of terrestrial DOC, and subsequent heterotrophic bacterial mobilization of terrestrial carbon in aquatic systems. We suggest that LMWC consumption can equal or exceed the importance of other processes for introduction of reduced carbon into pelagic lake food webs (i.e. phytoplankton production, slow BP on refractory terrigenous carbon, or detritus consumption) and that the LMWC pathway can contribute significantly to high reliance on terrestrial carbon by zooplankton and other consumers (Meili *et al.* 2000; Karlsson *et al.* 2003; Carpenter *et al.* 2005). In our example, LMWC was a more important organic carbon source for consumers than lake PP. LMWC subsidies should not be restricted to boreal lakes, as in our example, but should be considered in lakes which are located in forested catchments and have low PP. The link from terrestrial photosynthesis to secondary producers is in its principle identical to the aquatic microbial loop concept (Azam *et al.* 1983) stating that bacterial growth recycles carbon exudates from primary producers back to

the food web, although the loop in this case functions as a bridge across ecosystem barriers. Increasing terrestrial export of allochthonous DOC, e.g., related to global change (Roulet & Moore 2006; Monteith *et al.* 2007), may decrease the whole-lake PP and lake food webs will become more dependent on alternative inputs of carbon (Karlsson *et al.* 2009). The close link between terrestrial and aquatic carbon metabolism stressed in this study indicates that the function of ecosystems and the performance of lake organisms can be highly sensitive to terrestrial vegetation characteristics, short term and long term variations of the productivity in terrestrial ecosystems, and to hydrological prerequisites for allocation of LMWC from soils to aquatic systems. Such dependence makes lakes susceptible to land use activities and climate variation via mechanisms which have not been considered previously.

ACKNOWLEDGEMENTS

Financial support for this study was given by The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas) and The Swedish Research Council (VR). Financial support for laboratory equipment was obtained from the Knut and Alice Wallenberg Foundation. We thank Michael L. Pace and two anonymous referees for constructive criticism.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figure S1 Map of the Öre River and its catchment, with position of the studied lake (Örträsket) and the Torrböle sampling station. The upper two-thirds of the Öre River catchment area drains into Örträsket.

Figure S2 Export of terrestrial dissolved organic carbon (DOC) from the Örträsket catchment plotted against discharge for each snow melt + summer period between 1994 and 1997 (diamonds). For comparison, the mean \pm SD of all periods between 1987 and 2006 is indicated by square and error bars.

Figure S3 Absorbance at 420 nm (a_{420}) in Örträsket inlet water (interpolated between measurements) plotted against a_{420} measured at Torrböle ($R^2 = 0.87$, $n = 9$, $P < 0.01$). Örträsket values show the area weighted average of the sub-catchments represented by the two major inlets of the lake.

Figure S4 Performance of the BP_{LMWC} model shown together with measured data 1994–1997. (a) Characteristics of inflowing water: Runoff, a_{420} and DOC. (b) Lake mixed layer volume (left axis), i.e. the volume above the middle of the metalimnion, shown as the grey area. Mean temperatures above ('epi temp') and below ('hypo temp') the thermocline depth are read on the right axis. (c) Modelled values of

epilimnetic bacterial production based on LMWC (BP_{LMWC}) and measured epilimnetic bacterial production (BP) plus primary production (PP). Note that although the BP_{LMWC} model generated output for all days in 1994–1997, only the summer periods of 1994, 1995 and 1997 were selected for further analysis.

Table S1 Annual values of organic carbon fluxes ($\text{mg m}^{-2} \text{ day}^{-1}$) presented (as means) in Fig. 4 of the main paper.

Table S2 Zooplankton production ($\text{mg m}^{-2} \text{ day}^{-1}$) by taxa or group.

Appendix S1 Calculations and methodological details.

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Editor, James Grover

Manuscript received 23 November 2009

First decision made 30 December 2009

Second decision made 22 March 2010

Manuscript accepted 26 March 2010