

DR. FRANCISCO RIVERA VASCONCELOS (Orcid ID : 0000-0002-2327-9716)

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Bottom-up and top-down effects of browning and warming on shallow lake food webs

Running head: Browning and warming effects on shallow lake

Francisco Rivera Vasconcelos^{1,2}, Sebastian Diehl^{1,2}, Patricia Rodríguez^{1,3}, Per Hedström¹, Jan Karlsson¹ and Pär Byström¹

¹Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

²Integrated Science Lab – IceLab, Umeå University, Umeå, Sweden

³Austral Centre for Scientific Research (CADIC-CONICET), Ushuaia, Tierra del Fuego, Argentina

Corresponding author: telephone + 46 073 09 47 419; e-mail francisco.vasconcelos@umu.se

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Abstract

Productivity and trophic structure of aquatic ecosystems result from a complex interplay of bottom-up and top-down forces that operate across benthic and pelagic food web compartments. Projected global changes urge the question how this interplay will be affected by browning (increasing input of terrestrial dissolved organic matter), nutrient enrichment and warming. We explored this with a process-based model of a shallow lake food web consisting of benthic and pelagic components (abiotic resources, primary producers, grazers, carnivores), and compared model expectations with the results of a browning and warming experiment in nutrient-poor ponds harboring a boreal lake community. Under low nutrient conditions, the model makes three major predictions. (1) Browning reduces light and increases nutrient supply; this decreases benthic and increases pelagic production, gradually shifting productivity from the benthic to the pelagic habitat. (2) Because of active habitat choice, fish exert top-down control on grazers and benefit primary producers primarily in the more productive of the two habitats. (3) Warming relaxes top-down control of grazers by fish and decreases primary producer biomass, but effects of warming are generally small compared to effects of browning and nutrient supply. Experimental results were consistent with most model predictions for browning: light penetration, benthic algal production, and zoobenthos biomass decreased, and pelagic

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nutrients and pelagic algal production increased with browning. Also consistent with expectations, warming had negative effects on benthic and pelagic algal biomass and weak effects on algal production and zoobenthos and zooplankton biomass. Inconsistent with expectations, browning had no effect on zooplankton and warming effects on fish depended on browning. The model is applicable also to nutrient-rich systems, and we propose that it is a useful tool for the exploration of the consequences of different climate change scenarios for productivity and food web dynamics in shallow lakes, the worldwide most common lake type.

Introduction

In many northern lakes, ongoing global change is causing a rise in both surface water temperature and the concentration of colored ('brown'), terrestrial dissolved organic matter (tDOM) (Clark *et al.*, 2010; O'Reilly *et al.*, 2015). Temperature and tDOM are powerful drivers of numerous physical, chemical and biological properties of lakes (Woodward *et al.*, 2010; Read & Rose, 2013; Seekell *et al.*, 2015a). Their projected continued increase has therefore inspired experimental studies exploring the effects of 'browning' and warming on aquatic systems (Kratina *et al.*, 2012; Jones & Lennon, 2015; Zwart *et al.*, 2015). Still, while browning and warming have progressed simultaneously in many lakes, few experiments have investigated their interaction, and these experiments were performed on rather small spatial scales and/or have only focused on pelagic ecosystem components (e.g. Yvon-Durocher *et al.*, 2010; Winder *et al.*, 2012; Hansson *et al.*, 2013; Lefébure *et al.*, 2013). In contrast, we are not aware of any experiments that have evaluated browning and warming effects on entire lake food webs including both benthic and pelagic components at realistic

spatial scales. Yet, the responses of lake food webs to browning and warming are likely to involve complex bottom-up and top-down pathways that operate within and across the benthic and pelagic habitats.

Browning can be expected to affect lake food webs primarily from the bottom-up. Browning reduces benthic primary production by attenuating the light supply to the lake bottom (Ask *et al.*, 2009; Brothers *et al.*, 2014), which should propagate as negative browning effects to benthic grazers and carnivores (Karlsson *et al.*, 2009). In contrast, pelagic primary producers may benefit from browning, because they tend to be less light- and more nutrient-limited (Vadeboncoeur *et al.*, 2003; Ask *et al.*, 2009; Kissman *et al.*, 2013). Browning can supply nutrients to the pelagic habitat via at least two pathways. First, by releasing organic nutrients from tDOM (Cottingham & Narayan, 2013; Sanders *et al.*, 2015), and second, by shading out benthic producers and thus preventing them from intercepting the flow of nutrients from the sediment to the pelagic habitat (Hansson, 1990; Vasconcelos *et al.*, 2018). At moderate levels of browning, the resulting increase in pelagic primary production should then benefit pelagic grazers and carnivores (Lefébure *et al.*, 2013; Kissman *et al.*, 2013; Kelly *et al.*, 2016), whereas very high levels of browning can cause severe light limitation also of pelagic producers and the consumers that depend on them (Karlsson *et al.*, 2009; Finstad *et al.*, 2014; Karlsson *et al.*, 2015).

In contrast to browning, warming directly affects physiological rates of *all* organisms in the food web. The impact of warming on entire food webs will therefore depend on the balance of warming effects on growth and loss rates at different trophic levels (Yvon-Durocher *et al.*, 2010). In most organisms, resource uptake rates increase with warming up to an optimal temperature (Englund *et al.*, 2011; Rall *et al.*, 2012). Yet, consumer population

sizes may simultaneously decline, because population loss rates tend to increase faster with warming than resource uptake rates (Vázquez-Domínguez *et al.*, 2007; Yvon-Durocher *et al.*, 2012). The net impact of warming on top-down effects of consumer populations are therefore difficult to predict.

Predicting the consequences of browning and warming on lakes is further complicated by the dynamic coupling of benthic and pelagic habitats through the flow of light energy and nutrients across habitat boundaries and through active habitat choice by individual organisms. For instance, browning may shift the most productive habitat for fish from the benthic to the pelagic habitat (Karlsson *et al.*, 2009). Active habitat choice by fish could then lead to increased top-down control in the preferred, more productive habitat, but to prey release in the less productive habitat. Browning and warming might thus trigger complex dynamics, where top-down and/or bottom-up effects in one habitat propagate across habitat boundaries, potentially generating opposite responses to browning and warming in the two habitats.

In this paper we explore how browning and warming affect abiotic resources (light, nutrients) and the standing stocks of major food web components (primary producers, grazers, carnivores) in shallow lakes. We focus on shallow, thermally unstratified systems, because small shallow lakes are the most abundant lake type on Earth (Downing *et al.*, 2006), and they tend to be strongly influenced by inputs from the terrestrial catchment (Rasmussen *et al.*, 1989). We proceed in two steps. First, we develop a process-based model of a shallow lake ecosystem describing the dynamics of abiotic resources and food web components in both benthic and pelagic habitats. We explore numerically how browning and warming affect the equilibrium states of all ecosystem components, and we derive

analytical predictions for a relevant limiting case. Second, we report on a pond experiment with a boreal, shallow lake community in which we manipulated browning and warming in a factorial design and compare the experimental results with model predictions.

Materials and Methods

Model structure and analysis

Model description

The model is an extension of an existing model of competition between benthic and pelagic algae for light and a limiting nutrient (Jäger & Diehl, 2014; Vasconcelos *et al.*, 2016; Vasconcelos *et al.*, 2018) to which we added two grazers and a carnivore. One grazer feeds on benthic algae and the other grazer feeds on pelagic algae. The carnivore moves freely between habitats and can prey on both benthic and pelagic grazers.

The physical setting is a lake with uniform depth z_{max} . From the surface to z_{max} there is a well-mixed pelagic habitat. Between z_{max} and the sediment surface at depth z_{sed} there is a thin benthic habitat of depth z_{bent} . The sediment itself consists of an active surface layer of depth z_{ss} in which detrital nutrients are partially mineralized, and an inactive layer below. The model describes the dynamics of 11 variables: the biomasses of pelagic algae (A) and grazers (Z), benthic algae (B) and grazers (G), and carnivorous fish (C); light penetration to the bottom of the pelagic ($I_{z_{max}}$) and benthic ($I_{z_{sed}}$) habitats; the concentrations of dissolved mineral nutrients in the pelagic (R_{pel}) and benthic (R_{bent}) habitats; and the concentrations of particulate detrital (R_d) and dissolved mineral nutrients (R_{sed}) in the surface sediment. The model was parameterized for a scenario where phosphorus is the limiting nutrient, so all

nutrient compartments R_i , are in units of phosphorus. The dynamical equations are listed in Table 1 and the variables and parameters are defined in Table 2.

Nutrients are ultimately supplied from a surface inflow (eqn. T1.6), which delivers both mineral nutrients with concentration R_{surf} and dissolved organic nutrients with concentration $c_{DOM} * tDOM$ (where c_{DOM} is the phosphorus to carbon ratio of terrestrial dissolved organic matter $tDOM$). Because it is usually not known which fraction of tDOM-bound organic nutrients is available to primary producers, we explore two extreme, limiting cases: dissolved organic nutrients are either completely available and instantly mineralized upon entry into the lake (the default case) or completely unavailable, which is regulated by setting parameter $a_{0,1}$ in eqn. T1.6 (Table 1) equal to 1 or zero, respectively. In addition, nutrients are recycled and lost through various processes described further down and partially resupplied from the surface sediment, with mineral nutrient concentration R_{sed} , to the benthic habitat (eqn. T1.7).

Nutrient exchange rates between the sediment and the benthic habitat and between the benthic and pelagic habitats are proportional to the concentration differences between habitats and the rate constants D_{bent} , and D_{pel} , respectively. Nutrient and tDOM input from surface inflow occurs at the water exchange rate D_{surf} , which also represents the washout of pelagic nutrients, algae and grazers. Light attenuates with depth according to Lambert-Beer's law and is, at a given incoming light intensity I_0 , fully described by the light intensities I_{zmax} and I_{zsed} at the bottom of the pelagic and benthic habitats, respectively (eqn. T1.10, T1.11). Light is attenuated by pelagic and benthic algal biomass and by tDOM with attenuation coefficients k_A , k_B and k_{DOM} , respectively.

Pelagic and benthic algal production P_A and P_B depend on temperature T and are assumed to be co-limited by light and the nutrient as described by two multiplicative saturation functions (eqn. T1.12, T1.13). Growing algae take up mineral nutrients in proportion to algal production assuming constant pelagic and benthic algal nutrient to carbon ratios c_A and c_B (eqn. T1.6, T1.7). Pelagic algae sink out of the water column at temperature dependent velocity $v(T)$. Algae are consumed by grazers and suffer from additional losses (from maintenance, viral lysis etc.) at temperature dependent rates $l_A(T)$ and $l_B(T)$ (eqn. T1.1, T1.2).

Grazers and carnivores (eqn. T1.3-T1.5) feed with a type 3 functional response (Hill exponent $q > 1$) described by $a_{JK}(T)J^q / (1 + a_{JK}(T)h_{JK}(T)J^q)$, where $a_{JK}(T)$ is the clearance (or search) rate and $h_{JK}(T)$ the handling time of consumer K feeding on resource J (Uszko *et al.*, 2015). Both parameters are temperature dependent. The choice of type 3 rather than type 2 functional responses was motivated by empirical support (Kalinkat *et al.*, 2013; Uszko *et al.*, 2015) and by their greater propensity to yield stable equilibrium states (Williams & Martinez, 2004; Wollrab & Diehl, 2015). Preliminary analyses revealed that a Hill exponent of $q = 1.5$ yielded unstable dynamics in parts of the browning parameter space. We therefore used the conventional value $q = 2$, which yielded very similar biomass responses to browning, but stable dynamics. Each consumer K converts food J into own biomass with efficiency e_{JK} (when the carbon content of the food is growth limiting) or with efficiency c_J/c_K (when the nutrient content of the food is limiting) and suffers temperature dependent losses (from maintenance etc.) at rate $l_K(T)$.

Carnivorous fish can move between benthic and pelagic habitats. We assume that the rate at which fish leave a habitat depends inversely on the current habitat's size (affecting the probability of encountering a habitat boundary) and profitability (quantified as the difference in growth rates between the habitats), and positively on an inherent propensity S to move between habitats (de Roos *et al.*, 2002). As we assume a uniform depth, habitat volume is proportional to habitat depth. We assume that fishes searching for benthic prey do so from within the bottom layer of the water column (the lower 0.5m, or the entire water column if $z_{max} < 0.5m$), and when searching for pelagic prey, fishes do so within the entire water column (including the bottom layer). This means that the bottom layer contains both benthic and pelagic feeding fish, where search for benthic vs. pelagic prey is assumed to be mutually exclusive.

Individual habitat choice results in a fraction f_p of the fish feeding in the pelagic habitat and a fraction $1-f_p$ feeding in the benthic habitat (eqn. T1.5). Assuming that behavioral dynamics of fish are much faster than population dynamics of their prey, the habitat distribution of fish is in pseudo-steady-state with the current habitat conditions as described by expression f_p^* (Table 1, eqn. T1.14; following de Roos *et al.*, 2002). The parenthesis in the denominator of equation T1.14 expresses the difference in growth rate between the pelagic and benthic habitats (= relative profitability of the pelagic habitat). Parameter S governs the precision with which fishes track this difference in habitat profitability. When $S = 0$, habitat distribution is proportional to habitat volume but becomes, with increasing S , more influenced by habitat profitability until, at infinite S , all fish are found in the more profitable habitat.

The nutrient budget is closed through a variety of mineralization and loss processes.

Each consumer K assimilates only parts of the ingested nutrient content of prey J and excretes the unassimilated fraction $c_J - c_K e_{JK}$ in dissolved mineral form into the habitat in which it resides (eqn. T1.6, T1.7). Similarly, the nutrient content of a fraction f_i of the background losses of organism i , i.e. $c_i f_i l_i$, gets mineralized in the habitat in which the organism resides (eqn. T1.6, T1.7). The remaining fraction $c_i (1-f_i) l_i$ sinks to the bottom and becomes part of the detrital nutrient pool R_d in the surface sediment (eqn. T1.8), which is also replenished by sinking losses from pelagic algae (vA). Detrital nutrients are mineralized and enter the pool of dissolved nutrients in the surface sediment at rate rR_d and are buried (and thus permanently lost at rate bR_d^2) (eqn. T1.8, T1.9). The latter term can be thought of as a phenomenological description of the vertical redox gradient in the sediment, which becomes steeper, and thus speeds up the burial rate, the higher the concentration of detrital biomass in the surface sediment.

Model parameterization

Extensive sensitivity analyses revealed that the model's qualitative behavior is not very sensitive to the choice of parameter values describing traits of organisms [see Jäger & Diehl (2014) for algal traits and Appendix S3.1 for consumer traits]. For the analyses reported in this paper, we set all trait parameters to generic values yielding stable equilibria. To facilitate comparison with previous work, we set algal traits to the ambient temperature values in Vasconcelos *et al.* (2018), and consumer traits to the default values used in chapter IV of Vasconcelos (2017) (see Appendix S1.1). Environmental parameters (D_{surf} , temperature, l_0 and z_{max}) were set to their approximate values in the experimental system.

The values of the phosphorus to carbon quota (c_{DOM}) and the specific light attenuation coefficient (k_{DOM}) of tDOM are based on data in Dillon & Molot (1997) and Ask *et al.* (2009), respectively.

The temperature scaling of temperature dependent parameters is described in Appendix S1.2. We only consider the temperature range over which parameter values increase with warming, and used empirically derived Q_{10} values for the temperature range 17-20°C from the literature, focusing on relatively cold-adapted organisms that are relevant to the experimental study system (Table S1.1). This range covers the average temperatures in the ‘ambient’ and ‘warmed’ experimental treatments (see Fig. 3b), and is below the temperature optima of parameters that change in a non-monotonous way with temperature (e.g. the clearance rate coefficients of consumers; Uszko *et al.*, 2017). Note that, in this baseline parameterization (Tables 2, S1.1), loss rates of primary producers scale approximately similarly with temperature as do rates of primary production, whereas the loss rates of all consumer species are more sensitive to warming than their feeding and production rates. We performed additional sensitivity analyses in which the latter assumptions were reversed (see below).

Model analyses

Using the default parameter values listed in Table 2, we explored numerically how browning, warming and mineral nutrient supply affect our model system by manipulating three environmental parameters: the concentrations of tDOM (g C/m^3) and of dissolved mineral nutrients (R_{surf} , g P/m^3) in the surface inflow (subsequently called ‘browning’ and ‘nutrient supply’, respectively), and water temperature (T). We exhaustively explored the

parameter space of realistic tDOM and nutrient concentrations by varying $tDOM$ and R_{surf} independently in 200 arithmetically spaced steps over the range 1-50 g C/m³ and in 200 logarithmically spaced steps over the range 0.001–1 g P/m³, and did so for two (constant) water temperatures: ambient (= 17°C) and +6°C. All simulations were performed in Matlab version R2017b (Mathworks, Natick, Massachusetts, USA) and were run to equilibrium. To detect regions of alternative stable states, we ran simulations in both ascending and descending order across the $tDOM$ - R_{surf} parameter space, using the equilibrium values from the previous run as the starting values for the respective next run.

We performed four types of sensitivity analyses. First, we explored whether the model's qualitative behavior is robust against order of magnitude changes in the parameter values describing traits of consumers (see details in Appendix S3.1). In addition, we performed sensitivity analyses with respect to three alternative scenarios. (i) Setting parameter $\alpha_{0,1}$ to 1 or 0 (nutrients bound to tDOM are either fully available to algae (= default) or completely unavailable) allowed us to assess the potential contribution of tDOM-bound nutrients to the effects of browning. (ii) Setting parameter S to 200 (fish show near-optimal habitat choice = default) or 10 (fish use the benthic and pelagic habitats approximately in proportion to their volumes) allowed us to assess how system responses to environmental drivers depend on the precision with which fishes assess habitat quality. (iii) In order to assess how effects of warming depend on the relative temperature sensitivities of consumer production vs. loss rates, we explored alternative scenarios in which consumer feeding and production rates were assumed to increase either faster (= default) or more slowly with warming than loss rates (see Appendix S4).

Experimental setup, sampling and statistics

The experiment was performed at Umeå Experimental Ecosystem Facility (EXEF, 63°48' N, 20°14' E). EXEF includes a rectangular pond divided into 20 sections of which 16 were used for treatment establishment. Each section had a total volume of 110 m³, an area of 11.5 m x 6.7 m, was 1.6 m deep except for a narrow zone near the shoreline, and had its own, separate water supply system. In summer 2011, the pond was filled with groundwater and allowed to develop a spontaneously assembling community of pelagic and benthic algae, zooplankton and benthic invertebrates, and sparse floating leaf and submerged macrophytes. In addition, we inoculated mixed zooplankton from ponds that are located within tens of meters of the experimental pond. In May 2012, we stocked each section with a (subsequently reproducing and overwintering) fish population of three-spined stickleback (*Gasterosteus aculeatus*) and established two tDOM treatments: a 'low tDOM' control to which we continuously added groundwater, and a 'high tDOM' treatment to which we continuously added humic water from a mid-sized stream near the facility. The tDOM treatments were cross-classified with two temperature treatments: ambient temperature ('amb') and warming to 3°C above ambient temperature ('warm'). The latter was accomplished by continuously circulating water from the warmed sections through individual heat exchangers. For further details, see Rodrigues *et al.* (2016). Each tDOM by temperature treatment was replicated four times.

Warming and tDOM additions were maintained from May 10th to October 6th 2012, interrupted during winter to allow for a regular ice cover, and resumed from May 16th to October 3rd 2013 (Julian days 136-276). Here, we report results from the summer season 2013, which was characterized as follows. On May 16th 2013 water supply to both high and

low tDOM treatments was set to 4 m³/day to mimic a one-week spring flow. Thereafter a continuous input of 1.15 m³/day was applied, corresponding to a daily exchange rate of 0.9% of the water volume during the rest of the season. Humic stream water was 100 µm filtered prior to addition and was characterized by seasonal averages of 19.5 g/m³ of dissolved organic carbon (DOC), 0.05 g/m³ total phosphorus (TP), 0.01 g/m³ of soluble reactive phosphorous (SRP), and 0.26 g/m³ of dissolved inorganic nitrogen (DIN). Groundwater was characterized by seasonal averages of 1.5 g/m³ DOC, 0.003 g/m³ TP, 0.003 g/m³ SRP, and 0.3 g/m³ DIN. We cut and removed an existing sparse macrophyte cover on Julian day 156.

Sampling of abiotic and biotic variables

Water temperature and vertical profiles of photosynthetically active radiation (PAR, used to calculate the vertical light attenuation coefficient, k_d) were determined as in Vasconcelos *et al.* (2016). Temperature profiles indicated that the water column was always well mixed. We calculated light at the sediment surface ($I_{z_{\max}}$), expressed as a percentage of incident PAR, as

$$I_{z_{\max}} = 100 \cdot \exp(-k_d \cdot z_{\max}), \quad (1)$$

where z_{\max} is the depth of the water column.

Every third week, starting on Julian day 136, we took integrated water samples from the upper meter of the water column in each experimental section. Water samples were filtered (0.45 µm) prior to determination of SRP and DIN concentrations under Flow Injection Analysis (FIA, Foss, Denmark). The concentrations of dissolved organic carbon (DOC) and

chlorophyll *a* (Chl *a*) were determined as in Vasconcelos *et al.* (2016). Treatment effects on DIN are not further reported here because molar DIN:TP ratios exceeded 30 in 85% of all available measurements throughout the experiment, indicating that phosphorus was the limiting nutrient for primary producers (Bergström 2010).

Since it is not possible to efficiently separate benthic algae from soft sediment we monitored benthic algal biomass on square ceramic tiles (area 20.25 cm²) with a rough surface for algal colonization. On four occasions (Julian days 163, 183, 237, and 257) we deployed four tiles spread out on the sediment of each section. After three weeks, tiles were retrieved and sampled by scraping all material into a container after removal of invertebrates. The material was suspended in Milli Q water and analyzed for Chl *a* as described in Vasconcelos *et al.* (2016).

In each experimental section we estimated gross primary production (GPP) separately in the benthic and pelagic habitats (= benthic and pelagic GPP) from oxygen dynamics recorded during 48 h *in situ* incubations. Incubations were performed on four occasions (Julian days 161 - 165, 196 - 200, 242 - 247, and 273 - 277) as described in Rodríguez *et al.* (2016), and oxygen dynamics were converted into units of carbon as described in Vasconcelos *et al.* (2016).

We sampled benthic macroinvertebrates three times in the season (Julian days 168, 210 and 258) and crustacean zooplankton every third week. Benthic macroinvertebrates were sampled by pulling a 30 cm wide bottom net 70 cm along the bottom of each section. Samples were preserved in ethanol. Crustacean zooplankton was sampled by vertically pulling a net (100 µm mesh size and 25 cm diameter net opening) 133 cm through the water column. Samples were preserved in Lugol's solution. We measured the body length of

benthic and pelagic invertebrates and transformed them to dry weight (D.W.) using length-weight relationships (Dumont *et al.*, 1975; Bottrell *et al.*, 1976; Persson *et al.*, 1996).

Fishes were sampled on Julian days 127 and 280. Population densities were determined by the three-pass removal method (Zippin, 1956) after pulling a seine-net three times through each section. All captured fishes were placed in a container, photographed from above, and returned to their sections. Their numbers and body lengths were estimated using image analysis. Based on subsamples of 10-18 fishes from Julian day 280, we derived section-specific length vs. weight relationships in order to estimate wet fish biomass. When estimating the wet biomass of fish on Julian day 127, we used length-weight regressions from a sampling performed in October 2012.

Data analysis

We analyzed treatment responses using the temporally averaged mean values of all relevant variables over a time window ranging from Julian day 184 to 273 (July 03rd – September 30th). This is the largest time window for which data on all variables relevant to our hypotheses were available. Environmental conditions related to the treatments, i.e. water temperature and DOC concentration, did not show any strong temporal trends over this period, with the exception of a 6°C temperature decline in the last week (Fig. 3). Temporally averaged means were calculated by linear interpolation between all actual measurements taken during and (where available) immediately before and after the selected time window. Since fish were not sampled in summer, fish biomass during the time window was estimated by interpolating data from Julian day 127 to 280.

We analyzed the data using two-way ANOVA to test for treatment effectiveness (differences in tDOM/browning and temperature between treatments), for effects of the treatments on the availability of the resources light (characterized by $I_{z_{max}}$) and SRP, on the production and biomass of benthic and pelagic algae, and on the biomasses of crustacean zooplankton, benthic macroinvertebrates (zoobenthos), and fish. Data were log transformed when necessary to fulfill ANOVA requirements. All ANOVAs were run on R software using the ez package (R Development Core Team 2013, Lawrence 2015).

Results

Model output

In the following, we first describe predicted effects of browning for the baseline case of ambient temperature (17°C) and tDOM-bound nutrients being fully available to pelagic producers across a range of external nutrient supplies spanning three orders of magnitude (Fig. 1). Subsequently, we describe predicted effects of warming along the full range of browning conditions. Because browning is primarily an issue in relatively nutrient poor, boreal lakes, we focus on this scenario in the main text (Fig. 2). Scenarios with high external nutrient supply are also briefly described in the main text and shown in detail in Appendix S4. We finally describe the results of sensitivity analyses delineating the generality of the model expectations. For readers who want to skip the detailed descriptions and explanations of the modeling results, we have summarized the most salient and robust model predictions in the section *Summary of major model predictions*.

Effects of browning in nutrient poor systems

In clear and nutrient poor systems ($R_{surf} \leq 0.03 \text{ g P/m}^3$ and light attenuation $\leq 1.8 \text{ m}^{-1}$), sufficient light reaches the bottom of the lake to sustain benthic algae (Fig. 1a, c, 2a, e). Benthic algal production then intercepts most of the nutrient flux from the sediment to the water column, leading to nutrient limitation in the pelagic habitat and low pelagic algal biomass (Fig. 1b, d, 2b, f). Under these conditions, the biomass of benthic grazers is higher than zooplankton biomass, making the benthic habitat profitable for fish (Fig. 1e-g, 2g-i). Fish therefore exert strong top-down control on benthic grazers (Fig. 1e, 2g), thus releasing grazing pressure on benthic algae.

Browning has opposing effects on algal production by reducing light supply and increasing the supply with nutrients bound to tDOM (Fig. 1a-b, 2a-b). Nutrients released from tDOM do not only enrich the water column but also the surface sediment (from which benthic algae derive their nutrients) in the form of sinking pelagic algae and detritus. In the clearest systems, browning therefore has a net positive effect on both benthic and pelagic algae (Fig. 1c-d, 2c-f). However, with sufficient browning (near a light attenuation of 1.5 m^{-1} in Fig. 2e), the shading effects of tDOM become too strong and benthic algae decline with further browning. This triggers a positive feedback loop: Declining benthic algae intercept less of the nutrient flux from the sediment; this boosts the production of pelagic algae, resulting in further shading of benthic algae and an abrupt state shift to a system with low benthic and high pelagic algal biomass and production (Fig. 1c-d, 2c-f). The two states (dominance of benthic vs. pelagic algal biomass) exist as alternative states in a very narrow band near a light attenuation of 1.8 m^{-1} . Further browning drives benthic algae and grazers rapidly extinct (Fig. 1c, e, 2e, g).

At the state shift, fish switch abruptly over to the more profitable pelagic habitat (Fig. 1g-h, 2i-j) where they exert strong top-down control on zooplankton with further browning (Fig. 1f, 2h), thus releasing grazing pressure on pelagic algae. Pelagic algae therefore continue to respond positively to the increased supply with tDOM-bound nutrients that comes with further browning (Fig. 1d, 2f). Beyond the browning threshold where benthic grazers go extinct, fish continue to spend a small fraction of their time sampling the benthic habitat (Fig. 1g, 2i).

At yet higher browning (attenuation $> ca. 5.5 m^{-1}$), also pelagic algal production becomes severely light limited, and pelagic algae decline steeply with further browning to a point where a second state shift occurs; beyond this point, zooplankton production becomes too low to sustain a fish population, fish go abruptly extinct, and zooplankton controls pelagic algae at low levels (Fig. 1d, f, h, 2f, h, j). The two states (high vs. low algal biomass coupled with high vs. no fish biomass) exist as alternative states in the light attenuation range $ca. 5-7 m^{-1}$ (Fig. 1d, f, h, 2f, h, j, S2.1). These alternative states are a consequence of the type 3 response of zooplankton, which enable zooplankton to coexist stably with either a very low phytoplankton density (when zooplankton mortality is low) or a very high phytoplankton density (when mortality from planktivores is high). At sufficiently high browning the system will become so light limited that also zooplankton and pelagic algae go extinct (Fig. 1d, f, 2f, h).

Effects of browning in nutrient rich systems

The patterns described above change at higher external nutrient supply, because nutrients supplied to the water column benefit pelagic algae, which increasingly shade the benthic habitat. Consequently, as nutrient supply increases, the decline and extinction of the benthic food chain and the concomitant biomass increase of pelagic algae occur at increasingly lower levels of browning, until at $R_{surf} > 0.2 \text{ g P/m}^3$ benthic algae cannot persist even in the clearest waters (Fig. 1). At such high levels of external mineral nutrient supply, pelagic algal production is no longer stimulated by tDOM-derived nutrients and, instead, only suffers from increased light attenuation caused by browning. Production and biomass of pelagic algae are therefore highest in waters with the lowest tDOM concentrations and decline with browning until the threshold is reached where the system abruptly switches to the alternative state, with fish being extinct and grazers controlling pelagic algal biomass at very low levels (Fig. S4.1).

Effects of warming

Before we describe effects of warming on the model ecosystem in detail, we note two general observations. First, the just described qualitative predictions of browning and mineral nutrient effects hold also under warmer conditions (compare Fig. 1 with S3.2). Second, predicted effects of substantial warming (+6°C) are relatively small compared to the predicted effects of nutrient and light availability (Fig. 2, S4.1).

Several warming effects can be most easily understood if we first consider an isolated food chain in a single habitat. In this case, warming effects depend on the temperature scaling of growth and loss rates of consumers. In the baseline parameterization, at a given

prey density, the loss rates of consumers increase faster with warming than their feeding and growth rates (Table S1.1). Consequently, warming alleviates top-down control by fish and grazer biomass must increase, while algal biomass must decrease with warming, the underlying mechanisms working as follows (see Appendix S5 for formal derivations).

In an isolated food chain, fish control their prey at the level where prey intake yields a fish growth rate that exactly balances fish losses. Because clearance rate and handling time change more gently with warming than specific losses, fish require higher prey (= grazer) densities in order to achieve the feeding rates needed to balance higher losses at higher temperature. Higher grazer biomass and higher per capita feeding rates of grazers at higher temperatures then cause higher grazing pressure on algae. Algae must balance this increased grazing pressure through increased production. Because the specific gross production and background loss rates of algae (p_i and l_i , respectively) increase approximately equally with warming, this requires higher resource availability. Light and/or nutrient availability will, in turn, only increase if algal biomass decreases, thus alleviating intraspecific algal competition.

Importantly, the above predictions of relaxed top-down control by fish under warming extend, in the full model, directly to the habitat, where the bulk of the fish population resides. Thus, at low browning and low external nutrient supply R_{surf} , when fish forage extensively in the benthic habitat, benthic grazer biomass increases (albeit very slightly) and benthic algal biomass decreases with warming (Fig. 2e, g). Similarly, at higher browning or high external nutrient supply, when most fish forage in the pelagic habitat, zooplankton biomass increases and pelagic algal biomass decreases with warming (Fig. 2f, h, S4.1f, h).

We cannot derive possible analytical predictions for effects of warming on the remaining state variables. Numerical observations are, however, largely consistent across browning and nutrient enrichment. Specifically, because specific production increases with warming, this can more than compensate for lower algal biomass. Consequently, benthic algal production is only very weakly affected by warming, and both pelagic and total algal production increase with warming (Fig. 2c-d, l, S4.1d, l). Total fish biomass follows total primary production and increases with warming; yet, the browning threshold at which fish go extinct decreases slightly with warming (Fig. 2k-l, S4.1k-l). Warming effects on dissolved pelagic nutrients are negligible in nutrient poor systems and positive in enriched systems (Fig. 2, S4.1b).

Sensitivity analyses

In Appendix S3.1 we show that the above qualitative model predictions concerning the effects of browning do not depend on the specific choices we made for the values of the consumer parameters (attack rates, handling times, loss rates). When these parameter values were randomly drawn from order of magnitude ranges centered on their default values, we observed qualitatively similar responses to browning as for the default parameterization (compare Fig. S3.1 with Fig. 2). The variance observed in this analysis suggests that comparative data from real lakes (where organismal traits may differ geographically) should fall within fairly broad bands or wedges centered around median values similar to the deterministic lines in Fig. 2. The qualitative predictions also hold when the precision with which fish perceive habitat profitability is strongly reduced, with the exception that, by definition, fish then use the two habitats in proportion to habitat volume.

As a consequence, predation pressure on benthic grazers is reduced and grazing pressure on benthic algae is enhanced in very nutrient poor, clear waters (Fig. S3.3). The qualitative predictions of browning effects are also valid when nutrients bound to tDOM are assumed to be unavailable, but the persistence region of the pelagic food chain shrinks and alternative states disappear at low mineral nutrient supply ($R_{surf} < 0.02 \text{ g P/m}^3$; Fig. S3.4). This happens because, when mineral nutrient supply is scarce and tDOM nutrients are unavailable, pelagic production becomes strongly nutrient limited and relatively little shading by tDOM is sufficient to turn pelagic net production negative.

In Appendix S4 we explore three alternative scenarios in which the relative temperature sensitivities of consumer production vs. loss rates are partly or entirely reversed compared to the baseline scenario. We thus assume that clearance rates and handling times change faster with warming than loss rates for either fish (scenario 2) or grazers (scenario 3), or for both fish and grazers (scenario 4). These analyses reveal that the response of grazers to warming is entirely determined by the temperature sensitivity of their fish predators. Specifically, compared to the baseline scenario and scenario 3, the qualitative effects of warming on grazers are reversed (i.e. grazers decrease with warming in the more profitable habitat) when the loss rate of fish changes more slowly with warming than their clearance rates and handling times (scenarios 2 and 4, Fig. S4.2-S4.3). In contrast, effects of warming on algal biomass in the more profitable habitat are the same for all four scenarios (Fig. 2, S4.1-S4.3). We thus conclude that the prediction of negative effects of warming on benthic algal biomass at low levels of browning and on pelagic algal biomass at high levels of browning is highly robust and independent of whether consumer loss rates are more or less sensitive to warming than their clearance rates and handling times.

Summary of major model predictions

In summary, the following general predictions emerge concerning the effects of browning and warming on the model ecosystem. In systems with low mineral nutrient supply, benthic food web components dominate at low levels of browning but decline abruptly to extinction at moderate browning, whereas pelagic food web components show an overall unimodal browning pattern (Fig. 2, S4.2). Total (= benthic + pelagic) primary production also shows a distinct unimodal browning pattern, whereas the response of total fish biomass to browning is best described by a stepwise decreasing function (Fig. 2k-l, S4.2k-l). The level of browning at which benthic food web components go extinct decreases with increasing mineral nutrient supply, and pelagic food web components dominate at all levels of browning in extremely nutrient rich environments (Fig. 1, S4.1, S4.3).

The directions of most warming effects depend on the relative temperature sensitivities of the maximum growth and loss rates of consumers. The only consistent pattern is that algal biomass is predicted to decline with warming in the more productive habitat (i.e. the benthic habitat at low browning and the pelagic habitat at high browning, Fig. 2, S4.1-S4.3). Importantly, most warming effects are predicted to be weak compared to effects of browning and mineral nutrient supply and may therefore be difficult to detect empirically.

Experimental results

The manipulations of browning and temperature were effective (Fig. 3; Table 3). Averaged over the period July 3rd to September 30th, the concentration of dissolved organic carbon (DOC) was 2.7 times higher in the high vs. low tDOM sections, and water temperature was 2.8°C higher in the warmed vs. ambient sections. Low tDOM sections were

on average 0.3°C warmer than high tDOM sections (Table 3). Moreover, DOC concentrations tended to be lower in warmed than in ambient, high tDOM sections (Fig. 3a), but this effect was not statistically significant (tDOM*warming interaction in Table 3).

The browning treatment had a negative effect on light supply to the benthic habitat and a positive effect on nutrient availability in the pelagic habitat. The vertical light attenuation coefficient k_d was on average 2.4 times higher in high vs. low tDOM sections (Table 3).

Consequently, light supply to the benthic habitat ($I_{z_{max}}$) decreased from 26 to 4% of incoming light in high vs. low tDOM sections (Fig. 4a). There was a tendency for the vertical light attenuation coefficient to be lower in warmed than in ambient sections (indicated by higher values of $I_{z_{max}}$ in Fig. 4a), but this effect was only marginally significant (Table 3).

Nutrient availability in the water column increased with browning and decreased weakly with warming (Fig. 4b; Table 3). On average, SRP concentrations were 50% higher in high vs. low tDOM sections and about 15% lower in warmed vs. ambient sections (Fig. 4b; Table 3).

Benthic and pelagic algal production (GPP) responded in opposite directions to browning. Benthic GPP was 2.2 times lower and pelagic GPP was 2.2 times higher in the high vs. low tDOM sections (Fig. 4c-d; Table 3). The increase in pelagic GPP more than compensated for

the decrease in benthic GPP, and total (= benthic + pelagic) GPP increased 1.6 times with browning (Fig. 4j; Table 3). Benthic algal biomass (measured as Chl *a*) also tended to

decrease with browning, and pelagic algal Chl *a* increased with browning, but the former was not statistically significant (Fig. 4e-f; Table 3). Warming did not affect algal production, but decreased both benthic and pelagic Chl *a* (Fig. 4c-f; Table 3).

Benthic and pelagic grazers tended to show similar responses to browning as their algal resources. On average, zoobenthos was 1.85 times lower and crustacean zooplankton 1.94 times higher in high vs. low tDOM sections, but these responses were only marginally significant or non-significant (Fig. 4g-h; Table 3). Also, fish responded negatively to browning only at ambient temperature but not in the warmed treatment (Fig. 4i; tDOM*warming interactions in Table 3). The browning and warming responses of fish were thus ambiguous. Zoobenthos and crustacean zooplankton showed no clear responses to warming (Fig. 4g-h; Table 3).

Comparison of experimental results with model expectations

For several reasons, the comparison of model expectations and experimental results is not entirely straightforward, in particular with respect to a *quantitative* match. First, the model was parameterized for a generic lake system. Only a few environmental parameters (water depth, water residence time etc.), but none of the organismal traits, were tailored to the experimental system. Model predictions are therefore of a qualitative nature. Second, with the exception of warming effects on algal biomass, predicted effects of warming are weak and contingent on the assumption whether consumer loss rates increase faster or more slowly with warming than do growth rates. As a final complication, experimental warming tended to decrease the light attenuation coefficient by on average 0.47 m^{-1} in the high tDOM treatments. To illustrate this, we plotted the experimental data against the average light attenuation coefficients of the respective treatments (Fig. 4).

With these caveats in mind, a comparison of the experimental data with model expectations (in the relevant parameter range $R_{surf} \sim 0.01 \text{ g P/m}^3$ and light attenuation coefficient $\sim 0 - 3 \text{ m}^{-1}$) yields the following picture. For the lower food web compartments, experimental outcomes are in full agreement with qualitative model expectations. Consistent with expectations, light in the benthic habitat, benthic algal production, and benthic algal biomass all decreased with browning (the latter albeit non-significantly), and pelagic nutrients, pelagic algal production, and pelagic algal biomass all increased with browning (compare Fig. 2a-f with Fig.4a-f). Similarly consistent with expectations, warming had a relatively strong negative effect on benthic algal biomass in low tDOM systems and a relatively strong negative effect on pelagic algal biomass in high tDOM systems, but only weak or no effects on algal production, dissolved nutrients, and light (Fig. 2a-f, 4a-f). The picture is more mixed for consumers. In line with expectations, the biomasses of zoobenthos and fish decreased with browning, while the observed increase in crustacean zooplankton with browning was not significant and fish biomass decreased with browning only in the ambient treatment (Fig. 2g-h, k, 4g-i). Also in line with expectations, warming had only weak effects on the biomasses of zoobenthos and crustacean zooplankton, but a negative effect on fish biomass in low tDOM systems, which is opposite to expectations (Fig. 2g-h, k, 4g-i).

Discussion

The exploration of our dynamical model produced robust qualitative expectations on how benthic and pelagic food web components in shallow, non-stratified lakes might respond to browning and warming. These predictions differ between low and high

productive systems. Because browning is primarily an issue in relatively nutrient-poor, northern lakes, we focus most of the discussion on this lake type, which was also the target of our experimental study.

Effects of browning

Our model predicts that, in shallow lakes where sufficient light reaches the lake bottom to sustain benthic algal production under clear water conditions, browning should shift the more productive habitat from the benthic to the pelagic one, due to its contrasting effects on light vs. nutrient supply. These predictions are largely congruent with our experimental results and are also supported by comparative lake data, in which browning is positively related to light attenuation, pelagic nutrients, pelagic primary production and zooplankton biomass, and negatively related to benthic primary production, and benthic macroinvertebrate and fish biomass (Ask *et al.*, 2009; Karlsson *et al.*, 2009, 2015; Godwin *et al.*, 2014).

Our model also predicts that very high tDOM concentrations should cause light limitation also in pelagic producers, with negative consequences for pelagic secondary production. While such browning levels were not reached in our experiment, observational studies have indeed reported low levels of pelagic primary production and fish biomass at high levels of browning (Karlsson *et al.*, 2009; Finstad *et al.*, 2014; Benoît *et al.*, 2016). Yet, to unambiguously ascertain whether patterns of production and biomass of pelagic food web components are truly unimodal along the full browning gradient – as is predicted by our model (Fig. 2) and suggested by several comparative studies (Finstad *et al.*, 2014;

Seekell *et al.*, 2015a; Vasconcelos 2017) – will require the collection of more data, both observational and experimental.

Until now, relatively few experimental studies of browning have been performed. These studies have reported negative effects of browning on pelagic primary production when shading by tDOM was high (Carpenter *et al.*, 1998; Jones & Lennon, 2015), but positive effects on primary and zooplankton production (Kissman *et al.* 2013; Sanders *et al.* 2015; Kelly *et al.*, 2016) and neutral or positive effects on pelagic fish production (Lefébure *et al.*, 2013; Hansson *et al.*, 2013; Koizumi *et al.*, 2018) when browning was moderate. While these observations are compatible with model predictions, it is generally difficult to compare these studies with our model, because of inconsistencies in the temporal and/or spatial scales between model assumptions and experimental conditions. Thus, while model predictions are for equilibrium conditions in a system of dynamically coupled benthic and pelagic habitats, experiments have often focused on transient, seasonal dynamics, were performed at small spatial and on short temporal scales, lacked a benthic habitat, and/or did not report the responses of benthic ecosystem compartments (but see Koizumi *et al.*, 2018).

Our experiment overcame many of the above shortcomings. We want to emphasize, however, that the experiment was designed and carried out before we had fully developed the conceptual modeling framework. Given the strong non-linearities in the predicted patterns along the browning axis, future experiments should use a gradient design rather than a factorial design with only two levels of browning.

Interactions of browning and warming

Our model predicts that warming effects on shallow lake food webs should depend on browning. For the trophic structure assumed in the model, fish feeding on invertebrate grazers should preferentially forage in the more productive of the two habitats, i.e. the benthic habitat under relatively clear conditions, and the pelagic habitat under higher levels of browning. At equilibrium, warming is then expected to weaken top-down control of grazers by fish in the more profitable habitat, where the fish require higher prey (= grazer) densities to balance their increased metabolic losses. Such weakened top-down control propagates down the food chain and increases grazing pressure on primary producers in the more profitable habitat. The model therefore predicts that warming should reduce algal biomass in the benthic habitat at low levels of browning, and in the pelagic habitat at high levels of browning. On a first glance, this seems to contradict studies predicting an increase in algal blooms under warming (Jöhnk *et al.*, 2008, Paerl & Huisman, 2008). Yet, the latter predictions focus on (often transient) blooms of typically inedible algal taxa, whereas our model makes equilibrium predictions for algae that are susceptible to grazing.

While a negative impact of warming on benthic algae in the low tDOM treatment and on pelagic algae in the high tDOM treatment was indeed observed, the predicted underlying mechanisms (increased grazing pressure in the more productive habitat under warming) is not strongly supported by the experimental data. A possible reason for this discrepancy is that the predicted differences in grazer biomass in different warming scenarios (e.g. Fig. 2g, h) are so small as to be undetectable in noisy real data. This explanation appears plausible for benthic grazers at low levels of tDOM and for crustacean zooplankton in both tDOM treatments (Fig. 4g-h). Note, however, that crustacean zooplankton biomass was overall

extremely low. This suggests that feeding pressure from planktivorous fish was underestimated in the model, and that the observed very small absolute treatment differences in crustacean biomass may have produced ecologically insignificant differences in grazing pressure on pelagic algae. The observed difference in pelagic chlorophyll between the warmed and ambient high tDOM treatments could indeed also be explained by the difference in 'realized browning' between the two treatments. Recall that light attenuation was on average 0.47 m^{-1} lower in warmed (1.92 m^{-1}) than in ambient (2.39 m^{-1}) high tDOM treatments, and that pelagic algal biomass is expected to increase rather steeply with browning in that range of attenuation coefficients (compare Figs. 2f and 4f).

Extending the modeling framework

When comparing model expectations with the experimental data, one should keep in mind that real lake communities deviate from the model food web in that zoobenthos is not only comprised of grazers (as assumed in the model) but also of deposit feeders, which feed primarily on settled material from the water column. This flow of matter from the pelagic to the benthic habitat is not included in the model and may therefore contribute to deviating patterns. At intermediate levels of browning, deposit feeders should benefit from increased pelagic production and the concomitant increase in sedimentation from the pelagic habitat. In even higher tDOM systems, where benthic algae and grazers are predicted to be completely absent, deposit feeders should still persist and then also be attractive food for benthic feeding fish. Gut content analyses showed indeed that sticklebacks fed primarily on benthic invertebrates in all treatments, but that small amounts of crustacean zooplankton were also always included in the diet (P. Hedström *et al.*, unpublished data). This suggests

the possibility of an indirect mutualism between benthic deposit feeders and phytoplankton: benthic deposit feeders contribute to supporting a fish population that maintains high predation pressure on zooplankton; this releases phytoplankton from grazing pressure and thus increases the sedimentation flux of algae to the deposit feeders in the benthic habitat. This proposed positive feedback loop from deposit feeders on themselves will be included in future developments of the model.

Warming and browning have several additional, primarily physical, effects on aquatic systems that are currently not considered in our modeling framework, but could be incorporated in the future. For instance, in deeper lakes than considered in our experiment, warming and browning strengthen thermal stratification of the water column (Read & Rose, 2013), which reduces the transfer of nutrients from deeper waters across the thermocline (Lewandowska *et al.*, 2014). Conversely, browning can reduce photosynthetic oxygen production and increase heterotrophic respiration of tDOM in the hypolimnion of thermally stratified lakes, thus promoting anoxic conditions at the sediment surface that can boost the release of sediment nutrients to the water column (Brothers *et al.*, 2014). Similarly, warming may directly increase internal nutrient loading by speeding up mineralization rates in the sediment (Gudasz *et al.* 2010).

In our experiment, warming had a negative effect on the concentration of SRP, which is not consistent with model expectations. As our experimental pond was not thermally stratified, nutrient depletion caused by a more stable stratification (O'Reilly *et al.*, 2003; Lewandowska *et al.*, 2014; Solomon *et al.*, 2015) is not a plausible explanation. Possibly, increased phosphorus consumption by heterotrophic bacteria, which are not included in our model, can explain the reduced SRP concentrations in the warming treatment. Bacteria are

superior competitors for phosphorus compared to phytoplankton (Brown *et al.*, 1981), and their metabolic activity increases with warming (Kirchman *et al.*, 2005; Lopez-Urrutia *et al.*, 2006). To further explore this hypothesis, future extensions of the model could include bacteria and their organic carbon sources as additional dynamical state variables

Relevance to eutrophic systems

While we have focused the discussion primarily on relatively nutrient poor systems, the theory developed in this paper is equally applicable to more eutrophic shallow systems, which are often characterized by high internal nutrient loading from the sediment (Sondergaard *et al.*, 2001). Interestingly, under low tDOM – high nutrient conditions, the model can produce alternative states dominated by either benthic primary producers monopolizing nutrients and causing clear water conditions, or by pelagic primary producers causing high plankton turbidity (Fig. 1; Jäger & Diehl, 2014; Vasconcelos 2017; see Lischke *et al.* 2014 for a similar phenomenon in a model of terrestrial loading with *particulate* organic matter). Shallow eutrophic lakes are indeed known for their potential to exhibit either clear and macrophyte-dominated, or phytoplankton-turbid, alternative states (Scheffer *et al.*, 1993). Conceptually, benthic algae and macrophytes have similar ecological roles in this context, because the latter also reduce leakage of nutrients from the sediment to the water column, for example by preventing resuspension and taking up nutrients (Horppila & Nurminen, 2003).

Conclusions and outlook

We have developed a process-based model of a lake food web that describes dynamically coupled benthic and pelagic components. We used the model to explore responses of shallow lake ecosystems to browning, warming and nutrient enrichment, and compared these predictions with the results of a large-scale field manipulation of browning and warming of a nutrient-poor boreal system. Both the model and the experiment suggest that browning affects the food web from the bottom-up by reducing light supply to the benthic habitat and increasing nutrient supply to the pelagic habitat. The model also predicts that warming should alter top-down control by fish, but that such warming effects should be small compared to effects of browning and nutrient enrichment. Finally, the model can reproduce phenomena observed in nutrient-rich systems, such as alternative states dominated by benthic vs. pelagic primary producers. We therefore propose that the model is a useful tool for the exploration of the consequences of different climate change scenarios for productivity and food web dynamics in shallow lakes, the worldwide most common lake type. We have discussed several model extensions that could make the model useful also for other lake types such as thermally stratified lakes. This will be the focus of future studies.

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Table 1. Dynamical model. Differential and algebraic equations describing state variables, and functions describing specific algal production and habitat distribution of carnivores. Parameters are defined in Table 2 and their dependence on temperature (T) is indicated and further specified in Appendix S1.2 (Table S1.1).

Pelagic producer biomass (g C/m ³)	$\frac{dA}{dt} = \left[\frac{1}{z_{\max}} \int_0^{z_{\max}} P_A(T, I(z), R_{pel}) dz - \frac{a_{AZ}(T)A}{1 + a_{AZ}(T)h_{AZ}(T)A^2} Z - l_A(T) - \frac{v(T)}{z_{\max}} - \frac{D_{surf}}{z_{\max}} \right] A$	T1.1
Benthic producer biomass (g C/m ³)	$\frac{dB}{dt} = \left[\frac{1}{z_{bent}} \int_{z_{\max}}^{z_{sed}} P_B(T, I(z), R_{bent}) dz - \frac{a_{BG}(T)B}{1 + a_{BG}(T)h_{BG}(T)B^2} \frac{G}{z_{bent}} - l_B(T) \right] B$	T1.2
Pelagic grazer biomass (g C/m ³)	$\frac{dZ}{dt} = \left[\min \left(e_{AZ}; \frac{c_A}{c_Z} \right) \frac{a_{AZ}(T)A^2}{1 + a_{AZ}(T)h_{AZ}(T)A^2} - f_p^* \frac{a_{ZC}(T)Z}{1 + a_{ZC}(T)h_{ZC}(T)Z^2} \frac{C}{z_{\max}} - l_Z(T) - \frac{D_{surf}}{z_{\max}} \right] Z$	T1.3
Benthic grazer biomass (g C/m ²)	$\frac{dG}{dt} = \left[\min \left(e_{BG}; \frac{c_B}{c_G} \right) \frac{a_{BG}(T)B^2}{1 + a_{BG}(T)h_{BG}(T)B^2} - (1 - f_p^*) \frac{a_{GC}(T)G}{1 + a_{GC}(T)h_{GC}(T)G^2} C - l_G(T) \right] G$	T1.4
Carnivore biomass (g C/m ²)	$\frac{dC}{dt} = \left[\min \left(e_{ZC}; \frac{c_Z}{c_C} \right) f_p^* \frac{a_{ZC}(T)Z^2}{1 + a_{ZC}(T)h_{ZC}(T)Z^2} + \min \left(e_{GC}; \frac{c_G}{c_C} \right) (1 - f_p^*) \frac{a_{GC}(T)G^2}{1 + a_{GC}(T)h_{GC}(T)G^2} - l_C(T) \right] C$	T1.5
Dissolved pelagic nutrient concentration (g P/m ³)	$\begin{aligned} \frac{dR_{pel}}{dt} = & \frac{D_{pel}}{z_{\max}} (R_{bent} - R_{pel}) + \frac{D_{surf}}{z_{\max}} (R_{surf} + a_{0,1}c_{DOM}iDOM - R_{pel}) + c_A f_A l_A(T) A \\ & + c_Z f_Z l_Z(T) Z + c_C f_C l_C(T) \frac{C}{z_{\max}} + \left[c_A - c_Z \min \left(e_{AZ}; \frac{c_A}{c_Z} \right) \right] \frac{a_{AZ}(T)A^2 Z}{1 + a_{AZ}(T)h_{AZ}(T)A^2} \\ & + \left[c_Z - c_C \min \left(e_{ZC}; \frac{c_Z}{c_C} \right) \right] f_p \frac{a_{ZC}(T)Z^2}{1 + a_{ZC}(T)h_{ZC}(T)Z^2} \frac{C}{z_{\max}} \\ & + \left[c_G - c_C \min \left(e_{GC}; \frac{c_G}{c_C} \right) \right] (1 - f_p) \frac{a_{GC}(T)G^2}{1 + a_{GC}(T)h_{GC}(T)G^2} \frac{C}{z_{\max}} \\ & - \frac{c_A A}{z_{\max}} \int_0^{z_{\max}} P_A(T, I(z), R_{pel}) dz \end{aligned}$	T1.6

Dissolved benthic nutrient concentration (g P/m³)

$$\frac{dR_{bent}}{dt} = \frac{D_{bent}}{z_{bent}} (R_{sed} - R_{bent}) + c_B f_B l_B(T) B - \frac{D_{pel}}{z_{bent}} (R_{bent} - R_{pel}) \quad T1.7$$

$$+ c_G f_G l_G(T) \frac{G}{z_{bent}} + \left[c_B - c_G \min \left(e_{BG}; \frac{c_B}{c_G} \right) \right] \frac{a_{BG}(T) B^2}{1 + a_{BG}(T) h_{BG}(T) B^2} \frac{G}{z_{bent}} - \frac{c_B B}{z_{bent}} \int_{z_{max}}^{z_{sed}} P_B(T, I(z), R_{bent}) dz$$

Detrital nutrient concentration in surface sediment (g P/m³)

$$\frac{dR_d}{dt} = c_A \frac{v(T)}{z_{ss}} A + c_A (1 - f_A) l_A(T) \frac{z_{max}}{z_{ss}} A + c_B (1 - f_B) l_B(T) \frac{z_{bent}}{z_{ss}} B \quad T1.8$$

$$+ c_Z (1 - f_Z) l_Z(T) \frac{z_{max}}{z_{ss}} Z + c_G (1 - f_G) l_G(T) \frac{G}{z_{ss}} + c_C (1 - f_C) l_C(T) \frac{z_{bent}}{z_{ss}} C - rR_d - bR_d^2$$

Mineral nutrient concentration in surface sediment [g P m⁻³]

$$\frac{dR_{sed}}{dt} = rR_d - \frac{D_{bent}}{z_{ss}} (R_{sed} - R_{bent}) \quad T1.9$$

Light intensity at depth z_{max} (μmol photons m⁻² s⁻¹)

$$I_{z_{max}} = I_0 e^{-(k_A A + k_{DOM} t_{DOM}) z_{max}} \quad T1.10$$

Light intensity at depth z_{sed} (μmol photons m⁻² s⁻¹)

$$I_{z_{sed}} = I_{z_{max}} e^{-(k_B B + k_{DOM} t_{DOM}) z_{bent}} \quad T1.11$$

Specific production rate of pelagic algae (d⁻¹)

$$P_A(T, I(z), R_{pel}) = p_A(T) \frac{I(z)}{I(z) + H_A} \frac{R_{pel}}{R_{pel} + M_A} \quad T1.12$$

Specific production rate of benthic algae (d⁻¹)

$$P_B(T, I(z), R_{bent}) = p_B(T) \frac{I(z)}{I(z) + H_B} \frac{R_{bent}}{R_{bent} + M_B} \quad T1.13$$

Proportion of carnivores in pelagic habitat

$$f_p^* = \frac{z_{max}}{z_{max} + \min[0.5; z_{max}] \exp \left[-S \left(\frac{\min \left(e_{ZC}; \frac{c_Z}{c_C} \right) a_{ZC}(T) Z^2}{1 + a_{ZC}(T) h_{ZC}(T) Z^2} - \frac{\min \left(e_{GC}; \frac{c_G}{c_C} \right) a_{GC}(T) G^2}{1 + a_{GC}(T) h_{GC}(T) G^2} \right) \right]} \quad T1.14$$

Table 2. Symbols, definitions, values, and units of variables and parameters.

State variables/ parameters	Definition	Value (ambient temp., warmed +6°C)	units
A	Pelagic producer biomass		g C/m^3
Z	Pelagic grazer biomass		g C/m^3
B	Benthic producer biomass		g C/m^3
G	Benthic grazer biomass		g C/m^2
C	Carnivore biomass		g C/m^2
R_{pel}	Concentration of dissolved nutrient in the pelagic habitat		g P/m^3
R_{bent}	Concentration of dissolved nutrient in the benthic habitat		g P/m^3
R_{sed}	Concentration of mineral nutrients in the surface sediment		g P/m^3
R_d	Concentration of detrital nutrients in the surface sediment		g P/m^3
$a_{0,1}$	Availability of organic nutrients in tDOM for primary producers	1 (= default) or 0	dimensionless
$a_{AZ}(T)$	Clearance rate coefficient of pelagic grazer	ambient 20, warmed 23.301	$\text{m}^6 \text{d}^{-1} \text{g C}^{-2}$
$a_{BG}(T)$	Clearance rate coefficient of benthic grazer	ambient 0.0005, warmed 0.000583	$\text{m}^6 \text{d}^{-1} \text{g C}^{-2}$
$a_{ZC}(T)$	Clearance rate coefficient of carnivore feeding on pelagic grazers	ambient 6, warmed 7.088	$\text{m}^6 \text{d}^{-1} \text{g C}^{-2}$
$a_{GC}(T)$	Clearance rate coefficient of carnivore feeding on benthic grazers	ambient 0.8, warmed 0.945	$\text{m}^4 \text{d}^{-1} \text{g C}^{-2}$
b	Burial rate of detrital nutrients in the sediment	0.0005	$\text{m}^3 \text{d}^{-1} \text{g P}^{-1}$
c_A	Nutrient to carbon quota of pelagic producer	0.008	g P/g C
c_B	Nutrient to carbon quota of benthic producer	0.015	g P/g C
c_C	Nutrient to carbon quota of carnivore	0.025	g P/g C
c_G	Nutrient to carbon quota of benthic grazer	0.025	g P/g C
c_Z	Nutrient to carbon quota of pelagic grazer	0.025	g P/g C
c_{DOM}	Phosphorus to carbon quota of tDOM in surface influx	0.00176	g P/g C
D_{bent}	Nutrient flux rate coefficient sediment to benthic habitat	0.05	m/d
D_{pel}	Nutrient flux rate coefficient benthic to pelagic habitats	0.05	m/d
D_{surf}	Water exchange rate coefficient	0.01	m/d
e_{AZ}	Food carbon conversion of pelagic grazer	0.5	dimensionless
e_{BG}	Food carbon conversion of benthic grazer	0.5	dimensionless

e_{ZC}, e_{GC}	Food carbon conversion of carnivore feeding on pelagic and benthic grazer	0.6	dimensionless
f_A	Fraction of pelagic algal losses that is mineralized in the pelagic habitat	1	dimensionless
f_B	Fraction of benthic algal losses that is mineralized in the benthic habitat	0.5	dimensionless
f_C	Fraction of carnivore losses that is mineralized in the pelagic habitat	0.5	dimensionless
f_G	Fraction of benthic grazer losses that is mineralized in the benthic habitat	0.5	dimensionless
f_Z	Fraction of pelagic grazer losses that is mineralized in the pelagic habitat	0.5	dimensionless
H_A	Half-saturation constant of light-limited pelagic production	80	$\mu\text{mol photons m}^{-2} \text{s}^{-1}$
H_B	Half-saturation constant of light-limited benthic production	40	$\mu\text{mol photons m}^{-2} \text{s}^{-1}$
$h_{AZ}(T)$	Handling time of pelagic grazer	ambient 1.25, warmed 0.8541	d
$h_{BG}(T)$	Handling time of benthic grazer	ambient 3.8, warmed 2.596	d
$h_{ZC}(T), h_{GC}(T)$	Handling time of carnivore feeding on pelagic and benthic grazers	ambient 12, warmed 9.688	d
I_0	Light intensity at lake surface	300	$\mu\text{mol photons m}^{-2} \text{s}^{-1}$
k_A	Light attenuation coefficient of pelagic producer	0.3	$\text{m}^2/\text{g C}$
k_B	Light attenuation coefficient of benthic producer	0.5	$\text{m}^2/\text{g C}$
k_{DOM}	Light attenuation coefficient of tDOM	0.2	$\text{m}^2/\text{g C}$
$I_A(T), I_B(T)$	Loss rate of pelagic and benthic producers	ambient 0.1, warmed 0.1319	d^{-1}
$I_C(T)$	Loss rate of carnivore	ambient 0.01, warmed 0.0142	d^{-1}
$I_G(T)$	Loss rate of benthic grazer	ambient 0.03, warmed 0.0476	d^{-1}
$I_Z(T)$	Loss rate of pelagic grazer	ambient 0.09, warmed 0.1428	d^{-1}
M_A	Half-saturation constant of nutrient-limited pelagic production	0.003	$\text{g P}/\text{m}^3$
M_B	Half-saturation constant of nutrient-limited benthic production	0.005	$\text{g P}/\text{m}^3$
$v(T)$	Sinking velocity of pelagic producer	ambient 0.08, warmed 0.0997	m/d
$p_A(T), p_B(T)$	Maximum production rate of pelagic and benthic producers	ambient 1.5, warmed 1.913	d^{-1}
r	Mineralization rate of detrital nutrients in the sediment	0.05	d^{-1}
R_{surf}	Concentration of dissolved nutrient in surface influx	0.001 – 1	$\text{g P}/\text{m}^3$
S	Habitat choice parameter of carnivores	200 (= default) or 10	d
$tDOM$	Concentration of tDOM in surface influx	1 – 50	$\text{g C}/\text{m}^3$
Z_{bent}	Vertical extension of benthic habitat	0.01	m

Z_{max}	Depth at bottom of pelagic habitat	1.6	m
Z_{sed}	Depth of the lower bound of the benthic habitat (= upper bound of the surface sediment) below the water surface	1.61	m
Z_{ss}	Vertical extension of the surface sediment	0.01	m

Table 3. Summary of *P*-values (F statistics) from two-way ANOVAs of the effects of browning (tDOM), warming, and their interaction (tDOM*Warming) on dissolved organic carbon (DOC), water temperature, the light attenuation coefficient (*kd*), light in the benthic habitat ($I_{z_{max}}$), soluble reactive phosphorus (SRP), benthic, pelagic, and total (= pelagic + benthic) primary production (GPP), benthic and pelagic algal biomass (Chl *a*), and the biomasses of zoobenthos, crustacean zooplankton, and fish. *P*-values marked by * are statistically significant at *P* < 0.05, and *P*-values marked by † are marginally significant at *P* < 0.1. N = 16 and degrees of freedom are 1,12 in all columns.

Variables	Treatments, <i>P</i> -values and F-values		
	tDOM	Warming	tDOM*Warming
DOC	< 0.001* (F = 128.59)	0.35 (F = 0.94)	0.23 (F = 1.63)
Water temperature	< 0.05* (F = 6.33)	< 0.001* (F = 507.34)	0.37 (F = 0.88)
Light climate			
<i>kd</i>	< 0.001* (F = 98.28)	0.07† (F = 3.96)	0.12 (F = 2.84)
$I_{z_{max}}$	< 0.001* (F = 83.28)	0.22 (F = 1.67)	0.89 (F = 0.019)
SRP	< 0.001* (F = 33.13)	< 0.05* (F = 5.08)	0.77 (F = 0.09)
Benthic GPP	< 0.01* (F = 10.82)	0.92 (F = 0.01)	0.91 (F = 0.012)
Pelagic GPP	< 0.001* (F = 18.99)	0.22 (F = 1.67)	0.91 (F = 0.015)
Total GPP	< 0.05* (F = 9.03)	0.41 (F = 0.74)	0.93 (F = 0.008)
Benthic algal Chl <i>a</i>	0.19 (F = 1.91)	< 0.05* (F = 4.88)	0.59 (F = 0.31)
Pelagic algal Chl <i>a</i>	< 0.01* (F = 11.3)	< 0.05* (F = 5.88)	0.48 (F = 0.53)
Zoobenthos	0.08† (F = 3.75)	0.25 (F = 1.45)	0.46 (F = 0.58)
Crustacean zooplankton	0.21 (F = 1.72)	0.83 (F = 0.05)	0.40 (F = 0.77)
Fish biomass	< 0.01* (F = 10.25)	< 0.01* (F = 18.59)	< 0.001* (F = 28.39)

Figure 1. Equilibrium biomasses and resource levels of the model system as functions of browning (light attenuation in proportion to tDOM concentration, $k_{DOM} * tDOM$) and external nutrient supply (dissolved nutrient concentration in the surface inflow, R_{surf}). Shown are light availability at depth z_{max} (a), concentration of dissolved pelagic phosphorus (b), benthic (c) and pelagic (d) algal biomass, benthic (e) and pelagic (f) grazer biomass, and fish biomass in the benthic (g) and pelagic (h) habitats. Biomass and resource levels are logarithmically scaled as indicated by the scale bars. White lines mark two different regions of alternative states. (i) Between the upper two approximately horizontal lines, an alternative state exists where fish are not extinct, pelagic algal biomass is high, and nutrients and light are low. (ii) In the small, wedge-shaped area near $R_{surf} = 0.1$, an alternative state exists where benthic algae and grazers persist at high biomass; this alternative state continues to the left as a very narrow, horizontal band indicated by a single white line. The alternative states are shown in Fig. S2.1. Parameter values are as in Table 2 under default and ambient temperature conditions.

Figure 2. Equilibrium resource levels, algal production, and algal and consumer biomasses of the model system as functions of temperature and browning (expressed as light attenuation coefficient $k_{DOM} * tDOM$) at a nutrient concentration in the surface inflow $R_{surf} = 0.01 \text{g P/m}^3$. Shown are light at depth z_{max} as percentage of incident light (a), concentration of dissolved pelagic phosphorus (b), benthic (c) and pelagic (d) algal production, benthic (e) and pelagic (f) algal biomass, benthic (g) and pelagic (h) grazer biomass, fish biomass in the benthic (i) and pelagic (j) habitats, and total (= benthic + pelagic) fish biomass (k) and algal production (l). Temperatures are ambient (= 17°C, blue lines) and +6°C (red lines). Regions of alternative states are indicated by discontinuities between the dashed and solid lines. Parameter values are as in Table 2 under default conditions.

Figure 3. Concentrations of dissolved organic carbon (DOC) (a) and water temperatures (b) over the course of the experiment (Julian days 136-276 = May 16th - October 3rd). Shown are means ± 1 SE

(N=4) of the four experimental treatments. Vertical lines bracket the time window (Julian days 184-273) over which all response variables were averaged.

Figure 4. Responses to experimental browning and warming: light at depth z_{max} as percentage of incident light (a), concentration of dissolved pelagic phosphorus (b), depth-integrated production of benthic (c) and pelagic (d) algae, depth-integrated chlorophyll *a* of benthic (e) and pelagic (f) algae, zoobenthos (g) and crustacean zooplankton (h) dry biomass, fish wet biomass (i), and total algal production (j). Values are treatment means (± 1 SE, n=4) of measurements averaged over the time window shown in Fig. 3 (Julian days 184-273) and are plotted against the mean light attenuation coefficient k_d observed in the respective treatment. In panel (a) horizontal error bars indicate the standard error of k_d for each treatment.







