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**Accounting for littoral primary production by periphyton shifts a highly humic boreal lake towards net autotrophy.**

RH: Humic lake net autotrophy

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15 **Abstract**

1. The prevailing view that many humic lakes are net heterotrophic is commonly based on pelagic measurements alone. Poor light conditions in humic lakes are assumed to constrain littoral primary production (PP), such that the littoral zone has been considered an insignificant contributor to whole-lake PP. However, that assumption is based on models and inferences from pelagic processes which do not take littoral zone structure into account.

20 Many lakes have an extensive ring of aquatic vegetation lying near the water surface, which provides substratum for epiphytic algae under well-illuminated conditions.

2. We measured both pelagic and littoral PP and community respiration (CR) in Mekkojärvi, a small, highly humic headwater lake, in southern Finland throughout the open water season in 2012. We used a  $^{14}\text{C}$  incorporation technique to measure pelagic PP, while littoral PP was determined using changes in dissolved inorganic carbon (DIC) concentrations during *in situ* incubations. We then estimated whole-lake PP and CR for both the littoral and pelagic zones.

3. We found that littoral PP usually dominated whole-lake PP, contributing >90% to total PP in summer. A mean pelagic production to respiration ratio (GPP:CR) of 0.4 clearly indicated strong net heterotrophy, but a value of 2.2 for the littoral zone indicated strong autotrophy.

30 For both habitats combined, the mean whole lake GPP:CR was 1.6, indicating net autotrophy.

4. We suggest that littoral PP can contribute significantly to whole-lake PP even in highly humic lakes, and that the littoral contribution can shift some lakes which have been considered net heterotrophic to metabolic balance or even net autotrophy during the ice-free period. Small humic lakes like Mekkojärvi with rings of littoral vegetation are widespread, especially in the boreal zone, and at least for similar lakes, evaluating lake metabolism from pelagic measurements alone is likely to be misleading.

40 Keywords: Benthic Primary Production, Lake Metabolism, Heterotrophy, Autotrophy,  
Dissolved Organic Carbon.

## Introduction

Most studies concerning primary production (PP) in lakes have included only phytoplankton and have ignored benthic algae in littoral habitats (Vadeboncoeur, Vander Zanden & Lodge, 2002). Over the last decade, a consensus has emerged that littoral and pelagic food webs are linked and that a combination of the PP of phytoplankton, benthic algae and macrophytes together with allochthonous organic carbon (OC) forms the energetic base of lake food webs (Vander Zanden & Vadeboncoeur, 2002; Vadeboncoeur *et al.*, 2008; Reynolds 2008; Karlsson *et al.*, 2009; Cole *et al.*, 2011). Although the view of discrete pelagic and littoral food webs has changed, quantitative integrations of littoral processes into whole-lake dynamics remain under-represented in the literature (Vadeboncoeur & Steinman, 2002). Of the few studies investigating littoral productivity and dynamics, most are from clear-water lakes, both oligotrophic (eg. Ask *et al.*, 2009) and eutrophic (eg. Van de Bogert *et al.*, 2007), and only very few from dystrophic humic lakes. There is strong evidence that benthic algae can make substantial contributions to whole-lake PP in clear-water lakes (Vadeboncoeur *et al.*, 2003; Andersson & Brunberg, 2006; Ask *et al.*, 2009) and can provide a major food resource for consumers even in large lakes, despite a low benthic contribution to whole-lake PP (Hecky & Hesslein, 1995; Hobson & Welch, 1995; Vander Zanden & Vadeboncoeur, 2002; Devlin, Vander Zanden & Vadeboncoeur, 2013). In contrast, poor light penetration into humic lakes is considered to severely constrain primary production, and especially benthic primary production (Karlsson *et al.*, 2009).

Allochthonous (terrestrially derived) organic matter can affect several fundamental functions in lake ecosystems (e.g. constraining primary production) and allochthony increases along a humic gradient (Jones 1992; Carpenter *et al.*, 2005; Jansson *et al.*, 2007). Incorporation of allochthonous OC into lake food webs increases heterotrophy, leading to community respiration (CR) that exceeds gross primary production (GPP) and overall net

heterotrophy (del Giorgio & Peters, 1994; Duarte & Agusti, 1998). However, most studies investigating whole-lake carbon flux concern only pelagic habitats without measurements of benthic autotrophic production or metabolism in the littoral zone. Ask *et al.* (2009) measured biomass production of algae and bacteria in both pelagic and benthic habitats in subarctic clear-water lakes and found that pelagic habitats were net heterotrophic with respiration and net CO<sub>2</sub> production dominating carbon fluxes, whereas primary production was dominant in benthic habitats. Those authors also concluded that allochthonous OC supported a significant part of the total consumer biomass production in both pelagic and benthic habitats. Humic or highly turbid lakes, where light effectively limits phytoplanktonic primary production to the uppermost water layers, are expected to have very low benthic contribution to whole-lake PP (Vadeboncoeur *et al.*, 2008). This is especially pronounced if a lake has a high depth ratio (DR =  $\bar{z}/z_{\max}$ ) and lacks illuminated benthic habitats. Consequently, and possibly due to more demanding sampling and measurement techniques for benthic algae and benthic PP in complex littoral habitats compared to relatively simple pelagic PP measurements, inclusion of littoral habitats has been rare in studies of humic lakes.

We measured primary production and respiration in both pelagic and littoral habitats of a small, highly humic lake, Mekkojärvi, which has been well studied (e.g. Kairesalo, Lehtovaara & Saukkonen, 1992; Järvinen & Salonen, 1998; Salonen *et al.*, 2005; Taipale *et al.*, 2008). There are numerous similar lakes in Finland and globally, with the estimated total number of lakes with surface area from 0.1 to 1 ha being  $2.77 \cdot 10^8$  (Downing *et al.*, 2006). Finnish lakes are predominantly shallow due to flat topography and consequently allochthonous carbon inputs are diluted in a small volume of water resulting in higher TOC concentrations and water colour than in deeper lakes (Kortelainen, 1999). Climate change is expected to increase terrestrial exports of DOC to lakes (Tranvik & Jansson, 2002) affecting the light climate in these lakes. Previous studies have revealed that carbon fluxes in the

pelagic zone of Mekkojärvi are dominated by heterotrophic processes and the lake has been considered to be net heterotrophic. However, the littoral zone of Mekkojärvi consists of a surrounding floating moss bed with submerged, inert, sedge stems supporting profuse epiphytic algal mats (periphyton) under well-illuminated conditions in summer. The productivity of this periphyton has not been measured before. Species diversity and biomass of animals in the littoral zone of Mekkojärvi is much higher than in the pelagic zone, and those animal communities have been assumed to have strong reliance on periphyton (Kairesalo *et al.*, 1992). Our main hypothesis was that the periphyton productivity in the littoral zone should be high in order to support the abundant macroinvertebrate consumers, despite the argument that benthic PP should be low considering the trophic status, light regime and basin shape of the lake (Vadeboncoeur *et al.*, 2008). Our second hypothesis was that, although the pelagic zone in Mekkojärvi is strongly dominated by heterotrophic processes, the littoral zone is more dominated by autotrophic processes and would offset pelagic heterotrophy even to the extent of making the lake net autotrophic.

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## **Methods**

### *Study site*

The study was conducted at Mekkojärvi (61°13'N 25°3'E) in the Evo forest area in southern Finland (Fig. 1A) during the open water season in 2012. Mekkojärvi is a small (0.35 ha) and highly humic (water colour 300–800 mg Pt l<sup>-1</sup>) headwater lake with maximum depth of 4.3 m and mean depth of 2 m. The lake receives a high loading of terrestrial organic matter from its catchment area, and has high DOC concentrations and low pH (Table 1). Despite being so shallow, the very high water colour and shelter from wind by the surrounding coniferous forest cause the lake to develop a very steep temperature and oxygen stratification gradient in summer, when the thermocline lies between 0.5–1.0 m and anoxia generally

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occurs below 1.0 m. The lake cannot sustain fish populations due to complete under-ice anoxia during winter, and the absence of planktivorous fish has led to very dense populations of the large bodied cladoceran *Daphnia longispina* in summer. Our study was conducted as part of a whole-lake food web experiment in 2012, when Mekkojärvi was divided into two  
120 basins with a plastic curtain and adult perch (*Perca fluviatilis*) (n = 100) were introduced to one basin in early July, while the other basin remained fishless. Both lake basins were always sampled simultaneously.

Mekkojärvi has a depth ratio of 0.47 and lacks illuminated benthic surfaces due to its dark brown water colour and extremely low light penetration (light-attenuation coefficient,  $K_d$ , ranges from 4.5 to 7.5). Despite its moderate DR, Mekkojärvi does not have a clearly  
125 defined littoral zone, as the lake is surrounded by a floating moss bed with fallen submerged terrestrial sedges, and a water column lies underneath the vegetation mat leading to a more cylindrical lake morphometry than implied by the DR. The littoral zone is thus composed mainly of *Sphagnum* and *Warnstorfia* moss species, with submerged and emergent  
130 macrophytes such as *Menyanthes trifoliata*, *Phragmites australis*, *Carex* spp. and *Utricularia* sp. associated with the moss mat. The littoral vegetation mat does not extend further than ca. 1 m from the lake edge and not deeper than ca. 0.5 m, but it forms a complex physical structure, which is well-illuminated and has a large surface area for epiphytic algal development. Relatively thick (ca. 1 cm) periphyton communities, rich in pennate diatoms  
135 (Bacillariophyceae), develop early in June, and achieve their highest biomass from July to mid-August. The area of littoral vegetation mat, estimated from a satellite image by using an area calculator tool (in Retkikartta.fi, © Metsähallitus, MML, CGI 2015), is ca. 0.086 ha, which covers ca. 25% of the whole lake area and gives a ratio of pelagic to littoral zone by area of 3.0.

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### *Physical and chemical parameters*

Light attenuation was measured at each sampling period using a single planar LI-COR<sup>®</sup> (Li-192) Underwater Quantum light sensor. Light was measured at 0.5 m intervals from the surface to the bottom of the lake and light attenuation coefficients were calculated (Kirk, 2003). Temperature and oxygen concentration were measured during every sampling in 2012 and once in 2014 with an oxygen and temperature sensor (YSI 55 probe, Yellow Springs Instruments). Daily irradiance values (measured with a Kipp & Zonen B.V., model CM11) and day lengths were obtained from the Finnish Meteorological Institute measurement station in Jokioinen, ca. 110 km west from Mekkojärvi. Nutrient, DOC and POM samples were taken at each sampling period and were analysed at Lammi Biological Station.

### *Pelagic phytoplankton biomass, production and respiration*

Composite water samples were taken with an acrylic tube sampler (Limnos) by combining three pulls covering each of three strata (0–0.5, 0.5–1.5 and 1.5–3 m) corresponding to epi- meta- and hypolimnion in both basins of the lake. Samples were taken 10 times between May–October in 2012. Phytoplankton biomass was estimated as chlorophyll *a* (chl *a*) concentration in the composite water samples. Samples were filtered onto Whatman GF/C glass fibre filters and chl *a* was measured by UV-spectrophotometry (Shimadzu UV-1800) according to a standard spectrophotometric method (SFS 5772, Finnish Standards Association).

Primary production in the pelagic habitat was measured eight times from composite water samples from four strata (0–0.2 m, 0.2–0.5 m, 0.5–1 m and 1–3 m) from both basins according to the <sup>14</sup>C incorporation method described by Schindler, Schmidt & Reid (1972). Subsamples were pipetted into 20 mL glass vials (containing NaH<sup>14</sup>CO<sub>3</sub>) with four replicates

(one dark sample in each depth). Samples were then incubated *in situ* in each stratum for 24 h. The  $^{14}\text{C}$  activity was measured with a Packard Tri-Carb<sup>®</sup> liquid scintillation counter. These 24 h determinations were assumed to approximate most closely to net primary production (NPP). Primary productivity of the water column was converted from volumetric basis to areal basis by multiplying the values from each stratum by the total depth of the stratum and then summing over the whole water column. Whole-lake daily PP estimates were calculated by multiplying daily areal values by the lake surface area.

Pelagic community respiration (CR) was measured eight times, together with PP, as the increase in DIC concentration during dark incubations. Subsamples (two initials and two samples for dark incubation) were taken from composite water samples from each stratum into 50 mL glass BOD bottles. Half of the bottles were wrapped in aluminium foil and incubated *in situ* for 24 h in each stratum and the other half ( $t_{0h}$ ) were placed on ice and taken immediately to the laboratory, where DIC concentration was measured with a DIC-analyser (Salonen, 1981). This was repeated for  $t_{24h}$  samples the next day. Areal values and whole-lake estimates for CR were calculated as for pelagic PP. Pelagic NPP was converted to GPP as the sum of NPP and CR values in the photic zone, assuming that most of the CR was attributable to primary producers.

#### *Littoral primary production, respiration and periphyton biomass*

Primary production in the littoral habitats was measured eight times, concurrently with pelagic PP, from *in situ* incubations of periphyton samples in both dark and transparent 20 ml glass vials where the consumption or production of DIC over time indicates either respiration or production. Periphyton PP on moss and on sedges per unit dry mass of substratum was compared and there was no statistically significant difference in PP rates ( $t$ -test,  $t_{39} = -0.2005$ ,  $P = 0.8421$ , data not shown). This allowed us to sample routinely from

submerged sedges instead of from the more complex moss substratum. Furthermore, sampling of sedges was appropriate because while lying under the water surface they were metabolically inert. To insure that the sedge substratum was indeed metabolically inert, epiphyton was carefully removed from sedges and the cleaned substratum was incubated in both light and dark. No change in DIC was measured (data not shown). The lake was sampled at eight sites around the shoreline, four sites from each basin. Samples were collected by clipping random sedge pieces into 20 mL glass vials and filling with surrounding littoral water. Trial incubations of this littoral water without any epiphyton or substratum demonstrated no substantive changes in DIC concentration over time. Four replicate samples of surrounding water to obtain initial DIC concentrations were taken from each sampling site. Samples were incubated *in situ* for 2 h at noon, half of the samples in dark conditions and the other half in the surface water in the same light conditions as those from which the periphyton originated (barely submerged under the water surface). After the incubations, samples were put into ice and dark and taken immediately to the laboratory, where DIC was measured with a DIC-analyser (Salonen, 1981). Periphyton was then entirely removed from the collected substratum by scraping with a spatula and was filtered onto glass fibre filters (Whatman GF/F) and chl *a* was determined as described above for phytoplankton. Periphyton biomass was estimated as total chl *a* per dry weight of substratum in a sample. Substrata were dried at 60 °C for 24 h and dry mass was recorded.

Gross primary production (GPP) was calculated from the difference in DIC between dark and light samples ( $GPP = DIC_{\text{dark}} - DIC_{\text{light}} / \text{incubation time}$ ); CR was calculated from the difference in DIC between dark and initial samples ( $CR = DIC_{\text{dark}} - DIC_{\text{initial}} / \text{incubation time}$ ). Net primary production (NPP) was then calculated as  $NPP = GPP - CR$ , assuming that most of the CR was attributable to primary producers. Values for each incubated sample were normalized to mg C g dry weight (DW) substratum<sup>-1</sup>. To estimate whole-lake littoral primary

production, we quantified the availability of littoral substratum, which consisted of macrophytes and moss. Littoral substratum along 40 cm of lakeshore at 12 sites within each basin was entirely physically removed, carefully collected and dried at 60° C. We calculated the average dry weight of littoral substratum per meter of lake shore (20.1 and 22.5 g DW substratum m<sup>-1</sup>, respectively) in both basins and, since the substratum consists mainly of flat and horizontally aggregated macrophytes and moss leaves, we divided the weight by two in order to conservatively estimate the mass of the illuminated side of the substratum. It should be noted that more than half the substrate collected had substantial development of epiphyton and that this approach is likely to have yielded a conservative estimate of available substratum. We compared the use of this method of whole-lake extrapolation to a simple areal extrapolation method and found that the results were within 20% at the whole-lake scale. Given the vast oversimplification of defining the heterogeneous, extremely rugose and complex physical nature of the littoral substratum as a plane, we considered that extrapolation by substratum weight was more realistic. Daily estimates for periphyton PP were calculated from a slightly modified version (Eq. 1) of the calculation described by Vadeboncoeur *et al.* (2008). For whole-lake estimates, we calculated PP per m of lake shore and multiplied that by the total shoreline lengths of each basin (135 and 185 m, respectively). Daily estimates for periphyton respiration were calculated by multiplying the mean values at noon by 24.

235 Periphyton PP<sup>day</sup> =

$$\Delta t \sum_{\text{sunrise}}^{\text{sunset}} [\text{PP}_{\text{max}} \tanh(I_{zt}/I_k)]$$

(Eq. 1)

where  $\Delta t$  is the time increment (h),  $\text{PP}_{\text{max}}$  is the light-saturated primary production (mg C g dry-weighted substrate<sup>-1</sup> h<sup>-1</sup>) derived from incubating samples right under the surface at noon,  $\tanh$  is the hyperbolic tangent function,  $I_{zt}$  is the light at depth  $z$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and time  $t$  (h)

240 and  $I_k$  is the light intensity for onset of saturation, which was set to  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  according to Hill (1996). We used the irradiance data and day lengths obtained from the Finnish Meteorological Institute in Jokioinen. To define  $I_z$ , the photosynthetically active radiation (PAR) on the surface was multiplied by 0.75, which was the average fraction of light at the incubation depth over the whole sampling period (Fig. 1B).

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### *Statistical analyses*

Since the lake was divided into two basins with a plastic curtain, and one basin was fishless and the other had fish, we used multivariate repeated measures of ANOVA (RMA) to test if there were statistically significant differences in PP, CR and chl *a* between the sampling occasions and the basins. The data were log-transformed, when necessary, to achieve the requirements of parametric analyses. A non-significant basin effect (between-subject factor) revealed that the fish experiment and the lake division did not affect the production and respiration values, which allowed us to pool the data. The daily estimates for periphyton PP (Eq. 1) were performed using R project for Statistical Computing version 3.0 (R Core Team, 2013). Other tests were performed using IBM SPSS Statistics 20.0.0.2. If not expressly noted, all the descriptive statistics are means + S.E.

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## **Results**

### *Pelagic primary productivity, respiration and phytoplankton biomass*

260 Physical and chemical parameters are reported in Table 1. Light attenuation coefficient,  $K_d$ , ranged from 4.5 to 7.5. Pelagic NPP (Fig. 2A) was highest in late May ( $331 \pm 274 \text{ mg C m}^{-2} \text{ d}^{-1}$ ), indicating a clear spring maximum of phytoplankton. PP then decreased towards autumn, being lowest in late September ( $9.0 \pm 1.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). PP values for 19 July and 1 August include data from only one basin, as the data from the other basin were

265 unreliable. RMA was not executed for the pelagic PP data, since variation was substantial and assumptions for repeated measures were not met; however, a t-test showed no differences in mean PP for the whole sampling period between the two basins ( $t$ -test,  $t_{40} = 0.254$ ,  $P = 0.801$ ), or in pairwise comparisons between the basins on each date, allowing us to pool the data from the two basins.

270 Community respiration also varied substantially (Fig. 2A), and exhibited rates over one order of magnitude higher than those for PP. The highest mean CR on 18 June was  $3210 \pm 1655 \text{ mg C m}^{-2} \text{ d}^{-1}$ , of which the hypolimnetic fraction was 78%. The mean hypolimnetic fraction of the CR in the water column over the sampling period was  $77\% \pm 5$ . CR values for 1 and 15 August include values from only one basin. RMA for CR from May to August 275 showed a significant main effect of dates ( $F_{3, 48} = 11.88$ ,  $P < 0.01$ ), indicating change over time, but there was no significant interaction between the basins and the dates ( $F_3 = 2.03$ ,  $P = 0.12$ ), allowing us to pool the data from the two basins.

Chlorophyll  $a$  concentration in the epilimnion was rather constant from spring to autumn ( $8.0 \pm 1.1 \text{ mg m}^{-3}$ ) and substantially lower than in the metalimnion ( $27.2 \pm 6.2 \text{ mg m}^{-3}$ ) and hypolimnion ( $55.4 \pm 4.4 \text{ mg m}^{-3}$ ) (Fig. 3A). However, the high chl  $a$  concentrations in both meta- and hypolimnion presumably contain appreciable quantities of bacteriochlorophyll (BChl), which is abundant in Mekkojärvi and which overlaps with chl  $a$  in spectrophotometric determination (Karhunen *et al.*, 2013). Indeed BChl may also have contributed to epilimnetic chl  $a$ , as chl  $a$  did not follow the same pattern as pelagic PP. When 285 the basins were compared for the mean chl  $a$  over the sampling period, chl  $a$  was higher in the fishless basin ( $37.8 \pm 5.4 \text{ mg m}^{-3}$ ) than in the basin which had fish ( $22.6 \pm 4.2 \text{ mg m}^{-3}$ ) ( $t$ -test,  $t_{58} = -2.200$ ,  $P < 0.05$ ).

*Littoral primary productivity, respiration and periphyton biomass*

290 Littoral periphyton NPP was highest in spring and throughout the summer except for a  
rapid decrease in early July (Fig. 2C), and showed a pattern of decline towards autumn,  
decreasing substantially from late-August to late-September (Fig. 2B, C). The mean NPP at  
noon was  $35.8 \pm 3.2$  mg C g DW substratum<sup>-1</sup> h<sup>-1</sup> and the highest value was determined on 20  
July ( $47.2 \pm 11.0$  mg C g DW substratum<sup>-1</sup> h<sup>-1</sup>). RMA revealed a significant main effect of  
295 time ( $F_{7,98} = 6.940$ ,  $P < 0.01$ ), which was not affected by basin treatments ( $F_{7,98} = 1.098$ ,  $P =$   
 $0.366$ ). The only significant difference in NPP was observed between 30 August and 27  
September ( $F_{1,14} = 3.462$ ,  $P < 0.05$ ), although the main effect of basin was not significant ( $F_{1,$   
 $14} = 3.982$ ,  $P = 0.066$ ), allowing us to pool the data from both basins. Mean daily littoral NPP  
was  $364 \pm 66$  mg C g DW substratum<sup>-1</sup> d<sup>-1</sup> and the highest mean rates were observed on 20  
300 July ( $663 \pm 2$  mg C g DW substratum<sup>-1</sup> d<sup>-1</sup>), which was later than the highest noon rates  
observed on 4 July (Fig. 2B, C). This, as well as the decrease in daily NPP values on 30  
August, was caused by rapid changes in weather and light conditions, which gave lower daily  
estimates. NPP rates remained constant until August, when variation increased between the  
basins.

305 Littoral CR was low relative to the highest NPP rates (Fig. 2B, C). The mean CR at  
noon was  $16.7 \pm 2.4$  mg C g DW substrate<sup>-1</sup> h<sup>-1</sup>; the highest rates were observed on 4 July  
( $37.0 \pm 11.3$  mg C (g DW substratum)<sup>-1</sup> h<sup>-1</sup>) and the lowest on 27 September ( $4.6 \pm 1.3$  mg C  
(g DW substratum)<sup>-1</sup> h<sup>-1</sup>). RMA revealed no significant main effect of time ( $F_{2.88,40.36} = 1.530$ ,  
 $P = 0.222$ ) and no interaction between time and the basins ( $F_{2.88,40.36} = 0.252$ ,  $P = 0.852$ ), or  
310 any main effect of basin ( $F_{1,14} = 0.013$ ,  $P = 0.858$ ). When the daily CR values were  
calculated from the hourly rates, the mean CR over the sampling periods was  $395 \pm 65$  mg C  
(g DW substratum)<sup>-1</sup> d<sup>-1</sup>.

The mean periphyton chl *a* content over the sampling periods was  $0.7 \pm 0.1$  mg (g  
DW substratum)<sup>-1</sup>; the highest contents were observed on 30 August ( $1.3 \pm 0.3$  mg (g DW

315 substratum)<sup>-1</sup>) and the lowest on 27 September ( $0.2 \pm 0.3 \text{ mg (g DW substratum)}^{-1}$ ) (Fig. 3B).  
RMA revealed a significant main effect of time ( $F_{2,52, 35,36} = 5.705, P < 0.01$ ), but no  
interactions between time and basin ( $F_{2,52, 35,36} = 1.191, P = 0.323$ ).

#### *Whole-lake estimates for net primary production and respiration*

320 Whole-lake estimates showed that littoral contributions dominated whole-lake NPP  
from spring to early autumn (Fig. 4A, B). The mean littoral contribution to whole-lake NPP  
over the sampling period was  $81 \pm 8\%$ . Pelagic NPP contribution most early in the spring  
(24%) and in late autumn (54%), while in the summer the pelagic contribution varied from 2  
to 20%. The highest estimate for the whole-lake NPP in the littoral was  $4.1 \text{ kg C d}^{-1}$  on 21  
325 June and the lowest was  $17.5 \text{ g C d}^{-1}$  on 27 September, while the mean was  $2.4 \pm 0.7 \text{ kg C d}^{-1}$ .  
The highest whole-lake estimate for pelagic NPP was  $1.1 \text{ kg C d}^{-1}$  on 31 May and the lowest  
was  $32.4 \text{ g C d}^{-1}$  on 27 September, while the mean was  $338 \pm 165 \text{ g C d}^{-1}$ . Whole-lake  
estimates for July could not be calculated due to missing pelagic data from the fishless basin,  
but the littoral contributions in the basin with fish remained high in July (77 and 91%).

330 Whole-lake estimates of pelagic CR showed higher values in spring when the highest  
peak, observed on 21 June, was  $10.4 \text{ kg C d}^{-1}$  (Fig. 4C, D). The lowest estimate was  $385 \text{ g C}$   
 $\text{d}^{-1}$  on 30 August while the mean was  $3.2 \pm 1.9 \text{ kg C d}^{-1}$  over five sampling periods. Littoral  
CR was relatively stable, ranging from  $766 \text{ g C d}^{-1}$  in late September to  $4.4 \text{ kg C d}^{-1}$  in late  
August, while the mean was  $2.5 \pm 0.5 \text{ kg C d}^{-1}$  (Fig. 4C, D).

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#### *Production to respiration ratio (GPP:CR)*

The mean GPP:CR ratio in the littoral zone was  $2.2 \pm 0.4, n = 8$ ), but was  
significantly lower in the pelagic zone ( $0.4 \pm 0.1, n = 5$ ) (*t*-test,  $t_{11} = 3.185, P < 0.01$ ). The  
highest GPP:CR ratio in the littoral was 4.8 on 20 July, and the lowest was 1.0 on 27



340 September. For the pelagic zone, the highest GPP:CR ratio was 1.0 on 20 July, and the lowest  
was 0.2 on 16 August. The whole-lake average of five sampling periods was  $1.6 \pm 0.5$ . The  
results indicated net heterotrophy ( $P:R < 1$ ) in the pelagic zone but net autotrophy ( $P:R > 1$ ) in  
the littoral zone (Fig. 5). When whole-lake pelagic and littoral results were combined, the  
outcome indicated net autotrophy for the complete lake ecosystem (Fig. 5).

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## Discussion

Our results demonstrate an overwhelming dominance of littoral PP in whole-lake  
autotrophic production in Mekkojärvi. The lake is very humic, which limits light penetration,  
while its depth ratio and complex littoral structure leave the majority of the lake bottom in  
350 darkness. However, littoral vegetation lining the lake perimeter is well-illuminated and  
supports highly productive periphyton assemblages, with mean contribution to whole-lake  
NPP over 80% throughout the sampling period. Intense respiration of allochthonous OC in  
the pelagic habitat substantially exceeded phytoplankton PP, indicating strong net  
heterotrophy with low GPP:CR ratios in the open water of the lake. In contrast, well-  
355 developed and highly productive periphyton mats led to net autotrophy in the littoral habitat,  
and when incorporated into whole-lake PP the system GPP:CR ratio was net autotrophic.  
Estimating PP and CR for structurally complex littoral zones is very challenging, and our  
estimates of whole-lake littoral PP and CR undoubtedly have higher uncertainty than the  
pelagic values. Nevertheless, the littoral values are so high that the associated uncertainty  
360 cannot alter their essential message. Moreover, the values for littoral NPP must be  
underestimates, as we obtained these by subtracting CR from GPP, and the true respiration  
attributable to primary producers must be less than the CR. Hence our results demonstrate  
that, despite high terrestrial inputs of DOC and dominance of heterotrophic processes in the  
pelagic zone, some humic lakes can be metabolically balanced or even net autotrophic when

365 highly productive periphyton communities are included in measurements of whole-lake  
metabolism. Our findings challenge the current theoretical framework regarding whole-lake  
metabolism in humic systems and provide some answers to recently posed questions about  
the carbon budgets in lakes (Hanson *et al.*, 2014).

Lakes with high DOC, high colour and low pelagic primary production are often  
370 assumed to be heterotrophic due to the allochthonous OC (Cole *et al.*, 2000). However,  
littoral primary production is often overlooked in lakes like Mekkojärvi, as many factors that  
regulate possible littoral contributions to whole lake autochthony would appear to seriously  
constrain the potential significance of periphyton. Indeed, based on Mekkojärvi's depth ratio,  
light attenuation and P content, equations presented by Vadeboncoeur *et al.* (2008) predict  
375 that the overall contribution of littoral PP to whole-lake PP should be a maximum of 10%.  
However, these models do not account for sub-surface littoral vegetation lining the lake  
perimeter that provides substantial substratum for colonization by epiphytic algae.

Previous work demonstrating that benthic algal contribution to whole-lake PP  
declines rapidly with increasing DOC concentration in northern boreal lakes, offers a  
380 perspective for autotrophy in humic lakes when epiphytic benthic algae is not measured and  
included as a source of PP (e.g. Ask *et al.*, 2009). When metabolism on sediment and by  
periphyton colonizing only the lake bottom are measured, logically the reduced light  
penetration caused by high DOC concentrations explains why benthic algae could not  
contribute substantially to humic lake autotrophy. However, to fully account for and evaluate  
385 the contribution of benthic algae in humic lakes, the extremely productive, albeit easily  
overlooked, PP from shallow periphyton needs to be included.

It is still likely that large north temperate lakes are generally net heterotrophic, as  
bacterial respiration of allochthonous OC can proceed in the whole water column during the  
entire year, while photosynthesis in most of the lakes is restricted to the uppermost water

390 layers (Jansson *et al.*, 2000). That is evident if a lake does not have extensive littoral  
vegetation and the ratio of pelagic area to the area of littoral vegetation is very high.  
However, northern areas have millions of lakes with mean depth less than 3 m and a littoral  
zone that dominates the pelagic zone (Wetzel, 1990). In Finland, where ca. 10% of the  
surface area is covered by lakes, over 95% of the 190 000 lakes are smaller than 1 km<sup>2</sup>  
395 (Raatikainen & Kuusisto, 1990) and a majority of these are humic with a high concentration  
of organic matter (Kämäri *et al.*, 1991). Although our results are from only one lake, we can  
assume that in small humic lakes, where littoral vegetation comprising floating moss and  
macrophytes is a widespread characteristic, estimates of PP and lake metabolism based only  
on measurements from the pelagic zone and ignoring epiphytic PP are likely to be seriously  
400 erroneous.

Pelagic PP in Mekkojärvi was similar to that in previous studies of the lake (Salonen  
*et al.*, 2005; Taipale, Kankaala & Jones, 2007): a clear spring peak was followed by a  
decrease towards autumn with mean rates under 100 mg C m<sup>-2</sup> d<sup>-1</sup> and relatively high  
variation. Salonen *et al.* (2005) measured the CR in Mekkojärvi *in situ* from a 1 m water  
405 column in the epilimnion and found respiration rates 5.2 times higher than PP. Even so, they  
concluded that total water column CR was likely to be considerably underestimated, as CR in  
the anoxic hypolimnion has been shown to contribute significantly to whole-lake CR (Cole &  
Pace, 1995). Our finding of a 77% contribution from the hypolimnetic fraction to total  
pelagic CR, with a mean rate of almost 1 g C m<sup>-2</sup> d<sup>-1</sup> is consistent with this view. One of the  
410 greatest uncertainties in measuring PP by <sup>14</sup>C incorporation is whether it measures net or  
gross primary production, or something in-between (Marra, 2009). We used a <sup>14</sup>C  
incorporation method with 24 h incubation, as has been widely used at other nearby humic  
lakes (Arvola *et al.*, 1999), as a longer (24 h) incubation time has been considered appropriate  
in unproductive lakes, and such an incubation time should give values approximating NPP.

415 Other uncertainty is involved in deriving GPP from NPP by adding CR, as this includes the  
respiration of organisms other than autotrophs and gives an overestimate of GPP. The true  
autotrophic respiration must be less than CR and therefore the true PP:R ratios of the lake  
will be higher than our estimates; hence the lake must actually be more autotrophic and our  
interpretations remain conservative.

420 Oxygen data from the pelagic (Table 1) at noon demonstrate undersaturation of O<sub>2</sub> in  
the epilimnion at the relevant temperatures, indicating apparent heterotrophy. Although we do  
not have DO data from the littoral in 2012, we measured DO from both habitats in late-May  
2014 (Table 1). DO in the littoral was measured just above the moss from several sampling  
sites and from the epilimnion (0–0.5 m) in the pelagic. In the littoral zone oxygen saturation  
425 varied between 105 and 120%, whereas in the pelagic it was under 70%. These results give  
support to our high PP rates and demonstrate marked spatial heterogeneity in oxygen in the  
lake. Hence the undersaturation of oxygen in the open water is not inconsistent with an  
overall metabolic balance for the lake.

The extremely high littoral production we measured in Mekkojärvi is likely to support  
430 a productive littoral food web. Van Duinen *et al.* (2013) found that periphyton constituted a  
significant food resource for aquatic macroinvertebrates in small and highly humic bog pools  
in southwest Estonia. Lau *et al.* (2014) also showed that autochthonous resources are the  
main driver of secondary production in five dystrophic lakes in Sweden. While they did not  
directly measure primary production, our results of high epiphytic production support their  
435 findings. The most diverse and abundant macroinvertebrate community in Mekkojärvi lives  
within the littoral moss, and it is likely that periphyton is the basal food resource in this  
habitat. Moreover, the most widespread fish species in small humic lakes, European perch  
(*Perca fluviatilis*), relies mainly on littoral macroinvertebrates for food in such lakes (e.g.

Nyberg *et al.*, 2010). The contribution of periphyton to macroinvertebrate diets and the lake  
440 food web remains unclear in Mekkojärvi and deserves further study.

Our findings demonstrate that littoral zones in humic lakes offer a highly productive  
environment for lake biota, and are also as critical to whole-lake metabolism as the pelagic  
processes that have been much better documented in the past. Littoral primary production can  
dominate pelagic PP, and in doing so can offset the high heterotrophic pelagic respiration  
445 even to the extent of producing a balanced or net autotrophic whole-lake metabolism. This  
contradicts the most widely held current view (Del Giorgio, Cole & Cimbleris, 1997) and  
demonstrates that there is much more to be learned regarding the role of littoral processes in  
humic lake metabolism. However, our estimates cover only the ice-free period. Respiratory  
processes, mainly due to decomposition of OC, continue in boreal Finnish lakes at a low  
450 levels throughout the winter ice cover (Kortelainen *et al.*, 2006), which may still make these  
lakes net heterotrophic on an annual basis.

We estimated that the ratio of pelagic to littoral zone by area in Mekkojärvi is 3.0,  
which was derived from areal calculations of both habitats from satellite imagery. Littoral  
area was determined as originating at the land-water interface and ending at the edge of the  
455 vegetation. Although crude, we believe this approach provides a reasonable estimate. The  
number of lakes with the similar pelagic-littoral ratios approaches  $10^5$  worldwide (Peters &  
Lodge, 2010) with the majority other lakes having lower values. Yet, it is hard to give  
quantitative estimates of the prevalence of humic lakes ringed by similar floating vegetation  
with highly productive epiphyton as occurs in Mekkojärvi. Bryophyte mats and sedges are  
460 characteristic of oligotrophic humic lakes (Rintanen, 1996; Heino & Toivonen, 2008) and  
therefore there is a high probability that many lakes that are similar to Mekkojärvi in size and  
region contain similar vegetation features. Aquatic moss stands in small, humic Finnish lakes  
have expanded in recent decades showing a clear trend of filling the entire waterbody

(Rintanen, 1996). A recent overview of the biodiversity and ecosystem functioning in natural  
465 bog pools (Beadle *et al.*, 2015) highlighted the need for future studies, as knowledge of these  
ecosystems is limited. While lakes like Mekkojärvi differ in some regards from bog pools,  
there are relevant similarities in humic contents, vegetation and structure of the basins. Those  
bog pools are assumed to be net heterotrophic, even though there is evidence that  
invertebrates significantly rely on periphyton (Van Duinen *et al.*, 2013). We suggest that  
470 littoral primary production and respiration should also be taken into account in the future  
studies of humic systems, as our data demonstrate that they are likely to be more productive  
and less heterotrophic than previously assumed.

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Figure 1. A) Location and bathymetry (numbers indicate depth contours in m) of the study  
620 lake Mekkojärvi. Dashed line illustrates the lake division curtain and squares the sampling  
points in the pelagic measurements. B) The mean ( $\pm$  S.E.) light attenuation in Mekkojärvi in  
2012 ( $n = 13$ ).

Figure 2. Pelagic (A) and littoral (B, C) net primary production (bars) and community  
625 respiration (lines) in Mekkojärvi in 2012. Pelagic NPP represents areal means ( $\pm$  S.E.)  
combining both basins of the lake. Some dates (19 July and 6 August for pelagic NPP and 6  
August. for pelagic CR) have values only from one basin. Littoral NPP and CR represent  
mean ( $\pm$  S.E.) net primary production and community respiration of periphyton per gram dry-  
weighted substratum per hour (B) and per day (C). Differences in daily light regime account  
630 for inconsistencies in proportional scaling between hourly and daily rates on individual dates.

Figure 3. Pelagic (A) and periphyton (B) chl *a* in Mekkojärvi in 2012. Pelagic chl *a*  
represents mean ( $\pm$  S.E.) concentrations in three strata combining both basins. Periphyton chl  
*a* is expressed as mean ( $\pm$  S.E.) chl *a* content per gram dry-weighted substratum and  
635 combines both basins.

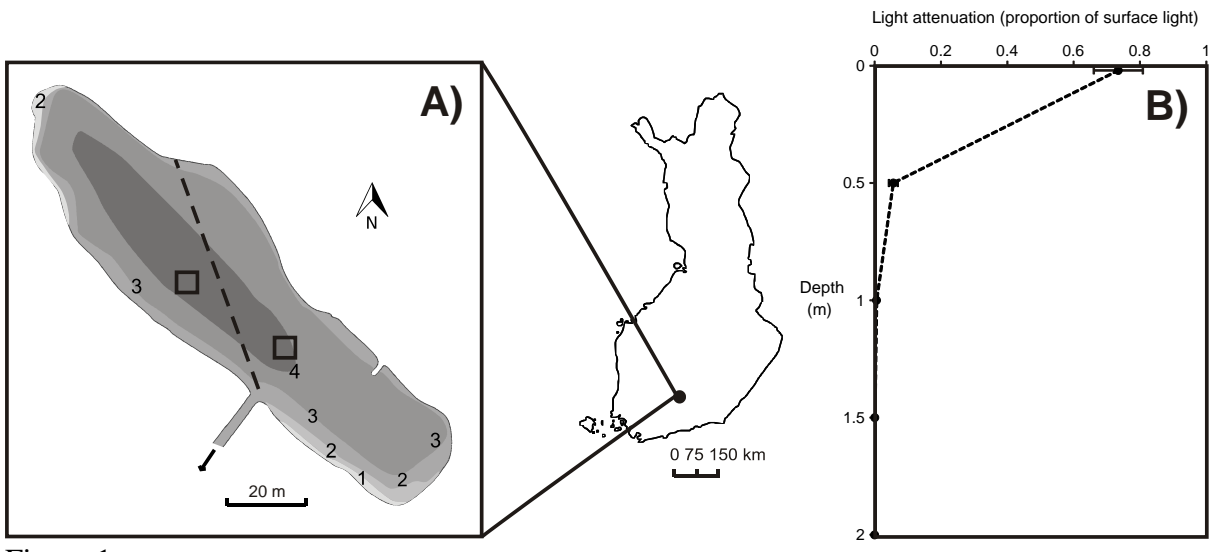
Figure 4. A) Estimates of the whole-lake littoral and pelagic net primary production and B)  
their proportions of whole-lake net primary production. C) and D) the same for the whole-  
lake community respiration.

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Figure 5. Comparison of whole-lake GPP and CR from pelagic and littoral habitats, both  
separately and in combination. The values are plotted on a logarithmic scale. The line  
represents a GPP:CR ratio of 1.

Table 1. Mean ( $\pm$  SE) values for some chemical parameters in the epi-, meta- and hypolimnion in Mekkojärvi during the open water period of 2012: chlorophyll *a* (Chl *a*), dissolved oxygen (DO), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), particulate organic carbon (POC), total phosphorus (Tot-P), ammonium (NH<sub>4</sub>-N) and combined oxidized inorganic nitrogen (NO<sub>2</sub>-N + NO<sub>3</sub>-N). pH is expressed as median. N refers to sampling occasions. Values from 2014 represent the mean ( $\pm$  SE) values from a single sampling occasion in late-May.

2012	N	0–0.5 m	0.5–1 m	1–3 m
pH	12	5.3*	5.4*	5.7*
Chl <i>a</i> ( $\mu\text{g L}^{-1}$ )	10	8.1 $\pm$ 0.0	27.2 $\pm$ 0.0	55.4 $\pm$ 0.0
DO ( $\text{mg O}_2 \text{ L}^{-1}$ )	9	4.8 $\pm$ 0.4	1.9 $\pm$ 0.5	1.0 $\pm$ 0.0
DOC ( $\text{mg C L}^{-1}$ )	10	32.0 $\pm$ 1.5	33.0 $\pm$ 1.1	30.0 $\pm$ 0.5
DIC ( $\text{mg C L}^{-1}$ )	8	2.9 $\pm$ 0.2	4.5 $\pm$ 0.9	8.6 $\pm$ 1.7
POC ( $\text{mg C L}^{-1}$ )	10	0.5 $\pm$ 0.0	0.8 $\pm$ 0.1	1.0 $\pm$ 0.0
Tot-P ( $\mu\text{g P L}^{-1}$ )	10	12.0 $\pm$ 0.7	15.0 $\pm$ 2.0	58.0 $\pm$ 4.4
NH <sub>4</sub> ( $\mu\text{g L}^{-1}$ )	10	34.0 $\pm$ 4.0	55.0 $\pm$ 9.4	384.0 $\pm$ 33.5
NO <sub>2</sub> + NO <sub>3</sub> ( $\mu\text{g L}^{-1}$ )	10	36.0 $\pm$ 6.9	65.0 $\pm$ 8.9	74.0 $\pm$ 9.5
2014	N	Pelagic	N	Littoral
DO ( $\text{mg O}_2 \text{ L}^{-1}$ )	2	7.3 $\pm$ 3.9	8	10.0 $\pm$ 0.5
Oxygen saturation (%)	2	68.0 $\pm$ 0.1	8	121.0 $\pm$ 4.1
Temperature ( $^{\circ}\text{C}$ )	2	11.5 $\pm$ 0.1	8	23.7 $\pm$ 0.3



655 Figure 1.



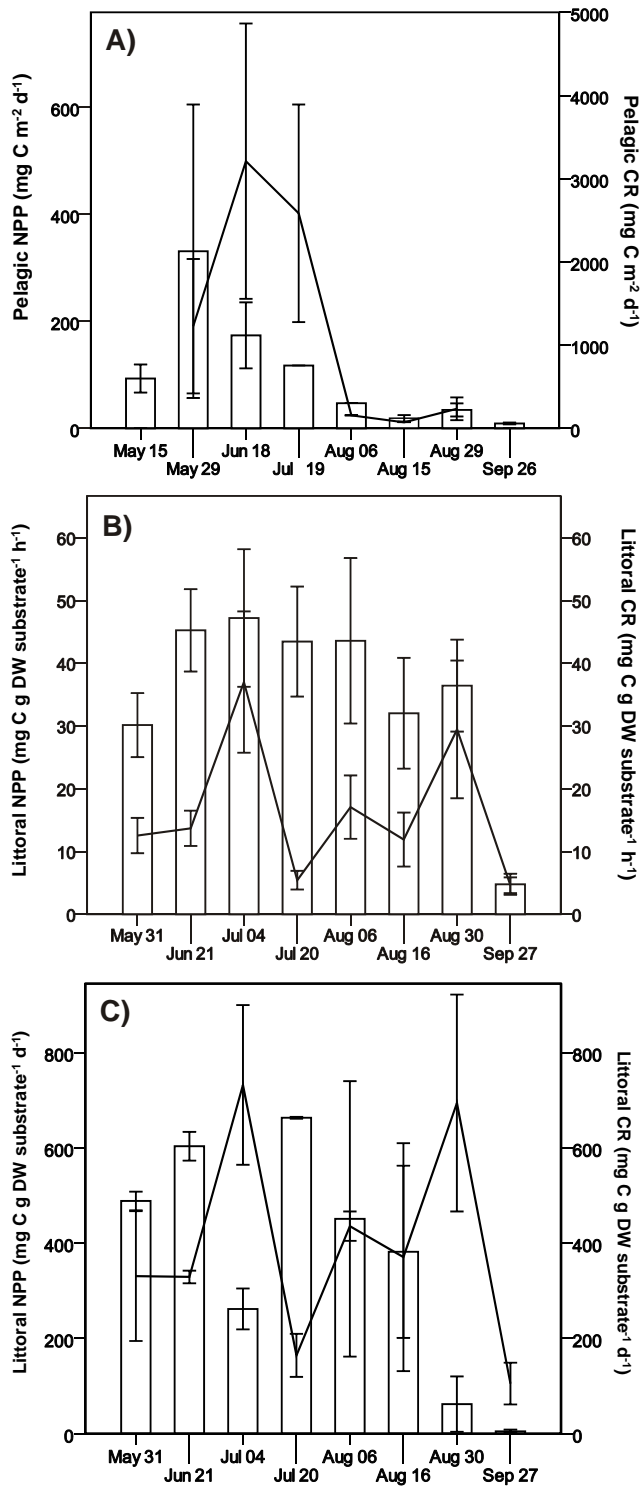
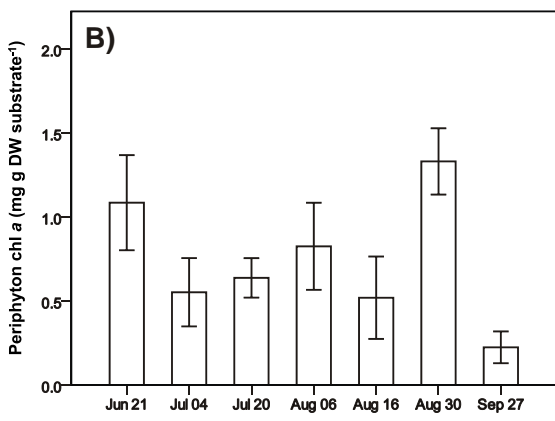
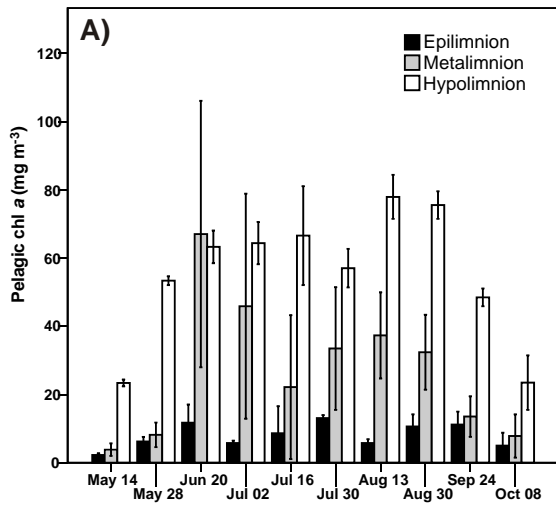
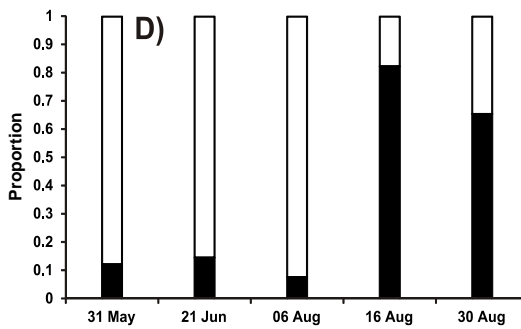
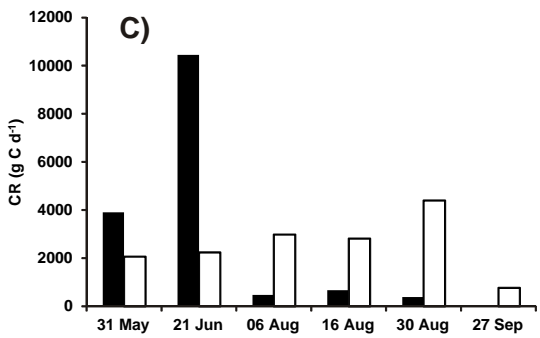
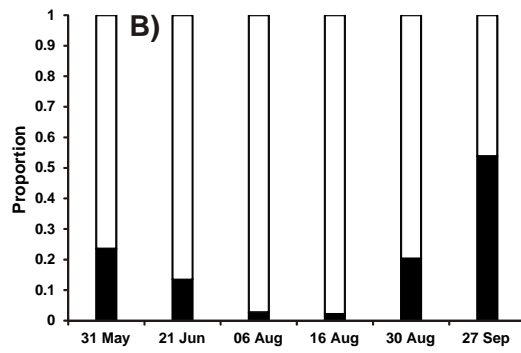
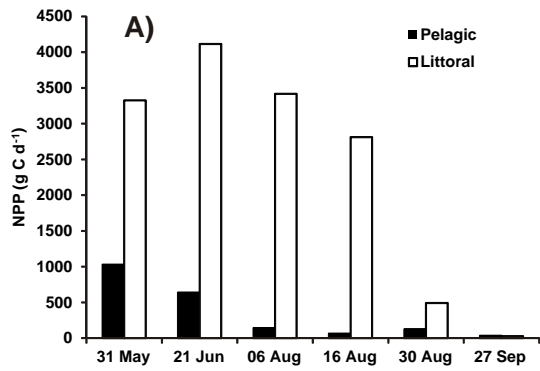


Figure 2.



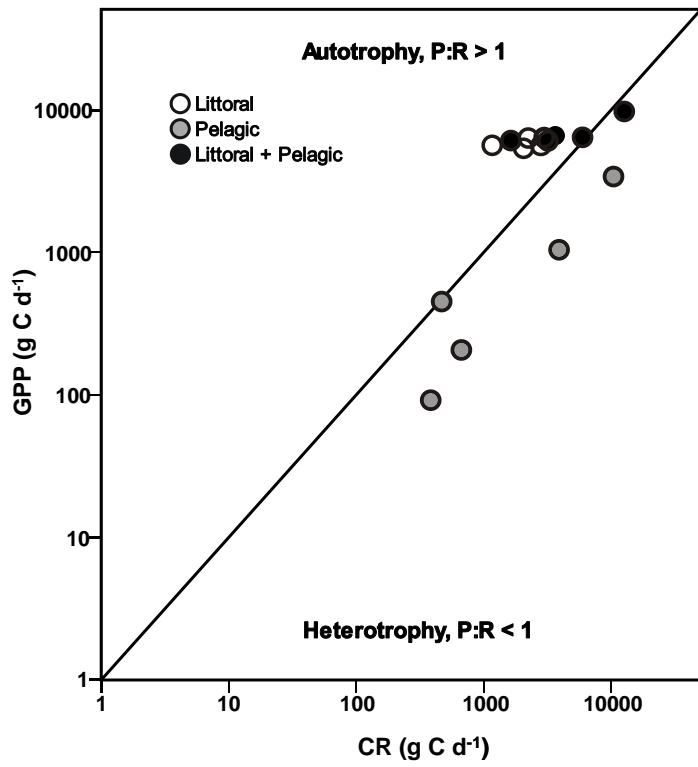
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Figure 3.



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Figure 4.



670 Figure 5.