LETTER

Unimodal response of fish yield to dissolved organic carbon

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Abstract

Here, we demonstrate a contrasting effect of terrestrial coloured dissolved organic material on the secondary production of boreal nutrient poor lakes. Using fish yield from standardised brown trout gill-net catches as a proxy, we show a unimodal response of lake secondary productivity to dissolved organic carbon (DOC). This suggests a trade-off between positive and negative effects, where the initial increase may hinge upon several factors such as energy subsidising, screening of UV-radiation or P and N load being associated with organic carbon. The subsequent decline in production with further increase in DOC is likely associated with light limitations of primary production. We also show that shallow lakes switch from positive to negative effects at higher carbon loads than deeper lakes. These results underpin the major role of organic carbon for structuring productivity of boreal lake ecosystems.

Keywords

Brown trout, DOC, light, limiting factors, production, *Salmo trutta*.

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INTRODUCTION

Productivity, the rate at which biological material is synthesised, is a cornerstone in ecosystem processes. In lakes, the bottom-up flux of energy and nutrients has attracted interest partly to understand drivers of (undesirable) algal blooms, but also because the transfer up the food chain is important for higher trophic levels such as fish. Nutrient availability as a key determinant of production in aquatic ecosystems has been a well-established paradigm for decades (Schindler 1974; Elser *et al.* 2007; Gruner *et al.* 2008). While light limitation clearly may constrain primary productivity with increasing depth, notably so in productive lakes, the general held view has been that phosphorous (P) and nitrogen (N) is the overall determinant of primary production (both volumetric and area-based) in oligotrophic lakes. Recently, this view has been challenged by empirical and theoretical evidence for a more general role of dissolved organic material (DOM) in governing lake primary and secondary productivity (e.g. Karlsson *et al.* 2009; Jones *et al.* 2012).

The level of photosynthetic active radiation (PAR) may be strongly controlled by coloured DOM of terrestrial origin, of which dissolved organic carbon (DOC) is the major component. The chromophoric properties of the humic, high molecular weight compounds, strongly affect light attenuation (Jones 1992; Bukaveckas & Robbins-Forbes 2000). Small, humic, nutrient poor lakes constitute a large proportion of the freshwaters in the boreal zone (Downing *et al.* 2006; Karlsson *et al.* 2009). Here, benthic primary production supports the majority of production at higher trophic levels (Vander Zanden & Vadeboncoeur 2002; Karlsson *et al.* 2009; Solomon *et al.* 2011), and it has been suggested that DOC-induced light-limitation pose major constraints on production at all trophic levels in these lakes (Karlsson *et al.* 2009).

The net effect of DOC on secondary production is not straight-forward, however. DOC could promote lake secondary production by energy subsidising and providing a major (yet recalcitrant) source of organic C (Hessen *et al.* 1990; Cole *et al.* 2006; Weidel *et al.* 2008; Berggren *et al.* 2010; Karlsson *et al.* 2012). Also, the screening off harmful UV-radiation imposed by DOC may increase productivity (Williamson *et al.* 1996). Finally, nutrient input to oligotrophic, boreal lakes is also closely associated with the input of DOC, in boreal catchments (Dillon & Molot 2005; Hessen *et al.* 2009).

The DOC-load to surface waters is largely driven by characteristics of the terrestrial ecosystems such as wetlands, primary production and vegetation structure (Larsen *et al.* 2011a). The predicted increase in temperature and precipitation for the next century will likely increase terrestrial vegetation coverage and runoff in northern, boreal regions (Larsen *et al.* 2011b). This will contribute to a severe increase in freshwater DOC concentration leading to a water 'browning' or 'brownification' (Larsen *et al.* 2011b; Granéli 2012), eventually also accompanied by browning caused by reduced acidification (Monteith 2007). Whether the net response to DOC in terms of lake secondary production is linearly positive, negative or unimodal is not settled, however, despite the long-lasting interest in the relative role of nutrient and light as limiting factors for lake primary and secondary productivity.

In this study, we empirically test how secondary production of fish vary along a natural gradient in concentrations of DOC. Particularly, focus is on the threshold between positive and negative effect of terrestrial vegetation density and DOC on fish yield. We hypothesise that increased production of terrestrial vegetation and increased carbon load at first will promote yield of nutrient poor lakes, due to increased energy subsidises, nutrient fluxes and/or reduced UV-radiation. Beyond a certain level, the net effects of DOC on fish yield will be negative due to light

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limitation of primary production, and the positioning of this threshold will depend upon lake bathymetry.

MATERIAL AND METHODS

We explored a range of Norwegian freshwater lakes and their adjacent catchments, and used large-scale data sets of populations of brown trout (*Salmo trutta* L.) biomass (measured as fish weight per unit effort) as a proxy for lake secondary productivity at the top trophic level. Fish biomass is a well suited sentinel for secondary production that integrates energy produced in both pelagic and benthic habitats (Karlsson *et al.* 2009). Brown trout is particularly suitable by being a highly generalist feeder, which in allopatric populations utilises all available niches of the lake ecosystem (Klemetsen *et al.* 2003). The distribution of brown trout in Norway is a result of both natural immigration and historical anthropogenic translocations and the species is found across all major environmental gradients (Hesthagen & Sandlund 2004).

Brown trout catches were extracted from a database of 458 Norwegian brown trout populations, sampled by Norwegian management and research institutions in the period 1972–1997 (Ugedal *et al.* 2005). Lakes with brown trout stocking or lakes influenced directly by hydropower regulation were excluded from the analyses, along with populations under suspicion of inference from acidity (Hesthagen *et al.* 1999). A subset of the data, for which relevant water chemistry data were available, was checked for relationships between pH ($N = 100$) or acid neutralising capacity (ANC, $N = 30$) (c.f. Lydersen *et al.* 2004) and brown trout biomass. No relationship was detected between neither pH or ANC and trout biomass (pH; Pearson $r = -0.05$, $d.f. = 98$, $P = 0.593$: ANC; Pearson $r = -0.03$, $d.f. = 28$, $P = 0.863$).

To avoid confounding effects of interactions with other fish species, only lakes where brown trout was the only fish species present (allopatric) were included in the analyses. The final analyses consisted of 168 lakes distributed throughout southern Norway from 59° to 66° N (Fig. 1), located at altitudes between 50 and 1352 metres above sea level. All lakes were fished with standardised series of gillnets consisting of either eight nets (25×1.5 m) with mesh sizes from 21 to 52 mm (knot to knot) (Jensen 1977) or multi-mesh gillnets (30×1.5 m) with mesh sizes between 5 and 55 mm (knot to knot) (Appelberg *et al.* 1995). To correct for differences in catchability among the two gill net series, type of series was entered as factor in the analyses (see below). The nets were distributed at different depths along the shoreline, and the lakes were fished during late summer or early autumn, with different effort (i.e. number of gillnet series) depending on lake size. Biomass caught per unit effort (bCPUE) was based on total weight of the brown trout catch per 100 m^2 gillnet area per night. bCPUE from gillnet catches in lakes correlates strongly with fish density estimated from mark-recapture study (Density = $3.91 + 0.19$ bCPUE, $F_{1,19} = 60.53$, $P < 0.001$, $R^2 = 0.75$, O. Ugedal unpublished results), and serves as a reliable correlate for fish production (Banse & Mosher 1980; Borgstrøm 1992; Downing & Plante 1993; Randall & Minns 2000; Smokorowski & Kelso 2002).
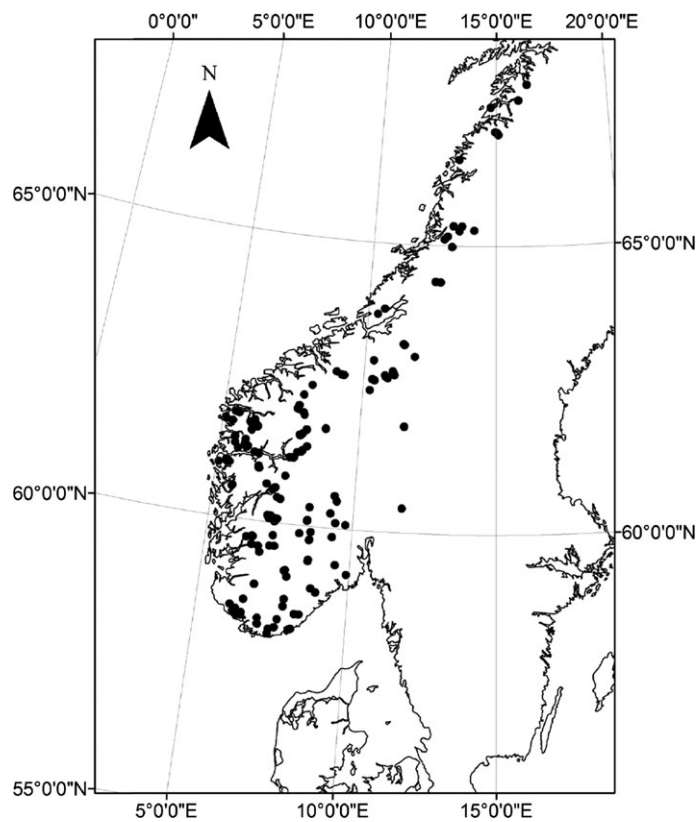

Figure 1 Positions of brown trout lakes included in this study ($N = 168$).

Bathymetric profiles were lacking for most of the lakes in the current data set. Instead, we used surrounding terrain slope (in a 100 m buffer along the lake shoreline) and lake area as proxies for lake morphology. We used a 25-m digital elevation model (DEM; from the Norwegian Mapping Authority, Statkart) to calculate slopes along the lake shoreline. Per cent slope was calculated by taking the difference in elevation (m) between adjacent cells, dividing by 25 m, and then multiplying by 100. Mean slope was extracted using a100 m buffer polygon outside the lake shoreline using ArcGIS Desktop 10.0 (ESRI, Redlands, CA, USA). Areas and lake shorelines were extracted from lake polygons provided by The Norwegian Water Resources and Energy Directorate (NVE). Surface area varied in size from 0.02 to 20.70 km^2 and terrain slope in a 100 m buffer surrounding the lake ranged from 1.4 to 26.4%. To verify the use of slope and area as bathymetric proxies, we analysed a calibration data set consisting of 194 Norwegian lakes with known depth profile obtained from NVE. Lake area (A, km^2) and surrounding terrain slope (S,%) together explained 49 and 46% of the among lake variation in maximum (D_{max}) and median (D_{median}) depth (m) respectively;

$$\ln D_{max} = 2.07 + 0.62 \ln S + 0.28 \ln A \qquad (1)$$

$$\ln D_{median} = 0.62 + 0.77 \ln S + 0.27 \ln A \qquad (2)$$

where $F_{1,191} = 96.98$, $P < 0.001$, $R^2 = 0.49$ for the maximum depth regression (eqn 1) and $F_{3,191} = 82.81$, $P < 0.001$, $R^2 = 0.46$ for the median depth regression (eqn 2). Despite a

substantial unexplained variance, there is a close functional link between shoreline slope and lake area and bathymetric profile (Håkanson & Peters 1995). Therefore these relationships do provide reliable proxies for lake mean and maximum depth.

Catchment areas upstream from each lake were delineated using a 25-m DEM and Hydrology tools in ArcGIS 10. Within each catchment, we averaged NDVI (Normalised Vegetation Density Index), mean annual air temperature (°C) and mean annual precipitation (mm/year). We also calculated fractional land cover statistics at 25-m resolution within each catchment area (percentage of bogs, agricultural land and forest) from digital maps (Norwegian Mapping Authority, Statkart).

The model verification was based on total organic carbon (TOC); however, we refer to output from our link models as DOC to keep the terminology consistent. In these boreal, low-productivity systems these metrics are almost substitutable since DOC typically constitutes 90 – 95% of TOC (Wetzel 2001; Wachenfeldt & Tranvik 2008). For the main analyses, TOC was estimated using previously established link models between catchment climate, NDVI and land cover raster's and TOC lake content, following the parameter choice and approach of (Larsen *et al.* 2011a,b), where the model was found to predict DOC with very high accuracy ($R^2 = 0.83$ for predicted vs. observed DOC) for nearly 1000 Norwegian lakes. For a subset of the lakes ($N = 30$) included in our analysis, we were able to obtain direct measurements of TOC (c.f. Henriksen *et al.* 1998), and this subset was used to test the model predictions. Comparable relationships, albeit with slightly lower fit due to fewer data points and less range in TOC values, were also observed within our data set when comparing predicted and observed TOC (linear regression, $R^2 = 0.68$, $P < 0.001$, $d.f. = 29$). Hence, we believe that our model should give a reliable estimate of TOC and hence DOC.

Lake catchments were delineated as areas upstream from each lake using a 25-m DEM and Hydrology tools in ArcGIS 10 (Finstad *et al.* 2011; Finstad & Hein 2012). The raster data used for linkmodel input and vegetation density proxy (NDVI) were the same as used by (Larsen *et al.* 2011a,b). Briefly, NDVI was obtained as monthly averages (1992–1993) at 480 m resolution from the US Geological Survey Eurasia Land Cover Characteristics database (http://edc2.usgs.gov/glcc/). Annual normal (long-term average for the period 1961–1990) mean temperature and precipitation at 1 km resolution were obtained from the Norwegian Meteorological Institute (Tveito *et al.* 2000). Runoff was based on mean yearly runoff for 1960–1990 on 1×1 km grid obtained from the Norwegian Water Resources and Energy Directorate. We also obtained the mean July air temperature at the centre point of each lake for the period 1961–1990 (Tveito *et al.* 2000) and used this metric as a proxy for ambient summer water temperatures.

We tested for the relationship between our secondary production proxy (trout bCPUE), and predicted lake DOC and terrestrial vegetation density (NDVI), by comparing a set of linear models. We entered normal July air temperatures at lake surface as a temperature proxy and gillnet series as a factor to standardise for temperature effects on production and differences in catchability among gillnet series. bCPUE, DOC,

NDVI and lake area were ln transformed before the analyses in order to stabilise variance. The hypothesised nonlinearity in the response of DOC and NDVI was tested by entering both a linear and quadratic terms for DOC and NDVI in the initial full model. We compared two different proxies for lake morphology. First, we tested for lake morphological modification of the relationship between DOC or NDVI and trout biomass using observed surrounding terrain slope and lake area directly as a morphological proxy, and entering a two-way interactions between DOC/NDVI and $DOC^2/NDVI^2$ and area or slope as well as the slope x area interaction. This yielded the following two sets of full models;

$$\ln bCPUE = \beta_0 + \beta_1 \ln X + \beta_2 \ln X^2 + \beta_3 S + \beta_4 \ln A + \beta_5 T$$
$$+ \beta_6 G + \beta_7 \ln X \times S + \beta_8 \ln X \times \ln A + \beta_9 \ln X^2 \times S$$
$$+ \beta_{10} \ln X^2 \times \ln A + \beta_{11} S \times \ln A + \epsilon$$

$$(3)$$

where X is either DOC or NDVI in each set of model, S is terrain slope in a 100 m buffer surrounding the lake, A is lake area, T is temperature and G is gillnet series (entered as factor), and β_0 to β_{11} are estimated coefficients.

Second, we illustrated the lake morphological modification of the relationship between DOC or NDVI and trout biomass using predicted median depth as a morphological proxy (eqn 2), and entering a two-way interactions between DOC/NDVI and $DOC^2/NDVI^2$ and median depth (D_{median}). This yielded the following two sets of full models;

$$\ln bCPUE = \beta_0 + \beta_1 lnX + \beta_2 \ln X^2 + \beta_3 D_{median} + \beta_4 T + \beta_5 G$$
$$+ \beta_6 \ln X \times D_{median} + \beta_7 \ln NDVI^2 \times D_{median} + \epsilon$$

$$(4)$$

where X is either DOC or NDVI in each set of model, T is temperature, G is gill-net series (entered as factor) and β_0 to β_7 are estimated coefficients.

Model selection was performed by stepwise removing terms to minimise AIC. Models with $\Delta AIC < 2$ were considered to have equal support (Burnham & Anderson 2002). Based on the parsimony principle, the simplest model with fewest terms was selected when two models were equally supported ($\Delta AIC < 2$). The final models were visually checked for spatial autocorrelation in residuals, without finding signs of violation of spatial independence. In order to test for the use of modelled DOC as proxy variable we also tested for a curve-linear relationship between measured DOC and trout biomass in a subset of lakes for which these data were available (see above). We did this by testing for the quadratic term of DOC in a linear regression model. Due to the relative low number of lakes available for this analyses ($N = 30$), we did not attempt expand the model further with other variables than the linear and quadratic term of DOC.

To obtain an empirical relationship between DOC (measured as TOC, see above), total P (TP) and total N (TN), we utilised a large database ($N = 1064$ and 1039 for TN and TP

respectively) with lake chemistry data covering the same area (but not the same lakes) as the fish survey presented here, for details, see Hessen *et al.* (2009). Here, TP and TN were regressed against DOC using linear regression. In addition, to illustrate the relationship between DOC, lake morphology and area of lake with net primary production, we utilised published relationships between organic carbon and vertical attenuation of PAR to calculate the compensation depth (deepest point of positive net primary production). The compensation depth was defined as $4.6/K_d$, where K_d is the PAR attenuation coefficient ($K_d = -0.09 + 0.19DOC$; Bukaveckas & Robbins-Forbes (2000), where DOC is in mg L^{-1}). The cumulative lake area above the compensation depth was modelled as a function of lake morphometric typology, defined by a dimensionless lake 'form factor' (V_d) defining the volume development of the lake with depth, given as the ratio between mean and maximum depth;

$$V_d = 3 \cdot D_{mean}/D_{max} \tag{5}$$

where D_{mean} is lake mean depth and D_{max} is lake maximum depth (Håkanson 2005). The cumulative area (A_d) above a given depth (D) for different lake morphologies was then given as follows:

$$A_d = A_{tot} - (A_{tot} \cdot ((D_{max} - D)/D_{max} + D \cdot \text{EXP}(3 - V_d^{1.5})))^{0.5/Vd} \tag{6}$$

where A_{tot} is the total lake area (Håkanson 2005). The area above compensation depth was then modelled as a function of DOC concentration by substituting D with the compensation depth in equation 6.

RESULTS

We found strong support for a unimodal relationship between fish biomass, measured as weight per unit effort of brown trout in gillnet catches, and concentrations of DOC or catchment terrestrial vegetation density (NDVI) (Table 1). The best model fits included both the linear and quadratic term of DOC and NDVI for all tested models.

For models using shoreline slope buffer and area as morphological proxies, we did not find support for the interactions terms between NDVI/DOC and lake area, or between slope and lake area (ΔAIC between second best and the selected model including NDVI $\times$ A and $DOC^2 \times$ A were 0.71 and 1.18 for the two model selections respectively). There was no support for further removal of terms (ΔAIC between final models excluding further terms > 7.02, with exception of removal of temperature, DOC: slope and DOC^2: slope relationship with ΔAIC = 4.76, 3.01 and 3.91 respectively).

For models using predicted median depth as morphological proxy, we did not find support for the interaction between median depth and $NDVI^2$ or DOC^2 (ΔAIC between models including $NDVI^2 \times D_{median}$ and $DOC^2 \times D_{median}$ and models without these interactions were 0.05 and 1.91 respectively). July temperature had only a weak effect in the two models including NDVI (ΔAIC between models with and without temperature was < 1.01 for both models). We did, however,

Table 1 Summary of best model explaining biomass of brown trout measured as ln weight per unit effort of gillnets (g^{-1} m^2) with either (a) total organic carbon or (b) normalised vegetation density index (NDVI) among the explanatory variables and lake shoreline slope and lake area as morphological proxies (eqn 1), and (c) total organic carbon or (d) normalised vegetation density index (NDVI) among the explanatory variables and predicted mean lake depth as morphological proxies (eqn 2). Model fit; (a) $F_{6,139} = 5.09$, $P < 0.001$, adjusted $R^2 = 0.20$; (b) $F_{9,139} = 5.88$, $P < 0.001$, adjusted $R^2 = 0.21$; (c) $F_{6,142} = 5.66$, $P < 0.001$, adjusted $R^2 = 0.15$; (d) $F_{6,142} = 5.36$, $P < 0.001$, adjusted $R^2 = 0.15$

		Parameter ($\pm$ SE)	t-value	P
(a)	Intercept	9.90 ($\pm$ 1.06)	9.32	<0.001
	ln TOC	3.63 ($\pm$ 0.93)	3.88	<0.001
	ln TOC^2	−0.67 ($\pm$ 0.19)	−3.45	<0.001
	Slope	−0.07 ($\pm$ 0.02)	−3.33	0.001
	Gillnet type	−0.67 ($\pm$ 0.25)	−2.70	0.007
	ln Lake area	−0.01 ($\pm$0.06)	−0.23	0.815
	Temperature	−0.13 ($\pm$0.05)	−2.54	0.012
	ln TOC $\times$ Slope	−0.03 ($\pm$ 0.01)	−2.18	0.030
	ln TOC $\times$ Lake area	−0.26 ($\pm$ 0.07)	−3.67	<0.001
	ln TOC^2 $\times$ Slope	0.03 ($\pm$ 0.01)	2.37	0.018
(b)	Intercept	−1.897 ($\pm$ 449.70)	4.21	<0.001
	ln NDVI	76.42 ($\pm$ 18.50)	4.13	<0.001
	ln NDVI^2	−76.38 ($\pm$ 19.04)	−4.01	<0.001
	Slope	98.68 ($\pm$ 33.35)	2.95	0.003
	Gillnet type	−0.87 ($\pm$ 0.26)	−3.39	<0.001
	ln Lake area	−6.64 ($\pm$ 1.82)	3.64	<0.001
	Temperature	−0.09 ($\pm$ 0.54)	−1.68	0.094
	ln NDVI $\times$ Slope	−41.22 ($\pm$ 13.93)	−2.95	0.004
	ln NDVI^2 $\times$ Slope	4.30 ($\pm$ 1.45)	2.95	<0.001
(c)	Intercept	9.41 ($\pm$ 0.58)	16.08	<0.001
	ln TOC	0.56 ($\pm$ 18.50)	2.76	0.006
	ln TOC^2	−0.29 ($\pm$ 0.20)	−3.19	0.001
	D$_{mean}$	−0.04 ($\pm$ 0.02)	−2.40	0.017
	Gillnet type	−0.62 ($\pm$ 0.25)	−2.51	0.013
	Temperature	−0.13 ($\pm$ 0.05)	−2.68	0.008
	ln TOC $\times$ D$_{mean}$	−0.07 ($\pm$ 0.02)	−3.47	<0.001
(d)	Intercept	−574.41 ($\pm$ 184.56)	−3.11	0.002
	ln NDVI	242.65 ($\pm$ 77.14)	3.14	0.002
	ln NDVI^2	−25.22 ($\pm$ 8.06)	−3.13	0.002
	D$_{mean}$	1.99 ($\pm$ 0.86)	2.30	0.023
	Gillnet type	−0.08 ($\pm$ 0.26)	−2.92	0.002
	Temperature	−0.09 ($\pm$ 0.05)	−1.51	0.133
	ln TOC $\times$ D$_{mean}$	−0.43 ($\pm$ 0.18)	−2.33	0.021

include temperature in the final model for coherency with the DOC model. There was no support for further removal of terms (all ΔAIC between final models and models excluding further terms > 6.67, with the exception of removal of gill net series factor and NDVI: mean depth relationship with ΔAIC = 4.46 and 3.56 respectively).

As expected, weight per unit effort was affected by gillnet type, and multi-mesh gillnets did on average yield lower catches than series of single mesh gillnets. The inclusion of gillnet series as factor thus accounts for potential different catch efficiency among the two different net series employed.

The full dataset analyses using link model proxies for DOC were supported by an observed unimodal relationship between DOC and trout biomass in the subsample of lakes from which measured DOC data were obtainable. The quadratic term was highly significant (ln $bCPUE = 8.13^{***} + 0.21^{NS}lnDOC$

-0.52lnDOC^2***, where NS annotates $P = 0.235$ and *** annotates $P < 0.001$, *d.f.* = 28, $R^2 = 0.28$). Regression parameters compared closely with those obtained using our DOC proxy variable (c.f. table 1). Non-significance of the linear term indicate that DOC level of maximum trout biomass not was significantly different from zero (on the natural log scale) in this analysis.

The effects of DOC or NDVI on fish biomass were modified by lake morphology. All final model fits included two-way interactions between DOC or NDVI and lake morphology proxies (Table 1), and the inclusion of one or more of these interactions in each model was in general well supported (ΔAIC > 5). The DOC or NDVI causing the predicted maximum fish biomass, given as the switch point between negative and positive effects in the unimodal relationship, was higher for lakes with a shallower bathymetry. This is illustrated by the effect of lake shoreline, slope or median depth (Fig. 2). For

lakes with low slope gradient (shoreline buffer slope) in the surrounding terrain, which indicates a large proportion of shallow areas in the lake, the DOC or NDVI switch from a positive to a negative effect on fish biomass was considerably higher than for lakes with steep slopes (i.e. lower proportion of shallow littoral areas). This is illustrated in Fig. 2. For example, lakes having a surrounding terrain slope of 1.4 and 14.3%, the predicted maximum fish biomass are given by 1.08 and 0.32 mg L^{-1} DOC, respectively, assuming a median lake area (0.7 km^2). For lakes with predicted median depth of 7 and 14 m, the maximum production is found at 2.21 and 0.51 mg L^{-1} DOC respectively.

The unimodal response in fish biomass over DOC suggests a trade-off between positive and negative effects of organic C. The positive effect could be attributed to increased nutrient availability with increasing carbon load as shown by exploring correspondence between DOC and total P (TP) and total N
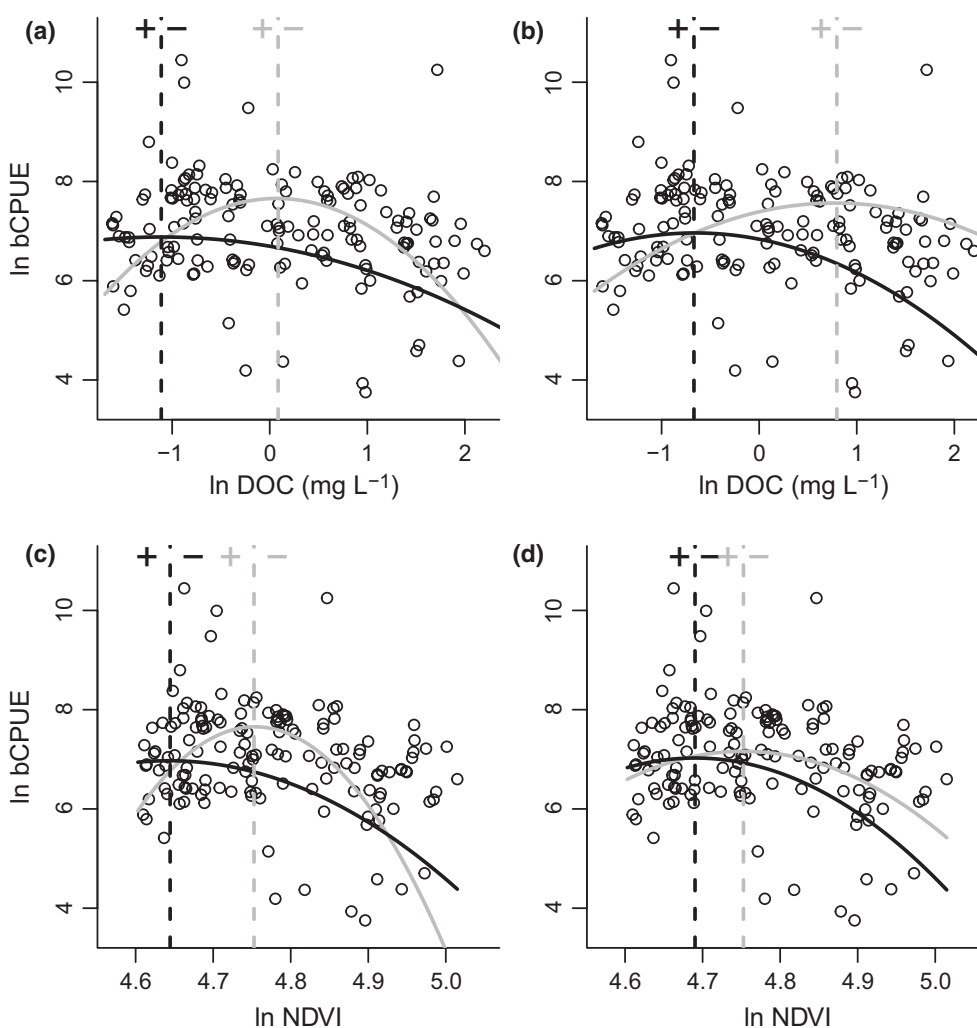

Figure 2 Biomass of brown trout (bCPUE g^{-1} 100 m^2) against predicted lake total organic carbon (ln DOC, a and b), and Normalised Density Vegetation Index (ln NDVI, c and d) (*N* = 168). Solid grey lines are predicted regression values (parameter values in Table 1) for shallow lakes with 1.4% shoreline buffer gradients (a and c), or 6.7 m median depth (b and d). Solid black lines are predicted regression values for deeper lakes (14.3% shoreline buffer gradients (a and c), or 14.0 m mean depth (b and d). Stippled grey and black lines indicate ln DOC and ln NDVI levels at maximum production for steep and shallow shoreline gradients or shallow or deeper median lake depth, respectively, with area to the left having a net positive (+) and to the right as having a negative (−) effect of DOC.

(TN) in the large water chemistry dataset. There was a positive correlation between TP and DOC; TP $(\mu g\ L^{-1}) = 2.0 + 0.75\,DOC\ (mg\ L^{-1})$ $(P < 0.001,\ r^2 = 0.19)$. For TN over DOC the relationship is even stronger; TN $(\mu g\ L^{-1}) = 94.5 + 35.2\,DOC\ (mg\ L^{-1})$ $(P < 0.001,\ r^2 = 0.37)$. Relative low r^2 values reflect other dominant sources of P and N for some of the lakes. Furthermore, the relationship between TP, TN and DOC broke down in more productive lakes $(> 10\ \mu g$ tot P $L^{-1})$.

The maximum fish yield related to DOC was governed by morphological features of the lake. The functional background for this can be illustrated by the area above compensation depth as a function of the lake's bathymetry (Fig. 3). Shallow lakes with low mean: maximum depth ratios will have a less reduction of areas above compensation depth with increasing DOC compared to lakes with high mean: maximum depth ratios. Hence, the point at which light becomes the limiting factor will occur at a higher carbon loads in lakes with a shallower bathymetry.

DISCUSSION

The large, empirical data set on brown trout biomass gave support to a unimodal response to DOC. The DOC level giving maximum fish yield, defining the turning-point between an initial positive response and a negative response, depends on lake bathymetry. This point, where DOC limited fish production, was higher in shallower lakes and in lakes with lower slope gradient of surrounding terrain compared to deeper lakes or lakes with steeper terrain gradient in the surroundings. The initial, positive response may depend on several factors, such as screening of harmful UV-radiation (Williamson *et al.* 1996), subsidising organic C to heterotrophic production (Hessen *et al.* 1990; Jones *et al.* 1999; Cole *et al.* 2011) or organic P and N being associated with DOC. Especially for shallow, clear-water lakes, a substantial fraction of the area could be negatively impacted by UV-radiation, but DOC causes a very efficient attenuation of short-wave radiation (Williamson *et al.* 1996). The 'subsidising' role of allochthonous DOC is much debated, while there is a general consensus that this is a refractory and low-quality source of C compared with autochthonous DOC; both radioisotope studies (Hessen *et al.* 1990) as well as stable isotope studies (Grey *et al.* 2000) have clearly confirmed that allochthonous DOC may also enter the food webs. In fact, ^{13}C-studies suggest that the subsidy of allochthonous DOC may be significant also at higher trophic levels such as fish (Jones *et al.* 1998).

In boreal, oligotrophic lakes surrounded by pristine catchments DOC are also a major contributor to total P and N (Hessen *et al.* 2009). However, while N and P are mostly on organic form and thus of low bioavailability, some fractions of these pools will eventually mineralise and thus support primary production. Hence, the hump-shaped response curves likely reflect the trade-off of DOC as a source of both nutrients and photon absorption.

The negative effect of DOC on primary productivity via photon absorption has been verified by several studies (e.g. Jones 1992; Carpenter *et al.* 1998) and this negative effect may propagate up to the level of fish (Karlsson *et al.* 2009). In a
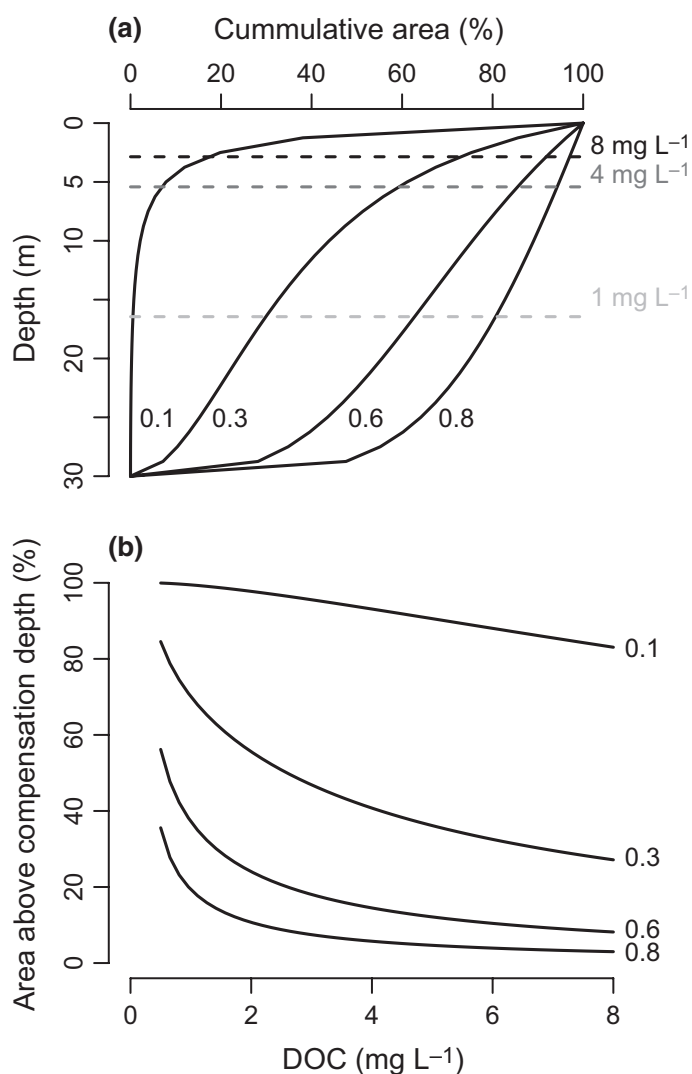

Figure 3 (a) Hypsographic curve (cumulative area above a given depth) for four different lake morphometric typologies defined by a mean depth/maximum depth ratio of 0.1, 0.3, 0.6 and 0.8. Depth of the compensation depth (positive net primary production) for total organic carbon content of 1, 4 and 8 mg L^{-1} are shown in light grey, grey and black stippled lines respectively. (b) Area above compensation depth (% of total lake area) is modeled as a function of DOC concentration, given the four different mean depth/maximum depth ratio illustrated in panel (a).

bio-optical model, Thrane *et al.* (subm) demonstrated the major role of total organic carbon as a photon absorber. On the average, DOC captured 56.3% of the available photons, but the fraction spanned from 36.9 to 76.2% and was positively correlated with DOC $(r = 0.63)$. The percentage of photons captured by DOC was on average 10 times higher than that captured by phytoplankton. Subsequently, Thrane *et al.* estimated areal primary production of phytoplankton (PP_A) based on incoming radiation and the photon budgets, and found a clear negative effect of DOC on PP_A, while a positive effect of total P. Thus, not only benthic primary production but also pelagic primary production is reduced under elevated DOC, and there is a clear trade-off between positive effects of total P and the negative effects of DOC. At very high levels of DOC,

also other negative impacts of allocththonous carbon may take effect, such as anoxic deep-waters (again due to high light attenuation), fluffy dy-like sediments offering poor substratum for benthos, as well as reduced pH and acid neutralising capacity owing to humic acids (Hessen & Tranvik 1998; Lydersen *et al.* 2004).

Despite an increasing interest in the magnitude and effect of terrestrial carbon subsidies to lakes, particularly in light of the recent focus on climate change impacts (e.g. Karlsson *et al.* 2009; Berggren *et al.* 2010; Larsen *et al.* 2011b), the perceived contrasting effects of terrestrial carbon subsidies remain poorly empirically investigated. Our study supports that of Karlsson *et al.* (2009) by demonstrating this negative role of DOC. However, by including a larger number of lakes, particularly with low DOC levels, and fish biomass estimates from a single dominant species, we further demonstrate the trade-offs between positive and negative impacts of DOC. Not at least, we show how these responses are shaped by lake morphometry, where fish production in deeper lakes is comparatively more susceptible to increased load of organic C ('browning') than that of shallower lakes. Thus, the browning effect is expected to be highly dependent on lake bathymetry since light limitation of benthic areas are determined by the relative proportion of the lake floor being above the compensation depth for photosynthetic production. These different DOC 'thresholds' may also reflect that shallow lakes support a higher relative share of benthic primary and secondary production compared with deep lakes, where planktonic primary production is likely to be more dominant. The fact that NDVI yielded corresponding responses reflects that vegetation density (primarily forest cover) is the main determinant of DOC in Norwegian lakes, and thus clearly demonstrates that increased forest cover or timberline due to climatic changes or forest planting may affect fish yield within the catchments. While the strong effect of NDVI may not be valid for other boreal regions, the DOC-effect should be fairly general.

Given the major role organic C has for structuring primary and secondary productivity of northern, boreal lake ecosystems (Stasko *et al.* 2012), and its expected increase with concomitant increased light attenuation, understanding the response to the observed and anticipated increased browning effects are of major importance and warrants further studies.

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AUTHORSHIP

AGF and DOH conceived the idea; AGF, IPH and DOH analysed the data; OU and TH compiled the fish biomass data set. All authors contributed to the writing of the article.

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