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An experimental test of climate change effects in northern lakes: Increasing allochthonous organic matter and warming alters autumn primary production

Mohammed Hamdan[1,2] [iD] | Pär Byström[1] | Erin R. Hotchkiss[3] [iD] |
Mohammed J. Al-Haidarey[4] [iD] | Jan Karlsson[1] [iD]

[1]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

[2]Department of Biology, Baghdad University, Baghdad, Iraq

[3]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, U.S.A.

[4]Department of Ecology, Faculty of Science, Kufa University, Najaf, Iraq

Correspondence
Mohammed Hamdan, Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, 901 87 Umeå, Sweden.
Email: mohammed.hamdan@umu.se

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Abstract

1. Climate changes are predicted to influence gross primary production (GPP) of lakes directly through warming and indirectly through increased loads of allochthonous coloured dissolved organic matter (cDOM) from surrounding landscapes. However, few studies have investigated this combined effect.

2. Here we tested the effects of warming (elevated 3℃) and cDOM input (three levels of humic river water addition) on GPP in autumn (2 months including open water and ice-covered periods) in experimental pond ecosystems.

3. The cDOM input decreased whole-ecosystem GPP at natural temperature conditions mainly as a result of lower benthic GPP not fully counteracted by an increase in pelagic GPP, while warming increased whole-ecosystem GPP due to a positive response of mainly pelagic GPP at all levels of cDOM input.

4. Warming delayed autumn ice cover formation by 2 weeks but did not affect light availability in the water column compared to ambient ice-covered treatments. Gross primary production during this period was still affected by warming and cDOM.

5. The results stress the importance of accounting for multiple climate drivers and habitats when predicting lake GPP responses to climate change. We conclude that climate change may shift whole-ecosystem GPP through different responses of habitat-specific GPP to increasing cDOM inputs and warming.

KEYWORDS
brownification, habitat-specific, limitation, rising temperature, whole productivity

1 | INTRODUCTION

Lakes in northern regions are rapidly warming (Niedrist, et al., 2018; Rose et al., 2016). Climate impacts lake gross primary production (GPP) in multiple ways, including direct temperature effects on metabolic rates of autotrophs and grazers (Kraemer et al., 2017; O'Connor et al., 2009; Yvon-Durocher et al., 2010) and indirect effects via terrestrial export of coloured dissolved organic

matter (cDOM) (Butcher et al., 2015; Creed et al., 2018; Rantala et al., 2016).

Warming could directly impact biomass growth and metabolic rates of autotrophs through increases in nutrient uptake and light saturation of photosynthesis (De Senerpont et al., 2014; Tilzer et al., 1986; Yvon-Durocher et al., 2015). Increased cDOM, by contrast, has multiple impacts on lake characteristics, including reduced light availability, but also increased macronutrients like nitrogen (N) and phosphorous (P) bonded to cDOM and increased carbon dioxide (CO_2) concentrations from cDOM mineralisation (Carpenter et al., 1998; Creed et al., 2018; Nydahl et al., 2019). Generally, elevated nutrient and CO_2 levels enhance GPP, mainly in the pelagic habitat, while reduced light penetration from brownification decreases GPP, mainly in benthic habitats (Ask et al., 2012; Brown et al., 2020; Genkai-Kato et al., 2012).

Climate change research on lakes and ponds has largely focused on the summer period, although measurements in the winter season are increasing (Denfeld et al., 2018; Hampton et al., 2017). Few studies have tested climate change impacts on ecological processes during autumn–winter transition, although this period is important ecologically and will experience warming-related changes such as increased water temperature and runoff as well as delayed ice cover formation (Bintanja, 2018; Veillette et al., 2010). Longer ice-free periods via warming could increase temperature of the water column (Niedrist et al., 2018) and increased runoff could elevate loading of cDOM to lakes (Klimaszyk & Rzymski, 2015). The combined consequences of warming and cDOM on GPP during autumn are largely unknown. While warming can stimulate metabolism, declining daily light irradiation in autumn may constrain the predicted positive temperature response of autotrophs, causing a mismatch between consumer energy demands and GPP as temperatures decline. This mismatch will probably be enhanced when browning-caused light limitation exceeds nutrient limitation, even when cDOM delivers critical nutrients.

Added to this, the reduced duration and thickness of ice and snow cover will increase light levels compared to a longer duration of a thick ice and snow cover, and will therefore potentially stimulate GPP in lakes (Lenard, 2015; Obertegger et al., 2017). Biogeochemical consequences of changes in ice phenology in spring have received increasing interest and studies have shown impacts on ecosystem dynamics and their contributions to whole lake ecosystem processes (Benson et al., 2012; Bertilsson et al., 2013; Hamdan et al., 2018; Hampton et al., 2017), while substantially less attention has been given to ecosystem processes during the late autumn/early winter transition.

The aim of this study was to experimentally test the direct (warming) and indirect (allochthonous cDOM) climate effects on lake GPP during autumn. We hypothesised that climate change will cause a mismatch between the effects of higher temperature and allochthonous cDOM on autumn GPP via asymmetric responses in GPP across habitats. We specifically predicted that: (1) warming stimulates GPP, but responses depend on availability of light and nutrients; (2) cDOM inputs impact habitat-specific GPP asymmetrically

by reducing benthic GPP (due to light limitation) while stimulating pelagic GPP (due to relaxing nutrient limitation); and (3) delay of ice cover formation promotes GPP via increasing light availability. To investigate our predictions, we increased water temperature and applied a gradient of inflow rates of stream water with high cDOM in a large-scale experimental pond system to monitor the response of whole-ecosystem and habitat-specific GPP.

2 | METHODS

2.1 | Study system and experiment design

The study was carried out at the Umeå University experimental ecosystem facility (EXEF) in northern Sweden (63°48′N, 20°14′E) for 2 months (1 October–4 December 2017). The EXEF is a large-scale experimental system (73 m long, 25 m wide, with an average depth of 1.5 m) divided into 20 experimental enclosures (12.5 × 7.3 m, 136 m³) by dark green PVC-sheet walls (Figure S1). Each enclosure includes a flat soft bottom benthic habitat and one natural shoreline (7.3 m long), has separate inlets and outlets and the facility allows for manipulation of input water chemistry and water temperature. The food web consists of benthic and pelagic primary producers, and a consumer community consisting of zooplankton (phylum Rotifera, Cladocera, and Copepoda) and zoobenthos (mainly larvae of chironomids, ephemeroptera, odonates and snails) (Koizumi et al., in preparation).

During autumn of 2017, we manipulated temperature and cDOM inputs in sixteen enclosures, while the four enclosures in the middle were left as a buffer. Eight enclosures followed the ambient autumn air temperature development and they started to be ice-covered on 30 October. The remaining eight enclosures were heated with the aim to reach 3°C above ambient water temperature during 1 October until 12 November when they started to become ice-covered (and warming treatment was terminated). Warming was carried out separately for each of the eight enclosures by circulating water through individual land-based heat exchangers and back to same enclosure. Separate temperature sensors in one of the ambient (i.e. natural season-dependent temperature development) and one heated enclosure continuously controls the closed flow system of heated media from an air-source heat pump. The temperature difference (ΔT) between the heating media in the closed flow system and the flow water from each warm enclosure was approximately 3°C.

A gradient of cDOM concentrations was created by varying the volume of naturally cDOM-rich water inputs from a small boreal river, Hörneån (63°57′N, 19°25′E). The water was collected and transported (three times within a 14-day interval) from the source in a tanker truck to the EXEF facility and kept in a 40-m³ tank. During the experimental period, all enclosures received the same rate (1.48 L/min) of continuous water inputs of either only clear groundwater (Umeå municipality groundwater source) or only cDOM water or a mix of both. The rate of cDOM water L/min in the total continuous

rate of water inputs from low to high was; 0 (two controls), 0.07 and 0.15 (low), 0.30 and 0.59 (medium), or 0.89 and 1.48 (high). Water chemistry and phytoplankton chlorophyll *a* biomass (Chl *a*; mean ± 1 *SD*, n = 3) of the cDOM river water during the experimental period were: dissolved organic carbon (DOC) 25.0 ± 3.0 mg/L, dissolved inorganic carbon (DIC) 262 ± 2.6 µM, pH 6.2 ± 0.1, total nitrogen (TN) 674.2 ± 82.8 µg/L, total phosphorus (TP) 54.5 ± 2.2 µg/L, nitrate (NO_3) 35.3 ± 1.8 µg/L, ammonium (NH_4) 13.3 ± 3.0 µg/L, phosphate (PO_4) 24.6 ± 0.9 µg/L, and Chl *a* 2.6 ± 0.9 µg/L. Corresponding groundwater input chemistry (mean ± 1 *SD*, n = 2) was: DOC 0.6 ± 0.1 mg/L, DIC 956 ± 65.2 µM, pH 7.4 ± 0.03, TN 74.5 ± 5.1 µg/L, TP 2.5 ± 0.4 µg/L, NO_3 28.7 ± 1.1 µg/L, NH_4 4.5 ± 0.02 µg/L, and PO_4 1.4 ± 0.2 µg/L. No measures of Chl *a* were done on the groundwater supply.

Warming was terminated on 13 November when the warmed enclosures became ice-covered. Clear and cDOM water input to ambient enclosures was terminated on the 31 October in connection to ice cover formation, while it was terminated on the 13 November in warm enclosures. Measures of additional response and explanatory variables were terminated on 4 December.

2.2 | Sampling and analyses

We used logging sensors to record high-frequency patterns in light, water temperature, dissolved oxygen, and wind speed. Light intensity (photosynthetic active radiation [PAR, µmol m^{-2} s^{-1}]) was continuously measured every 10 min over the whole study period by light sensors (SQ-110, UT, U.S.A.) which were deployed at 0.8 m depth at each enclosure and recorded with loggers (Delta-T Devices, Cambridge, U.K.). Dissolved oxygen and water temperature were measured at 10-min intervals by logging sensors (PME MiniDOT, CA, U.S.A.), which were deployed as free loggers at 0.5 m below the water surface in the centre of each enclosure, as well as fixed loggers, which were placed inside the incubation chambers during incubations for pelagic and benthic measurements. Water temperature and PAR were calculated as daily average for each enclosure. Then, we calculated the daily average of water temperature for the eight ambient and heated enclosures respectively, for whole study period. The daily average of PAR was calculated for the two enclosures of each subgroup within the main groups. Wind speed was recorded every 10 min by a climate station positioned on the shoreline of EXEF.

For chemical analyses and Chl *a*, 1-L water samples were collected in the middle of each enclosure from the upper meter of the water column on four occasions during the study period (every second week). Partial pressure of CO_2 in the enclosures was manually measured in situ at the same four times with a hand-held non-dispersive infra-red CO_2 sensor (CARBOCAP GM70 Vaisala Inc., Helsinki, Finland). Subsamples for TP and TN analysis were taken and stored in the freezer (−20℃). Total P was measured according to Murphy and Riley, (1962), by using potassium persulfate for digesting the samples. For DOC, 50 ml of water sample was filtered

through burnt (550℃, 4 hr) acid washed 0.45 µm Whatman GF/F filters, acidified with 500 µl 1.2 M HCl, and stored at 4℃ until analyses. For DOC and TN, water samples were analysed using a combustion chamber (IL550 TOC/TN analyser, Duesseldorf, Germany). For NO_3, PO_4, and NH_4, water was filtered (GF/F as above) and stored in freezer until analysis with photometric flow injection analysis method (Gray et al., 2006). Chlorophyll *a* was extracted (95% ethanol for 24 hr in the dark) from the Whatman GF/F filter and measured with a spectrofluorometer (Perkin Elmer LS-55, MA, U.S.A.) with the excitation wavelength set to 433 nm and emission wavelength to 673 nm.

2.3 | Whole-ecosystem and habitat-specific GPP estimates

Sensor oxygen concentrations in each enclosure were used to estimate daily whole-ecosystem GPP over the study period. Gross primary production was calculated with inverse modelling and Bayesian parameter estimation using a similar parameter estimation approach as for diel dissolved oxygen in streams (Hotchkiss & Hall, 2014), but modified for ponded waters as in Hamdan et al., (2018):

$$mO_i = mO_{i-1} + \left(\frac{GPP}{zmix} * \frac{PAR_i}{PAR} \right) + \left(\frac{ER}{zmix} * \Delta t \right) + K_i \left(O_{sat,i} - mO_{i-1} \right) \Delta t \tag{1}$$

where mO_i is modelled dissolved oxygen at time *i* (g O_2/m^3) given parameter estimates of GPP and ecosystem respiration (ER; g O_2 m^{-2} d^{-1}). Because changes in dissolved oxygen are a function of GPP, ER, and gas exchange, we calculated daily air–water oxygen fluxes based on oxygen saturation and the temperature-corrected gas exchange velocity for oxygen (K_i, d^{-1}). K_i was estimated from K_{600} derived from wind speed (Vachon & Prairie, 2013). For estimating whole-ecosystem GPP of ice-on period, the emission flux of oxygen ($K_i \left(O_{sat,i} - mO_{i-1} \right) \Delta t$) to or from the atmosphere was fixed at zero. z_{mix} was the mean enclosure depth (m) given the enclosures are shallow and no thermal stratification (no shift >0.4°C/m in water temperature) was noticed during the experiment. The metabolism model used a *random walk* metropolis algorithm and Markov chain Monte Carlo sampling from the *metrop* function in the *mcmc* package of the statistical program R (Geyer & Johnson, 2013) to find the best fit between measured and modelled dissolved oxygen data given model estimates of GPP and ER. Each parameter estimate was derived from 10,000 model iterations after removing an initial 1,000 iterations of *burn-in* from parameter starting values. Then, we checked for convergence of parameter estimates and removed days with negative GPP and with poor fits between measured and modelled dissolved oxygen.

In each enclosure, pelagic incubations were carried out in transparent cylindrical chambers (1.9 L, diameter 85 mm) suspended vertically 0.5 m below the water surface by a metal wire fixed above and in the centre of all enclosures. Benthic incubations were performed in semi-spherical transparent chambers (12 L, diameter 350 mm) equipped with a thin metal frame (3 cm high) allowing them to be

inserted *c*. 3 cm into the sediment. Pelagic and benthic 48 hr in situ incubations were performed on four occasions (8 October, 23 October, 6 November, and 20 November). The obtained oxygen data from these incubations were used to estimate habitats specific GPP (pelagic and benthic). Gross primary production was estimated as for whole-ecosystem rates (same model as above), but the emission flux of oxygen ($K_i \left(O_{sat,i} - mO_{i-1} \right) \Delta t$) to or from the atmosphere was fixed at zero for closed chambers used to measure pelagic and benthic primary production. The term z_{mix} also was not considered for pelagic and benthic incubations.

For comparison with habitat-specific incubation periods, daily whole-ecosystem GPP estimates were grouped into four periods. Further, the average of habitat-specific and whole-ecosystem GPP for whole study period was calculated for each enclosure to estimate the relative contribution of habitat-specific GPP (benthic and pelagic) to whole-ecosystem GPP.

2.4 | Statistical analyses

Statistics (SPSS 20) were based on enclosure-specific means of measured environmental and response variables. The gradient design of the cDOM treatment implicitly calls for a regression-based statistical analysis. For water chemistry responses in the enclosures to cDOM treatments, we used linear regressions; we tested differences in water chemistry between ambient and heated enclosures with pairwise *t*-test on mean concentrations over the whole experimental period. We also used regression analysis of the average daily GPP response to the gradient of cDOM input in ambient and heated enclosures over the whole experimental period. Three regression models were applied on the results and we moved from a simple linear model to an exponential decay model ($f = y0 + a * exp(-b * x)$) and to a non-mechanistic hump-shaped Gaussian curve ($f = y0 + a * exp\left(-0.5 * \left(\frac{x-x0}{b}\right)^2\right)$) and chose the model with the best fit for GPP responses. However, to account for the time effect (4 subsequent measures over time) and for simplicity by avoiding extended and complicated model selections for the GPP responses and warming effects over the time periods, we grouped our cDOM treatment into four groups (control, low, medium, and high) and analysed GPP responses over time to experimental treatments with Two-way repeated-measures ANOVAs. Note that this approach renders cDOM groups (part from the controls) to be artificially grouped and therefore not true replicates. Further, two-way ANOVAs were used to test the responses of GPP to the treatments during the period (31 October–12 November) when ice cover started to form in the ambient but not warm enclosures, and the period (13 November–3 December) following ice formation in both enclosures. To test for differences between ambient and heated groups within specific experimental periods (i.e. ice-free and ice-on periods), standard *t*-tests were used. The correlations between selected variables were calculated using Pearson correlation coefficient (*r*). Whole-ecosystem and habitat-specific GPP values were $\log_{10}$ transformed to achieve homogeneity of variances.

3 | RESULTS

3.1 | Physical and chemical variables

Warming and cDOM treatments altered temperature, light, and nutrient conditions in the enclosures. Warming delayed the start of the ice cover formation 13 days (30 October in ambient and 12 November in heated enclosures) and increased water temperature by on average 2.4℃ (1 October until 12 November: *t*-test; *df* = 42, *t* = −30.6, *p* < 0.001). For the period when ambient enclosures became ice-covered while heated enclosures were still ice-free (31 October–12 November), the water temperature was on average 1.8℃ warmer in heated enclosures (*t*-test; *df* = 12, *t* = −17.2, *p* < 0.001). Finally, when all enclosures became ice-covered and warming was ended (13 November–3 December), water temperature was similar in the heated and ambient enclosures (*t*-test; *df* = 20, *t* = 0.6, *p* = 0.60, Figure 1a,b). Water temperature was similar at shallow (0.5 m depth) and deep (1.5 m depth) water (Δ water temperature was 0.36 ± 0.07 and 0.18 ± 0.06℃ for ambient and warm enclosures, respectively) and did not change along the gradient of cDOM input (Linear regression; shallow water: *p* = 0.62 and 0.63; deep water: *p* = 0.50 and 0.67 for ambient and heated enclosures, respectively).

Light conditions (PAR) were not affected by warming or by the interaction of cDOM × warming (two-way repeated-measures ANOVA; warming: $F_{1, 8}$ = 3.9, *p* = 0.08, cDOM × warming: $F_{3, 8}$ = 0.15, *p* = 0.9). Photosynthetic active radiation decreased with increasing cDOM inputs (until 13 November) and over time with shorter days, reaching the lowest value at the end of the experiment (two-way repeated-measures ANOVA; cDOM: $F_{3, 8}$ = 304.4, *p* < 0.001; Figure 1a,b). Furthermore, PAR did not differ between ambient and heated enclosures by same cDOM treatments (control, low, medium, and high cDOM, Figure 1a,b) during the period (31 October to 12 November) when ambient, but not heated, enclosures were ice-covered (*t*-test; *df* = 12; *t* = −0.3, *p* = 0.73; *t* = 0.03, *p* = 0.97; *t* = −1.4, *p* = 0.17; *t* = 0.4; *p* = 0.72, respectively) or when all enclosures were ice-covered (Figure 1a,b; *t*-test; *df* = 20; *t* = −0.6, *p* = 0.53; *t* = −1.6, *p* = 0.12; *t* = −1, *p* = 0.32; *t* = −0.5; *p* = 0.65, for same cDOM treatments respectively).

Over the experiment, DOC concentration was positively affected by increasing cDOM input (Figure 2; Table 1) but not by warming (*t*-test; *df* = 7, *t* = 0.4, *p* = 0.6, Figure 2). The pCO_2 increased with increasing cDOM input (Figure 2; Table 1) and was lower in heated enclosures (*t*-test; *df* = 7, *t* = 5.2, *p* = 0.001, Figure 2). Concentration of TN, TP, NO_3, PO_4, and NH_4 was affected (increased) by increasing cDOM input (Figure 2; Table 1) but not by warming (*t*-test; *df* = 7; *t* = 0.2, *p* = 0.8; *t* = 0.8, *p* = 0.4; *t* = −0.6, *p* = 0.5; *t* = 0.3, *p* = 0.7; *t* = −0.6, *p* = 0.5, respectively; Figure 2). Concentrations of TN, TP and NO_3 for ambient and heated enclosures generally increased over time in cDOM treatments compared to the clearwater (two-way repeated-measures ANOVA; Time: $F_{3, 24}$ = 3.42 and *p* = 0.03; $F_{3, 24}$ = 7.89 and *p* = 0.001; $F_{3, 24}$ = 15.84 and *p* < 0.001, respectively, Figure 2). pCO_2, TN, TP, NO_3, PO_4, and NH_4 were positively correlated with DOC concentration (*r* = 0.6, *p* < 0.001; *r* = 0.9,
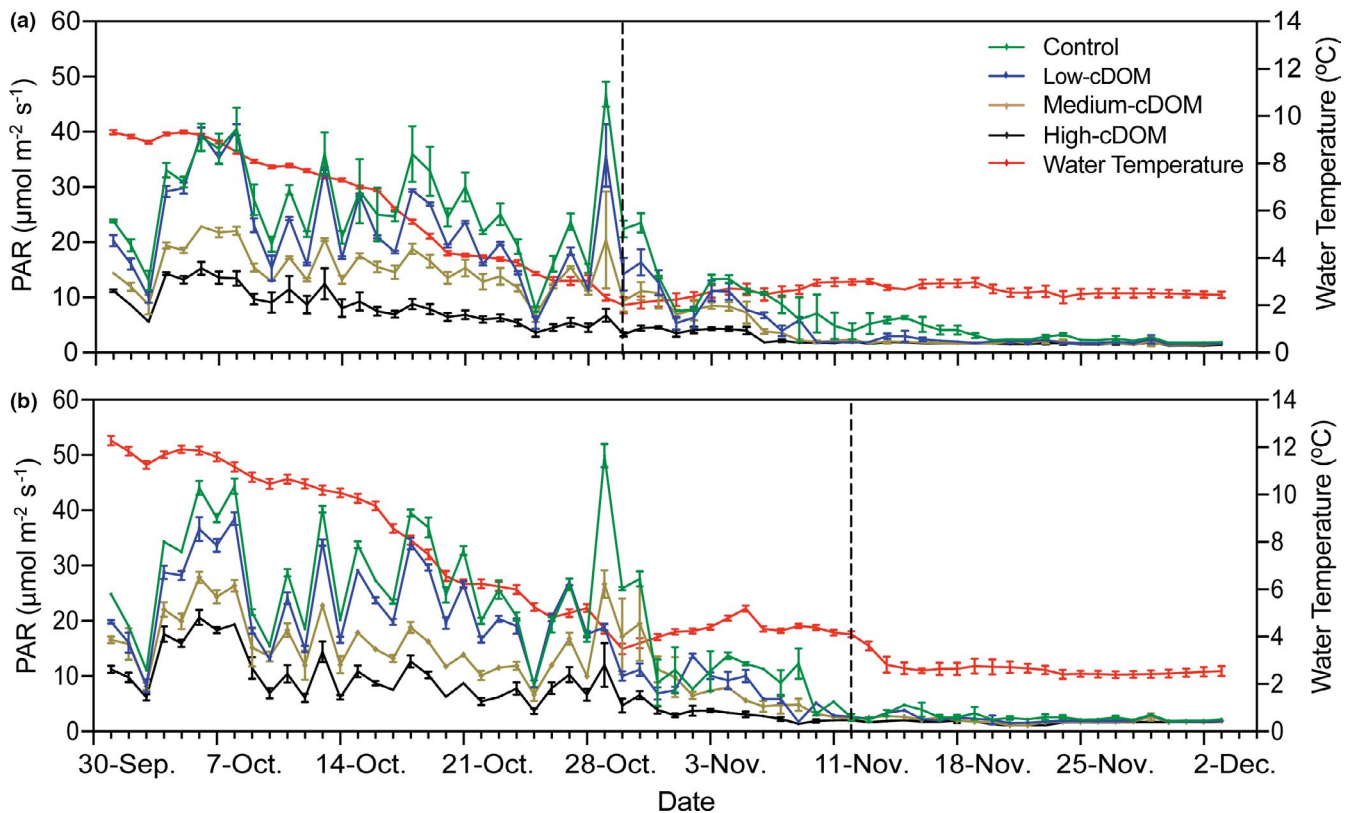
FIGURE 1 Daily mean (±1 SD) of water temperature (0.5 m depth) and photosynthetic active radiation (PAR, 0.8 m depth) in ambient (a) and warm (b) enclosures. Water temperature represents an average of all enclosures in ambient and warm enclosures because there were no differences in temperature within allochthonous coloured dissolved organic matter (cDOM) inputs. The vertical dashed lines refer to when the enclosures of each group became ice-covered. The experiment was carried out from 1 October to 3 December 2017

$p < 0.001$; $r = 0.8$, $p < 0.001$; $r = 0.6$, $p < 0.001$; $r = 0.6$, $p < 0.001$; $r = 0.7$, $p < 0.001$, respectively).

3.2 | Whole-ecosystem and habitat-specific GPP

Whole-ecosystem GPP decreased with increasing cDOM input in ambient enclosures, while GPP in warm enclosures increased with low and medium cDOM inputs but decreased at high input (Figure 3a,b; Table 2). Increasing cDOM input caused pelagic GPP to increase at low and medium levels but decrease at the high level and the response was substantially stronger with warming (Figure 3d,e; Table 2). Benthic GPP decreased with increasing cDOM input and was not affected by warming (Figure 3g,h; Table 2).

The gradient of cDOM input in heated enclosures caused hump-shaped responses of mean whole-ecosystem and pelagic GPP over the whole experimental period (Gaussian curve; $r^2 = 0.88$, $p = 0.02$ and $r^2 = 0.99$, $p < 0.0001$, respectively), while in ambient enclosures the gradient of cDOM input negatively affected whole-ecosystem GPP (linear model; $r^2 = 0.73$, $p = 0.006$) and did not affect pelagic GPP (linear model; $r^2 = 0.10$, $p = 0.42$; Figure 3c,f). In contrast, mean benthic GPP over the whole experiment was affected negatively by the gradient of cDOM input (exponential decay model; $r^2 = 0.52$, $p = 0.04$ and $r^2 = 0.95$, $p = 0.0006$) in ambient and heated enclosures,

respectively (Figure 3i). The sum of habitat-specific GPP agreed closely (90–100%) with estimates of whole-ecosystem GPP, yet their relative contributions changed with the treatments (Figure 3). Mean pelagic GPP contribution to whole-ecosystem GPP increased (and benthic GPP contribution decreased) with increasing cDOM input (control, low, medium, and high) and warming treatment (ambient: 40, 50, 65, 60%; heated: 45, 55, 70, and 65%; Pairwise t-test pelagic GPP contribution: $df = 3$, $t = -21$, $p < 0.001$).

The gradient of cDOM input caused a hump-shaped response in phytoplankton Chl a biomass in heated enclosures ($r^2 = 0.82$, $p = 0.05$), but not in ambient (Linear model; $r^2 = 0.15$, $p = 0.33$; Figure S2a). Pelagic GPP-to-Chl a ratios did not differ between ambient and heated enclosures along the gradient of cDOM input (t-test; $df = 7$, $t = 0.50$, $p = 0.62$; Figure S2b).

During the period when ambient enclosures were ice-covered and heated enclosures ice-free (third sampling period), whole-ecosystem GPP showed similar responses to the treatments as the two former sampling periods (significantly affected by cDOM input and warming), while, for habitat-specific GPP, only the effects of cDOM input were evident (Figure 3; Table 2). When both ambient and heated enclosures were ice-covered, whole-ecosystem and habitat-specific GPP were affected by cDOM input (Figure 3; Table 2). During this period, whole-ecosystem, pelagic, and benthic GPP were all positively correlated to PAR ($df = 7$; $r = 0.8$, $p = 0.003$; $r = 0.7$,
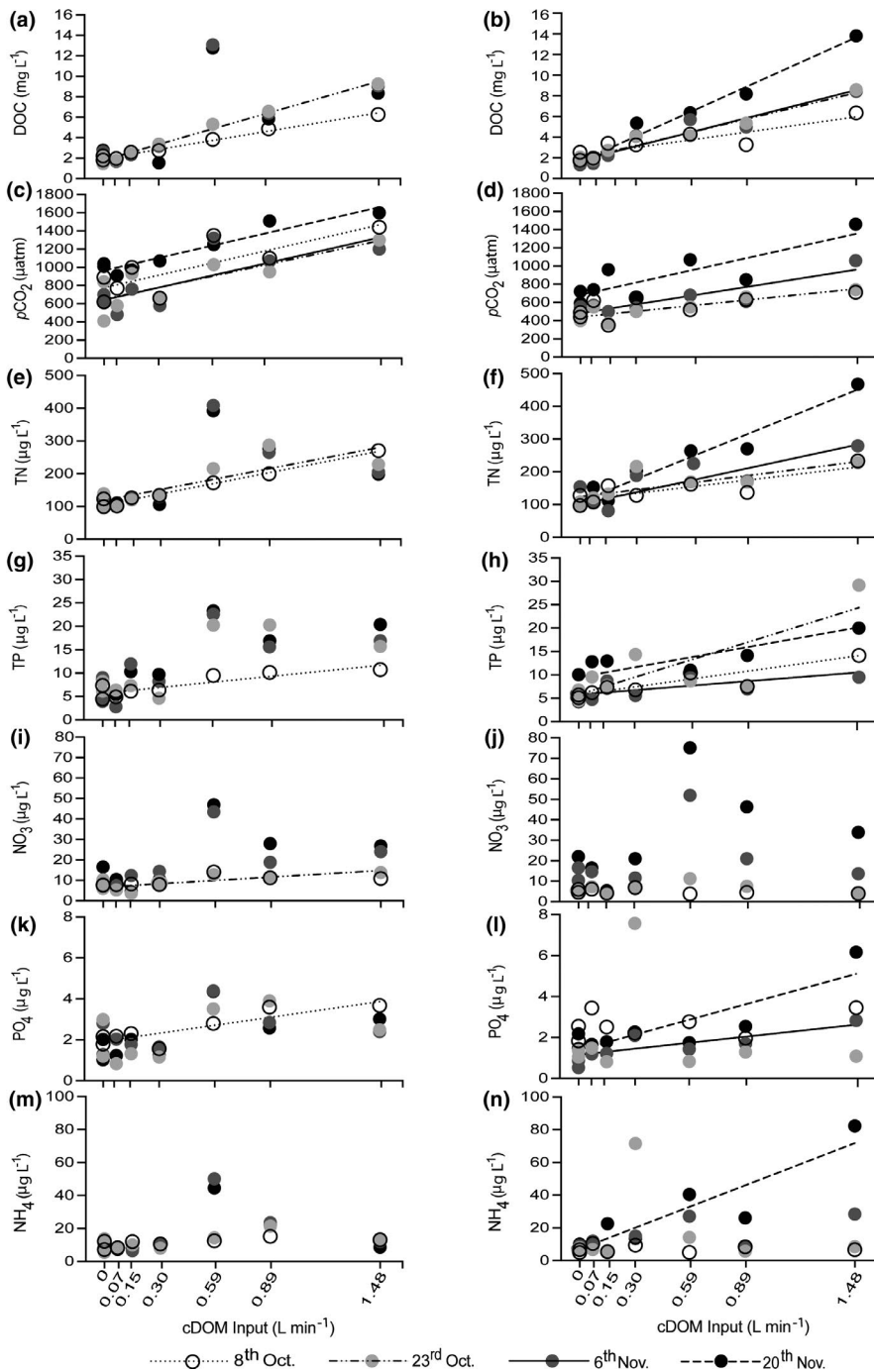
FIGURE 2 Water chemistry in ambient (a, c, e, g, i, k, and m) and warm (b, d, f, h, j, l, and n) enclosures at different allochthonous coloured dissolved organic matter (cDOM) inputs over the course of the experiment. All variables abbreviations are reported. Note the different scales of the y-axis among panels. DOC, dissolved organic carbon; TN, total nitrogen; TP, total phosphorous

$p = 0.02$; $r = 0.8$, $p = 0.03$) across ambient enclosures as well as across heated ($r = 0.8$, $p = 0.02$; $r = 0.9$, $p < 0.001$; $r = 0.8$, $p = 0.01$), respectively.

4 | DISCUSSION

Our results show that autumn GPP was affected by both cDOM input and warming. Increased cDOM input decreased whole-ecosystem GPP at ambient conditions by reducing benthic GPP more than stimulating pelagic GPP, while warming increased whole-ecosystem GPP across all levels of cDOM due to the stimulation of

mainly pelagic GPP. Differences in benthic and pelagic responses to warming and cDOM input emphasise the need to study the impacts of multiple environmental changes at both habitat-specific and the whole-ecosystem level to understand climate change effects on lake productivity.

The increase in pelagic GPP at low and medium cDOM input suggests that phytoplankton growth was nutrient limited and that the macronutrients bonded to the cDOM promoted phytoplankton growth. The fact that PO_4 did not increase with cDOM input, despite the high TP content in DOM, indicates high phytoplankton demand for phosphorus. The increased CO_2 concentration with cDOM input could potentially also have contributed to the increase

TABLE 1 Effect of the gradient in allochthonous coloured dissolved organic matter (cDOM) input on water chemistry of ambient and warm enclosures over the experiment tested by linear regression analysis. $^{(+)}$ denotes a positive effect

Variable	Ambient enclosures		Heated enclosures	
	r^2	p	r^2	p
DOC (mg/L)	0.71 $^{(+)}$	0.008	0.95 $^{(+)}$	<0.001
pCO_2 (µatm)	0.80 $^{(+)}$	0.002	0.88 $^{(+)}$	<0.001
TN (µg/L)	0.45 $^{(+)}$	0.03	0.89 $^{(+)}$	<0.001
TP (µg/L)	0.58 $^{(+)}$	0.02	0.77 $^{(+)}$	0.004
NO_3 (µg/L)	0.40	0.09	0.17	0.29
PO_4 (µg/L)	0.40	0.08	0.28	0.17
NH_4 (µg/L)	0.15	0.33	0.49	0.05

Note: r^2, coefficient of determination; *p*-values and all variables abbreviations are reported.
Abbreviations: DOC, dissolved organic carbon; TN, total nitrogen; TP, total phosphorous.

in pelagic GPP (Hamdan et al., 2018; Jansson et al., 2012) due to its important role as a carbon source for photosynthetic enzymes (Badger et al., 1998). In enclosures with the highest cDOM input, and highest nutrient and CO_2 levels, pelagic GPP decreased to levels similar to clearwater enclosures. We attribute this to be mainly an effect of a shift to light limitation, which prohibits further positive effects of increasing nutrients and CO_2 on pelagic GPP. We acknowledge that the responses in pelagic GPP to our treatments could have been influenced by changes in phytoplankton community composition (Flöder et al., 2002; Kissman et al., 2013). However, although it was not designed to reveal and conceptualise the exact mechanisms for the observed patterns, our study provides a strong experimental support for shifts from nutrient- to light-limited pelagic GPP with increasing cDOM inputs (Bergström & Karlsson, 2019; Kelly et al., 2018; Vasconcelos et al., 2018).

In contrast to the hump-shaped response in pelagic GPP, benthic GPP declined with increasing cDOM, suggesting light availability was the primary control on benthic GPP in the enclosures. Soft bottom-dwelling benthic algae in general, including those in the experimental ponds (Vasconcelos et al., 2018), have access to nutrients from the sediment and sediment–water interface but also experience lower light conditions compared to phytoplankton (Bonilla et al., 2005; Daniels et al., 2015). Thus, benthic algae are not expected to benefit from additional nutrient inputs in most soft bottom-dominated lake ecosystems (Bonilla et al., 2005). While we do not have nutrient data from the sediment, we cannot exclude the possibility of nutrient availability to also constrain benthic GPP at least when light is readily available.

The combined asymmetric effects of nutrient and light limitation on habitat-specific GPP resulted in a shift in the relative contributions of the habitats to whole-ecosystem GPP, moving from benthic dominance in clearwater ponds to increasing pelagic contributions with higher cDOM input. The decline in benthic GPP was countered by an increase in pelagic GPP at low and medium levels of cDOM. In

contrast, at high cDOM input when light-limited benthic GPP, light limitation exceeded the positive effects of increased nutrients on pelagic GPP and whole-ecosystem GPP declined. Taken together our study provides experimental support for the suggested mechanism behind observed patterns in whole-ecosystem GPP with increased DOC concentrations (Finstad et al., 2014; Karlsson et al., 2009; Seekell, Lapierre, Ask, et al., 2015).

In our study, warming increased whole-ecosystem GPP at all levels of cDOM input, probably due to the direct stimulating effect of warming on physiological processes involved in photosynthesis (Porter et al., 1996; Yvon-Durocher & Allen, 2012). Due to the counteracting effects on limiting resource availability by cDOM (positive for nutrients and negative for light), whole-ecosystem GPP increased with warming when nutrients increased at low and medium levels of cDOM input, but this response was moderate because of decreased light availability with higher cDOM. In fact, warming shifted the overall negative effects of increased cDOM on whole-ecosystem GPP to a hump-shaped response with increasing cDOM. This response was in turn mainly driven by the increase in pelagic GPP. Although we do not have the data to test the underlying mechanisms, the positive response in pelagic GPP with warming concomitant with an increased nutrient supply from the cDOM water treatment may be because warming enhances nutrient uptake rates (Malik & Saros, 2016; Reay et al., 1999; Rhee & Gothan, 1981). Warming did not affect benthic GPP along the gradient of cDOM input, probably primarily due to light availability limiting benthic GPP and especially so at high cDOM input. At the highest cDOM levels, light limitation probably also became strong enough to counteract any positive temperature response in GPP even in the pelagic habitats. Still, the lack of a significant temperature response in benthic GPP in the clearwater enclosures is somewhat surprising. However, nutrient levels in the sediments of our ponds may be fairly low compared to many lakes (Vasconcelos et al., 2016), which explains the lack of temperature response in benthic GPP of the clearwater enclosures. This may suggest that nutrient availability in benthic systems could be an additional factor causing modest GPP responses in clearwater systems (McCormick et al., 2019). Variation in thermal stratification could be another factor that influences interpretations and mechanistic explanations of our results. However, the absence of thermal stratification in our enclosures, probably due to their shallow nature, gives at hand that our results cannot be explained by differences between treatments in stratification properties. Still, we acknowledge that in deeper systems, increased cDOM can cause changes in thermal stratification (Read & Rose, 2013) and impact GPP via for instance affecting nutrient movement across the water column (Staehr et al., 2012).

Warming also extended the duration of the ice-free period by tw2 weeks and during this period GPP was higher in the heated ice-free compared to ambient ice-covered enclosures. Similar to the preceding ice-free period we attribute the differences in habitat-specific and whole-ecosystem GPP to increased photosynthetic rates following higher temperatures in ice-free versus ice-covered enclosures during this period. Surprisingly, there was no significant
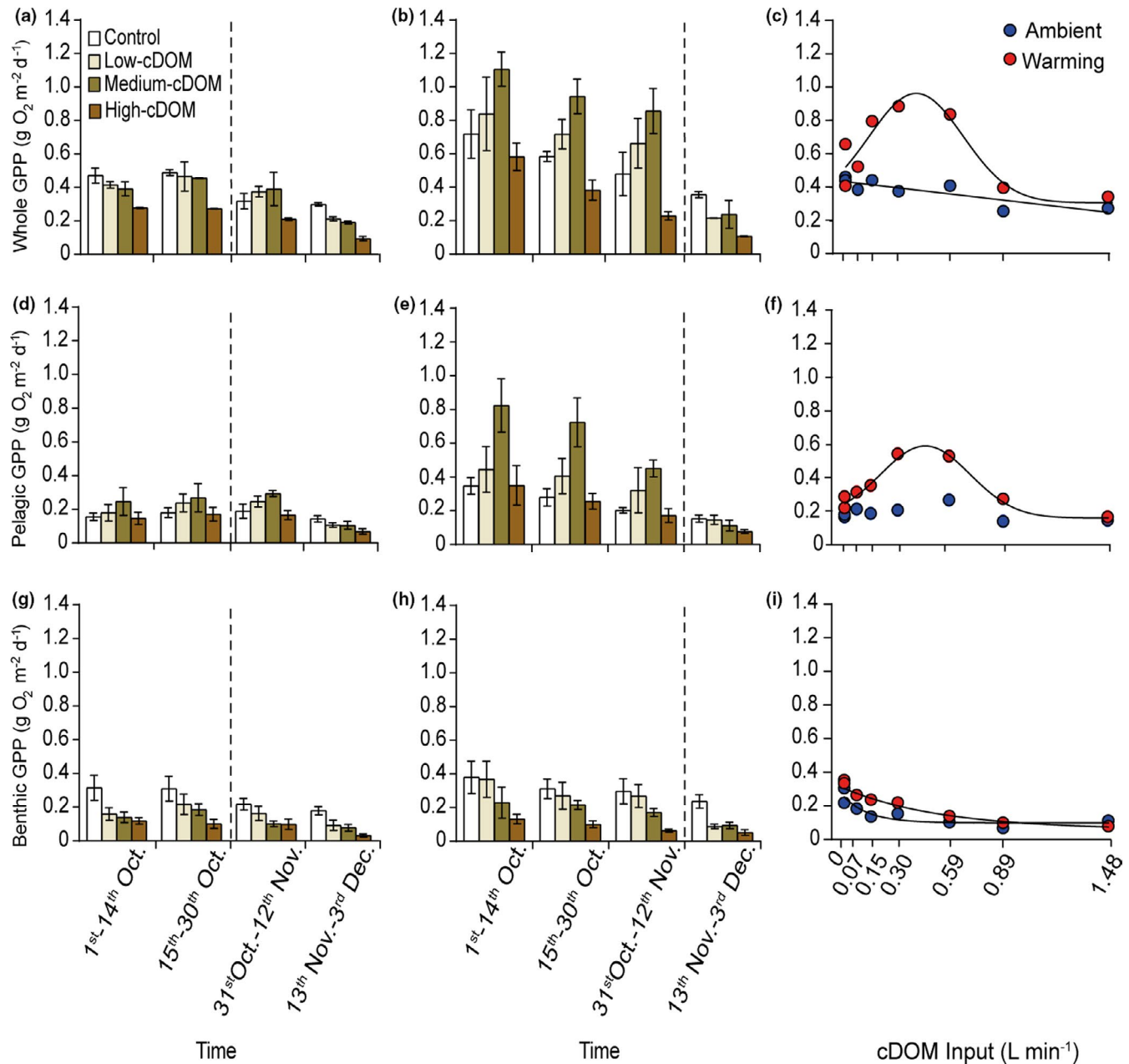
FIGURE 3 Mean (± 1 *SD*) gross primary production (GPP) at the different levels of allochthonous coloured dissolved organic matter (cDOM) inputs over time in ambient (a, d, and g) and warm enclosures (b, e, and h) for whole-ecosystem, pelagic, and benthic habitat, respectively, as mean time-integrated GPP of whole-ecosystem (c), pelagic (f), and benthic habitat (i) in both ambient and heated enclosures along the gradient of cDOM inputs. Dashed line indicates transition between sampling periods of ice-free to ice-on conditions

difference between ambient and heated enclosures in incoming light intensity, presumably because the ice cover was clear and transparent (i.e. no snow cover) with low ability to intercept incoming light (Bolsenga & Vanderploeg, 1992). Hence, it is likely that with thicker and more opaque ice or snow cover than in our experiment, decreased light conditions would result in additional negative impacts on GPP.

The results of this study advance our understanding of how climate change affects aquatic productivity. This is important since lakes and ponds in northern regions are experiencing rapid and ongoing climate change (Finstad et al., 2016; Niedrist et al., 2018; Rose et al., 2016). Our findings suggest that both cDOM inputs, presumably via associated changes in availability in light, nutrients, and CO_2 as well as warming have strong effects on lake GPP and provide experimental evidence for the predicted hump-shape response of GPP to increasing cDOM inputs (Hanson et al., 2003; Seekell et al., 2015; Solomon et al., 2015). Warming in autumn is also likely to have positive effect on whole-ecosystem GPP. Hence, we conclude that climate change may

TABLE 2 Results of two-way repeated-measures ANOVA (for whole experiment period) and two-way ANOVAs (for the third and fourth sampling periods) for whole-ecosystem, pelagic, and benthic gross primary production showing effect of time, allochthonous coloured dissolved organic matter (cDOM) input, warming, and their interactions

	Gross primary production (g O_2 m^{-2} d^{-1})								
	Whole-ecosystem			Pelagic			Benthic		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Whole experiment									
Time	3, 24	61.2	<0.001	3, 24	29.8	<0.001	3, 24	27.1	<0.001
cDOM	3, 8	11.7	0.003	3, 8	13.4	0.002	3, 8	19.4	<0.001
Warming	1, 8	17.1	0.003	1, 8	39.4	<0.001	1, 8	4	0.08
cDOM × Warming	3, 8	1.1	0.39	3, 8	1.1	0.39	3, 8	0.4	0.74
Time × cDOM	9, 24	1.9	0.10	9, 24	1.6	0.17	9, 24	1.1	0.38
Time × Warming	3, 24	4.6	0.01	3, 24	5.4	0.006	3, 24	0.6	0.61
Time × cDOM ×Warming	9, 24	0.8	0.62	9, 24	0.2	0.99	9, 24	0.9	0.48
Third sampling period									
cDOM	3, 15	5.4	0.02	3, 15	5.2	0.02	3, 15	10.6	0.004
Warming	1, 15	8.4	0.02	1, 15	1.4	0.27	1, 15	2	0.19
cDOM × Warming	3, 15	1.2	0.37	3, 15	0.3	0.80	3, 15	1.8	0.21
Fourth sampling period									
cDOM	3, 15	23.7	<0.001	3, 15	4.9	0.03	3, 15	14.4	0.001
Warming	1, 15	1.5	0.25	1, 15	1	0.34	1, 15	1.6	0.23
cDOM × Warming	3, 15	0.1	0.94	3, 15	0.2	0.9	3, 15	0.3	0.82

Note: *df*, degrees of freedom; F, ratio of mean squares; *p*-values are reported.

alter patterns of autumn whole-ecosystem GPP through asymmetric responses of habitat-specific GPP to warming and increasing cDOM inputs.

CONFLICT OF INTEREST
All authors have no conflict of interests.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available by the corresponding author upon request.

ORCID
Mohammed Hamdan https://orcid.org/0000-0003-4068-2109
Erin R. Hotchkiss https://orcid.org/0000-0001-6132-9107
Mohammed J. Al-Haidarey https://orcid.org/0000-0001-5135-9345
Jan Karlsson https://orcid.org/0000-0001-5730-0694

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