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**Aquatic Sciences**  
Research Across Boundaries

ISSN 1015-1621  
Volume 78  
Number 4

Aquat Sci (2016) 78:717-725  
DOI 10.1007/s00027-015-0463-y



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# Do warming and humic river runoff alter the metabolic balance of lake ecosystems?

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Received: 21 January 2015 / Accepted: 9 December 2015 / Published online: 24 December 2015  
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**Abstract** Global warming is expected to influence lake gross primary production (GPP) and ecosystem respiration (R) by increasing water temperature and terrestrial export of organic material and inorganic nutrients from the catchment. We experimentally tested the effects of warming (3 °C) and natural humic river runoff, separately and in combination, on habitat-specific and whole ecosystem net ecosystem production (NEP = GPP – R) in replicated large scale (136 m<sup>3</sup>) experimental pond ecosystems over one open water season. Pelagic NEP was reduced by warming and increased with humic river water addition. Littoral NEP (benthos, macrophytes, periphyton) showed an opposite pattern with increasing NEP following warming and decreasing NEP following humic river water addition. These changes were a result of changes in GPP with warming (negative in pelagic, positive in littoral) and with humic water addition (positive in pelagic, negative in littoral), while no effects were observed on pelagic respiration. As a result of the counteracting effects on NEP in pelagic and littoral habitats, whole ecosystem NEP was not affected by the treatments. The study suggests that climate mediated changes in temperature and river runoff have relatively small effects on the overall metabolic balance of shallow aquatic ecosystems but there may be large habitat-specific effects.

**Keywords** Warming · Humic river runoff · Pelagic habitat · Littoral habitat · Whole ecosystem metabolism

## Introduction

Inland waters play an important role in carbon cycling by releasing substantial amounts of carbon (mainly as CO<sub>2</sub>) to the atmosphere (Battin et al. 2009). The net exchange of carbon with the atmosphere is to a large extent controlled by the difference between gross primary production (GPP) and community respiration (R), i.e., the net ecosystem production (NEP). When GPP exceeds R, NEP is positive and the system is autotrophic (net CO<sub>2</sub> consumption), and when R is higher than GPP, NEP is negative and the system is net heterotrophic (net CO<sub>2</sub> production) (Chapin et al. 2006). Sustained net heterotrophy implies that ecosystem respiration is subsidized by allochthonous organic matter, i.e., produced beyond the ecosystem boundaries (del Giorgio et al. 1999; Cole et al. 2000).

Surprisingly few studies have been carried out on the control of aquatic NEP by climate change related factors. Based on current knowledge it could be anticipated that climate has pronounced effect on metabolic processes in aquatic ecosystems via its direct effect on water temperature but also via indirect effects on terrestrial export of organic matter and nutrients (IPCC 2014; Sobek et al. 2005; Kosten et al. 2010). The increase in water temperature is expected to alter aquatic metabolism by promoting R more than GPP (Allen et al. 2005; López-Urrutia et al. 2006). Similarly, runoff of terrestrial organic matter is expected to increase R over GPP, mainly due to mineralization of the external C input but potentially also by negative consequences on GPP by decreasing light and nutrient availability for primary producers (Jones 1992;

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Ask et al. 2009). On the other hand, the runoff from the catchment also brings inorganic nutrients into the aquatic ecosystems which may favour GPP (Carpenter et al. 1998; Vadeboncoeur et al. 2003; Allan 2004), potentially counteracting negative effects of terrestrial organic matter on GPP. The net outcome of increased temperature and interacting effects of nutrients and terrestrial organic matter on NEP is therefore hard to predict a priori, especially in shallow ecosystems where the light absorption by organic matter may have lower impact on the overall light climate compared to what happens in deep lakes.

Although comparative studies across climate gradients (e.g., Jansson et al. 2008; Ask et al. 2012) have provided important knowledge on the relationship between terrestrial organic carbon inputs and net ecosystem production in lakes, these studies can not distinguish which factor is driving, among many uncontrolled variables, the processes behind the observed patterns. On the other hand, it is also difficult to study climate impacts in controlled experiments at the scale necessary to comprehend whole ecosystem processes (Carpenter et al. 1995). In order to estimate the impact of increased temperature and input of terrestrial organic matter, either alone or in combination on NEP in aquatic ecosystems, we performed a large scale pond experiment over a whole growing season. The treatments consisted of an increase in water temperature to 3 °C above the natural seasonal temperature development, i.e. ambient conditions, and an input of humic river water from a boreal river in a full factorial design. Measurements included pelagic, benthic and whole ecosystem NEP and R from which GPP was calculated and littoral (benthos, macrophytes, periphyton) metabolic rates estimated.

## Methods

### Experimental system

This study was performed at the Umeå University Experimental Ecosystem Facility (EXEF) situated close to Umeå University, northern Sweden (63°48'N, 20°14'E) from June to September 2012. EXEF is a large-scale experimental system (73 m long, 25 m wide, with an average depth of 1.49 m) divided into 20 sections (12.5 × 7.3 m, 136 m<sup>3</sup>) (Fig. 1). Each section contains a natural, benthic soft-bottom habitat, benthic and pelagic producers and consumers including a reproducing fish top-consumer population of three-spined sticklebacks (*Gasterosteus aculeatus*). Each section has separate in- and outlets for water supply, allowing manipulation of input water, and eight of the sections are heated with individual closed circular systems connected to heat exchangers. Water from each warm pond sections are circulated through the heat exchangers and



**Fig. 1** Aerial picture of EXEF (Umeå University Experimental Ecosystem Facility). The pond system (73 m long, 25 m wide) is divided into 20 sections (12.5 × 7.3 m, 1.49 m average depth). The facility allows for warming with heat exchangers (a), and manipulations of input water characteristics; in (b) is shown the tank where the humic river water is stored

back to each pond section. Separate temperature sensors in one of the ambient (i.e. natural season-dependent temperature development) and one heated section continuously controls the closed flow system of heated media from an air-source heat pump (to the individual heat exchangers). The  $\Delta T$  of the closed flow system and the flow of water from each warm pond section was approximately 3 °C.

During the ice-free season (May to October) of 2012, eight sections were heated (+3 °C above ambient temperature, 4 “warm” and 4 “warm × humic” sections), eight remained at ambient temperature (4 “control” and 4 “humic”), and the 4 intermediate sections served as thermal buffers to isolate temperature treatments (Fig. 1). Four heated and four ambient sections received natural humic river water (seasonal average: 23 mg L<sup>-1</sup> in dissolved organic carbon [DOC], 21 µg L<sup>-1</sup> in soluble reactive phosphorus [SRP], 69 µg L<sup>-1</sup> in total phosphorus [TP] and 662 µg L<sup>-1</sup> in total nitrogen [TN]) from a mid-sized stream in the vicinity of the city of Umeå, and the other eight enclosures received clear water (seasonal average: 1 mg L<sup>-1</sup> in DOC, 3.8 µg L<sup>-1</sup> in TP, and 71 µg L<sup>-1</sup> in TN) from the municipal water supply (ground water). Thus, the humic river water treatment (“humic”) contains inorganic nutrients and coloured organic matter, and it is used here to represent climate-change induced terrestrial runoff into freshwater systems. Hence, the study system has a full factorial experimental design with four replicates per treatment combination (control, warm, humic, warm × humic). Initially, the humic runoff and clear water supply was set to mimic a 2 week spring flow input (4 m<sup>3</sup> day<sup>-1</sup>) and thereafter a continuous input (0.57 m<sup>3</sup> day<sup>-1</sup>) for the rest of the season. Total nutrient



concentrations did not differ among the sections pre-assigned to the different treatments before the treatments were applied (Two way ANOVA,  $p > 0.05$  for TP and TN). Initial TP values ranged from 1.70 to 16.3  $\mu\text{g L}^{-1}$ ; whilst TN concentrations varied between 185 and 336  $\mu\text{g L}^{-1}$ .

### Sampling and analyses

Water temperature and incoming irradiance were recorded (loggers from Delta-T Devices, UK) every 1 min during the whole study with sensors TH2-F from UMS (Germany) and SQ-110 from Apogee (USA), respectively, located at 0.5 m depth in the centre of each section. Physicochemical variables were monitored, and one integrated water sample from the top 70 cm was taken weekly from each section. Photosynthetic available radiation (PAR) was measured every 25 cm with a Li-250A radiometer equipped with a spherical quantum sensor Li-193SA (Li-Cor, Lincoln, USA) in order to calculate the vertical attenuation coefficient,  $k_d$ , as the slope of the linear regression of the natural logarithm of PAR versus depth (Kirk 2011).

Water samples were stored in the freezer ( $-20\text{ }^\circ\text{C}$ ) and sub-sampled in the laboratory to assess the concentrations of TP and TN. Total phosphorus was determined according to Murphy and Riley (1962) after digestion of the sample with potassium persulfate. DOC and TN were analysed using an IL 550 TOC/TN analyser (Hach-Lange GmbH, Dusseldorf, Germany). Water samples for DOC determination were filtered after sampling through pre-combusted ( $400\text{ }^\circ\text{C}$ , 3 h), acid washed Whatman GF/F filters and acidified with HCl before the analysis, within ca. 2 months of being taken.

### Pelagic, benthic, and whole ecosystem metabolism

Estimations of metabolism in benthic and pelagic habitats, were performed once per month (July, August, and September) inside the sections through 48 h in situ incubations. For pelagic incubations, 2 L (32 cm height, 8.6 cm inner diameter) transparent acrylic tubes were held vertically 50 cm below the water surface. For the benthos, 12 L semi-spherical transparent polycarbonate chambers (34 cm inner diameter) were deployed. The chambers were equipped with a metal frame underneath that allowed them to be inserted into the sediment surface in an area without macrophytes. Oxygen ( $\text{O}_2$ ) loggers (MiniDOT, PME, Vista, CA, USA), which registered  $\text{O}_2$  concentration every 1 min, were placed inside the tubes and chambers during incubations. For estimating whole ecosystem metabolism the  $\text{O}_2$  loggers, which registered  $\text{O}_2$  concentrations every 10 min, were deployed at 50 cm below the water surface for 1 week close to chamber measurements.

### Calculations

We estimated net ecosystem production (NEP) from the changes in oxygen concentration ( $\Delta\text{O}_2$ , in  $\text{g m}^{-3}$ ) over an specific time interval ( $\Delta t$ , in h) as:

$$\text{NEP} = \Delta\text{O}_2/\Delta t - F/Z_{\text{mix}} \quad (1)$$

where  $F$  ( $\text{g m}^{-2} \text{h}^{-1}$ ) is the  $\text{O}_2$  exchange between the water and the atmosphere and  $Z_{\text{mix}}$  is the mixing depth (Staehr et al. 2010). The  $Z_{\text{mix}}$  was assumed to be equivalent to the maximum depth of the enclosures given that the ponds are shallow and no thermal stratification (no change  $>0.5\text{ }^\circ\text{C}$  per meter) was observed during the warmer periods.  $F$  was estimated as:

$$F = k(\text{O}_{2\text{measured}} - \text{O}_{2\text{sat}})$$

where  $k$  ( $\text{m h}^{-1}$ ) is the gas exchange coefficient for  $\text{O}_2$ ,  $\text{O}_{2\text{measured}}$  is the oxygen concentration in the water and  $\text{O}_{2\text{sat}}$  is the saturation concentration of dissolved oxygen at ambient temperature and atmospheric pressure. The gas exchange coefficient ( $k$ ) was estimated based on wind speed data measured at a height of 10 m recorded at Umeå airport (ca. 4 km from EXEF) and the relationship between Schmidt numbers (Jähne et al. 1987; Cole and Caraco 1998). Hence, NEP as defined in Eq. (1), was estimated for day and night periods as the slope of the curve of  $\text{O}_2$  concentration versus time. The term  $F/Z_{\text{mix}}$  (1) had relatively small effect on the oxygen dynamics and was ca. 24.4 and 25.2 % of NEP (1) during day and night hours, respectively.  $\text{NEP}_{\text{daytime}}$  was thus calculated as the slope of the curve of  $\text{O}_2$  concentration versus time during the day, when both primary production and respiration occurs, and then integrated over the day hours. During the night, when  $\text{GPP} = 0$ , NEP (1) represents the sum of autotrophic and heterotrophic respiration (i.e., community respiration,  $R$ ). For further calculations it was assumed that the respiration rate during the night was equal to respiration during the day, and then integrated over day ( $R_{\text{daytime}}$ ) and night periods ( $R_{\text{night-time}}$ ) in order to obtain daily rates (Cole et al. 2000, Staehr et al. 2010). The length of the night and day periods were assumed to coincide with the periods of decrease and increase of  $\text{O}_2$  concentration through time, respectively. Daily rates of GPP and NEP, integrated in the water column were obtained for each habitat from (2) and (3) respectively:

$$\text{GPP} (\text{g O}_2 \text{m}^{-2} \text{day}^{-1}) = \text{NEP}_{\text{daytime}} + R_{\text{daytime}} \quad (2)$$

$$\text{NEP} (\text{g O}_2 \text{m}^{-2} \text{day}^{-1}) = \text{GPP} - (R_{\text{daytime}} + R_{\text{night-time}}) \quad (3)$$

For benthic and pelagic incubations that were carried out in closed systems, the term  $F/Z_{\text{mix}}$  in (1) was not considered. For estimating benthic metabolism we subtracted

pelagic metabolic rates in the overlying water in the chambers. We estimated the metabolic rates of the habitat comprised of macrophytes and the associated periphyton by difference among whole ecosystem rates and benthic plus pelagic habitats. To estimate littoral (benthos, macrophytes and periphyton) GPP and R, the respective pelagic rates were subtracted from whole ecosystem estimations and littoral NEP was obtained as littoral GPP – R.

**Statistical analysis**

We initially tested our results for monthly effects with Repeated Measures ANOVA but, as these analysis showed similar results and did not change the interpretation and conclusions drawn, we choose to report statistics and results for time averaged data only. Hence, factorial ANOVA was used to test for differences on time-averaged physicochemical variables and pelagic, benthic, macrophytes + periphyton, littoral (benthos, macrophytes + periphyton) and whole ecosystem GPP, R and NEP between treatment combinations and their interaction (warm × humic). Tukey post hoc tests were used to detect which treatments differed from the others. Pearson correlations and *t* test between specific treatments were used when appropriate. Variables were Log<sub>10</sub> transformed to fulfil assumptions of homogeneity of variances when needed. SPSS 20 package was employed for running most of the analyses.

**Results**

**Physicochemical variables**

Water temperature over the season was on average 2.7 °C higher in heated sections (Table 1; Fig. 2). In both heated and non-heated sections, the highest temperature was recorded in the beginning of July (22.6 and 20.1 °C, respectively) and the lowest at the end of September (10.3 and 8.3 °C, respectively). The light attenuation coefficient

(*k<sub>d</sub>*) and DOC were higher in humic sections (Table 1; Fig. 2). The percentage of incident light that reached the bottom was, on average, 5.3 and 6.4 %, in humic and warm × humic sections, respectively, and 33.3 and 29.2 %, in control and warm sections, respectively. Both TP and TN concentrations were lower in warm sections and TN concentrations were higher in sections receiving humic river water input (Table 1).

**Habitat-specific and whole ecosystem metabolism**

Warming had a negative effect on pelagic gross primary production (pGPP) whereas humic river water input had a positive effect on pGPP but only in non-heated sections (Table 2; Fig. 3a). In contrast, pelagic respiration (pR) was not affected by any of the treatments (Table 2; Fig. 3a). Overall pelagic net ecosystem production (pNEP) was lower in heated sections and humic river water input had a positive effect on pNEP, especially in the non-heated sections (Table 2; Fig. 3b).

Benthic gross primary production (bGPP) and respiration (bR) were negatively affected by both warming and humic river water addition (Table 2; Fig. 3a). Benthic NEP was negatively affected by humic river water addition but only in the non-heated sections (Table 2; Fig. 3b). The GPP and NEP in the habitat comprised of macrophytes and the associated periphyton were positively affected by warming whilst no effects were detected on R (Table 2; Fig. 3a, b).

Benthic and pelagic GPP were similar in control and warm treatments (*t* test, *p* > 0.05 in both cases). In contrast, when humic water was added, pGPP was higher than bGPP (*t* test, *p* < 0.001 for both humic and warm × humic). Littoral GPP (benthos, macrophytes and periphyton) increased with warming and was negatively affected by humic river runoff, whereas respiration was not affected by any treatment (Table 2). Littoral NEP (INEP) was higher when both temperature and humic water input were increased whereas humic runoff negatively affected INEP in non-heated sections (Table 2). Following the contrasting

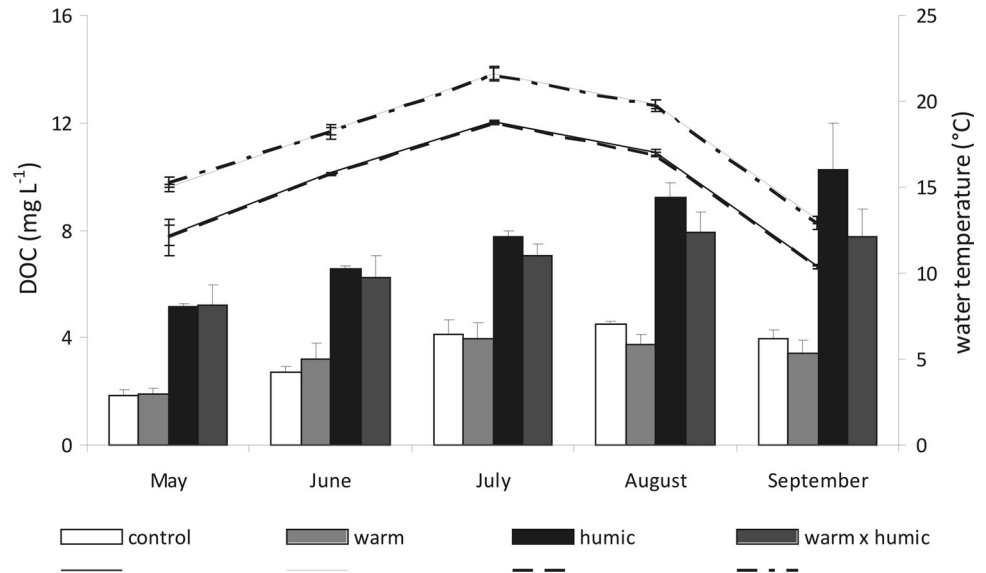
**Table 1** Mean (±1 SD) values and ANOVA results for the physicochemical variables in the sections

	Treatments				ANOVA		
	Control	Warm	Humic	Warm × humic	Warm	Humic	Warm × humic
Water temperature (°C)	15.3 ± 0.07	15.2 ± 0.13	17.9 ± 0.21	17.9 ± 0.29	581.4**	0.47	0.04
<i>k<sub>d</sub></i> (m <sup>-1</sup> )	0.74 ± 0.13	0.86 ± 0.26	1.99 ± 0.31	1.86 ± 0.36	0.004	65.4**	0.79
DOC (mg L <sup>-1</sup> )	3.86 ± 0.21	3.57 ± 0.44	8.57 ± 0.51	7.30 ± 0.77	9.0*	261.5**	3.50
TP (µg L <sup>-1</sup> )	20.9 ± 2.13	17.4 ± 5.75	23.3 ± 4.07	16.4 ± 4.00	6.17*	0.10	0.69
TN (µg L <sup>-1</sup> )	241.7 ± 15.3	204.7 ± 10.9	317.2 ± 13.9	289.7 ± 29.0	11.9*	74.2**	0.26

The statistic *F*<sub>1,12</sub> is shown with \* for *p* < 0.05 and \*\* for *p* < 0.001

*k<sub>d</sub>* vertical attenuation coefficient of light, *DOC* dissolved organic carbon, *TP* total phosphorus, *TN* total nitrogen

**Fig. 2** Monthly variation in dissolved organic carbon (DOC) concentration (*left axis*) and water temperature (*right axis*) during the study period. Each bar and data point represent the average  $\pm$  or  $\pm 1$  SD, respectively



**Table 2** Factorial ANOVA results for pelagic, benthic, macrophytes and periphyton and littoral habitats and whole ecosystem gross primary production (GPP), ecosystem respiration (R) and net ecosystem production (NEP)

	Warm	Humic	Warm × humic
<b>Pelagic</b>			
GPP	47.7**	15.6*	7.53*
R	2.52	0.03	0.004
NEP	29.5**	14.1*	5.82*
<b>Benthos</b>			
GPP	9.53*	24.6**	0.27
R	9.76*	16.8**	1.46
NEP	0.26	4.20	5.80*
<b>Macrophytes + periphyton</b>			
GPP	11.5*	1.74	3.25
R	2.56	0.003	0.82
NEP	14.3*	4.61	3.78
<b>Littoral</b>			
GPP	6.64*	9.48*	4.60
R	0.13	2.68	0.17
NEP	14.8*	9.91*	9.45*
<b>Whole ecosystem</b>			
GPP	0.31	1.91	0.94
R	0.32	1.86	0.16
NEP	0.03	0.25	2.37

The statistic  $F_{1,12}$  is shown with \* for  $p < 0.05$  and \*\* for  $p < 0.001$

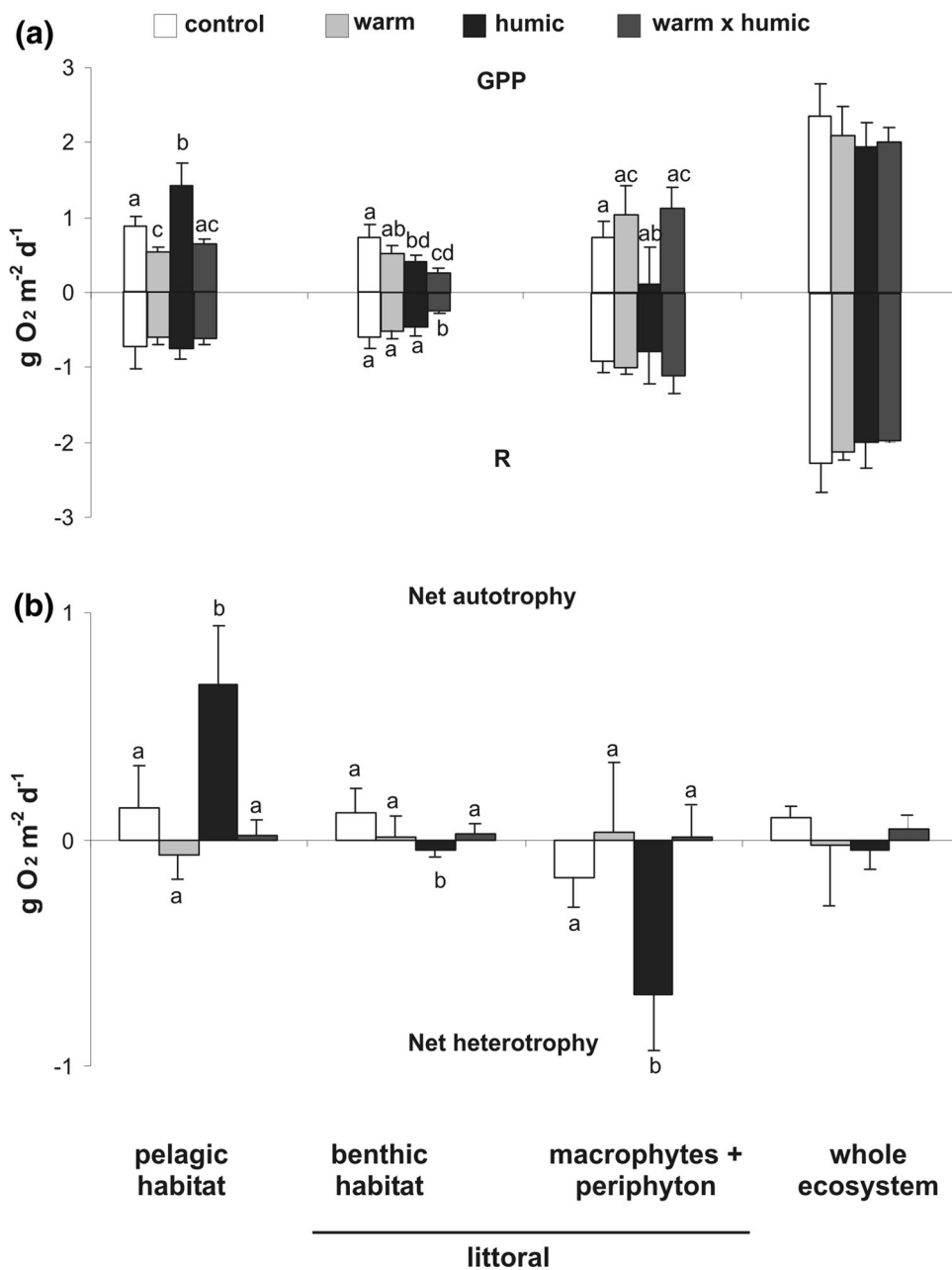
effects of the treatments on NEP in the different habitats, there was a negative correlation between pNEP and INEP across all treatments (Fig. 4). At the whole ecosystem level, no treatment effects were detected in GPP, R or NEP (Table 2; Fig. 3a, b).

## Discussion

We found that warming and increased terrestrial runoff input had strong, counteracting, effects on habitat-specific NEP in pelagic and littoral habitats. Given the make-up of our model ponds these counteracting effects result in no effect on whole ecosystem NEP. These results largely contrast current knowledge and predictions and strongly emphasize the importance of integrating responses in both littoral and pelagic habitats in order to make accurate estimates and predictions on the response of whole ecosystems metabolism to environmental change.

The increased light absorption by humic matter following addition of river water was apparently not enough in our study to result in decreased pelagic GPP in the mixed water column. Instead, pelagic GPP was stimulated by humic water input, most likely as a result of increased nutrient supply that accompanied the river water. Our results differ from small scaled mesocosm studies where lake humic water has been added and pelagic chlorophyll and productivity diminished as a consequence of shading (Nicolle et al. 2012; Kritzberg et al. 2014). However, in those cases, the supplied humic water was not accompanied by additional inorganic nutrients as in our experiment, where the negative effects of light reduction most likely were counteracted by increased nutrient input. Accordingly, in a recent experimental study, dissolved organic matter extracted from leaves have been shown to stimulate phytoplankton biomass in nutrient limited boreal lakes (Daggett et al. 2015). On the other hand, in our study, benthic GPP decreased with humic river water input, probably due to the decrease in light availability at the sediment surface (Ask et al. 2009). The contrasting effects

**Fig. 3** Average rates (+1 SD,  $n = 3$ ) of gross primary production (*positive values*) and ecosystem respiration (*negative values*) (a), and net ecosystem production (b) for the pelagic, benthic and macrophytes plus periphyton habitats and at the whole ecosystem metabolism scale. The benthos, macrophytes and periphyton represent the littoral habitat. *Different letters* indicate which treatments differed from each other (Tukey post hoc comparison)

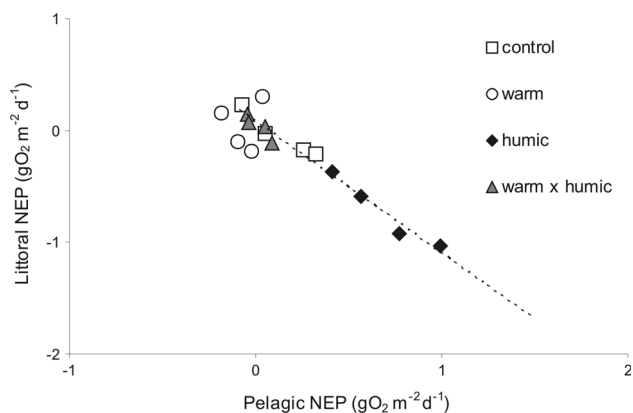


on benthic and pelagic GPP were likely due to the fact that algae in those habitats were limited by different resources, i.e. light and nutrients respectively (Vadeboncoeur et al. 2001; Karlsson et al. 2009). Our results contrast with studies along DOC gradients where whole lake GPP decrease along with colour, and also with surveys that show that lake primary production decrease with the increase in DOC concentration above certain thresholds of either 4.8 or 5.96  $mg L^{-1}$  (Ask et al. 2012; Seekell et al. 2015a, b). The DOC concentrations in the sections that received humic river runoff were well above those concentrations but still pelagic GPP increased with humic river runoff. Most likely this is due to the shallow nature of the

ponds which mitigates any effects of light limitation for pelagic primary producers, in contrast to deeper lakes where the light extinction has a stronger effect when considering production integrated in the whole water column.

In contrast to general predictions, the input of humic river water did not stimulate respiration and net heterotrophic conditions in our study. Instead, the experimental ecosystems remained close to metabolic balance. Terrestrial organic carbon (OC) is partly mineralized by heterotrophic bacteria in recipient aquatic systems (Tranvik 1992), and the main cause of net heterotrophic conditions in many low productive lakes (del Giorgio and Peters 1994). A plausible explanation for the unexpected result in





**Fig. 4** Relationship between NEP in littoral (benthos, macrophytes and periphyton) and pelagic habitats. The *trend line* shows the overall correlation using data for all treatments ( $p < 0.05$ ,  $r = -0.94$ ). Each data point represents the average over the study period ( $n = 3$ )

this study can be that the supply of OC with river water was relatively low ( $145 \text{ mg C m}^{-2} \text{ day}^{-1}$ ) compared to ecosystem GPP ( $743 \text{ mg C m}^{-2} \text{ day}^{-1}$ ), suggesting that the major part of ecosystem R was based on autochthonous rather than on allochthonous OC. Assuming that as much as 50 % of the OC delivered in river water could be respired during the summer (Algesten et al. 2004) suggests that allochthonous OC only supported around 10 % of the total respiration in the sections receiving river water. Hence, only a 10 % decrease in R of autochthonous OC (i.e., 10 % of GPP accumulates) would be needed to counteract the estimated R of humic river water OC. Irrespective of the cause for the observed patterns the data suggest that, for realistic mineralization rates and bioavailability of terrestrial OC, the supply of allochthonous OC has to be relatively high compared to GPP in order to induce net heterotrophic conditions. Moreover, if exported terrestrial OC is accompanied by inorganic nutrients as in our study, this stimulates GPP which could potentially offset the increased R based on terrestrial OC. Therefore, both in deeper systems, or in systems with low inorganic nutrient supply, an increased respiration based on allochthonous organic matter is less likely to be counteracted by increased GPP (Ask et al. 2012). Thus, terrestrial export of nutrients and organic matter, as well as the physical properties of recipient aquatic ecosystems, needs to be considered in order to understand and predict the effects of changes in catchment conditions on carbon cycling in aquatic ecosystems.

In this study, warming did not increase ecosystem R and GPP, and thus did not alter the metabolic balance of the ecosystems. Temperature per se is expected to increase organism's metabolic rates and to stimulate R more than GPP (Allen et al. 2005). The unexpected lack of stimulation of metabolism by warming reflect that the strong

temperature responses observed in small scale experimental systems (e.g., Moss et al. 2003; Yvon-Durocher et al. 2010; Kritzberg et al. 2014) are not necessarily realized at larger scales. In natural systems, where other factors like variation in nutrient supply and resource competition, cross habitat exchanges, food web interactions and ecosystem feedbacks may constrain metabolic rates and thereby override direct temperature effects (O'Connor et al. 2009; Kratina et al. 2012; Shurin et al. 2012). Despite no ecosystem level effects on GPP, warming affected habitat-specific GPP, with positive effects on littoral GPP and negative effects on pelagic GPP. The effect on littoral GPP agrees with previous studies that show that aquatic plants can benefit from warming (McKee et al. 2002; Feuchtmayr et al. 2009). Phytoplankton in shallow systems are regarded to be primarily limited by nutrients and the decrease in pelagic GPP in heated sections was accompanied with a decrease in TN and TP. It is plausible that the stimulation of littoral GPP was the ultimate cause for the repression of pelagic GPP in the warm treatments via its effects on the nutrient availability in the water (Moss 1990).

To summarize, in this study we found unanticipated consequences of warming and humic river water input on metabolic rates. Major effects were observed by both warming and humic river runoff on the metabolism in littoral (benthos, macrophytes, periphyton) and pelagic habitats. Nevertheless, at the whole ecosystem level, NEP was not affected by the treatments as NEP in different habitats had opposite directions. Hence, the results suggest that the metabolic balance of shallow lakes and ponds may be relatively resistant to climate change effects. Still, in more benthic or pelagic dominated systems than studied here the consequences of climate change may potentially alter the balance between GPP and R in the habitat-specific directions shown in this study. However, such habitat-specific based predictions should be treated with caution as processes in respectively habitat are intertwined and may cause counterintuitive effects at the whole ecosystem level.

**Acknowledgments** Thanks to Anders Jonsson and Marcus Klaus for their help both in the laboratory and in the field. This study was supported by Grants from Conicet (Argentina) to Patricia Rodríguez (Postdoctoral fellowship, May 2012–April 2013 and PIP 64). Contribution no. 2 from Umeå University Experimental Ecosystem Facility (EXEF). EXEF is financed by the strategic research program ECOCHANGE and the Kempe foundation to Pär Byström, the Swedish Research Council (dnr. 621-2011-3908) to Jan Karlsson and the Swedish Research Council and the Wallenberg foundation to Lennart Persson.

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