Catchments, Carbon, and Climate Connections

- a limnological perspective

Dissertation for the degree of Ph.D.
by

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Ex nihilo nihil fit

(Nothing comes from nothing)

- Parsimedes

PREFACE

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RCN project 165139 “Biogeochemistry in Northern Watersheds, a Reactor in Global Change”

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Lastly, I want to thank Kristine again - for keeping me on track.

Søren Larsen
Blindern, March 2010

LIST OF PAPERS

The thesis is based on the following list of publications and manuscripts, which will be referred to in the text by their Roman numerals:

I LARSEN, S., ANDERSEN, T., HESSEN, D.O. *(submitted to Limnology and Oceanography)* **Predicting organic carbon in lakes from climate drivers and catchment properties.**

II LARSEN, S., ANDERSEN, T., HESSEN, D.O. *(Global Change Biology, in print)* **Severe impacts of climate change on organic carbon in lakes.**

III LARSEN, S., ANDERSEN, T., HESSEN, D.O. *(submitted to Global Biogeochemical Cycles)* **pCO_2 in lakes; DOC as a global predictor?**

IV HESSEN, D.O., ANDERSEN. T., LARSEN, S., SKJELKVÅLE, B.L., de WIT, H.A., *(Limnology and Oceanography, 54(6 part 2), 2009, 2520-2528)* **Nitrogen deposition, catchment productivity, and climate as determinants of lake stoichiometry.**

V TRANVIK, L. J., DOWNING, J. A., COTNER, J. B., LOISELLE, S. A., STRIEGL, R.G., BALLATORE, T. J., DILLON, P., FINLAY, K., FORTINO, K., KNOLL, L. B., KORTELAINEN, P. L., KUTSER, T., LARSEN, S., LAURION, I., LEECH, D. M., MCCALLISTER, S. L., MCKNIGHT, D. M., MELACK, J. M., OVERHOLT, E., PORTER, J. A., PRAIRIE, Y., RENWICK, W. H., ROLAND, F., SHERMAN, B. S., SCHINDLER, D. W., SOBEK, S., TREMBLAY, A., VANNI, M. J., VERSCHOOR, A. M., VON WACHENFELDT, E., WEYHENMEYER, G. A. *(Limnology and Oceanography, 54(6 part 2), 2009, 2298-2314)* **Lakes and reservoirs as regulators of carbon cycling and climate.**

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1. SUMMARY

This thesis starts out investigating the key drivers behind the concentration of organic carbon in lakes. The analysis leads to a novel finding of catchment vegetation density (Normalized Difference Vegetation Index, NDVI) as a key parameter, which is rational, but never has been used before in this context. NDVI is also a key component in a follow-up analysis, where the thesis sets out to elucidate the impacts of climate change on the organic carbon flow through a boreal region. The study demonstrates some severe consequences of climate change, with important implications for aquatic ecosystems and human use of surface waters. The examination continues by establishing DOC as the major causal factor for the evasion of carbon dioxide from Norwegian lakes. It also presents a new modeling approach to the connection between organic carbon and the amount of CO_2 in lakes, offering a possible answer to the inconsistencies observed between studies worldwide. The thesis then examines how human alterations of the nitrogen cycle also impact the flux of energy and matter through watersheds. Finally, the thesis presents a synthesis that clarifies the significant role of lakes as regulators of the global carbon cycle and climate.

2. INTRODUCTION

The flow of organic carbon through ecosystems is a fundamental aspect of large scale ecology, and the central role of carbon in a climate change perspective has intensified the focus on the global carbon cycle. The boreal zone accounts for a large part of the global cycling of carbon (C) between organic and inorganic states and though lakes occupy a relatively small fraction of the circumboreal land area, increasing evidence suggests that they may still be significant regulators of C flow in ecosystems (Battin *et al.*, 2009, Cole *et al.*, 2007). Dissolved organic carbon (DOC) is, by far, the largest pool of organic C in most boreal lakes (Figure 1)(Hessen, 2005, Hessen *et al.*, 1990, Meybeck, 1982, Wetzel, 1975). and the major part is believed to originate from terrestrial primary production in the catchment (Hongve, 1999, Jansson *et al.*, 2008, Kritzberg *et al.*, 2006).

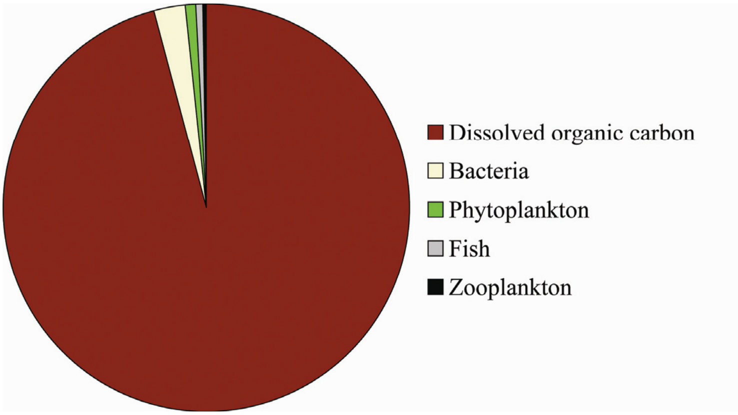

Figure 1: Carbon pools typical of the different active organic carbon pools in lakes of southern Quebec (Prairie, 2008). Similar partitioning of organic carbon has also been demonstrated for Norwegian lakes (Hessen, 2005).

2.1 The role of organic carbon in lakes

DOC plays a fundamental and multifaceted role in the functioning of lake ecosystems due to its influence on physical, chemical and biological lake properties. It is beyond the scope of this introduction to describe the whole host of ways in which DOC affects lakes, but here follow some examples which highlight different aspects of lake DOC.

For the non-limnologist, one of the most apparent outcomes of an elevated DOC concentration is the brown color of the water due to colored DOC (ie. humic substances).

This coloration has more than just aesthetic consequences; DOC is an important factor for light attenuation in the water column and constrains the depth of light penetration (Fee *et al.*, 1996). The absorbed light is mostly transformed into heat energy such that the concentration of DOC acts as a co-determinant of the vertical heat distribution in the water column. Consequently, the depth of the thermocline and the duration of stratification, and thus the overall thermal budget of a lake, is potentially affected by the concentration of DOC (Snucins & Gunn, 2000).

Through its effect on availability of light for primary production, DOC may have a strong impact on the proliferation of benthic algae and the in-lake production of organic carbon (Karlsson *et al.*, 2009). However, it also modifies the spectral properties of the light available to aquatic organisms and, in particular, the strong UV absorbance of DOC offers a shield of photo-protection for aquatic organisms (Hessen, 2005, Rautio & Korhola, 2002).

Absorption of UV-radiation induces photo-chemical degradation of DOC, which may result in highly reactive end-products such as hydroxyl radicals and hydrogen peroxide (Febria *et al.*, 2006). Despite both substances being toxic to many organisms (Drabkova *et al.*, 2007), they are important for the breakdown of recalcitrant organic compounds (Pullin *et al.*, 2004).

Thus, the optical properties of DOC have a wide range of consequences for the physical and biological traits of a lake, but the intricate effects of DOC on lake chemistry are also pervasive. The chelating properties (i.e. the ability to bind certain trace elements) of DOC gives it a major role in the cycling of metals and organic contaminants, modifying their retention and bioavailability in aquatic ecosystems (Mierle & Ingram, 1991; Skjelkvaale et al., 2001).

The bioavailability of allochthonous DOC is generally low, but the vast amount still makes it an important energy source for bacterial production (Jansson *et al.*, 2000). This alleviates the bacterial dependence on in-lake primary production as a carbon source and sets the foundation for a microbial loop which bypasses the autotrophic links in the pelagic food chain. High ratios of DOC to available phosphorus or nitrogen lower bacterial growth efficiency and cause a general increase in heterotrophic respiration. As DOC also reduces the absolute and relative primary production, it ultimately controls the ratio of pelagic autotrophic to heterotrophic production (Cimbleris & Kalff, 1998). Thus, lake stoichiometry (ie. DOC to nutrient ratio) is one of the major determining factors for the metabolic balance of lakes (ie. whether lakes are net sources or sinks of carbon dioxide) and studies suggest that that lakes shift from net autotrophic to net heterotrophic at a concentration around 5 mg DOC L^{-1} (Hanson *et al.*, 2003, Jansson *et al.*, 2008, Prairie *et al.*, 2002, Sobek *et al.*, 2006)

The relationship between organic carbon and lakes is bilateral. Though the amount of DOC is crucial for a wide range of lake properties, lakes also play an important role in the global cycling of carbon.

2.2 The role of lakes as regulators of carbon cycling

Organic carbon produced by the terrestrial ecosystem will, generally speaking, be stored, oxidized, or exported via hydrological pathways. Lakes and rivers act as efficient shunts of organic carbon from the terrestrial ecosystem to the sea (Kawasaki *et al.*, 2005). Recent work suggests that lakes should not be considered to be passive transport vectors, but rather as active reactors which mineralize, modify, and store significant amounts of organic carbon (Cole *et al.*, 2007).

The mineralization of DOC by biological or photochemical induced oxidation and subsequent gas evasion through the surface to the atmosphere is believed to account for most of the organic carbon loss in lakes (Cole & Caraco, 1998). A significant amount of organic carbon ends up in lake sediments. The annual sedimentation of organic carbon in lakes globally is assumed to be approximately 20% of the carbon stored in terrestrial biomass and soils (Battin *et al.*, 2009). The relatively constant environment of the hypolimnetic sediments, with cold and often anoxic conditions, provides for a very low carbon turnover rate (millennia), compared to the faster carbon turnover (centuries) in the more variable environment of soils (Einsele *et al.*, 2001).

An increasing number of studies argue that inland waters play a significant, but often neglected, role in the global carbon cycle, and that the sequestration, transport, and mineralization of organic carbon in lakes and rivers needs to be integrated into the representation of the carbon cycle for optimal management of climate change mitigation (Algesten *et al.*, 2004, Battin *et al.*, 2008, Battin *et al.*, 2009).

2.3 Rationale

From a lake ecology perspective, DOC is one of the fundamental parameters for ecosystem functioning. Fluxes of carbon through rivers and lakes integrate a range of terrestrial biogeochemical processes. Better quantification of aquatic carbon exports could thus provide additional constraints for reducing the uncertainties in global ecosystem budgets (Battin *et al.*, 2009, Ciais *et al.*, 2008, Luyssaert *et al.*, 2009).

Freshwater is a critical resource world-wide, and the quality of surface waters are of vital importance for ecosystem properties, productivity, and ecosystem services (e.g. aesthetic aspects, drinking water supply). There is a growing demand for robust models explaining the large scale variations in DOC and nutrients between lakes (Roehm *et al.*, 2009). This thesis aspires to address this demand.

The foundation for the majority of this work (Papers I, II and IV) is a large dataset including water quality parameters from a national lake survey by the Norwegian Institute for Water Research (NIVA). The dataset comprises ~1000 lakes which were selected to span the large variation in lake attributes across Norway (Henriksen *et al.*, 1998). The challenge was to use the information derived from this sample to confidently infer environmental conditions in the remaining ~450000 lakes in Norway. The large number of lakes and catchments with their wide range of physical, chemical and biological properties should also make these assessments relevant to boreal lakes in general.

Lakes are spatially auto-correlated, meaning that nearby lakes are more likely to be similar than lakes further apart ("the first law of geography"). Using the geographical coordinates for all the lakes, it would have been possible to apply geostatistical techniques (e.g. kriging) to spatially interpolate water chemistry parameters for unsampled lakes located in the Euclidean space spanned by those which had been sampled. The problem with this approach is that it builds on an assumption of linear spatial dependence and ergodicity, while location per se does not influence any aspects of lakes. Furthermore, spatial interpolation does not state anything about causes of the observed values, nor can it be extrapolated to regions outside the sampled geographical space.

Lakes receive water either directly as precipitation on the water surface, or indirectly as runoff from the surrounding catchment. Lakes occupy ~3% of the world's continents (Downing *et al.*, 2006), such that the amount of precipitation falling directly on the water surface usually has little influence on the overall water budget of a lake. As a consequence, almost all lake water has been filtered through the catchment and thus been exposed to a multitude of processes which influence the chemical properties of the water (Cresser *et al.*, 2000, Mattsson *et al.*, 2003, Quinn & Stroud, 2002). Thus, it seems reasonable to assume that there will be some correlation between catchment properties and the physicochemical properties of the receiving lake (Andersson & Nyberg, 2009, Kortelainen *et al.*, 2006).

Due to the complex interactions between biogeochemical processes in the catchment and their drivers (e.g. temperature, precipitation, N-deposition), it is hard to use strictly mechanistic models to determine how the aquatic environment is influenced by catchment properties. Still, considerations based on general aspects of the catchment give some hints on what to expect. For example, peat bogs contain relatively large pools of organic carbon, which makes it seem reasonable to expect that an increase in peat bog coverage would have a positive correlation with the amount of organic carbon exported from the watershed. Likewise, precipitation is virtually devoid of organic carbon such that increased precipitation should act as a DOC diluting agent. However, since precipitation is also the main vector for DOC export and is directly related to soil moisture content, it may also influence the decomposition rate of particulate organic carbon (e.g. litter fall). Due to these factors, we do expect that precipitation has a variety of synergistic and antagonistic effects on lake DOC, but currently do not have enough knowledge to elucidate a more precise estimate on the actual net outcome of these interactions (Yuan *et al.*, 2009).

An alternative approach to spatial interpolation is to use detailed catchment information from the sampled lakes to model their water chemistry properties, and subsequently use these same catchment variables to predict the water chemistry in the un-sampled lakes. Thus, instead of using a single parameter (proximity) this approach is based on a number of explanatory variables (figure 2). This means that the predictive model also has some potential for identifying causal relationships between catchment properties and water chemistry. Furthermore, the prediction model is applicable outside the original sample space; for example, a model based on Norwegian lakes could be applied to Canadian lakes. Using this approach, it is not only possible to test the model performance but also to examine the validity of theoretical causalities implied from the model.

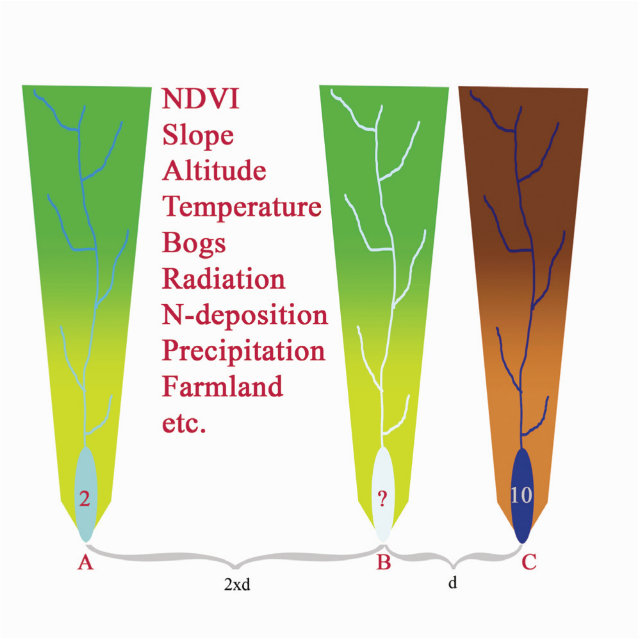

Figure 2: Conceptualization of the spatial interpolation and catchment property approaches to estimating lake water properties. A, B and C represents lakes (blue-hued ovals) with respective catchments (adjacent polygons). The coloration of the catchments represents values of catchment properties (some examples are listed in the figure).The numbers in A and C are arbitrary values for a sampled lake water property (e.g. DOC concentration), while B is an un-sampled lake. The distance between A and B (2d) is twice the distance between B and C (d). Spatial interpolation, based on proximity alone, would predict that B is more similar to C. The catchment approach use models based on detailed catchment information to predict lake water properties. Hence, this approach would infer that B actually shares characteristics with A.

Knowledge about the impact of climate change on lake DOC is so far provisional. An integrative approach, using large scale variations in lake DOC over wide gradients of climate parameters, could potentially bypass the complexity of the biogeochemical processes involved and still provide insight to the large scale consequences of climate change. We used a detailed survey of ~1000 lakes and their catchment properties to model their DOC concentrations. This resulted in robust and accurate predictions for DOC concentrations and exports of organic carbon in other lakes (paper I). Based on a space-for-time approach, the model was then refined and optimized for integrating climate related parameters. This allowed us to use projections from current climate change scenarios to predict major climate induced changes in lake concentrations and organic C discharge in boreal areas (paper II).

Most lakes in the boreal zone are supersaturated with CO_2 and function as vents of CO_2 to the atmosphere (Sobek *et al.*, 2005). The emission of CO_2 is recognized as one of the most important pathways for the export of C from lakes, and is an essential process for the role of lakes in the global carbon cycle (Prairie, 2008). However, the causes behind the elevated partial pressure of CO_2 in this environment are still under debate (Humborg, 2009, Roehm *et al.*, 2009). We used direct measurements of the partial pressure of CO_2 in the surface waters of lakes, which integrates all metabolic processes affecting the gas balance of the lake water column, together with the catchment approach to elucidate the key drivers for pCO_2 (paper III).

Changes in the global carbon cycle are a major concern, but the stoichiometry of carbon and nutrient fluxes through the watershed has far reaching implications for the recipient limnic and marine aquatic ecosystems. Still, only a modest number of studies have been dedicated to gauging the combined effects of climate change and anthropogenic alteration of biogeochemical cycles (e.g. nitrogen fixation), especially with respect to the stoichiometric composition of surface waters. We used an integrative approach including remote sensing data and comprehensive information on the chemical composition of a large number of lakes, and were able to elucidate the drivers behind the stoichiometry of their key elements (paper IV).

3. MAIN RESULTS

3.1 DOC interpolated in space (paper I)

Paper I aims to determine the key catchment properties which regulate DOC concentration in lakes. The starting point for this study was a dataset of the total concentration of organic carbon (TOC) in ~1000 lakes which were sampled by the Norwegian Water Research Institute (NIVA) in a national lake survey.

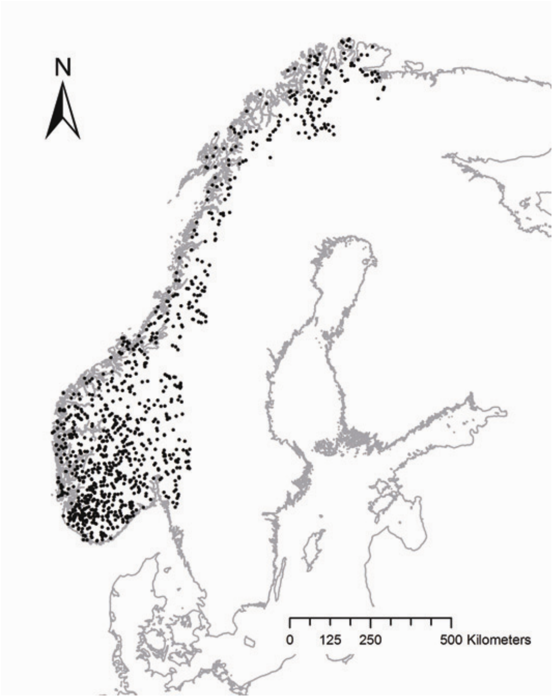

Figure 3: The geographical distribution of the ~1000 lakes which were samples in 1994 during a national lake survey by the Norwegian Institute for Water Research (NIVA).

The study concept was based on the fact that the major component of lake DOC is allochthonous (i.e. produced in the catchment); thus it would not be unreasonable to assume that variation in properties of the catchments determines the variation in lake DOC concentrations.

To obtain detailed information on the catchment properties of each of the 1000 lakes, we defined the catchments of all the lakes as polygons in a digital map by using a geographical information system (GIS). The delineation of the polygons were primarily based on the REGINE dataset (courtesy of Norwegian Water Resources and Energy Directorate (NVE)), which contains a hierarchical system of ~20000 catchments covering the entire mainland of Norway. Whenever the smallest REGINE sub-unit referred to a larger catchment than the sampled lake we corrected the polygons manually, using digital elevation models (DEM) and map-layers of rivers and streams as guides. We used the resulting polygon layer to extract highly detailed information about a wide range of catchment specific properties.

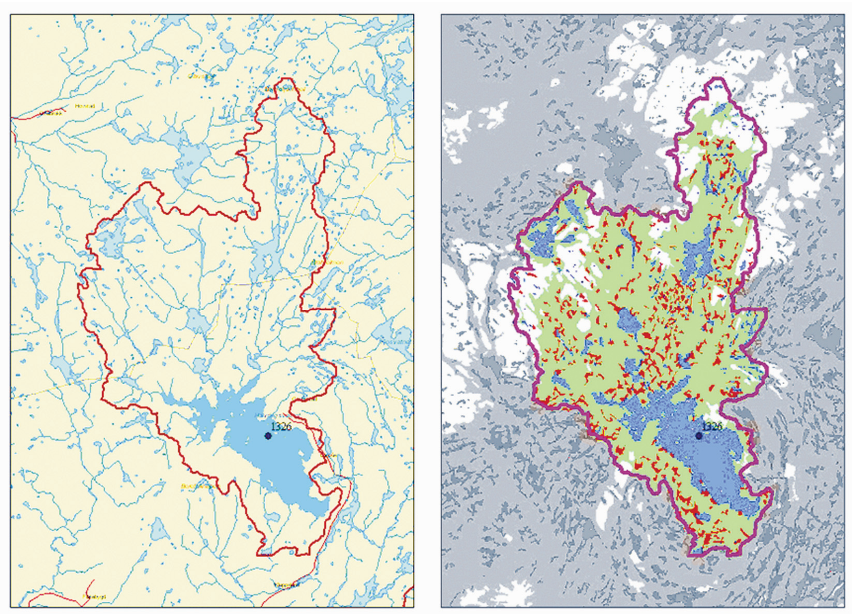

Figure 4: A catchment defined by a polygon (red line) on two different map layers. The map in the left panel shows lakes, rivers and streams (blue areas). It was used as a guide in the delineation of the catchment (together with the REGINE catchment data). The right pane shows an example of how the catchment polygon was superimposed on maps with different content to extract catchment specific information. Here the underlying map represents land use categories forest (green), bogs (red) and bedrock (white). The area outside the polygon is in grey tones for visual representation only. The resulting statistic of the GIS analysis contained information on the area coverage of the different categories represented on the map.

After an initial screening of different modeling approaches we ended up using a multivariate linear regression model. The final model was constructed by stepwise backward elimination using the Bayesian Information Criterion (BIC) for model selection (Johnson & Omland, 2004). The model was tested by imputation and re-sampling tests which demonstrated that it was very robust and unbiased with respect to sample size and representation.

The final model included 8 significant predictor variables, which explained 83% of the variation in the dataset (R^2 = 0.83, n = 962). The model variables were: mean air temperature, catchment area, specific runoff, terrain slope, vegetation density, atmospheric nitrogen deposition, water residence time, and catchment area fractions of bogs and arable land. Vegetation density, expressed as NDVI (Normalized Difference Vegetation Index), was by far the strongest and most important predictor variable, while area fraction of bogs in the catchment also showed a strong positive effect on organic C concentrations (figure 5).

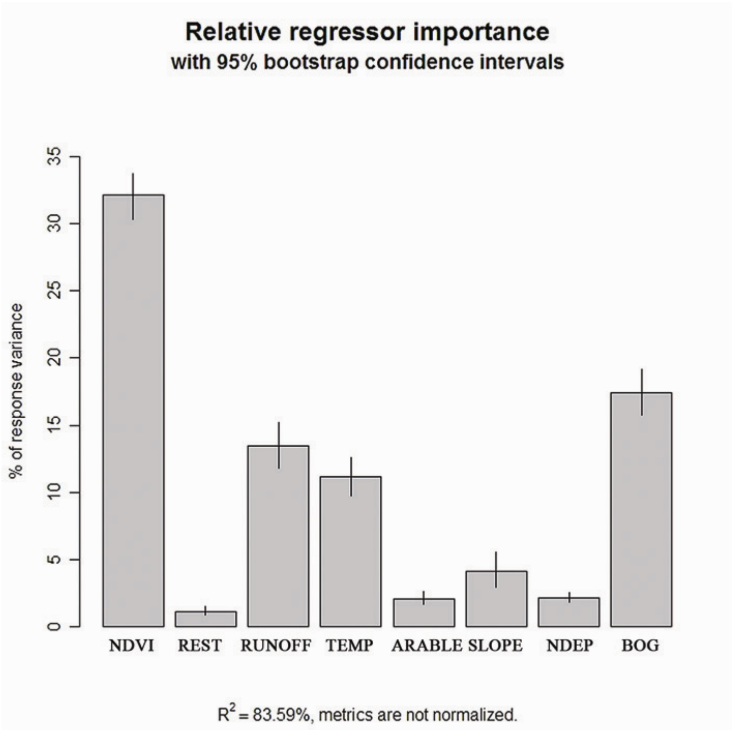

Figure 5: The relative importance of explanatory variables in predicting DOC concentrations in the 1000 lake survey. Bar height indicates pecentage of variance explained by after averaging sequential sums of squares over orderings of the respective predictor variables. (Bacher, 1983)

The robustness and high explanatory power of the model made it reasonable to extract catchment specific information and use it to estimate DOC concentration for all REGINE-units. This gave us not only an overview of the spatial pattern in DOC concentration, but combined with catchment specific runoff it provided us with an estimate on the total flux from the mainland of Norway (2.6 g m^{-2} yr, 0.8 Mt C yr^{-1}). Figure 6 demonstrates the geographic pattern of the most important predictor variable, NDVI, and the model estimates for concentration and flux of DOC. It is visually evident from the figure that high NDVI mostly translates into high DOC concentration, while some regions (e.g. along the south west coast) display high values of NDVI but relatively low DOC concentrations. This apparent inconsistency is explained by the geographic patterns in the map representing DOC flux; the low values of DOC are due the fact that the DOC has been transported away. Taken together, the DOC concentration and DOC flux complement the general pattern in NDVI. The figure also exemplifies that it is not possible to deduce DOC flux from DOC concentration alone or vice versa.

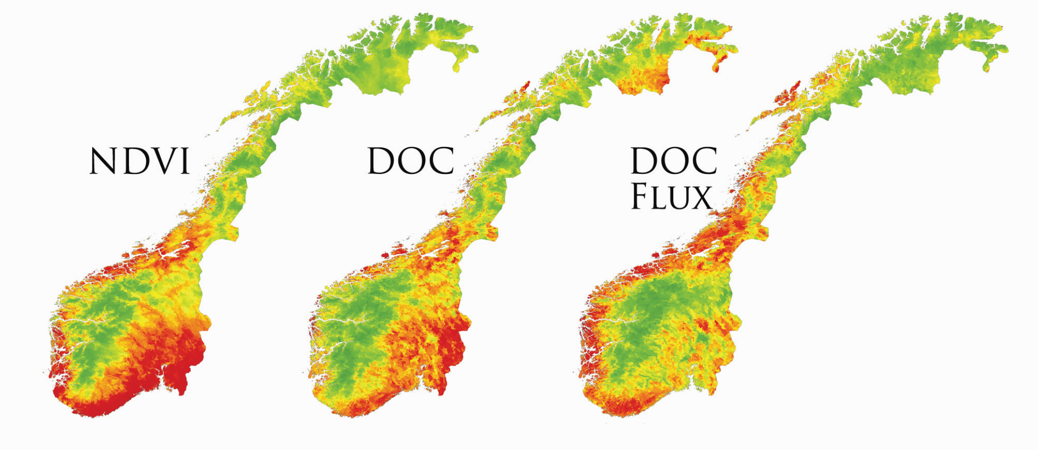

Figure 6: Geographical pattern of NDVI, DOC concentration and DOC flux. Red and green colors represent high and low values, respectively.

Given that the catchments spanned a wide range of geographic locations, local climates and land uses, the high explanation power was remarkable. Intriguingly, the model included several parameters which were directly related to climate change, such as mean annual temperature and surface runoff. Furthermore, NDVI was the parameter which, by far, had the largest effect on DOC variation (figure 5 and 6). This was no surprise, as terrestrial photosynthesis is the ultimate origin of allochtounous carbon in lakes, but it seemed reasonable to assume that NDVI would also depend on climatic parameters. If we were able to model NDVI from climatic parameters we could produce climate change projections for some of the most important predictor variables for DOC. This line of reasoning was followed up in paper II.

3.2 DOC extrapolated in time (paper II)

Paper II addresses the impact of climate change on organic carbon in lakes. Alterations in precipitation patterns and temperature are first order elements in climate change. According to the findings in paper I, both parameters were significant drivers for the amount of DOC in lakes, but their combined importance was dwarfed by NDVI. Climate change projections do not relate directly to NDVI, but it seemed reasonable to assume that NDVI is dependent on temperature and precipitation. Based on this, we extracted values on NDVI, temperature and precipitation from all REGINE-catchments and were able to establish a model for NDVI. The model was fairly simple (a quadratic response surface with 8 parameters, R^2 = 0.78, 17 335 degrees of freedom), and explained 78% of the variation in NDVI with annual precipitation and mean temperature as predictor variables. The model demonstrated that NDVI was consistently increasing with temperature. Increases in the low range of precipitation were also translated into increased NDVI, while high amounts of precipitation would have the opposite effect, especially at low temperatures (which hints at this effect being due to prolonged snow-cover).

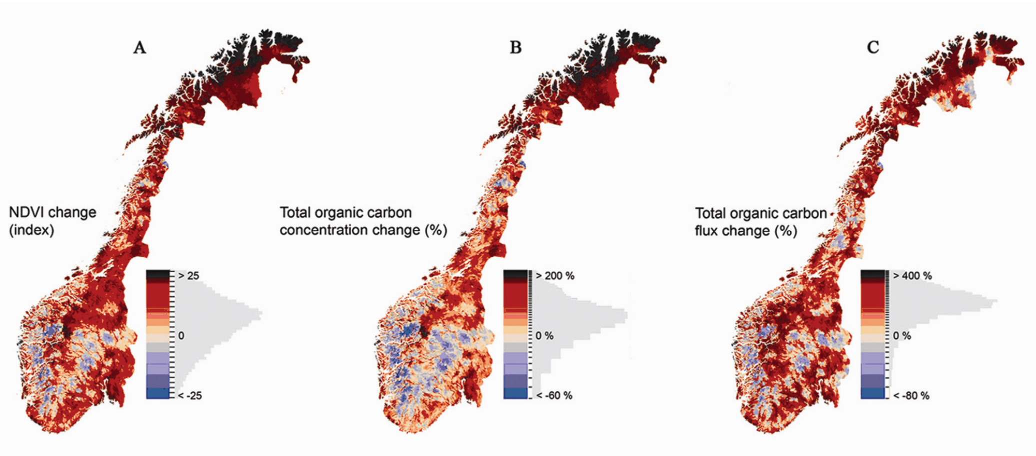

Figure 7: Regional patterns under climate change projections of NDVI, DOC, and DOC flux in Norway, based on fitting a linear model to data from 1000 lakes, and extrapolating to the >20 000 non-sampled catchments in the same area. A) projected change in NDVI (% of current); B) projected change in total organic carbon (% of current); C) projected change in total organic carbon flux (% of current).

The DOC model developed in paper I was refined and optimized for climate variables by removing low impact parameters which were not related to climate change. The final model which explains ~80% of the observed variation in DOC contained the variables runoff, NDVI, temperature, and wetland coverage (i.e. bogs).

The Norwegian Water Resources and Energy Directorate (NVE) provided us with downscaled climate projections for runoff, precipitation and annual mean temperature (based on the IPCC B2 scenario). The geographical patterns of NDVI projections were as expected:

increasing precipitation at high altitudes (where temperature is low) resulted in declining NDVI values, while there otherwise was a general increase in NDVI. Now we had everything needed to elucidate the impact of climate change on concentration and fluxes of DOC.

The projections from the climate-optimized DOC-model demonstrated that even under this moderate scenario, changes in climatic variables would have severe impacts on the organic carbon in lakes (figure 7). In summary, the study projected that the median lake DOC would be expected to increase from 2.0 to 3.2 mg C L^{-1} – a dramatic 65% increase. Increases in lake DOC were inversely related to projected changes in runoff, yielding an estimated 28% overall increase in DOC export.

These findings are relevant for boreal lakes in general and demonstrate significant consequences of climate change that concern both ecosystem functioning and human water utilization. Thus, we demonstrated that changes in climatic variables will have severe impacts on organic carbon in lakes, but to what extend does DOC explain the CO_2 super-saturation in boreal lakes? This question is addressed in paper III.

3.3 DOC, a global predictor for pCO2? (paper III)

Generally speaking, circum-boreal lakes are supersaturated in CO_2, which means that they are net sources of CO_2 to the atmosphere. Consensus is building that in-lake mineralization of allochtonous DOC is the main source of water column CO_2, but some studies suggest that other factors, such as inflow of groundwater supersaturated in CO_2, are of equal importance (Humborg, 2009, Rantakari & Kortelainen, 2008). Furthermore, the correlation between DOC and pCO_2 is inconsistent among studies from different regions, but it should be noticed that statistical methods also differed between studies.

The study presented in paper III addresses these issues and includes a wider range of predictor variables for pCO_2. We took direct measurements of pCO_2 in 112 lakes and also sampled them for a range of in-lake water chemistry parameters (total phosphorus, total nitrogen, chlorophyll, pH, and sulfate). One essential advantage of using partial pressure of gases to evaluate lake metabolism is that it integrates all metabolic and chemical processes in the lake. We also gathered information on physical lake properties (surface area, altitude, depth, drainage area ratio), and watershed characteristics (runoff, annual air temperature, NDVI, slope, and the catchment proportions of bog, forest and farmland). With this broad range of inputs, it was possible to study the relative importance of in-lake processes, physical properties and watershed characteristics on the pCO_2 in lakes.

First we addressed the issue of how to model correlations between DOC and pCO_2. We found that the most adequate approach was to model pCO_2 as a linear function of DOC without forcing pCO_2 to approach zero with zero DOC. To account for the heteroscedasticity in the data, without compromising the assumption of linearity, we used a generalized linear model (GLM-model) with a gamma distribution and an identity link function for the independent variables. The general approach has been to log-transform both variables (to attain homeoscedasticity in the data set), which models the correlation as a power function model and also entails that pCO_2 should approach zero with DOC (figure 8) (see paper III for details). Our approach is in agreement with a priori knowledge, which dictates that even if a lake is totally devoid of DOC or any biochemical processes it would still contain some CO_2 due to equilibration with the atmosphere.

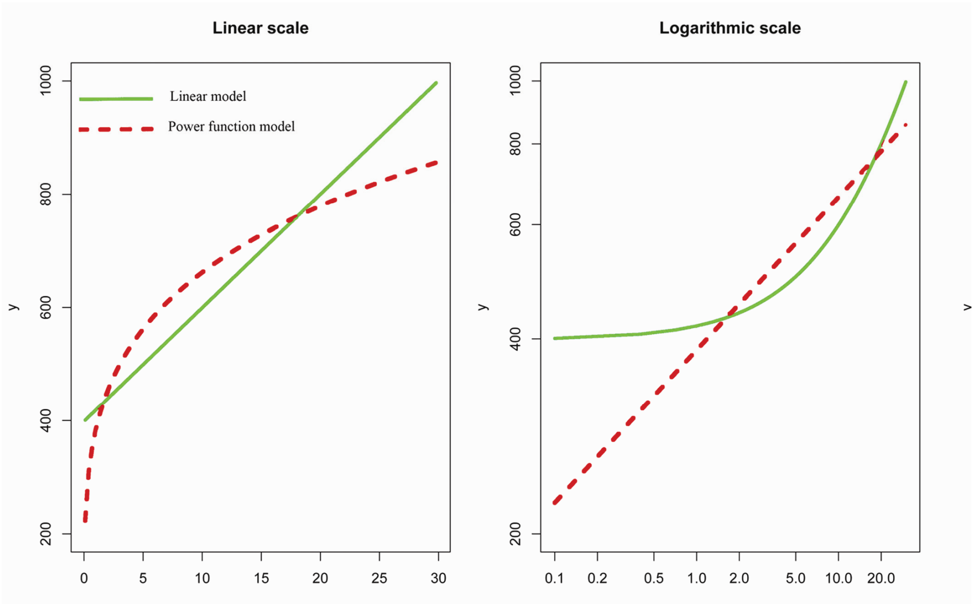

Figure 8: Visualization of linear and power function models on two different scales. The linear model (green solid line) is a straight line on a linear scale (left pane) while it displays curvature horizontal asymptote on a logarithmic scale (right pane). The power function model (red punctured line) displays a curvature on a linear scale, but is a straight line on a logarithmic scale. A model of log-transformed values of pCO_2 modeled as a linear function of log-transformed values of DOC is consistent with the red line in the right panel. This implies that the relation has a vertical asymptote at the origin on a linear scale.

The data analysis revealed that DOC was, by far, the most influential predictor variable of lake pCO_2 (R^2 = 0.73, n = 112). For comparison, variables related to the influence of groundwater explained 27% of the variation in pCO_2, which clearly demonstrated that groundwater influence was comparatively low for the lakes in this study.

The comparison between the different modeling approaches revealed that the GLM was considerably more robust regarding the range of input data, and that differences between models from different regions could be due to the modeling approach (figure 9).

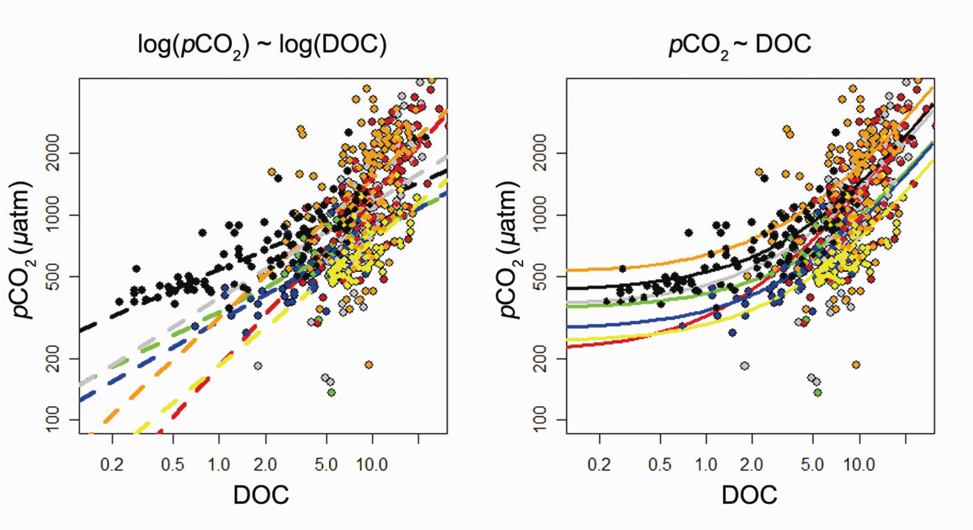

Figure 9: The relation between literature values of DOC and pCO_2. Left panel demonstrates that the power function approach generates models with a highly variable intercepts and slopes, while the right panel shows that the identity link gamma-GLM approach reduces the apparent dissimilarity between models based on data from different regions. Green lines: del Giorgio (1999); red lines: Sobek (2003); blue lines: Jonsson (2003); yellow lines: Roehm et al. (2009)black lines: This study, orange lines: Humborg et al. (2009); grey lines: all data

3.4 The stoichiometry of watershed fluxes (paper IV)

As discussed above, DOC per se is a significant factor for ecosystem functioning, but the relative concentration of C to other nutrients affects the nature of elemental limitation which has consequences for community composition and for lake ecosystem functioning.

In paper IV we study how catchment properties affect the ratios and export fluxes of C, N, P and Si. We used GIS and remote sensing data for obtaining a range of key catchment properties for ~1000 lakes with known concentrations of C, N, P and Si.

We found that terrestrial productivity, N deposition, climate and a few key catchment properties (e.g. proportion of the catchment composed of bogs) explained a major fraction of the variability of element export to surface waters. Since the different predictor variables affect element exports in different ways, they also have profound effects on the stoichiometry of the key elements in lakes (figure 10).

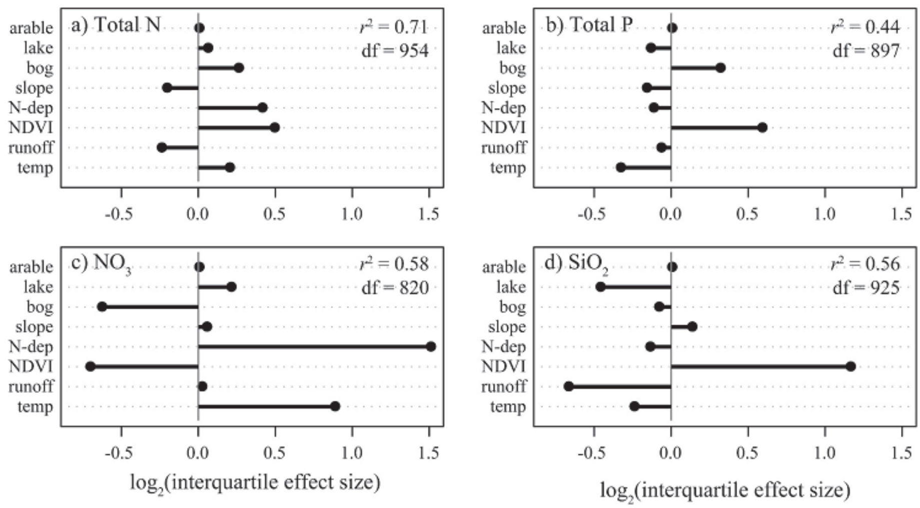

Figure 10: Effect size plots for the independent variables in regression models of lake-water concentrations of a) total N, b) total P, c) NO_3, and d) SiO_2. Effect sizes are computed as regression coefficients x interquartile ranges of the different independent variables. "arable", "lake" and "bog" is the fraction of catchment area covered with farmland, lake surface and bogs, respectively, while "temp" is mean annual air temperature.

Precipitation contains virtually no P, Si or organic N, such that areas with high precipitation levels had significantly lower amounts of these elements in their surface waters. Thus, precipitation acts as a dilution factor for most elements, but since precipitation also functions as a vector for atmospheric NO_3 deposition there is a positive correlation between runoff (which depends on precipitation) and lake water NO_3 concentration

This study demonstrated that changes in catchment properties, such as percentage of bog and forest cover, and weathering rates, will regulate the flux and fate of C, N, P, and Si in catchments on a long-term scale. On a shorter time scale (years to decades), changes in precipitation and temperature, as well as anthropogenic influences on the biogeochemical cycle (e.g. atmospheric N and S deposition), will dominate the stoichiometry of element fluxes in watersheds. This study focused on the drivers for elemental ratios in lakes with fairly pristine catchments. In more cultivated regions the signal from N deposition will be less significant. In any case, it may be hard to distinguish the intertwined responses and interactions of these drivers directly in the catchments, but down-stream lakes will pick up and integrate these stoichiometric signals.

The studies described so far have considered different compartments of the cycling of carbon in and out of lakes and revolved around studies of Norwegian lakes, which can be considered representative for circum-boreal lakes in general. Paper V expands this scale and integrates the interactions between lakes and the global carbon cycle.

3.5 The role of lakes in the global carbon cycle (paper V)

Paper V is mainly based on a compilation of studies worldwide and offers a synthesis where we examine the general mechanisms influencing the flux, fate, and transformation of lake carbon in the different biomes of the world. Using available literature, we explored the role of lakes in global carbon cycling and reviewed the mechanisms affecting carbon pools and transformations in lakes. This led to a revision of the "the active pipe" concept (figure 11), which argues that lakes and rivers are not merely transport vectors for terrestrial DOC. Instead, inland waters should be considered as reactors which actively control the fate of the imported carbon. According to our revision, two thirds of the carbon entering lakes and rivers are either stored in lake sediments or emitted to the atmosphere. For comparison, the amount of carbon emitted from inland waters to the atmosphere is similar in magnitude to the net production of the global terrestrial ecosystem, and equal in scale to the uptake of CO_2 by the oceans. Furthermore, the global sedimentation of organic carbon in lakes exceeds organic carbon sequestration on the ocean floor. The scale of lake induced perturbations clearly signifies that the concept of the active pipe should be incorporated into current models of the global carbon cycle.

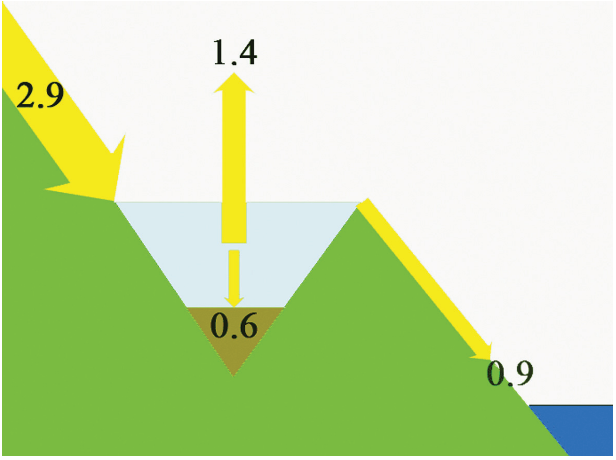

Figure 11: Values represent annual transport of C (Pg), based on a revision of the "active pipe" (Cole, 2007). Lakes receive 2.9 Pg C yr^{-1} from the terrestrial environment. 1.4 Pg C is emitted from lakes to the atmosphere, while 0.6 Pg C ends up in lake sediments. 0.9 Pg C yr^{-1} (or ~30 %) of the total pool of C entering lakes are exported to the oceans.

The investigations discussed above led to further discussions about the future role of lakes in the biosphere. We considered how the fate of carbon in the lakes is expected to adjust in reaction to climate change and human activities. The ongoing construction of impoundments, which accumulate large quantities of carbon in sediments, will likely increase the global in-lake carbon dioxide and methane production of which a large part is emitted to the atmosphere. We thus expect that inland water will add strong positive feedback effects to current projections of the future climate system.

The review validates the importance of the previous studies. Lakes are dynamic and important regulators of the global carbon cycle and climate. Without a comprehensive understanding of the flux and fate of carbon in lakes we cannot adequately and proactively manage the challenges imposed upon lake biota, and the rest of us, by future climate change.

4. MAIN FINDINGS

Paper I establishes NDVI as the key parameter for predicting DOC in lakes. This is a novel finding, but the causal connection is consistent with a priori understanding. NDVI data are available with global coverage and with time series covering decades. Our study thus provides new research tool, not only for the carbocentric limnologist (see Prairie, 1998), but for all research fields which consider the flux of carbon through ecosystems.

Paper II is, to our knowledge, the first study which, based on empirical studies, indicates strong impacts of climate change on DOC concentrations in and fluxes through lakes. We face a future with browner lakes which will have far-reaching consequences for ecosystem productivity, for fluxes of organic bound heavy metals and organic pollutants, and for human use of surface waters.

Paper III provides a piece of the puzzle of CO_2 super-saturation in inland waters, and identifies DOC as the causal driver of pCO_2 in Norwegian lakes. Additionally, and maybe more importantly, we demonstrate that the apparent inconsistencies between the numerous studies in the field might be alleviated by applying an alternative modeling approach, which is also more consistent with a priori knowledge.

In Paper IV we present the first assessment of the combined impact of human alterations of biogeochemical cycles and climate change on the stoichiometry of watershed flux. Lakes are valuable sentinels for detecting global changes. We apply a novel approach, which should be relevant to boreal lakes in general.

Paper V provides a revised estimate of the flux, mineralization and sequestration of carbon in lakes worldwide, which clarifies the significant role of lakes for the fate of carbon. The synthesis emphasize the role of lakes as important regulators of the global carbon cycle and climate.

5. FUTURE PERSPECTIVE

The demonstration of the close connection between NDVI and organic carbon in lakes is promising. A first natural step would be to extend the scope beyond the Norwegian borders, which are irrelevant for the boreal ecosystem. Our approach requires a relatively small investment in terms of workload since comparable lake survey datasets are available for lakes in Finland and Sweden. This could not only validate the method outlined in this thesis, but also increase our knowledge on current and future flux of carbon through boreal ecosystems.

With just two parameters, our model explained the major fraction of NDVI variation, but additional research is required to assess the regional validity of this model. Though we expect that the model needs to be calibrated for different biomes, it seems reasonable to assume that precipitation and temperature are significant for the vegetation density on a global scale. If this holds true, it would also allow us to estimate global changes in NDVI from climate projections. Thus, combining NDVI with the flux of carbon through lakes could provide us with a valuable tool for global scale evaluations of organic carbon in lakes and increase our understanding about an important part of the global carbon cycle.

Our modeling approach to the correlation between pCO_2 and DOC suggested an answer to the inconsistencies observed between studies worldwide. Future research should aim to compile available data from different regions and use our method to investigate if the apparent difference in the nature of DOC among regions is real or a result of statistical methodology.

The interplay between lakes, catchments and the atmosphere demonstrated here clarifies the need to bridge the gap between aquatic and terrestrial sciences. This would deepen our knowledge of causes and effects of ecological processes in general, and their consequences for the flux of energy and matter in particular. For example, paper IV showed that terrestrial N deposition yielded lower lake concentrations of P. It is intriguing to speculate about the cause behind the observation. A hypothesis could be that: *increased N deposition translates into increased terrestrial biomass production. Though terrestrial biomass has relatively low C to P ratio, the increase in biomass is bound to sequester some amount of P and the signal reverberates to the flux of P through lakes and rivers.* A test of the hypothesis requires the combined efforts from the fields of limnology and terrestrial vegetation ecology.

6. CONCLUSION

We demonstrated that lake DOC values can be interpolated in space (paper I) and extrapolated in time (paper II). We established DOC as the key determinant for lake pCO_2 and provided a new modeling approach, which is consistent with a priori knowledge and may alter the understanding of regional differences in the nature of DOC (paper III). We also clarified the impact of human alterations of biogeochemical cycles on the flux of energy (i.e. C) and matter through a boreal ecosystem (paper IV). Lastly, we signified that lakes are important regulators of the global carbon cycle and climate (paper V).

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