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Constrained microbial processing of allochthonous organic carbon in boreal lake sediments

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Abstract

We investigated sediment bacterial metabolism in eight lakes with different inputs of allochthonous and autochthonous organic carbon in south-central Sweden. Sediment bacterial production, mineralization, and biomass were measured seasonally and along a lake depth gradient in lakes with different water and sediment characteristics. Sediment bacterial metabolism was primarily controlled by temperature but also by the quality and origin of organic carbon. Metabolism was positively correlated to measures of autochthonous influence on the sediment organic carbon, but did not show a similar increase with increasing input of allochthonous organic carbon. Hence, in contrast to what is currently known for the water column, increasing terrestrial organic carbon influence does not result in enhanced sediment bacterial metabolism. The role of allochthonous organic carbon as the main driver of sediment bacterial metabolism suggested so far is contrary to our findings. Meio- and macrobenthic invertebrate biomass were, at most, weakly correlated to bacterial metabolism and biomass, suggesting limited control of sediment bacteria by grazing. Bacterial metabolism in boreal lake sediments is constrained by low temperatures and by the recalcitrant nature of the dominant organic carbon, resulting in sediments being an effective sink of organic carbon.

The organic carbon of lakes is, to a large extent, of terrestrial origin (Wetzel 2001). Many studies have shown that terrestrial organic carbon supports the metabolism of heterotrophic bacteria in the water column and that increasing amount of dissolved organic carbon (DOC) sustains increasing metabolism (Tranvik 1988; Jansson et al. 2007). Bacteria can mediate further transfer of the energy to higher trophic levels (Carpenter et al. 2005). Studies of the role of terrestrial organic matter as a subsidy to aquatic food webs have, so far, focused mainly on the pelagic habitat. It has long been recognized that lake sediments are an essential component of the organic carbon processing (Lindeman 1942). One of the latest syntheses on sediment bacterial metabolism in lakes suggested that the energy flow in lake sediments is driven by allochthonous organic carbon (Schallenberg and Kalff 1993). Still, the organic carbon metabolism in lake sediments has received relatively limited interest, compared to corresponding processes in the water column (Vadeboncoeur et al. 2002; Gudasz et al. 2010).

Most of the organic carbon in boreal lakes arrives in dissolved state, imported from the drainage area. The flocculation of the DOC followed by sedimentation represents a major source of sediment organic carbon in boreal lakes (von Wachenfeldt and Tranvik 2008).

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The majority of the sediment bacterial metabolism (i.e., production and mineralization) occurs in the uppermost layers (Haglund et al. 2003). There are several different ideas about how sediment bacterial activity and mineralization is regulated, but all these processes (including bacterial production, bacterial abundance and sediment mineralization of organic carbon) are typically not studied together. For example, a few recent studies show that the sediment mineralization is primarily constrained by temperature (Bergström et al. 2010; Gudasz et al. 2010) but also by total phosphorus (TP) concentration in the water, a proxy of autochthonous organic carbon, (Pace and Prairie 2005; Gudasz et al. 2010). However, these studies do not consider bacterial production and biomass. The quantity and origin of organic carbon is also considered to be important, but its influence is poorly understood. Cole et al. (1988) first showed that bacterial production is related to sediment organic carbon content and bacterial biomass but no direct causal relationship could be established, and sediment mineralization was not studied. In a cross-system comparison of boreal Canadian lakes and literature data, Schallenberg and Kalff (1993) found that sediment bacterial biomass was mainly explained by water content and hydraulic flushing rate. Sediment bacterial abundance was negatively correlated with the sediment C : N ratio (an indicator of the origin and quality of the organic carbon) and positively related to the sediment organic matter content. The authors found little support for relationship between indicators of planktonic biomass such as chlorophyll *a* (Chl *a*) and sediment bacterial biomass in lakes.

The constraints on lake sediment bacterial production, bacterial biomass, and mineralization, as well as the link between them, are not well-understood. In particular, the quantitative importance of the large terrestrial organic carbon pool in the sediments, and the subsequent subsidy

Table 1. Characteristics of the eight lakes investigated in south-central boreal Sweden between spring 2007 and winter 2008. Dissolved organic carbon (DOC) and total phosphorus (TP) concentration in the water represent annual averages. The absorbance at 420 nm (A420) was measured on samples collected during autumn. The C : N ratio by mass in the bulk sediment represents annual average at the deepest point. Z_{max} and Z_{mean} are the maximum and mean depth in lakes.

Lake	Area (km^2)	Z_{max} (m)	Z_{mean} (m)	DOC (mg L^{-1})	A420 (m^{-1})	C : N sediment	TP (μg L^{-1})
Valloxen	2.90	9.0	3.8	17.5±0.9	1.08	8.1±0.03	46.7±2.9
Lötsjön	0.63	11.2	6.0	12.1±0.5	0.47	8.4±0.10	28.1±8.8
Strandsjön	1.30	4.0	1.7	20.8±5.4	2.37	8.5±0.03	41.3±8.3
Fälaren	2.05	2.6	1.5	34.3±14.5	4.63	12.0±0.04	20.5±7.6
Ljustjärn	0.12	11.0	4.8	3.6±0.7	0.56	12.5±0.30	12.1±1.5
Lilla Sångaren	0.24	17.0	6.6	6.5±1.9	1.25	14.3±0.15	11.4±3.2
Oppsveten	0.65	10.0	3.5	19.1±1.1	5.95	16.1±0.28	15.4±1.1
Svarttjärn	0.07	7.0	3.6	28.0±4.8	9.65	16.6±0.08	15.1±6.1

to benthic food webs, is not clear (Solomon et al. 2008; Premke et al. 2010). Temperature and the organic carbon quality and origin are important drivers of sediment bacterial metabolism and biomass (Sander and Kalff 1993; Schallenberg and Kalff 1993; Gudasz et al. 2010). In particular, statistical constraints (e.g., correlated variables; Schallenberg and Kalff 1993) and the lack of more extensive data sets limit our understanding of the regulation of sediment bacterial metabolism and biomass. Currently, there is no model of sediment bacterial metabolism and biomass to describe these functional relationships.

To overcome these limitations, we investigated lakes with different influence of terrestrial organic carbon and indigenous primary production (TP), providing a broad spectrum of sediment types and environmental conditions. This allowed us to quantify the connection between sediment bacterial metabolism, including overall organic matter mineralization, bacterial production, and bacterial biomass and a large number of environmental variables. We suggest that the commonly described (Jansson et al. 2007) terrestrial organic subsidy to water-column heterotrophs is not paralleled in lake sediments, where the input of terrestrial organic matter can be substantial but still only results in limited metabolism and subsidy to benthic food webs.

Methods

Study site, sampling, and lakes characteristics—Eight lakes in south-central boreal Sweden were investigated on a seasonal basis between spring 2007 and winter 2008. DOC concentration ranged from 3.6 mg C L^{-1} to 34.3 mg C L^{-1}, and TP concentration ranged from 11.4 μg L^{-1} to 46.7 μg L^{-1} (*see* Table 1). For more information regarding the lake characteristics, *see* Premke et al. (2010) and Steger et al. (2011).

Intact sediment cores were sampled with a corer (inner diameter = 59 mm; Uwitech) along a depth gradient. We used three sampling stations to represent each lake with profundal (Sta. 1, depth from 2.7 m to 16.5 m), intermediate (Sta. 2, depth from 1.4 m to 9 m) and littoral (Sta. 3, depth from 1 m to 2.5 m). The depths of the sampling station were selected based on the local summer temperature profiles, which differed among lakes. Hence, a station located at 5-m depth in one lake does not necessarily reflect same conditions in another lake at the same depth (e.g., if it is below or above the thermocline during summer stratification). At each station, three replicate cores were sampled and the upper 0–5-cm layer was collected for further analyses. Subsamples of well-mixed sediment were retained for bacterial production, bacterial biomass, total carbon (TC), total nitrogen (TN), TP, and Chl *a*. The incubations for bacterial production were started within a few hours from sampling, while the rest of the sediment was kept frozen at −20°C until analysis. The upper layer of the sediment (0–5 cm) was also used for meiofauna analysis. Subsamples were taken with a 20-mL cut syringe (inner diameter, 21.5 mm) and fixed with formaldehyde (4% final concentration). To estimate the macrofauna biomass, four additional cores were taken at each station and the upper 5 cm of the sediment were used for analyses.

Surface-water samples for TP, DOC, absorbance, and Chl *a* analyses were collected with a Ruttner sampler. Temperature and dissolved oxygen concentration and saturation were measured every meter with an OxyGuard Handy Delta oxygen meter (OxyGuard International A/S).

During the summer period, only Ljustjärn, Lilla Sångaren, Lötsjön, Oppsveten, and Svarttjärn were stratified. The depth of the thermocline in these lakes (defined as the depth at which the temperature changed ≥ 1°C per m depth interval) was 5 m, 4 m, 5 m, 4 m, and 2 m respectively. The hypolimnetic temperatures varied between 5°C and 13°C.

The water content of the sediment was in most cases above 90% except in the sediments from Sta. 3, in Ljustjärn, Valloxen, and Lilla Sångaren, where the water content was 36%, 56%, and 60%, respectively.

Sediment mineralization—Sediment organic matter mineralization comprises a number of different processes, including aerobic oxidation as well as different anaerobic oxidation pathways that lead to the release of CO_2 or methane. Our study focuses on the net effect of all these processes, represented by the dissolved inorganic carbon (DIC) efflux. Therefore, we will refer to sediment mineralization as the net release of DIC at the sediment surface. The sediment mineralization was measured through DIC production in the dark. Undisturbed sediment cores containing the upper 10-cm layer were incubated in the

dark, in situ, or at in situ temperatures. All sediment cores were incubated under oxic conditions. The method was described in detail previously (Gudasz et al. 2010). Of all the sediment mineralization rates measured, in all lakes and at all stations ($n = 78$), only six data points derive from an anoxic hypolimnion.

Sediment mineralization was measured as DIC efflux at the sediment–water interface in cores that contain the upper 10 cm of sediment, whereas bacterial production and bacterial biomass and different sediment characteristics were measured in bulk sediment samples homogenized over 0–5 cm. This setup was for practical reasons, and due to the difficulty in reproducible slicing and incubation of these soft and water-rich sediments. Bacterial activity strongly decreases with depth and typically most of the activity occurs in the upper 0–5-cm sediment layer (Marten 1985; Haglund et al. 2003). Thus, we regarded the activity (DIC production and bacterial production) in the 5–10-cm layer to be of minor influence.

Methane was analyzed by gas chromatography–flame ionization detector (GC–FID). The GC–FID (Shimadzu 8A) was equipped with a 500-μL injection loop and a 2-m, 3.2-mm stainless steel column packed with HayeSepQ 80/100. The column oven temperature was 40°C.

Bacterial production—We estimated bacterial production as leucine incorporation into bacterial protein (Smith and Azam 1992). Three replicates and one blank were used from each sampled core. In order to avoid high blank values, the sediment was diluted 1 : 10 with 0.2-μm filtered lake water. We used L-[4,5-^{3}H]leucine (TRK510; Amersham) diluted with unlabeled L-leucine (Sigma), to reach a total L-leucine concentration of 250 μmol L^{-1}. Tests confirmed that this concentration saturated the uptake rate. The amount of labeled isotope added varied between 24.5 and 30 $\times$ 10^6 disintegrations per minute (DPM). A volume of 100 μL of diluted sediment was used in the incubations. The samples were incubated for 180–229 min. The incubations were carried out in the dark and at in situ temperatures $\pm$ 2°C. To terminate the incubation, 1.7 mL of borax buffered 4% formaldehyde was added. Samples were then centrifuged and washed, one step with 5% trichloracetic acid (TCA) and one step with 80% ethanol, following a similar procedure to that described by Ask et al. (2009). Finally, 1 mL of Optiphase 'HiSafe' 2 (PerkinElmer) scintillation cocktail was added. The radioactivity was measured with a Packard Tri-Carb 2100TR liquid scintillation analyzer (PerkinElmer Life Sciences). The net DPM counts were converted to nmol leucine incorporated into proteins expressed per square meter per day.

Bacterial biomass—The microbial biomass was measured by analysis of phospholipid fatty acids (PLFA). For the extraction, the sediment samples were freeze-dried and between 0.1 g and 2.7 g (higher amounts for littoral samples) of dry weight were analyzed by a modified one-phase Bligh & Dyer method (Frostegård et al. 1991). After lipid fractionation, the phospholipids in the polar fraction were converted to fatty acid methyl esters (FAME) by a mild alkaline methanolysis. The fatty acid 19:0 (nonadecanoic acid methyl ester) was added to the samples as an internal standard. The organic fractions were dried and stored at −20°C prior to gas chromatography analyses. Identification and quantification of FAME have been described previously (Steger et al. 2011). Total bacterial PLFA of the sediment represents a good estimate of the bacterial biomass and has been reviewed in Steger et al. (2011). A conversion factor for PLFA to living microbial biomass of 100 μmol of PLFA in 1 g dry weight of bacterial cells was used, and carbon was assumed to constitute 50% of the dry cell biomass (White et al. 1979).

Meiofauna and macrofauna biomass—To estimate the meiofauna biomass, animals were extracted from sediment by the Ludox centrifugation technique (Burgess 2001), and sieved through a 30-μm-mesh net. The samples trapped on the net were fixed with 4% formaldehyde (final concentration) and stained with Bengal Rose. Organisms were identified to group level (oligochaetes, tardigrades, nematodes, rotifers, ostracodes, gastrotriches, copepods, nauplii) and counted in preserved samples at 40× magnification (Zeiss). We used published values for individual carbon content of the different groups (Bott and Borchardt 1999) to calculate carbon biomass.

To estimate the macrofauna biomass, the sediment was sieved using a 500-μm net and preserved in 70% ethanol. In the laboratory, macroinvertebrates were counted, measured and determined to lowest possible taxonomic level (*Caenis*, *Cloen*, *Ephemera*, *Notonecta*, *Corixidae*, *Zygoptera*, *Anisoptera*, *Molanna*, *Leptoceridae*, *Holocentropus*, *Oxyethira*, *Haliplus*, *Limnius* larvae, other *Coleoptera* larvae, *Platambus*, *Pseudoplatambus*, *Sialis*, *Tabanus*, *Anopheles*, *Ceratopogonidae*, *Chironomidae*, *Chaoborus*, *Hydracarina*, *Cladocera*, *Gammarus*, *Asellus*, *Erpobdella*, *Helobdella*, *Glossiphonia*, other *Hirundinea*, *Planaria*, *Pisidium*, *Dreissena*, *Theodoxus*, *Ancylus*, *Bythinia*, *Valvata*, *Gyraulus*, *Radix peregra*, *Viviparus*, *Hydra*). Biomass (dry weight) was calculated using published mass–length relationships (Smock 1980; Benke et al. 1999; Johnston and Cunjak 1999). Dry weight of all macrofauna invertebrates was converted to carbon assuming a carbon content of 45% (Wetzel 2001).

Chl a—The Chl *a* content of the water samples was analyzed according to the ISO 10260 (1992) standard. Sediment Chl *a* was measured according to Jespersen and Christoffersen (1987) and ISO 10260 (1992) standard.

DOC and absorbance—The DOC concentration in the water was measured with a Sievers 900 TOC analyzer (GE Analytical Instruments). The absorbance of the water samples was measured in 1-cm quartz cuvettes, on a Perkin Elmer Lambda 40 ultraviolet-visible spectrophotometer. The water was filtered through glass-fiber Whatman GF/F filters and the absorbance read at 250 nm, 365 nm, and 420 nm. The DOC-specific ultraviolet absorbance (SUVA) at 254 nm was used as an indicator of aromaticity (Weishaar et al. 2003). We also calculated the 250 : 365 absorbance ratio, which has been found strongly correlated with the total aromaticity and average molecular weight of the humic solutes (Peuravuori and Pihlaja 1997).

Elemental analysis—TC and TN were determined with a CHN analyzer (NA 1500; Carlo Erba instruments). Acetanilide standard was used to check the instrument performance over time. The accuracy of the instrument was $< 0.3\%$, whereas the precision was $< 5\%$. The sediment TP was measured by igniting dried sediment at 550°C, followed by a subsequent P analysis according to Murphy and Riley (1962). The sediment C : N and C : P ratios by mass were calculated by dividing percent carbon to percent nitrogen and phosphorus. The TP concentration in the water was determined according to Murphy and Riley (1962).

Units and conversions—In order to avoid a strong bias caused by the standardization of bacterial and sediment attributes per gram dry weight (Sander and Kalff 1993), we converted our results per unit sediment area. With the exception of the sediment mineralization data, which are the flux per unit area of 10-cm-deep sediment cores, the reported areal values of sediment and bacterial attributes, meiofauna, and macrofauna, reflect the integrated values over the 0–5-cm sediment layer.

Statistical analyses—We used multivariate linear regression by means of partial least-squares projections to latent structures (PLS; Eriksson et al. 2006). The performance of the PLS model is expressed in terms of R^2Y and Q^2. R^2Y is comparable to R^2 in linear regression, and Q^2 is a measure of the predictive power of the model (the closer Q^2 values are to R^2Y, the higher the predictive power). To summarize the influence of every X-variable for the Y-model, across the extracted PLS components, we have used the variable influence on projection (VIP). The VIP scores of every model term (X-variables) are cumulative across components and weighted according the amount of Y-variance explained in each component (Eriksson et al. 2006). X-variables with VIP larger than 1 (i.e., the average influence), are most influential for the model. A cut off around 0.8 separates moderately important X-variables, whereas those below this threshold can be regarded as less influential. Scaled and centered PLS coefficients were used for interpreting the influence of the X-variables on every Y-variable in the model where Y-variables are re-expressed as multiple regression models of the X-variables (Eriksson et al. 2006). In order to test whether the models predict better than chance, we performed a model validation for every Y-variable. The Y-variables were permuted 100 times. In order to achieve normal or approximately normal distribution of the data and, therefore, improve the model performance, skewed variables were log- or log (X + 1)-transformed. PLS modeling was done based on the soft independent modeling of class analogy (SIMCA), in SIMCA-P+ version 12.0 software (Umetrics AB).

The univariate data analysis was done in SigmaPlot 10.0 and Statistica 9.0 software. We used Type III model for one-way ANOVA analysis. A modified Tukey test was used for post hoc test for unequal sample size. The data were log-transformed and tested for the homogeneity of variance.

Results

There was a clear seasonal pattern in sediment bacterial metabolism (Fig. 1), but no significant spatial distribution within lakes (Fig. 1). Along the gradients of increasing sediment C : N (Fig. 2A,D,G) and TP concentration in the water (Fig. 2B,E,H) there was a distinct pattern across lakes. A group of lakes (Ljustjärn, Lilla Sångaren, Oppsveten, Svarttjärn, and Fälaren) had relatively similar and lower median sediment mineralization, bacterial production, and bacterial biomass with C : N ratios (by mass) at around 12 and TP concentrations below 20 μg L^{-1} (*see* Table 1), whereas the other group of lakes (Valloxen, Lötsjön and Strandsjön) had generally higher median values of sediment mineralization, bacterial production, and bacterial biomass.

We measured methane production simultaneously with sediment mineralization, but found it to be negligible (*see* Gudasz et al. 2010). The fraction of the carbon in CH_4, as compared to CO_2, was on average only 2.3% (median 0.02%, $n = 180$).

Along the gradient of increasing DOC concentration, sediment bacterial metabolism and biomass increased only toward intermediate DOC concentrations (i.e., around 17.5 mg L^{-1}), and then decreased with increasing DOC (Fig. 2C,F,I).

Different proxies of the allochthonous organic carbon such as absorbance at 420 nm and 250 : 365 absorbance ratio, and autochthonous organic carbon such as TP concentration in the water, were generally well-reflected in the sediment composition as indicated by the C : N ratio (Fig. 3).

Temperature was positively correlated with sediment mineralization, bacterial production, and bacterial biomass (Fig. 4). Furthermore, different measures of sediment bacterial mineralization, production, and biomass were correlated with each other (Fig. 5).

To identify the main factors related to sediment bacterial metabolism and biomass, we performed PLS analysis of data matrices with all the temporal and spatial data collected during the survey of the eight boreal lakes, and a number of different parameters describing sediment and water characteristics, as well as total biomass of meiobenthos and benthic macrofauna (Table 2). The PLS regression model describing the response in benthic microbial metabolism (Fig. 6) extracted three significant components that explained, in total, 74% of the variance ($R^2Y_{cum} = 0.74$). The contribution of each component or Y-variable (bacterial production and sediment mineralization) to the model is described in Table 3. The model predictability power was high ($Q^2_{cum} = 0.70$). The model validation showed that the background correlation (i.e., amount of explained variance that resulted due to chance) was low for both bacterial production ($R^2Y = 0.071$) and sediment mineralization ($R^2Y = 0.085$). The model depicted in Fig. 6 shows that the Y-variables, bacterial production, and sediment mineralization were well-correlated. Temperature was the most important predictor of the benthic bacterial metabolism. Based on the VIP scores, other important predictors include bacterial biomass, TP,

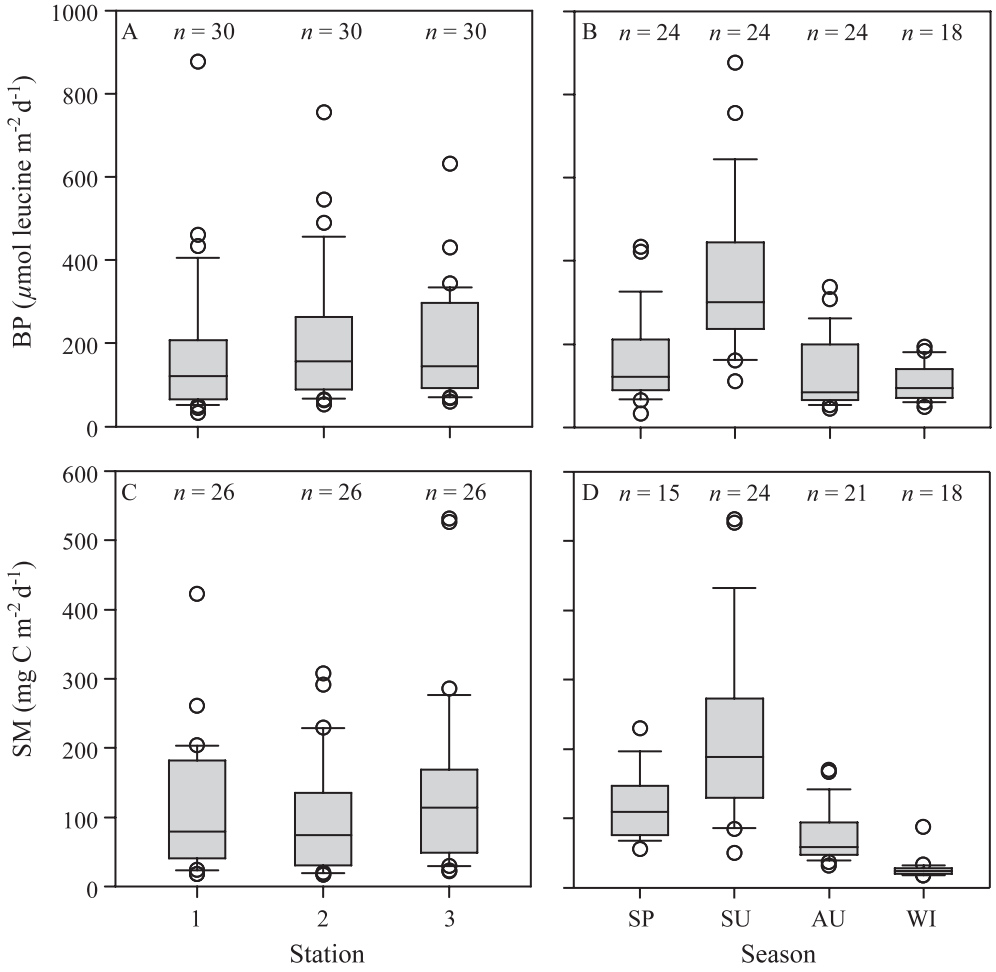

Fig. 1. Box plots representing patterns of (A, B) bacterial production (BP) and (C, D) sediment mineralization (SM) within lake-depth gradient: Sta. 1 (profundal), Sta. 2 (intermediate), Sta. 3 (littoral), and across seasons (SP = spring, SU = summer, AU = autumn, WI = winter) in boreal lake sediments. The box plots of spatial and seasonal data shown here were pooled across lakes. The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles and symbols indicate outlying points. There were no statistically significant differences among stations for both BP and SM ($p = 0.36$ and $p = 0.38$, ANOVA). The BP across seasons was statistically different only during summer ($p < 0.0001$, ANOVA), whereas SM was statistically significant across all seasons ($p < 0.05$, ANOVA).

and Chl *a* in the water, the 250 : 365 absorbance ratio (positively correlated), and the C : N ratio (negatively correlated; Fig. 6).

The PLS model also describes the correlation structure of the X-variables. Variables reflecting the organic carbon origin and quality from both water column and sediment were well-correlated with each other (Fig. 6). Thus, different indicators of both autochthonous organic carbon (TP and Chl *a* in the water) and allochthonous organic carbon (C : N and C : P ratios, A420, and SUVA) were well-correlated (positively) as indicated by their close position to each other in the loadings plot (Fig. 6). The 250 : 365 absorbance ratio, an indicator of allochthonous organic carbon, showed an inverse relationship with similar parameters of organic carbon origin such as C : N and C : P ratios, A420, and SUVA. The strong influence of organic carbon origin is sustained also by the positive correlation of the TP and Chl *a* concentration in the water with the bacterial biomass and the Y-variables, in particular with the bacterial production.

Parameters with a moderate influence (i.e., below average) on sediment metabolism include meiofauna biomass (positively correlated) and C : P ratio, SUVA, and A420 (negatively correlated). Other variables considered in our model such as: depth, station, A250, A365, TC, TP, TN in the sediment, Chl *a* in the sediment, and macrozoobenthos biomass and DOC concentration in the water, had little influence upon the benthic microbial metabolism.

The analysis of the PLS coefficients for the first PLS component (the most significant component; Table 2)

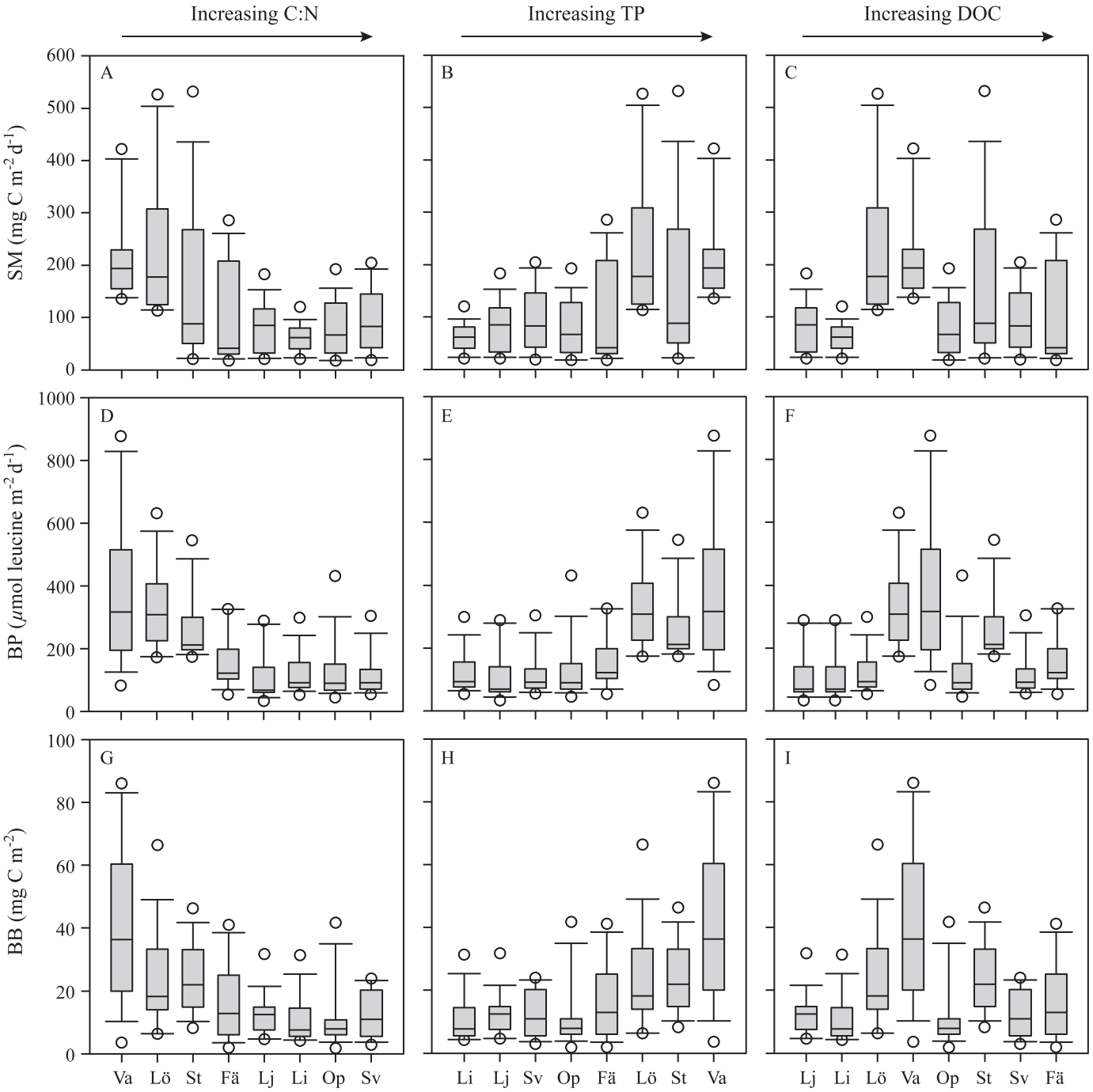

Fig. 2. Patterns of sediment mineralization (SM), bacterial production (BP), and bacterial biomass (BB) along the gradients of (A, D, G) sediment C : N ratio, (B, E, H) TP, and (C, F, I) DOC concentration in the water in boreal lakes (Va = Valloxen, Lö = Lötsjön, St = Strandsjön, Fä = Fälaren, Lj = Ljustjärn, Li = Lilla Sångaren, Op = Oppsveten, Sv = Svarttjärn). The gradient spans from low to high values (i.e., left to right), and data can be found in Table 1. The box plots of SM, BP, and BB data, shown here across lakes, were pooled from seasonal and spatial lake data.

showed that the same variables explained bacterial production and sediment mineralization, because those emerged as influential based on the VIP scores analysis.

The second PLS model describes the benthic bacterial biomass (Fig. 7). The PLS analysis extracted one significant component that explained only 41% of the variance ($R^2Y = 0.41$) with good predictability ($Q^2 = 0.36$) relative to the R^2Y and low background correlation ($R^2Y = 0.05$). Based on the VIP scores, the most influential variables for the sediment bacterial biomass were: bacterial production, sediment mineralization, Chl *a* and TP concentration in the water, temperature, TN, 250 : 365 ratio and Chl *a* concentration in the sediment (positively correlated), and C : N ratio (negatively correlated). Variables with some-

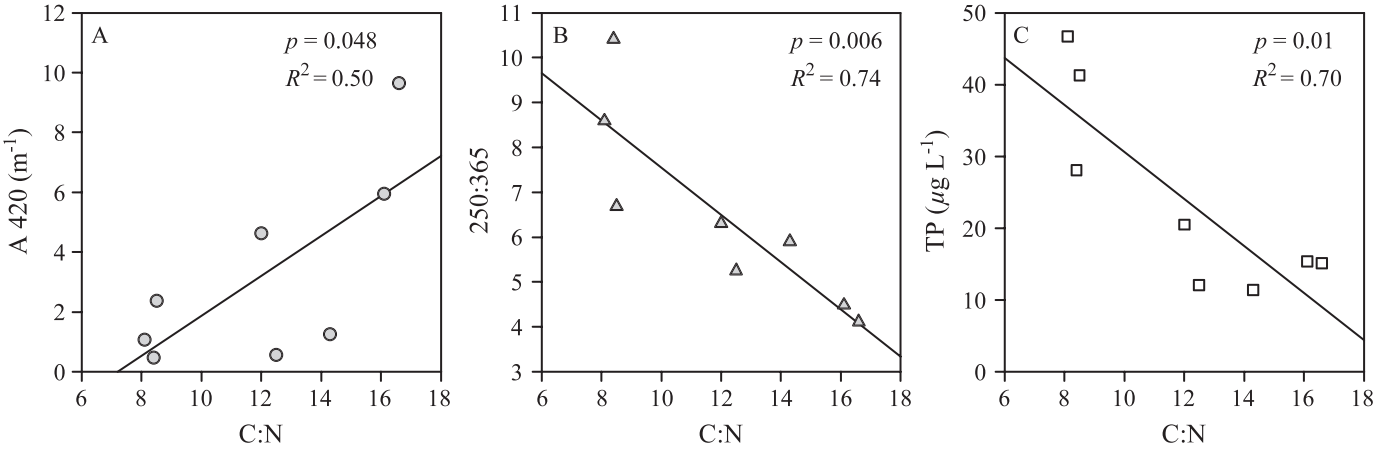

Fig. 3. Relationship of sediment C : N ratio and (A) water color, (B) absorbance ratio 250 : 365, and (C) TP concentration in the water in boreal lake sediments.

what moderate influence were meiofauna biomass (positively correlated) and SUVA (negatively correlated).

Discussion

Two separate and well-correlated groups of proxies of organic carbon origin emerged, which correlated either negatively (TP, Chl *a* concentration in the water, and 250 : 365 absorbance ratio) or positively (A420, SUVA) with the sediment C : N ratio (Figs. 3, 6, 7). The C : N ratio of the sediment organic carbon reflects the proportion of terrigenous or algal material (Meyers and Ishiwatari 1993; Wolfe et al. 2002). In general, high C : N ratios (> 20, atomic) indicate a sediment containing a higher proportion of terrestrial recalcitrant humic material, while low C : N ratios (4–10, atomic) indicate a higher contribution of algal organic carbon based on the properties of these two organic carbon sources (Meyers and Teranes 2001). The use of the C : N ratio as an indicator of organic carbon origin can be problematic in certain cases such as the adsorption of nitrogen as NH_4^+ to clay particles. However, in most freshwater sediments, inorganic nitrogen concentrations are low compared to those of organic nitrogen (Meyers and Teranes 2001). In most cases, the sediment organic carbon content in our lakes was in the range of 10–40%. Other factors, such as preferential degradation of either carbon or nitrogen compounds, can decrease or increase the C : N ratio during the postdepositional diagenesis (Meyers and Teranes 2001). The C : N ratio can also decrease due to the input of low C : N bacterial biomass (Lehmann et al. 2002). However, Meyers and Teranes (2001) showed that changes in the elemental composition of sedimentary organic carbon are not large enough to erase the large C : N differences determined by the organic carbon origin. Essentially, sediment organic carbon of a humic lake showing strong allochthonous influence (C : N ratio above 20, atomic) and high water content (> 80–90%), cannot be altered to a degree by which it could be confounded with sediment of an eutrophic lake dominated by high phytoplankton influence (C : N ratio of 4–10, atomic).

Parameters measured in the water column, reflecting high allochthonous influence on the organic carbon (A420, 250 : 365 absorbance ratio) and high autochthonous production (TP concentration in the water), correlated with the

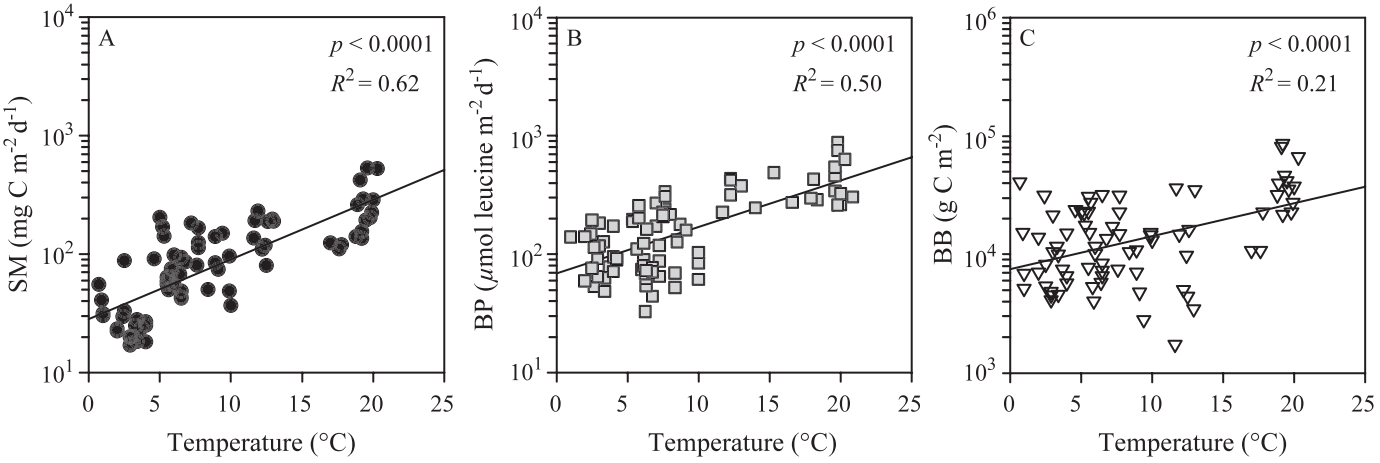

Fig. 4. The temperature dependence of (A) sediment mineralization, (B) bacterial production, and (C) bacterial biomass in boreal lake sediments. Data shown here were pooled across lakes, seasons, and stations, and are represented on a log scale.

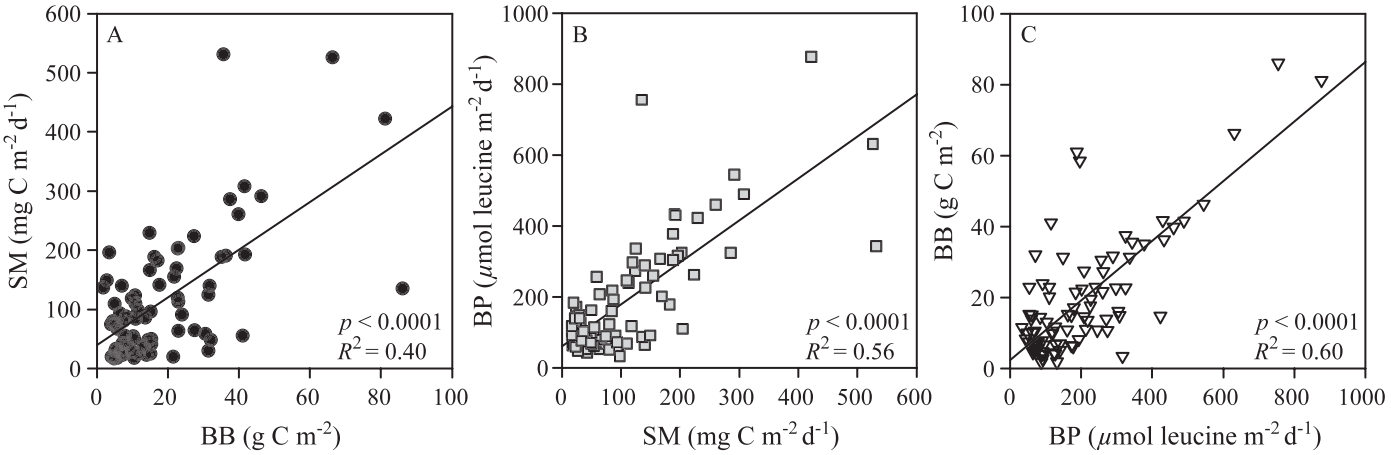

Fig. 5. Relationship of (A) sediment mineralization, (B) bacterial production, and (C) bacterial biomass in boreal lake sediments. Data shown here were pooled across lakes, seasons, and stations.

sediment C : N ratio in a pattern (Fig. 3) consistent with a strong allochthonous influence on sediment organic carbon in lakes with high concentrations of allochthonous DOC. This corroborates previous findings that the sediments of these lakes are dominated by terrestrial organic matter as a consequence of flocculation of DOC (von Wachenfeldt and Tranvik 2008).

Benthic bacterial metabolism and biomass varied more across seasons and between lakes, compared to the variation within lakes. A similar pattern has been observed for bacterial biomass (Steger et al. 2011). Within lakes there was no statistical difference among habitats, as represented by sampling stations at different depths (Fig. 1). This is in contrast to the higher variability of sediment areal carbon mineralization within lakes than among lakes reported by den Heyer and Kalff (1998). Habitat differences can be attributed to a number of factors that vary spatially within lakes. In particular, temperature has a strong effect on sediment metabolism (Gudasz et al. 2010), resulting in differences between epi- and hypolimnetic sediments. Moreover, the access to dissolved oxygen is a limiting factor for bacterial mineralization of OC, which becomes increasingly pronounced in sediments with more recalcitrant organic matter (Kristensen et al. 1995). However, the lack of statistically significant differences between different habitats within lakes may be a consequence of moderate temperature gradients within lakes at most sampling occasions (*see* Methods). Sediment mineralization in the

Table 2. Variables used in the PLS analysis.

Variable in PLS model	Description	Category
SM	Sediment mineralization	Y, X
BP	Bacterial production	Y, X
BB	Bacterial biomass	Y, X
A250	Absorbance at 250 nm	X
A365	Absorbance at 365 nm	X
A420	Absorbance at 420 nm	X
250 : 365	Ratio between the absorbance at 250 and 365 nm	X
SUVA	Specific ultraviolet (UV) absorbance	X
C : N	Ratio between percent carbon and percent nitrogen in bulk sediment	X
C : P	Ratio between percent carbon and percent phosphorus in bulk sediment	X
Chl *a* S	Chlorophyll *a* concentration in bulk sediment	X
Chl *a* W	Chlorophyll *a* concentration in surface water	X
D	Depth	X
DOC	Dissolved organic carbon concentration in surface water	X
ME	Meiofauna carbon biomass	X
MZB	Macrozoobenthos carbon biomass	X
Sta. 1	Station 1 (profundal)	X
Sta. 2	Station 2 (intermediate)	X
Sta. 3	Station 3 (littoral)	X
TC	Total carbon content in bulk sediment	X
Temp BP	Water temperature for bacterial production measurements	X
Temp SM	Water temperature for sediment mineralization, in situ conditions	X
TN	Total nitrogen content in bulk sediment	X
TP	Total phosphorus content in bulk sediment	X
TP W	Total phosphorus concentration in surface water	X

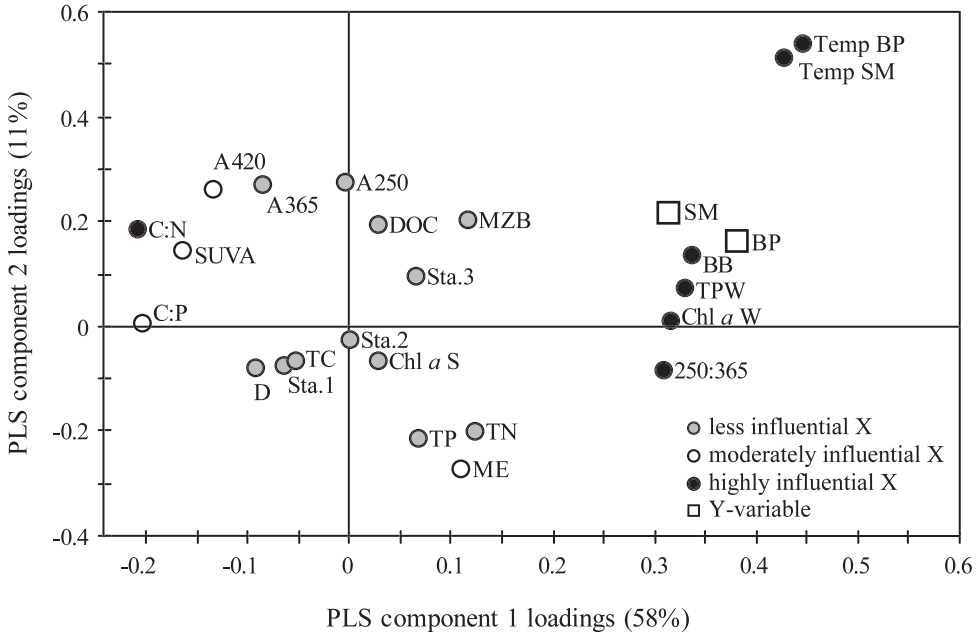

Fig. 6. Loadings plot of the PLS regression analysis of the benthic heterotrophic microbial metabolism. The graph shows how Y-variables (squares) correlate with X-variables (circles), and the correlation structure of the Xs and Ys. The X variables are classified according to their VIP, cumulative across components: highly influential (black circles), moderately influential (white circles), and less influential (grey circles). The plot can be read by drawing a line from a Y-variable through the origin and across the plot and projecting the X-variables on this line. Thus, the X-variables along this line situated far away from the origin of the plot (on the positive or negative side) are highly correlated with Y and are the most influential for the model. Variables close to the origin of the plot are poor predictors of the Y-variables. The Y-variables close to each other are positively correlated. The X-variables situated near Y-variables are positively correlated to them and those situated on the opposite side are negatively correlated. For the explanation of the abbreviations *see* Table 2.

littoral samples could potentially be biased by benthic algal respiration. However, the PLS model of sediment bacterial metabolism (Fig. 6) can be mainly predicted from temperature, TP, and C : N ratio. This supports that the measured mineralization derives mainly from heterotrophs.

Temperature was the primary constraint on sediment bacterial metabolism, followed by different indicators of sediment or water organic carbon origin and quality (Figs. 4, 6), in accordance with previous studies (Sander and Kalff 1993; Bergström et al. 2010; Gudasz et al. 2010).

Table 3. The model contribution of the PLS analysis of the sediment bacterial metabolism. Note that R^2Y and Q^2 numbers are cumulative (cum) for the addition of PLS components.

Model contribution	PLS component	R^2Y(cum)	Q^2(cum)
Total	1	0.58	0.56
	2	0.70	0.66
	3	0.74	0.69
BP	1	0.67	0.65
	2	0.76	0.72
	3	0.76	0.72
SM	1	0.47	0.46
	2	0.62	0.59
	3	0.72	0.66

Sediment bacterial metabolism and biomass along the DOC concentration gradient increased only toward intermediate DOC concentrations, and then decreased with increasing DOC (Fig. 2C,F,I). We suggest that this is caused by increasing influence of autochthonous organic carbon upon metabolism up to about 17 mg L^{-1}, followed by increasing allochthonous dominance at higher concentrations. The pattern in sources of DOC is supported by corresponding changes in TP and humic absorbance as indicated by the watercolor parameter A420 (*see* Table 1), an index of dissolved humic substances in the water (Tranvik 2009). Although Valloxen and Oppsveten had similar DOC concentrations, they were well-separated in terms of watercolor as indicated by the absorbance at 420 nm (Table 1).

Sediment bacterial metabolism decreased with increasing C : N of the sediment, which is in accordance with increasingly allochthonous sediments supporting decreasing bacterial metabolism (Fig. 2A,D). Accordingly, indicators of high aromaticity and terrestrial origin of organic carbon (A420, SUVA, and sediment C : N ratio) were negatively correlated with sediment bacterial metabolism (Fig. 6). The 250 : 365 absorbance ratio, which is inversely related to the aromaticity and molecular size of the aquatic humic solutes (Peuravuori and Pihlaja 1997), was positively correlated to sediment bacterial activity, which further

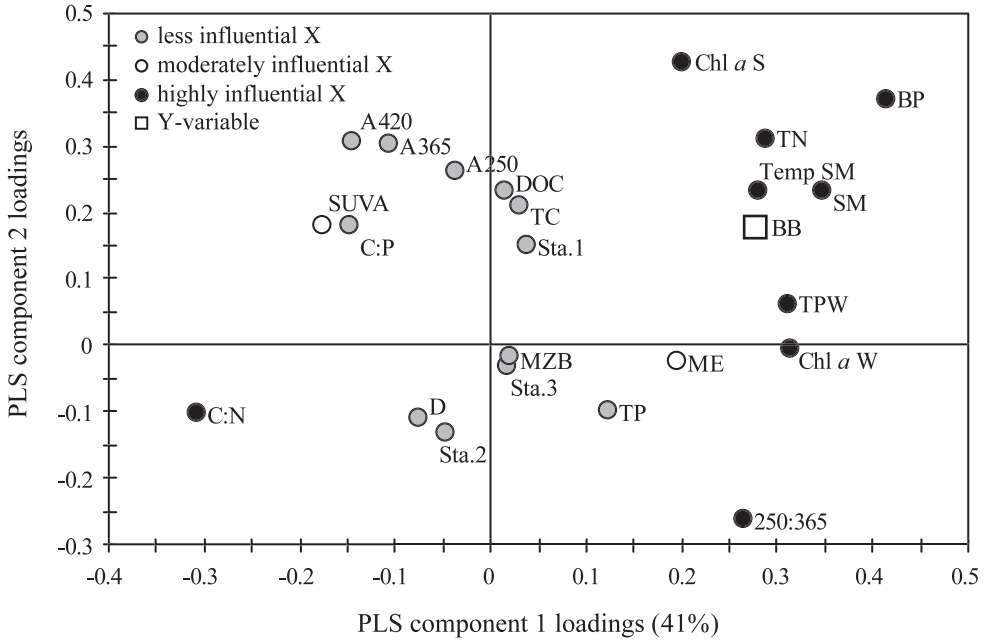

Fig. 7. Loadings plot of the PLS regression analysis of the sediment bacterial biomass. The PLS component 2 is not significant, but has been included to make the separation along the component 1 visible. The graph shows how Y-variables (squares) correlate with X-variables (circles), and the correlation structure of the Xs and Ys. The X variables are classified according to their VIP: highly influential (black circles), moderately influential (white circles), and less influential (grey circles). The plot can be read by drawing a line from a Y-variable through the origin and across the plot and projecting the X-variables on this line. Thus, the X-variables along this line situated far away from the origin of the plot (on the positive or negative side) are highly correlated with Y and are the most influential for the model. Variables close to the origin of the plot are poor predictors of the Y-variables. The X-variables situated near Y-variables are positively correlated to them and those situated on the opposite side are negatively correlated. For the explanation of the abbreviations *see* Table 2.

supports that the microbial metabolism is low in boreal sediments with a strong influence of terrestrial organic matter. In contrast, the sediment metabolism was positively correlated to the TP concentration in the water (Figs. 2B,E; 6), which is an indicator of autochthonous organic carbon. It has previously been shown that P is limiting phytoplankton production in the lakes in the studied region (Bergström et al. 2005) suggesting that TP is a useful proxy for autochthonous organic carbon. Moreover, the good correlation between TP and Chl *a* concentration in the water (*see* Fig. 6) supports the use of TP as a proxy of autochthonous organic carbon in these lakes. This is in accordance with the tight coupling between bacterial metabolism and biomass, and indicators of autotrophic biomass such as Chl *a* and TP previously described for water-column bacteria (Cole et al. 1988).

In lakes with a sediment C : N ratio above about 12 (by mass), sediment mineralization, bacterial production, and bacterial biomass were at similarly low levels with increasing influence of the allochthonous organic carbon (Fig. 2A,D,G), suggesting a threshold where increasing terrestrial influence to the sediment does not result in any increase in sediment heterotrophic metabolism. The sediment C : N ratio was previously shown to be an important predictor of sediment bacterial abundance (Schallenberg and Kalff 1993), but due to the partial autocorrelation of bacterial abundance with sediment organic matter, the authors recommended caution in drawing conclusions. Our study shows that increasing terrestrial dominance on the sediments of boreal lakes only to a limited extent supports increasing sediment mineralization and microbial production.

In pelagic environments, increasing amounts of terrestrial organic carbon result in an increase in bacterial metabolism (Tranvik 1988; Jansson et al. 2007). The slow utilization of an abundant source of terrestrial detritus may lead to metabolic stability in aquatic ecosystems. This baseline metabolism is independent of the more intermittent pulses of autochthonous organic carbon (Wetzel 1984; Tranvik 1992), and is higher at higher levels of import of allochthonous organic carbon (McCallister and del Giorgio 2008). In contrast, we show the lack of a similar response in sediment bacteria (Fig. 2). Although our data suggest differences in the utilization of allochthonous carbon in the sediment and water column, this may be related to a different fraction of the allochthonous organic carbon reaching the sediment, compared to the fraction that is utilized by bacteria in the water column.

When comparing across lakes, a pattern emerges with a low sediment bacterial metabolism based on allochthonous

organic carbon, which does not increase with increasing allochthonous organic carbon influence (Figs. 2, 6). In contrast, the sediment bacterial metabolism increased with rising autochthonous organic carbon influence. Similarly, Ask et al. (2009) failed to identify higher sediment metabolism with increasing contribution of terrestrial organic carbon, but found a clear response to indigenous primary production. Consequently, differences in sediment bacterial production and mineralization between lakes with a relatively high allochthonous influence may result largely from temperature and fresh labile organic carbon produced within lakes (Gudasz et al. 2010). Thus, our results are in contrast to the findings of Schallenberg and Kalff (1993), which suggested that benthic bacterial processes in lakes are driven by allochthonous organic carbon inputs and that benthic and pelagic cycling of organic carbon are strongly decoupled.

Bacterial biomass followed the same pattern as bacterial metabolism along the C : N, TP and DOC gradients (Fig. 2G–I), suggesting that bacterial biomass contained mainly viable, active biomass. The PLS analysis did not yield a strong model (Fig. 7) with only 41% of the variability explained ($R^2Y = 0.41$). However, bacterial biomass was essentially correlated with the same factors, following the same pattern, as in the case of bacterial metabolism. Bacterial metabolism, organic carbon origin and quality, and temperature were the best predictors of bacterial biomass (Fig. 7). Among the bacterial biomass grazers, only meiofauna were, at most, of moderate importance as predictors of bacterial biomass with a positive effect (Fig. 7). Together with the rapid change in the composition of the bacterial communities across seasons (Steger et al. 2011), this implies that the bulk sediment biomass was not heavily grazed but rapidly recycled. The relatively strong relationship between sediment mineralization and bacterial biomass further supports limited importance of bacterivory (Fig. 5).

Different components of the sediment fauna (meiofauna, macrofauna, and micrograzers) consume bacteria (Goedkoop et al. 1997). Accordingly, a strong positive relationship between benthic macrofauna and sediment bacterial biomass has been shown (Schallenberg and Kalff 1993; Wieltschnig et al. 2008). Our results do not corroborate this relationship; on the contrary, macrozoobenthos was of minor importance and, at most, meiofauna had a moderate influence on sediment bacterial metabolism and biomass (Figs. 6, 7).

Meiofauna and bacteria compete for sediment organic carbon (Goedkoop et al. 1997). Experiments show that when sediment organic carbon is diluted the bacteria dominate its utilization, whereas when the sediment organic carbon is more concentrated, benthic fauna gains control (van Nugteren et al. 2009). Schallenberg and Kalff (1993) showed that at sediment water content $> 80\%$, the sediment bacterial abundance is constrained by dilution. Majorities of surface sediments in the boreal zone are highly organic and typically exhibit a water content of $>$ 80–90%. We suggest that this high water content affects not only the bacteria, but interferes also with exploitation of both detrital organic carbon and bacterial biomass by the meiofauna and macrofauna.

In the investigated lakes, only six macrofauna taxa were abundant (Chironomidae, Ceratopogonidae, Gastropods, Pisidium, Anisoptera, Ephemeroptera; data not shown). Parallel studies based on deeper Ekman grab samples showed no other taxa than those described above. Out of these six taxa, only chironomids burrow deeper into the sediment. However, many studies of chironomid vertical distribution indicated that the greatest chironomid larvae abundance and biomass occurs in the upper few centimeters of substrate (Takács and Tokeshi 1994). Furthermore, Sherfy et al. (2000) found that chironomids were most abundant in the 0–5-cm layer, and that abundance and biomass in 10-cm cores were predicted strongly by biomass and abundance in the upper 5-cm layer. Thus, a 5-cm core sample yields a useful quantification of benthic fauna.

Even though chironomids, the only bioturbating organisms in our samples, contributed about 70% of total macrozoobenthos biomass in the profundal, they only had an average length of 4.4 mm $\pm$ 2.9 mm (data not shown). Thus, they were too small to burrow deeply into the sediment and to substantially influence microbial processes. Similarly, they contributed about 50% of total macrofauna biomass in the littoral zone, with an average length of 6.3 mm $\pm$ 1.9 mm. Also sampling deeper in the sediment with an Ekman grab did not reveal other sizes than described above.

Boreal lakes store large amounts of organic carbon and, after peatlands, contain the second largest pool of organic carbon in the biome (Benoy et al. 2007). Moreover, much of the organic carbon stored in boreal lakes is dominated by inputs from terrestrial sources (von Wachenfeldt and Tranvik 2008). Hence, the constraint on the microbial mineralization of sediment organic carbon is a key factor in the carbon biogeochemistry. We suggest that increasing terrestrial organic carbon influence does not result in enhanced sediment bacterial metabolism. Hence, sediments are an effective sink of allochthonous organic carbon, in accordance with the large amounts of organic carbon stored in boreal lakes. Boreal lake sediments emerge as a low-temperature and low organic-carbon-quality environment, constituting a hot spot of organic carbon preservation at the landscape scale (Kortelainen et al. 2004; Benoy et al. 2007).

Pace and Prairie (2005) showed that sediment mineralization can be predicted based on the TP or Chl *a* concentration in the water, and that the percent of sediment organic carbon respired is exponentially declining, from oligotrophic to eutrophic lakes. This suggests that long-term organic carbon burial is increasingly important in more eutrophic lakes. In contrast, a comparison over a wider range of lakes showed higher burial efficiency in lakes receiving higher loads of terrestrial organic carbon (Sobek et al. 2009), in line with our results. The model of Pace and Prairie (2005) did not consider the contribution of terrestrial organic carbon. At a global scale, terrestrial organic matter is a dominant component of inland water sediments, as exemplified by boreal lakes (Benoy et al. 2007). We suggest that this terrestrial organic carbon, compared to autochthonous organic carbon, only supports limited bacterial metabolism and contributes strongly to carbon burial.

In conclusion, we find that bacterial production and sediment mineralization in boreal lake sediments are strongly constrained. A large influence of allochthonous organic matter, at most, results in a weak subsidy to heterotrophic bacteria, and additionally the transfer of energy to benthic fauna is limited. With generally low temperatures setting the scene for low sediment bacterial metabolism, the dominant and recalcitrant allochthonous organic matter constraints even further the potential bacterial metabolism in boreal lakes. Lake sediments are widely recognized as sinks of organic carbon. We demonstrate that this is particularly important for terrigenous organic carbon, which efficiently escapes conversion to bacterial biomass, and transfer to higher trophic levels, as well as mineralization.

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