Warming alters food web-driven changes in the CO₂ flux of experimental pond ecosystems

Journal: Biology Letters

Manuscript ID: RSBL-2015-0785.R1

Article Type: Research

Date Submitted by the Author: 06-Nov-2015

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Subject: Ecology < BIOLOGY, Environmental Science < BIOLOGY

Categories: Global Change Biology

Keywords: trophic cascades, biosequestration, climate change, carbon cycling
Title: Warming alters food web-driven changes in the CO$_2$ flux of experimental pond ecosystems

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Evidence shows the important role biota play in the carbon cycle, and strategic management of plant and animal populations could enhance CO₂ uptake in aquatic ecosystems. However, it is currently unknown how management-driven changes to community structure may interact with climate warming and other anthropogenic perturbations to alter CO₂ fluxes. Here we show that under ambient water temperatures, predators (Three-Spined Stickleback) and nutrient enrichment synergistically increased primary producer biomass, resulting in increased CO₂ uptake by mesocosms in early dawn. However, a 3°C increase in water temperatures counteracted positive effects of predators and nutrients leading to reduced primary producer biomass, and a switch from CO₂ influx to efflux. This confounding effect of temperature demonstrates that climate scenarios must be accounted for when undertaking ecosystem management actions to increase biosequestration.

Keywords: trophic cascades, biosequestration, carbon cycling, climate change

1. INTRODUCTION

In freshwater ecosystems, projected increases in water temperatures (3-5°C) [1] are likely to interact with bottom-up and top-down processes to modify community structure [2] and CO₂ dynamics [3,4]. Heterotrophs contribute to the net carbon balance of ecosystems by consuming organic matter and respiring it as CO₂. Predators and herbivores can further influence carbon balance by directly or indirectly (via trophic cascades) shifting the balance between heterotrophic respiration and photosynthesis. However, warming and eutrophication can modify food web structure by increasing species extinctions, especially at higher trophic levels [5], altering species
interactions. Phytoplankton blooms caused by eutrophication and trophic cascades can only
enhance long-term carbon storage if plant matter escapes mineralization and is buried in
sediments; however, higher water temperatures increase metabolism and remineralization rates.
Because temperature modifies food web structure with consequences for CO\textsubscript{2} assimilation and
remineralization [6], alterations to animal and plant populations could cause complex climate
feedbacks in a warmer world.

We tested two hypotheses of how elevated water temperatures could alter the effects of
top-down and bottom-up manipulations on the CO\textsubscript{2} flux of freshwater pond mesocosms.
Mesocosm food webs contained phytoplankton, periphyton, zooplankton, benthic
macroinvertebrates and in treatments containing fish, \textit{Gasterosteus aculeatus} (Three-Spined
Stickleback; Table S1). First, warming would increase the strength of trophic cascades and
decrease mesocosm CO\textsubscript{2} emissions. We predicted that warming would increase indirect positive
effects of predators on primary production [7,8] leading to higher CO\textsubscript{2} influx in treatments
containing predominantly odd-numbered food chains with top predators. Second, warming
would alter interactive effects between eutrophication and predators on primary producers and
CO\textsubscript{2} flux. In a previous study we described the temporal response of phytoplankton to the same
three variables, showing that warming reduced the positive effects of nutrients on primary
producers [7]. We predicted that this interaction between nutrients and warming would lead to
increased CO\textsubscript{2} emissions [9]. However, because our previous study also showed that warming
enhanced top-down control [7], it is difficult \textit{a priori} to predict the combined effects of all three
stressors on CO\textsubscript{2} flux.

2. MATERIALS AND METHODS

(a) Experimental set-up
We manipulated water temperature, nutrients, and the presence of Stickleback in a 2x2x2 design using 40, open-air, well mixed, 1,136 L Rubbermaid plastic mesocosms (0.6 m deep, 1.5 m in diameter) to test their independent and interactive effects on consumer biomass, producer biomass and CO₂ flux. Each treatment was replicated 5 times. Water temperatures were either ambient or 3.04° ± 0.05° C (mean ± s.e.) above ambient. Mesocosms had either ambient nutrient levels or were meso-eutrophic (N:P ratio of 22) with monthly additions of both nitrogen and phosphorus (264 µg of nitrogen/L as NaNO₃ and 27 µg of phosphorus/L as KH₂PO₄). Finally, mesocosms contained either five Stickleback (54.4 ± 0.05 mm standard body length) or no fish. Detailed experimental methods can be found in Supplementary Material.

(b) Organism sampling and CO₂ measurements

Primary producer biomass, consumer biomass (not including fish), and water CO₂ concentrations were collected one year (May) and 16 months (October) following the start of the study. Phytoplankton and periphyton biomasses and benthic and pelagic consumer biomasses were combined for total primary producer and total consumer biomasses, respectively.

Water samples for dissolved CO₂ were extracted at dawn using 50-mL gas-tight syringes and headspace equilibrium analysis. CO₂ concentrations were measured on a 5890 Series II gas chromatograph within 24 h.

CO₂ flux (mg C m⁻² d⁻¹) to the atmosphere was calculated as follows:

\[ \text{CO}_2\text{flux} = (\text{CO}_2\text{water} - \text{CO}_2\text{sat}) \times k \]

Here CO₂water is the temperature corrected CO₂ concentration of the water, CO₂sat is the concentration the water would have if it were at equilibrium with the atmosphere (390 ppm), k is
the CO₂ exchange velocity coefficient (0.63 m d⁻¹), which was estimated using literature values for our study sites average wind speed (2.8 ± 0.09 m s⁻¹) [10].

(c) Statistical analyses

Treatment effects on primary producer biomass, consumer biomass, and CO₂ flux were tested using linear mixed-effects models (α = 0.05) in R 3.1.1 (R Development Core Team, 2014). Individual mesocosms and date were treated as random factors. Date was included as a random factor to account for non-independence between dates and because our sampling design did not have sufficient power to describe temporal differences. In order to understand how treatment-mediated changes to food web structure influenced CO₂ flux, it was imperative to analyse only dates where pelagic and benthic organisms and CO₂ were sampled at the same time. Because of the highly destructive nature of benthic sampling on the community (see supplementary for detailed methods) we limited our collections to only two occasions.

3. RESULTS & DISCUSSION

Under ambient water temperatures, we detected independent and interactive effects of nutrients and predators on total consumer and producer biomass that led to increased CO₂ influx (Table 1, Fig. 1). Increased CO₂ influx was likely the result of predator- (in predator only) and nutrient-induced (in nutrient addition treatments only) increases in primary production [9,11]. In the absence of predators, nutrient additions doubled consumer and plant biomass, which would have increased both primary production and respiration (Tables S2). However, because increases in CO₂ influx were still observed in these treatments, the effect of nutrients on CO₂ assimilation appears greater than their effect on respiration. Fish reduced consumer biomass by 70% and increased primary producer biomass by 32% (Table S2). Trophic cascades were enhanced by
nutrient enrichment, with a 27-fold increase in producer biomass (Table S2). Similar to Cole et al. [10], mesocosms with both nutrient additions and top predators had the greatest CO$_2$ influx. In general, warming had strong negative effects on trophic cascade strength and the influence of nutrients on primary producers, generating top-heavy food webs with reductions in CO$_2$ influx (Table 1; Fig. 1). Higher emissions in warmed mesocosms likely resulted from positive effects of warming on respiration rates [3] and observed negative effects of warming on primary producers. Contrary to our prediction, warming only strengthened trophic cascades in non-fertilized mesocosms. In fertilized mesocosms, warming dampened consumer effects resulting in similar CO$_2$ fluxes as mesocosms without predators (Fig. 1, Table S2). The negative effect of warming on primary producers was strongest in mesocosms with nutrient additions and especially large in mesocosms with nutrients and predators. Warmed mesocosms containing both added nutrients and predators had 90% less primary producer biomass compared to ambient temperature mesocosms (Table S2). The negative effect of warming on primary producer biomass in our study and others [3,12] may have been the result of increased consumption by herbivores under warmer temperatures [6,8], or the replacement of productive phytoplankton taxa by stress tolerant, but less productive taxa. Although further studies are needed to understand the mechanisms by which increased temperatures alter CO$_2$ cycling, our results suggest that future increases in temperatures could reduce biosequestration by aquatic ecosystems.

Mesocosms are well suited to explore complex interactions between global change drivers that are otherwise difficult to study in natural systems. Nevertheless, the use of mesocosms and our context-dependent results should be considered. First, our mesocosms did not receive large terrestrial subsidies, which can make up > 50% of the dissolved organic C pool.
in natural ecosystems [13]. Thus, respiration in natural lentic ecosystems is not constrained by *in situ* primary production, as was the case in our mesocosms. Because respiration rates have a stronger temperature-dependence than photosynthetic rates [3], the positive effects of warming on CO$_2$ efflux seen in our study may be conservative. Second, the effects seen on communities and ecosystem process in this study may be only short-term, transient responses to perturbations that could greatly differ from long-term ones. Future studies should investigate whether the effects seen in our study are consistent across diurnal cycles and longer time scales within a myriad of aquatic ecosystems. Finally, the direction and magnitude of predator effects on food webs and carbon cycling may depend on predator identity, food chain length, and species diversity [8]. Despite these limitations our study is the first to our knowledge to unravel the cumulative effects of eutrophication, warming, and alterations to top predators on the CO$_2$ flux of an ecosystem.

Our findings support other studies [9,14] which suggest that maintaining viable predator populations in odd-numbered food webs and/or adding nutrients could increase natural biosequestration. However, our results reveal how previously unknown interactions between warming, nutrients, and changes to top predators could create positive climate feedbacks by reducing the capacity of top-down and bottom-up forces to reduce the production of *in situ* CO$_2$. The number of freshwater ecosystems experiencing negative or undesirable anthropogenic impacts is likely to increase in the future due to a combination of a 2.4-2.7 fold increase in eutrophication [15] and increased rates of trophic downgrading [16]. As most freshwater ecosystems are sources of CO$_2$, our results suggest that CO$_2$ emissions from aquatic systems could increase as temperatures rise.


**Ethics** This work was conducted with the approval by the University of British Columbia’s Animal Ethics Committee (animal ethics permit #A08-0220)

**Data accessibility** Raw data are available from the Dryad digital repository (http://dx.doi.org/10.5061/dryad.1f090)

**Author contributions** T.B.A., E.H., H.S.G., P.K, J.B.S., J.S.R contributed to study design and writing of the manuscript. Data were collected by T.B.A., E.H., H.S.G. and P.K. All authors gave final approval for publication, and agreed to be accountable for all aspects of the work.

**Funding** This research was funded by the Natural Sciences and Engineering Research Council (Canada) grants to J.B.S., J.S.R. and P.K., and the New Zealand Foundation for Research, Science & Technology Fellowship (UBX0901) to H.S.G.
Acknowledgments We thank P L Thompson and A. J. Klemmer for help with setting up the ponds and assisting in collections.

Competing interests statement We have no competing interests.
Figure Legend

**Figure 1** Interaction plots illustrating the impacts of warming, nutrient additions, and predators on community biomass and CO$_2$ flux of mesocosms. Effects of nutrients and warming on consumer biomass (a), primary producer biomass (c), and CO$_2$ flux (e) in food webs where fish are absent. Effects of nutrients and warming on consumer biomass (b), primary producer biomass (d), and CO$_2$ flux (f) in food webs containing fish. Dotted lines in graphs (e) and (f) represent CO$_2$ source/sink boundaries. Means ± 95% C.I.s represent fixed effects and were approximated using the “predictSE.lme()” function in the “AICcmodavg” package in R.
Table 1 Summary statistics of linear mixed-effects models for individual and interactive effects of warming (W), nutrient additions (N), and predators (P) on consumer biomass, primary producer biomass, and CO$_2$ flux of mesocosms. $P$-values in bold are statistically significant.

<table>
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<tr>
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<th>Consumer biomass</th>
<th>Primary producer biomass</th>
<th>CO$_2$ flux</th>
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<tr>
<td></td>
<td>$F_{1,32}$</td>
<td>$P$</td>
<td>$F_{1,32}$</td>
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<td>26.756</td>
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