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Riverine sources of bioreactive macroelements and their impact on bacterioplankton metabolism in a recipient boreal estuary

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The loading of terrestrially derived macroelements, such as dissolved organic carbon (DOC), total nitrogen (N), and total phosphorus (P), to inland and estuarine waters is increasing in the northern hemisphere. These macroelements often limit heterotrophic bacterioplankton metabolism (production and respiration), which in turn influence food web structures, exchange of greenhouse gases between the atmosphere and aquatic systems and oxygen consumption in estuarine ecosystems. In order to predict the impact of increasing macroelement inflows on the function and structure of boreal aquatic ecosystems it is vital to understand the potential sources of macroelements and their regulation of bacterioplankton metabolism.

In this thesis, I aimed to determine whether terrestrially derived macroelement loadings to inland and estuarine waters can be utilized by bacterioplankton. In addition, I assessed how riverine influxes of DOC, N and P, alone or combined, regulate estuarine bacterioplankton metabolism. For this purpose, I applied a bioassay approach to measure bacterioplankton respiration (BR) and production (BP) on samples from boreal freshwaters and estuarine systems. Terrestrially derived macroelement availability in brown-water lakes increased from DOC to N to P and averaged 2%, 31% and 49%, respectively. Although extremely low, relative DOC bioreactivity increased with downstream transit for rivers with long water residence time and high fractions of urban and agricultural land use. Riverine bioreactive DOC was not the primary source of energy supporting bacterioplankton respiration at the Öre estuary, confirming the low bioreactive DOC exports expected for the Öre river. Instead riverine nutrients showed a more important effect on BR through stimulation of primary production, which in turn derived the organic carbon utilized by the bacterioplankton in the estuary. However, BP at the Öre estuary was in general limited by P and BR by carbon. In light of expected increases in riverine loadings of DOC and P, and decreases of estuarine primary production, estuarine BP is expected to increase, as well as estuarine BR of riverine DOC inputs. These bacterioplankton responses may be exacerbated by combined increases of riverine inflows of DOC, N and P. In summary, terrestrially derived macroelements can have a substantial impact on freshwater and estuarine bacterioplankton metabolism. Given the large role of bacterioplankton on the structure and function of aquatic systems, continuous changes in the input of terrestrial macroelements may have large consequences for boreal aquatic ecosystems.

Key words: Dissolved organic carbon; aquatic ecology; bacterial respiration; bacterioplankton production; dissolved organic matter; nutrient bioavailability; DOC bioreactivity

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Coverphoto: The Öre estuary.

(Photo: A. Soares)

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Abstract

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In summary, terrestrially derived macroelements can have a substantial impact on freshwater and estuarine bacterioplankton metabolism. Given the large role of bacterioplankton on the structure and function of aquatic systems, continuous changes in the input of terrestrial macroelements may have large consequences for boreal aquatic ecosystems.

Popular Science Summary

The loading of macroelements such as, dissolved organic carbon (DOC), total nitrogen (N) and total phosphorus (P) from terrestrial soils to aquatic systems is increasing in the northern hemisphere. This phenomenon has several ecological and biogeochemical consequences for inland and coastal water systems, which are linked to bacterial cycling of DOC, N and P. During growth, bacteria assimilate macroelements into biomass (a process known as bacterial production), removing DOC, N and P from the water column and channelling these elements to consumers. Bacteria can also utilize organic carbon as a source of energy for respiration. For this purpose they take up oxygen dissolved in the water and release CO_2 to the atmosphere. Increases in bacterial production have consequences for aquatic food web structures, whereas increases in bacterial respiration have implications for greenhouse gas emissions and for oxygen concentrations of estuarine waters. Currently, it is still unclear the degree to which land derived macroelements can be utilized by bacteria. Moreover, it is also not understood how bacterial metabolism (production and respiration) will respond to increased terrestrial macroelement fluxes.

In this thesis, I aimed to determine the fraction of the terrestrially derived macroelement loading that can be utilized by bacteria. Moreover, I investigated whether riverine inflows of DOC, N and P, alone or combined, limited the metabolism of bacteria in estuarine waters. I found that on average only 2% of the DOC exported from land was utilized by bacteria for production of biomass during a seven-day period. This share amounted to approximately 50% in the case P, which was thus the macroelement mostly available to bacteria among the three macroelements studied. Yet, the relatively low DOC quality increased downstream for rivers with long river water residence time and high catchment proportions of agricultural and urban land. These riverine catchment features are thus important to predict the export of oxygen consuming organic carbon (C) from rivers to estuaries.

The DOC transported in the Öre river, was less important for support of bacterial respiration than nutrients. These findings agree well with predictions of DOC quality for the Öre river, based on the its catchment features. Riverine nutrients stimulated primary production at the Öre estuary, which in turn supplied organic carbon to bacteria. In general, bacterial production in the Öre estuary was limited by P, while bacterial respiration was limited by organic C. In light of predicted increases of riverine macroelement deliveries and expected reductions of estuarine primary production, bacterial production will likely increase, as well as the bacterial respiration of riverine delivered organic C. Both estuarine bacterial production and respiration are expected to increase the most in response to combined increases of riverine deliveries of DOC, N and P.

In summary, land derived macroelements can be substantially available to freshwater and estuarine bacteria and impact their metabolism. Given the large role of bacteria in food web structures and aquatic CO_2 emissions, continued changes in the input of terrestrial macroelements may have large implications for boreal aquatic ecosystems.

Contents

List of papers

This thesis is based on the following manuscripts, which are referred to in the text by their Roman numerals:

Paper I Soares, A. R. A., Bergström, A.-K., Sponseller, R. A., Moberg, J. M., Giesler, R., Kritzberg, E. S., Jansson, M. & Berggren, M. 2017. New insights on resource stoichiometry: assessing availability of carbon, nitrogen, and phosphorus to bacterioplankton. *Biogeosciences* 14, 1527-1539.

Paper II Soares, A. R. A., Lapierre, J.-F., Selvam, B. P., Lindström, G. & Berggren, M. Controls on dissolved organic carbon bioreactivity in river systems. *Manuscript.*

Paper III Soares, A. R. A., & Berggren, M. Importance of riverine dissolved organic matter for bacterioplankton respiration in a boreal estuary. *Manuscript.*

Paper IV Soares, A. R. A., Kritzberg, E.S., Custelcean, I., & Berggren, M. 2017. Bacterioplankton responses to increased organic carbon and nutrient loading in a boreal estuary—separate and interactive effects on growth and respiration. *Microbial Ecology*.

The contribution of Ana Soares to the papers included in this thesis was as follows:

I Had the main responsibility for running the experiment, data handling, data analyses, interpretations, and writing.

II Planned the study together with co-authors. Performed the field work together with co-authors. Had the main responsibility for running the experiment, data handling, data analyses, interpretations, and writing.

III Planned the study together with co-author. Had the main responsibility for running the experiment, data handling, data analyses, interpretations, and writing.

IV Planned the study together with co-authors. Had the main responsibility for running the experiment, data handling, data analyses, interpretations, and writing.

Abbreviations

BP	Bacterioplankton production
BR	Bacterioplankton respiration
C	Carbon
CDOM	Colored dissolved organic matter
CO_2	Carbon dioxide
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
LTBR	Long-term bioreactivity
N	Nitrogen
P	Phosphorus
SE	Standard error
SEM	Structural equation modelling
STBR	Short-term bioreactivity
SUVA	Dissolved organic carbon specific UV absorbance at 254 nm
tDOC	Terrestrial dissolved organic carbon
tDOM	Terrestrial dissolved organic matter
TP	Total phosphorus
WRT	Water residence time

1. Introduction

1.1 Macroelement export from land to aquatic systems

Over the past decades a browning trend has been observed in inland and coastal surface waters of North America and Northern Europe (Monteith et al. 2007). This trend has been mainly ascribed to increased loadings of terrestrial dissolved organic matter (DOM), which consists of a mixture of plant, soil and organism remains. In Sweden, for example, terrestrial DOM concentrations in aquatic systems have increased as much as 60 % since the late 1980s (Kritzberg and Ekström 2012), and projections are that this increase will continue (de Wit et al. 2016). Several mechanisms have been suggested as drivers of the change in terrestrial DOM loadings to the aquatic environment, including increases in air temperature (Weyhenmeyer and Karlsson 2009), changes in land-cover patterns (Kritzberg 2017), increases in precipitation and runoff (Erlandsson et al. 2008), and a decline in atmospheric sulphate deposition (Monteith et al. 2007). The browning of aquatic systems has marked socio-environmental impacts on drinking water production costs (Eikebrokk et al. 2004), on global biogeochemical cycles (da Cunha et al. 2007), on the metabolism of aquatic organisms (Zwart et al. 2016), among others. Particularly, increased loadings of terrestrial DOM to aquatic systems imply an increase in the supply of elements of special importance to living organisms (i.e. macroelements), such as organic carbon (C), nitrogen (N) and phosphorus (P; Hessen et al. 2010). Since bacteria are the main biological agents of the assimilation and mineralization of macroelements (Cho and Azam 1988; Pomeroy et al. 1991), it is essential to understand the regulation of such processes in light of changes in macroelement loadings.

1.2 Reactivity of land-derived macroelements to bacterioplankton

Heterotrophic bacterioplankton (hereafter referred to as bacterioplankton), which consist of the bacteria in the water column that depend on external supply of chemical energy, represent an important entry point of C, N and P to aquatic heterotrophic food webs (Azam et al. 1983). They remove macroelements from the water column to support their growth (or production), and are in turn grazed upon, supplying macroelements to higher trophic levels of the food web (Jones 1992). Bacterioplankton production (BP) represents a major transfer of energy and nutrients in which the rest of the food web depends on, especially in northern aquatic systems where the amount of energy derived from primary production is low (Jansson et al. 2000). Despite the large amounts of terrestrially derived macroelements received by inland waters, macroelement availability is often a factor limiting BP (Jansson et al. 2012). In fact, only a variable share of land-derived macroelement flux can be accessed by bacteria for production (i.e. is bioavailable; Jansson 1998). For example, a fraction of the N and P transported in the terrestrial DOM may be bound to organic compounds and be thus unavailable to bacteria (Jansson et al. 2012; Stepanauskas et al. 2000). Despite the importance of macroelement bioavailability at the ecosystem level, knowledge on the topic is limited, mostly due to difficulties in determining the bioavailable pool size (Berggren et al. 2015). This knowledge makes it difficult to predict biological and ecological pathways of this increasing C, N and P flux (Eilola et al. 2011).

The role of bacterioplankton on the cycling of C has received special interest during the last decades. This is especially due to the increase of CO_2 concentrations in the atmosphere and associated impact on global climate (Ciais et al. 2014). Dissolved organic carbon (DOC) compromises the major pathway of C from terrestrial soils to freshwater systems, and ultimately to coasts (Cole et al. 2007). Dissolved organic carbon may be further added within aquatic systems by algae and macrophytes (Guillemette and del Giorgio 2011). The total amount of C annually exported from soils to aquatic systems is now well integrated into the global C cycle, and it is estimated to be approximately half of that sequestered by terrestrial primary producers every year (Battin et al. 2009). During transit through inland waters, a large amount of DOC can be respired by bacterioplankton (Cole et al. 2007). Bacterioplankton respiration (BR) is a process involving a series of redox reactions in order to produce energy, during which oxygen is consumed from water and CO_2 released to the atmosphere. The degree to which DOC can support BR is variable, and the mechanisms underpinning its bioreactivity at the end of inlands waters remain unclear (Bauer et al. 2013; Regnier et al. 2013). This knowledge gap is mainly due to a limited understanding of how physical processes, such as water residence time (WRT), together with biogeochemical macroelement cycling, as function of landscape and climate change, influence DOC bioreactivity properties at river mouths (Ward et al. 2017). Although traditionally DOC bioreactivity is known to decrease with increases in WRT (Middelburg 1989), recent literature suggests that other environmental factors may well play a large role for DOC bioreactivity (Evans et al. 2017). The inadequate understanding of the DOC pool that can potentially be mineralized has major implications for estimates of inland water CO_2 emissions and estimates of oxygen-consuming riverine DOC exported to estuarine areas, which are currently associated with a large degree of uncertainty (Ward et al. 2017).

1.3 Impact of riverine inputs of bioreactive macroelements on estuarine bacterioplankton metabolism

Increased loadings of riverine DOM are expected to have a profound effect on estuarine bacterioplankton production and respiration (Figueroa et al. 2016; Nydahl et al. 2013). This is expected to be the case for estuarine areas that are highly influenced by riverine DOM inflows, such as boreal estuaries (Andersson et al. 2015). In response to increased riverine DOM deliveries, BP will likely increase (Figueroa et al. 2016). This change in BP may alter estuarine food web structures, and overall productivity of estuaries, which are among the most productive ecosystems on Earth (Canuel et al. 2012). Moreover, increases in estuarine BR can lead to increased CO_2 emissions from estuarine waters and reduce the concentration of dissolved oxygen in the water column (Diaz and Rosenberg 2008; Panigrahi et al. 2013). While the importance of increasing riverine DOM influxes to estuarine systems is evident, little is known regarding the potential utilization of riverine transported macroelements inputs by bacterioplankton. Moreover, it is also unclear how riverine macroelements, alone or combined, regulate estuarine bacterioplankton metabolism (production and respiration; Andersson et al. 2015). This limited understanding hampers the prediction of how the structure and function of boreal estuaries will respond to changes in riverine macroelement deliveries.

2. Aims of the thesis

The overall purpose of this thesis is to determine the potential reactivity of the increasing terrestrially derived macroelement exports to bacterioplankton, and to determine its effect on estuarine bacterioplankton metabolism. The specific aims of the thesis were to:

- Determine the potential bioavailable size of the dissolved organic carbon, nitrogen and phosphorus pool in aquatic systems dominated by terrestrial dissolved organic matter inputs (paper **I**)
- Assess the effect of landscape patterns and water residence time on dissolved organic carbon bioreactivity in river systems (paper **II**)
- Determine the relative importance of direct and indirect effects of riverine dissolved organic matter for bacterioplankton respiration in a boreal estuary (paper **III**)
- Assess the single and interactive effects of increasing macroelement loadings on bacterioplankton respiration and production in a boreal estuary (paper **IV**)

3. Materials and methods

3.1 Study area and sampling

This study was conducted on brown-water lakes, rivers and on a boreal estuary within Sweden. Specifically, the study presented in Paper **I** was conducted in epilimnion samples of four lakes located in northern of Sweden (Övre Björntjärnen, Lillsjöliden, Struptjärnen and Stortjärnen; Fig. 1). Samples were taken between September 2012 and September 2014. The lakes have a similar size and are located within the same region. The catchments of these lakes are mainly composed of different portions of coniferous forest (Scots Pine, *Pinus sylvestris*; Norway spruce, *Picea abies*) and wetlands (mires).

The study presented in Paper **II** was conducted on samples from 18 river outlets that drain to the Kattegat or into the Baltic Sea. Samples were taken once, during low flow conditions, between June and August 2013. River catchments fall between latitudes 68˚ N and 56˚ N and span a 1800 km climate gradient, which includes a subarctic climate in the north and a more temperate climate in the south. The size of the sampled catchments varied from 131 to 48136 km^2. Land use and land cover varied from mountainous, wetland and forested areas in the North, to more agricultural and urban areas in the South (Sponseller et al. 2014).

The research presented in papers **III** and **IV** was conducted at the Öre estuary, located in the northwestern part of the Bothnian Sea (Baltic Sea). The estuary consists of a semi-enclosed area with no tides, of roughly 50 km^2, an average depth of 16 m and a volume of 1.0×10^9 m^3 (Wikner et al. 1999). For the study presented in paper **III**, samples were taken along a fresh-marine water transect, which included the Öre river (sampled at 1 m depth), the Öre estuary (sampled at 1 m and 15 m depth), and a marine site (sampled at 1 m). Samples for this study were taken between March and September of 2014. The study presented in paper **IV** includes samples taken between March 2014 and March 2015 at 1 m depth from two estuarine sites, which differ in terms of proximity to the Öre river mouth.

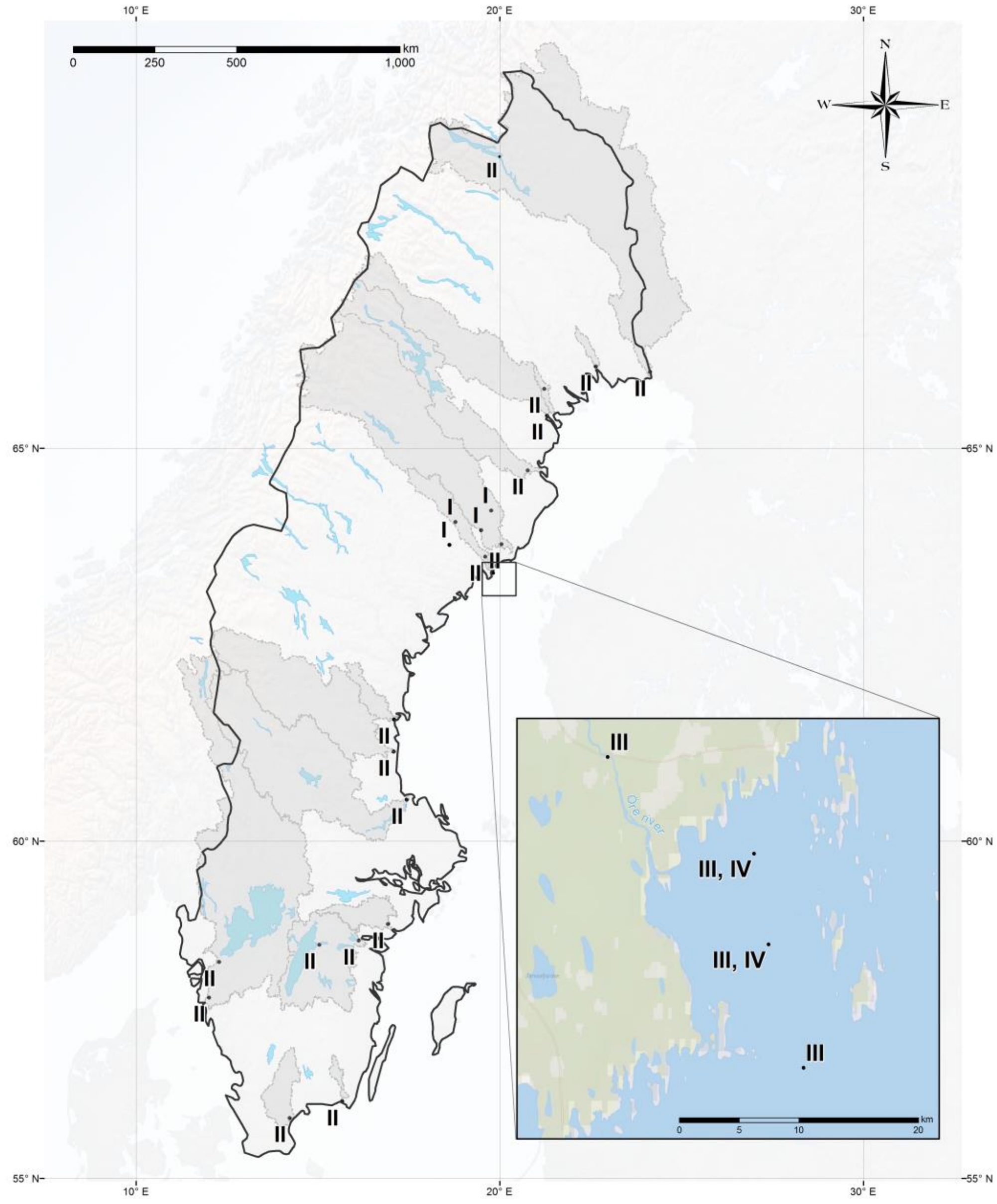

Figure 1. Geographic location of the lakes sampled for paper I (legended as I), the river outlets sampled for paper II (II), the freshwater-seawater transect sampled for paper III (III) and the Öre estuary sampled for paper IV (IV).

3.2 Experimental setup

Bioavailable concentrations of terrestrially derived C, N and P from lakes dominated by tDOM inputs were determined with enrichment bioassays, in which strong macroelement limitation was induced (paper **I).** The response of bacteria was measured by the leucine incorporation of ^{3}H-leucine according to the method developed by Kirchman et al. (1985) over seven days. Total amounts of ^{3}H-leucine incorporated were converted into concentrations of bioavailable C, N or P based on standard bacterial growth curves, which described the amount of leucine incorporated per unit of bioavailable limiting macroelement.

The DOC bioreactivity at the end of river outlets (paper **II**) was determined as the amount of DOC lost during short- (0-6 days) and long-term (23-365 days) dark bioassays. Losses of DOC were either calculated from differences in DOC or oxygen concentrations. Data on catchment WRT was derived following the method described in (Lindström et al. 2017), and proportions of land use and land cover were retrieved from the Swedish Meteorological and Hydrological Institute. Causal links between landscape and WRT and bioreactive DOC were tested using structural equation modeling (SEM). These relationships were mediated by other variables which were also included in the SEM: primary production (PP), specific ultraviolet absorption at 254 nm ($SUVA_{254}$), colored dissolved organic matter (CDOM) and total phosphorus (TP).

Single and interactive effects of increasing C, N and P on estuarine BR and BP were tested with a full-factorial experiment (paper **III**). Sample sub-volumes were added to glass vials and standard solutions of C (glucose), N (ammonium nitrate) and P (disodium phosphate) were amended. Responses of BR were determined from changes in oxygen concentration during three days and responses of BP were measured by leucine incorporation of ^{3}H-leucine (Kirchman et al. 1985).

For the purpose of assessing the direct and indirect impacts of riverine DOM on the source of organic C used for BR at the Öre estuary (paper **IV**), the stable isotopic composition (δ^{13}C) of the bioreactive DOC was determined. Changes in concentration and δ^{13}C of DOC were recorded over time in long-term dark experiments, and the Keeling plot method (Keeling 1958) was used to estimate the δ^{13}C of the bioreactive organic C. The results were compared with estimates of δ^{13}C values of bioreactive organic C from terrestrial and marine sources.

4. Main results and discussion

4.1 Availability of dissolved organic carbon, nitrogen and phosphorus to bacterioplankton in brown-water lakes (paper I)

The concentration of bioavailable macroelement in tDOM-rich lakes increased from C to N and from N to P. Specifically, macroelement absolute concentrations varied between 104 and 692 µg C L^{-1}, 23 and 287 µg N L^{-1}, and 0 and 16 µg P L^{-1}. In relation to the total pool, the average share of bioavailable macroelement was 2 %, 31 % to 49 % for C, N and P, respectively (Fig. 2). Phosphorus was thus the most available macroelement, suggesting that in terrestrial DOM-rich systems P availability may be higher than previously thought (Jansson et al. 2012).

Organic N represented on average 80% (± 13 SE) of the total bioavailable N share, while approximately 61% (± 46 SE) of the bioavailable P pool was organic. Bacterioplankton were thus able to take up large fractions of organic macroelements and to utilize them for support of production. Total nutrient ratios were higher in comparison to bioavailable ratios (dependent t test, $p < 0.05$, $n = 26$). For example, average total carbon-to-nitrogen ratio (55 ± 9 SE) was ca. 13 times higher than the average bioavailable carbon-to-nitrogen ratio (4 ± 3 SE). Likewise, average total carbon-to-phosphorus ratio was (4774 ± 2135 SE) was ca. 12 times higher than the average bioavailable carbon-to-phosphorus ratio (369 ± 915 SE). These results highlight that total nutrient fractions are poor forecasters of resource bioavailability in boreal freshwater ecosystems. Due to a high degree of C recalcitrance, predictions of macroelement limitation based on total macroelement ratios may be inadequate when C is part of the ratio.

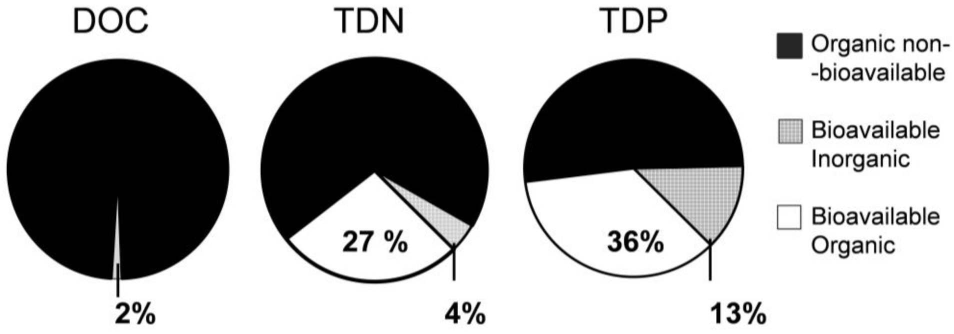

Figure 2. Share of organic non-bioavailable, organic bioavailable and inorganic nutrient pools of dissolved organic carbon (DOC), total dissolved nitrogen (TDN) and total phosphorus (TP)

4.2 WRT and landscape influence on riverine bioreactive DOC (paper II)

Bulk DOC concentrations measured in surface waters varied from 0.8 to 20.6 mg C L^{-1}. Concentrations of short-term bioreactive (STBR) DOC varied between 0.04 and 0.45 mg C L^{-1} and concentrations of long-term bioreactive (LTBR) DOC varied between 0.52 and 7.75 mg C L^{-1}. While bulk DOC concentrations were negatively related to WRT, bioreactive pools were independent of WRT (Fig. 3).

The variation of the STBR was strongly related to land cover and land use classes such as forest, agriculture and urban, as function of surface water P concentrations. High P concentrations in turn stimulated the production of a short-term bioreactive C pool towards the end of riverine networks (r^2=0.52; $p<0.05$; Fig. 3). These findings agree well with those from paper **I** by showing that P derived from forested soils had a high potential to support aquatic productivity. In addition, they revealed that agricultural and urban land were also important sources of bioavailable P to adjacent waters, which in turn stimulated the phytoplankton supply of short-term bioreactive C, typically preferred by bacteria to support of metabolic processes (Amon and Benner 1996). Since these two land types are typically located close to river mouths (Weyhenmeyer and Conley 2017), they play an important role for the bioreactivity of the C and P exported that into estuarine zones.

Variation of the LTBR was explained by both land use and WRT, as function of $SUVA_{254}$ and CDOM (r^2=0.78; $p<0.05$; Fig 3). Long photochemical processing of the aromatic, recalcitrant C substrates (paper **I**) likely fueled the LTBR pool observed at river mouths. While these results agree with previous reports of preferential loss of colored recalcitrant terrestrial DOM during water transit time (Kellerman et al. 2015; Weyhenmeyer et al. 2012), they also contradict the general notion that DOC bioreactivity decreases with increased WTR (Middelburg 1989). Although absolute DOC concentrations declined over time, the DOC measured at river mouths was relatively more bioreactive.

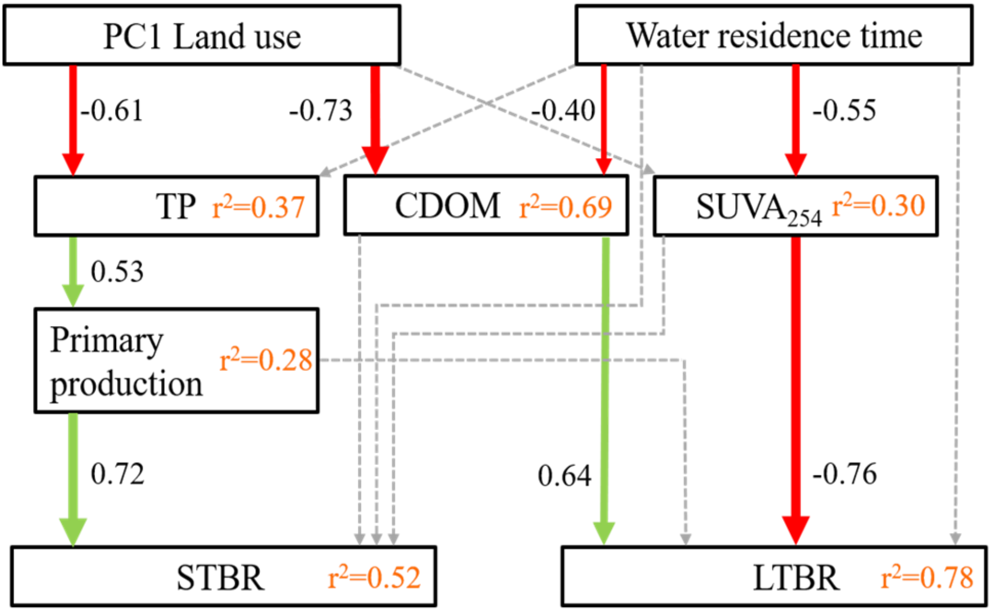

Figure 3. Structural equation model relating short- (STBR) and long-term bioreactive (LTBR) DOC pools with land use and water residence time (WRT). Red arrows show negative, while green positive relationships. The coefficients translate the rate at which the response variable changes in response to a change in its predictor. Significant links are considered at $p < 0.05$ level. Dashed grey arrows represent non-significant pathways. Forest, agricultural and urban land exhibited high negative loadings on principal component one (PC1).

4.3 Relative importance of direct and indirect effects of riverine dissolved organic matter on estuarine bacterioplankton respiration (paper III)

The average signature of the $\delta^{13}C$ of the bioreactive DOC consumed in the estuary (–22 ‰ ± 1SE) resembled that of organic C derived from marine phytoplankton (–22 to –21 ‰; Peterson and Fry 1987). These results indicate that BR in the Öre estuary was not primarily supported by riverine DOC, but rather supported by organic C derived from marine phytoplankton production. Even during high flow periods, such as during spring flood, when bioavailable riverine DOC exports to the estuary are highest (Wikner and Hagstrom 1999), marine-derived organic C was the main source of energy supporting BR. The isotopic signal of the bioreactive DOC was positively related to riverine DOC and nutrient concentrations, which in turn were positively related to riverine flow. These findings suggest that riverine discharge had an important indirect role as source of nutrients to marine primary producers, which was greater than its role as direct source of energy to estuarine bacterioplankton. High riverine nutrient loadings likely contributed to increased primary productivity which in turn derived the main pool of bioreactive organic C utilized by bacterioplankton in the estuary. These findings match well the predictions of low oxygen consuming organic C exports from the Öre river, which has short WRT, and catchment proportions of agricultural and urban land (paper **II**). Despite riverine nutrients being bound to organic matter, paper **I** showed that a large fraction of the total N and total P can be bioavailable. Moreover, the bioavailability of nutrients bound in the terrestrial DOM may increase when entering the saline coastal environmental; for example, estuarine photolysis can increase organic nutrient bioavailability to phytoplankton (Bushaw et al. 1996).

Nutrient availability is currently the limiting factor to primary productivity at the Öre estuary during growing season (Andersson et al. 1996). However recent studies suggest that increased riverine DOM inflows are expected to decrease primary production due to a decrease in water column light attenuation (Andersson et al. 2013; Wikner and Andersson 2012). Moreover, increased riverine C loadings may decrease the reliance of bacterioplankton on organic carbon derived from primary production (Jansson et al. 2007), increasing bacteria competition with primary producers for N and P. Since bacteria are superior nutrient competitors (Vadstein 2000), bacteria will likely outcompete primary producers, which will in turn further contribute to a possible decrease of primary production in estuaries (Andersson et al. 2015; Carney et al. 2016; Meunier et al. 2017).

4.4 Single and interactive effects of increasing DOC, nitrogen, and phosphorus loadings on bacterioplankton respiration and production in a boreal estuary (paper IV)

Bacterioplankton respiration increased on average 2.2 times in response to single organic C amendments in both estuarine sites. In contrast, amendments of N and P alone did not have a significant effect on BR. These results are in line with the general idea that organic C is the main driver of BR, and that nutrients alone have a marginal impact on estuarine BR (Asmala et al. 2013; del Giorgio and Newell

2012). In light of predicted increases of riverine DOC supplies to estuarine areas, and considering the relatively high bioreactive DOC patterns found at Baltic Sea river mouths (paper **II**), an increases in estuarine BR of riverine DOC supplies is expected.

Bacterioplankton production varied between the two studied estuarine sites. At the site located close to the river mouth, BP increased on average 1.8 times in response to single P amendments, however it did not increase in response to amendments of organic C or N. These results highlight the role of P as limiting macroelement for BP in the estuary. Although resource limitation studies conducted in coastal and offshore areas of the Baltic Sea suggesting overall N-limitation (Kivi et al. 1993; Vaquer-Sunyer et al. 2015), N did not limit bacterioplankton metabolism in the estuary. This is most likely due to the riverine discharge received by the estuary being characterized by high total nitrogen to total phosphorus ratios, which thus lead to a P shortage (Graneli et al. 1990). Considering that P exported from terrestrial soils can be highly bioavailable (paper **I**), the predicted increases of riverine P deliveries are expected to increase BP. At the estuarine site located furthest away from the river mouth, BP was not limited by P but instead was weakly limited by organic C. These results suggest that the fractions of bioreactive organic C in the estuary (paper **III**) were likely depleted at the site close to the estuary, which then led to organic C-limitation of BP at site located furthest away from the from the river mouth.

The combined amendments of organic C, N and P led to the highest observed BP and BR responses in both estuarine sites. Organic C, N and P further showed an interactive effect on all variables, but on BP at the site near the river mouth, where P had a main effect. These results suggest that the three macroelements have a costimulating effect on bacterial metabolism. In light of the predicted increase of riverine macroelement inflows it is thus likely that estuarine BP and estuarine BR of riverine DOM will be in the future intensified.

5. Concluding remarks

This thesis showed that terrestrially derived macroelement loadings have large influence on bacterioplankton metabolism. The bioavailability of terrestrially derived macroelements increased from organic C to N to P in terrestrial DOM-rich lakes, suggesting that in such systems organic C bioavailability is extremely low. Yet, organic carbon bioavailability changed during water transit to river mouths, where a relatively high bioreactive organic C pool was observed. Changes in organic C bioreactivity occurred in river catchments with long water residence time and high portions of agricultural and urban land. These findings suggest that such catchment characteristics must be considered for improved forecasting of riverine inflows of oxygen-consuming organic carbon to estuarine ecosystems. The indirect effect of riverine bioavailable N and P inflows on estuarine bacterioplankton respiration was relatively more important than that of riverine bioreactive organic C. These results matched well the predictions of low bioreactive organic C deliveries from the Öre river based on its catchment characteristics. Instead, riverine nutrients stimulated estuarine primary production which in turn supplied organic carbon to estuarine bacterioplankton. Overall, estuarine bacterioplankton respiration was primarily limited by C and estuarine bacterioplankton production was primarily limited by P. In light of continued increases of riverine P supplies, bacterioplankton production will likely increase, thus shifting the estuary towards net-heterotrophy. Expected decreases of estuarine primary production combined with increased exports of riverine organic C, will likely increase the bacterioplankton respiration of riverine organic C, therefore increasing estuarine emissions of riverine organic carbon-based CO_2. Combined inputs of riverine organic C, N and P may further exacerbate the expected effects of bacterioplankton metabolism on the structure and function of boreal estuarine ecosystems.

6. Outlook

Northern aquatic systems are experiencing increased loading of terrestrially derived macroelements with ecological and biogeochemical significance linked to the bacterial cycling of DOC, N and P (Andersson et al. 2015). To forecast the impact of such increasing flux it is important to improve knowledge on the available C, N and P shares, and to consider the inclusion of this pool on water monitoring programmes.

Moreover, from this thesis it became clear that a high share of the terrestrially derived P is bioavailable, and that P was an important driver of aquatic productivity at river outlets and in the Öre estuary. However, one aspect not covered in this study but related to its findings is the impact of iron-phosphorus interactions on P bioavailability, since iron has the potential to immobilize P. Because terrestrial exports of iron are increasing (Kritzberg and Ekström 2012), this topic should be addressed in future studies.

While this thesis addressed the effect of C, N and P increases on bacterioplankton metabolism, other drivers associated with the increase of terrestrial DOM may also have an impact on bacterioplankton metabolism. For example, the increase of terrestrial DOM is expected to change surface water temperature due to its light absorbing properties and to decrease estuarine salinity (Nydahl et al. 2013). To account for the impact of multiple factors on bacterioplankton metabolic responses, more mesocosm experiments should be employed.

Paper IV proved the role of organic C derived from primary producers for support of estuarine BR. This shows that bacteria and phytoplankton can be coupled even in estuaries that are recipients of high loadings of terrestrial DOM. Due to the strong effect of terrestrial DOM on the bacterioplankton to phytoplankton ratio (Wikner and Andersson 2012), more knowledge is needed on the impact of the expected increases of terrestrial DOM loadings on overall basal production (bacteria and phytoplankton) and more emphasis should be given to secondary aquatic production by water monitoring programmes.

Finally, more importance should be given to the effects of land cover change and management on increasing export fluxes of terrestrial DOM. For example, afforestation and forest practices such as harvesting, clear-cutting, logging and ditching have a large influence on land export of macroelements to aquatic systems (Laudon et al. 2009; Oni et al. 2015; Rantakari et al. 2010), and should be better considered in the future management of boreal aquatic resources.

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