

Carbon metabolism in clear-water and brown-water lakes

Jenny Ask



Department of Ecology and Environmental Science
Umeå University
901 87 Umeå
Umeå 2010

Copyright©Jenny Ask

ISBN: 978-91-7264-954-5

Frontcover: Marina Becher (*a sediment core from a clear-water lake*)

Backcover: Jenny Ask (*sediment cores from a brown-water lake*)

Printed by: VMC-KBC

Umeå, Sweden 2010

Till Per och Orvar

LIST OF PAPERS

This thesis is a summary of the following papers that are referred to in the text by their Roman numerals:

- I. **Ask, J.**, J. Karlsson, L. Persson, P. Ask, P. Byström and M. Jansson (2009). Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. *Ecology* 90: 1923 – 1932.
- II. Karlsson, J., **J. Ask** and M. Jansson (2008). Winter respiration of allochthonous and autochthonous organic carbon in a subarctic clear-water lake. *Limnology and Oceanography* 53: 948 – 954.
- III. **Ask, J.**, J. Karlsson, L. Persson, P. Ask, P. Byström and M. Jansson (2009). Terrestrial organic matter and light penetration: Effects on bacterial and primary production in lakes. *Limnology and Oceanography* 54: 2034 – 2040.
- IV. **Ask, J.**, J. Karlsson and M. Jansson. Net ecosystem production in clear-water and brown-water lakes. *Manuscript*.

Papers I, II and III are reproduced with kind permission from Ecological Society of America (I) and American Society of Limnology and Oceanography (II, III).

Table of Contents

Introduction	7
Pelagic production	7
Benthic production	9
Respiration and metabolic balance	11
Aims	12
Study area	13
Methods	14
Results and discussion	15
Autotrophic basal production	15
Heterotrophic basal production	17
Whole-lake metabolic balance	18
Concluding remarks	20
Acknowledgements	20
Sammanfattning (Swedish summary)	20
References	23
Tack!	30

Abstract

The trophic state of lakes is commonly defined by the concentration of nutrients in the water column. High nutrient concentrations generate high phytoplankton production, and lakes with low nutrient concentrations are considered low-productive. This simplified view of lake productivity ignores the fact that benthic primary producers and heterotrophic bacteria can be important basal producers in lake ecosystems.

In this thesis I have studied clear-water and brown-water lakes with respect to primary production, respiration and bacterial production based on allochthonous organic carbon. These processes were quantified in pelagic and benthic habitats on temporal and spatial scales. I also calculated the net ecosystem production of the lakes, defined as the difference between gross primary production (GPP) and respiration (R). The net ecosystem production indicates whether a lake is net heterotrophic ($GPP < R$), net autotrophic ($GPP > R$) or in metabolic balance ($GPP = R$). Net heterotrophic lakes are sources of carbon dioxide (CO_2) to the atmosphere since respiration in these lakes, by definition, is subsidized by an external organic carbon source. External organic carbon is transported to lakes from the terrestrial environment via inlets, and can serve as a carbon source for bacteria but it also limits light availability for primary producers by absorbing light.

On a seasonal scale, four of the clear-water lakes studied in this thesis were dominated by primary production in the soft-bottom benthic habitat and by respiration in the pelagic habitat. Concentrations of dissolved organic carbon (DOC) were low in the lakes, but still high enough to cause the lakes to be net heterotrophic. However, the lakes were not low-productive due to the high production in the benthic habitat. One of the clear-water lakes was studied also during the winter and much of the respiration under ice was supported by the benthic primary production from the previous summer. This is in contrast to brown-water lakes where winter respiration is suggested to be supported by allochthonous organic carbon.

By studying lakes in a DOC gradient (i.e. from clear-water to brown-water lakes) I could draw two major conclusions. The lakes became less productive since benthic primary production decreased with increasing light extinction, and the lakes became larger sources of CO_2 to the atmosphere since pelagic respiration was subsidized by allochthonous organic carbon. Thus, lake carbon metabolism can have an important role in the global carbon cycle due to their processing of terrestrial organic carbon and to their possible feedback effects on the climate system.

Keywords: clear-water lakes, brown-water lakes, primary production, bacterial production, benthic, pelagic, net ecosystem production, allochthonous organic carbon, CO_2 , DOC

Introduction

A general opinion concerning lakes and lake productivity is that phytoplankton form the base of the foodweb and are limited by phosphorous. Almost every textbook in limnology demonstrate positive correlations between phosphorous in the water column and pelagic chlorophyll or primary productivity. The view of phosphorus-limited, phytoplankton dominated lakes is also reflected by the fact that the study by Schindler (1977), which stresses that primary productivity in lakes depends on phosphorous, is one of the most cited papers in limnology (over 1000 citations in Web of Science ©). However, this view is far from general when considering that it ignores other nutrients than phosphorous, primary producers that are not phytoplankton, and heterotrophic bacteria. Recent research shows that phytoplankton in natural oligotrophic lakes are limited by nitrogen (Bergström & Jansson 2006, Elser *et al.* 2009). Also the opinion that the dominant pathway of energy in lakes is via pelagic primary producers is eroding (Reynolds 2008, Karlsson *et al.* 2009) since both periphytic algae and heterotrophic bacteria can be important mobilizers of energy for higher trophic levels in oligotrophic lakes.

Pelagic production

Primary production in lakes is the process where aquatic plants are using solar energy and nutrients to transform inorganic carbon into biomass. This process is fundamental in aquatic ecosystems, mainly since phytoplankton has been regarded as the main food source for higher trophic levels (Reynolds 2008 and references therein). Nutrients have been recognized as a limiting factor for pelagic primary production (Wetzel 2001) since they mostly occur in low concentrations and almost always increase primary production when added to lake water (Schindler 1977, Jansson *et al.* 1996, Jansson *et al.* 2001). Lakes are classified based on nutrient concentrations, and lakes with high levels of nutrients and phytoplankton are termed eutrophic. Light is crucial for the photosynthetic process and primary production increases linearly with light during short-term incubations, but experiences photoinhibition at high light intensities during long-term light exposure (Harris & Piccinin 1977). Temperature also increases primary production, provided sufficient light and nutrients concentrations are at hand, until reaching optimal levels (Harris & Piccinin 1977, Davison 1991). However, algae are found in many environments, including ice (Haecky & Andersson 1999), and different species have different temperature optima (DeNicola 1996) indicating that temperature *per se* is not as limiting as light or nutrients. It is suggested that dissolved organic carbon (via light extinction, Jones 1992, Jansson *et al.* 2000) and grazing pressure (Carpenter

et al. 1998) are the main factors, besides nutrients, determining pelagic primary production in lakes.

However, heterotrophic bacteria have been convincingly shown to be important basal producers in lake foodwebs (Salonen 1981, Hessen 1985, Tranvik 1989, Jansson *et al.* 2000), supporting a significant part of the zooplankton biomass in both humic and clear-water lakes (Hessen *et al.* 1990, Karlsson *et al.* 2003). Heterotrophic bacteria can use both autochthonous and allochthonous organic carbon as an energy and carbon source. Autochthonous organic carbon is produced within the lake by primary production and is available for bacteria via algae exudates (Cole *et al.* 1982, Baines & Pace 1991), via “sloppy feeding” by grazers (Lampert 1978), and via biomass degradation. Autochthonous organic carbon is generally thought to be highly available for bacteria, and bacterial production is often positively correlated to chlorophyll (White *et al.* 1991) or primary production (Cole *et al.* 1988) in the lake water. Allochthonous organic carbon originates from primary production in the terrestrial environment and is transported to lakes via inlets, groundwater and/or superficial run-off (Hope *et al.* 1994, Laudon *et al.* 2004). A major part of the dissolved organic carbon (DOC) pool in unproductive lakes are of terrestrial origin (Jones 1992, Karlsson *et al.* 2003) and the input of available allochthonous organic carbon for pelagic bacteria will ultimately depend on the source of the terrestrial carbon and the hydrology in the catchment. Allochthonous organic carbon is composed of a mixture of low-molecular weight (highly available) and high-molecular weight (highly refractory) compounds, that are more or less coloured (McKnight & Aiken 1998). The potentially low availability of allochthonous organic carbon is compensated by high concentrations (Tranvik 1988), and positive correlations between DOC and bacterial biomass (Hessen 1985, Tranvik 1989) and bacterial production (Jansson *et al.* 2000, Karlsson *et al.* 2001) are common in oligotrophic lakes.

The bacterial use of different types of carbon has implications for the role of bacteria in lake foodwebs (Jansson *et al.* 2007). Bacteria using autochthonous organic carbon are recycling organic carbon that has already been mobilized by photosynthesis (Fig. 1). This process, i.e. the microbial loop (Azam *et al.* 1983), does not mobilize new organic carbon for the foodweb. In contrast, bacteria using allochthonous organic carbon for growth (Fig. 1) introduces new organic carbon into the lake foodweb (Tranvik 1988), thereby serving as energy mobilizers or basal producers analogous to algae (Jones 1992, Jansson *et al.* 2000). The access to an external carbon source also means that bacteria no longer have to rely on phytoplankton for growth, and the decoupling from phytoplankton also means that pelagic bacteria become effective competitors for nutrients (Vadstein 2000, Blomqvist *et al.* 2001).

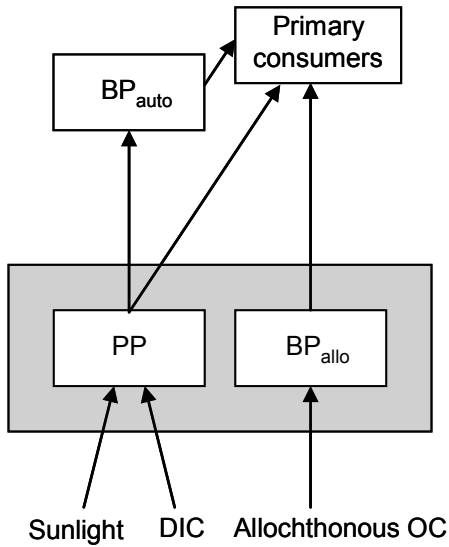


Figure 1. New biomass production, or energy mobilization, (shaded area) is the sum of primary production (PP) and bacterial production based on allochthonous organic carbon (BP_{allo}). BP_{auto} is the bacterial production on autochthonous organic carbon (in the microbial loop) and was calculated from the part of the primary production available for bacteria and the bacterial growth efficiency on autochthonous organic carbon (see Appendix A, paper I). Redrawn from paper I.

Benthic production

By far the most common way of assessing lake productivity is by measuring pelagic primary production thereby disregarding benthic algae and bacteria (Vadeboncoeur *et al.* 2002). However, a majority of lakes world-wide are small (Downing *et al.* 2006) with potentially large areas suitable for growth of benthic algae. Benthic algae, or periphyton, are classified based on the substrate on which they grow (Kalff 2002). Epipelton (growing on sediments) is fundamentally different from epiphyton (growing on plants), epilithon (growing on rocks), epipsammon (growing on sand) and epixylon (growing on wood) etc, since the epipelton has access to the nutrients stored in the sediments (Jansson 1980, Bonilla *et al.* 2005). Pore waters can contain nutrients at concentrations one to several magnitudes higher than in the lake water (Enell & Löfgren 1988). Hence, other factors than nutrients, such as temperature, light or inorganic carbon, are the major regulating environmental variables for epipellic production. Grazing has, to my knowledge, not been shown to strongly regulate epipellic production although it is an important structuring factor for epilithic production (Hillebrand & Kahlert 2002). Epipelton and epipellic production will henceforth be denoted as benthic algae and benthic production, respectively.

It has been shown in both experiments and field surveys that benthic algal production and biomass do not increase following nutrient additions (Björk-Ramberg 1984, O'brien *et al.* 1992, Vadeboncoeur *et al.* 2001, Bonilla *et al.* 2005) or correlate with water column nutrients (Vadeboncoeur *et al.* 2003, Vadeboncoeur *et al.* 2006). Other types of periphyton, such as epilithon or epixylon, do increase with nutrients in the same manner as

phytoplankton (Blumenshine *et al.* 1997, Vadeboncoeur *et al.* 2001) thus emphasizing the fundamentally different character between epipelon and other types of periphyton. Boundary-layer effects may be more pronounced for attached algae or macrophytes than for phytoplankton, although many plants display different compensation strategies to overcome this constraint (Sand-Jensen & Borum 1991, Kalff 2002). Instead, benthic algal production has been shown to be controlled by light availability (Hansson 1992, Vadeboncoeur & Lodge 2000, Liboriussen & Jeppesen 2003) or light and temperature (Stanley 1976, Sorsa 1979, Björk-Ramberg 1983).

Whole-lake (i.e. both pelagic and benthic) primary production is rarely considered, but in clear-water lakes benthic primary production can be substantially higher than pelagic primary production (Welch & Kalff 1974, Björk-Ramberg & Ånell 1985, Vadeboncoeur *et al.* 2003, Andersson & Kumblad 2006). Clear-water lakes are thus not as unproductive as previously thought, and phosphorous might not be such a strong predictor of lake primary production as pelagic studies indicate (Vadeboncoeur *et al.* 2003). It can be hypothesized that benthic primary production will respond negatively to an increased input of allochthonous organic matter due to decreasing light availability at the lake bottoms. The magnitude of this decrease, and whether or not it will be compensated for by other basal production modes, has not been studied previously.

Pelagic bacteria are frequently measured in studies of lakes, but benthic bacteria are seldom considered on a whole-lake scale. That benthic bacteria often substantially outnumber pelagic bacteria has been shown in both lakes and rivers (Schallenberg & Kalff 1993, Fischer & Pusch 2001, Wetzel 2001), and higher densities of bacteria usually have a larger proportion of active cells (Haglund *et al.* 2002). Fischer & Pusch (2001) showed that benthic bacterial production was higher in a river with low input of allochthonous organic matter compared to a river with high allochthonous input (Findlay *et al.* 1986). They also came to the conclusion that temperature, oxygen availability and quantity and quality of organic matter are important structuring factors for benthic bacterial production (Fischer & Pusch 2001 and references therein). On hard substrates, algae and bacteria are tightly coupled (Carr *et al.* 2005) and bacteria did not outcompete algae for nutrients even when supplied with an external carbon source (Rier & Stevenson 2002). Hence, nutrient limitation or nutrient competition between algae and bacteria are unlikely in sediments of aquatic systems. The few studies that are available for lakes show that benthic bacteria make a substantial contribution to whole-lake production (Brunberg *et al.* 2002). However, to what extent benthic bacteria use autochthonous or allochthonous organic carbon in lakes and how this scales to whole-lake basal production in different types of lakes is virtually unknown.

Respiration and metabolic balance

Bacterial respiration, considered to be the major contributor to community respiration in unproductive lakes (Pace & Cole 2000, Biddanda *et al.* 2001, Roberts & Howarth 2006), seems to be more regulated by the quantity of organic carbon than by its quality (Berggren *et al.* 2009b, a). Indeed, there is a strong correlation between pelagic respiration and DOC (Hanson *et al.* 2003), but in many cases also with chlorophyll, temperature and nutrients (Pace & Prairie 2005). What controls benthic respiration in lakes is far less studied than what controls pelagic respiration (Pace & Prairie 2005), although oxygen concentrations and temperature (Graneli 1978, Baulch *et al.* 2005) and lake (pelagic) productivity are discussed as important factors (Pace & Prairie 2005). The contribution of benthic respiration to whole-lake respiration is not straight forward. Some studies show that benthic respiration is highly important (Welch & Kalff 1974, Kortelainen *et al.* 2006), whereas others find pelagic respiration to be the most important contributor to whole-lake respiration (den Heyer & Kalff 1998, Algesten *et al.* 2005). The differing results may be due to the depth of lakes, since benthic respiration will be more important in shallow lakes (den Heyer & Kalff 1998), or to the amount of benthic primary production. However, the coupling between benthic respiration and benthic primary production needs further evaluation.

Respiration (of all organisms) and primary production determine the metabolic balance of lakes. This balance is defined as the difference between gross primary production (GPP) and community respiration (R), and the net ecosystem production can thus be calculated as $NEP = GPP - R$ (del Giorgio *et al.* 1999). Negative net ecosystem production values indicate that a lake is net heterotrophic and thus also a source of CO_2 to the atmosphere (Cole *et al.* 1994), whereas positive values indicate net autotrophy. Most lakes worldwide are indeed net heterotrophic (Kling *et al.* 1991, del Giorgio *et al.* 1999, Prairie *et al.* 2002, Jonsson *et al.* 2003), which, by definition, means that respiration is subsidized by allochthonous organic carbon. However, net heterotrophy is often indicated by the partial pressure of CO_2 (pCO_2) (Cole *et al.* 1994) and using pCO_2 can be biased by external inputs of CO_2 -rich water (Riera *et al.* 1999, Stets *et al.* 2009) or photo-oxidation of terrestrial organic carbon (Graneli *et al.* 1996). A compilation of world-wide estimates of pCO_2 in lakes reveal positive correlations with lake water concentrations of DOC (Roehm *et al.* 2009), which indirectly emphasizes the bacterial respiration of allochthonous organic carbon. Experimental studies also lend support to the direct connection between bacterial respiration of allochthonous organic carbon and CO_2 release from lakes (Lennon 2004).

Most studies (above) imply that the net heterotrophy of lakes is a result of bacterial respiration of allochthonous organic carbon in the pelagic habitat. However, the pCO_2 of lakes is the net result of metabolic processes

in all habitats and benthic processes also contribute to whole-lake metabolism (Lauster *et al.* 2006, Van de Bogert *et al.* 2007). However, direct and simultaneous measurements of the metabolic processes in the different habitats of lakes, scrutinizing between primary production and respiration in benthic and pelagic habitats, are still scarce and further efforts are needed.

An important consequence of net heterotrophy is that it denotes lakes as links between the terrestrial habitat and the atmosphere (Algesten *et al.* 2004, Cole *et al.* 2007) since respiration of terrestrial (allochthonous) organic carbon in lakes return terrestrially fixed CO₂ to the atmosphere (Cole *et al.* 1994). In this way, lakes can be a potentially important part of the global carbon cycle (Battin *et al.* 2009). The release of CO₂ from lakes to the atmosphere is often based on summer values, but lakes may be an even greater source of CO₂ to the atmosphere on an annual scale due to insignificant primary production during the winter. High CO₂ accumulation during winter has been observed in both clear-water and brown-water lakes (Kling *et al.* 1992, Striegl *et al.* 2001), and the magnitude of the CO₂ accumulation has been explained by the concentration of DOC in the lake water (Striegl *et al.* 2001). The carbon sources responsible for CO₂ accumulation during winter in clear-water lakes are yet to be discovered.

Aims

The overall objective of this thesis is to assess the contribution of different habitats and modes of basal production to whole-lake productivity and metabolic balance. The processes are studied in clear-water and brown-water lakes. In particular, I address the following questions:

- * What is the relative importance of autotrophic and heterotrophic basal production in pelagic and benthic habitats of clear-water lakes during the ice-free season?
- * What is the organic carbon source for respiration and the metabolic balance in a clear-water lake during winter?
- * How does the contribution of benthic basal production to whole-lake basal production change with increasing input of terrestrial organic matter?
- * How does the metabolic balance of lakes change with increasing input of terrestrial organic matter?

Study area

All of the studies included in this thesis were carried out in small lakes situated in the alpine and boreal regions of northern Sweden (Fig. 2). Four lakes in the Abisko (68°21' N, 18°49' E) region, Lakes Almberga, Tjabrak, Ruozutjaure and Vuorejaure, were used in a seasonal study in the summer of 2005. Sampling was continued in Lake Almberga also during the winter 2005/2006. Lakes Almberga and Tjabrak are situated in the sub-alpine vegetation belt and Lakes Ruozutjaure and Vuorejaure in the low-alpine belt and the lakes are surrounded by alpine birch forest or alpine heaths, respectively. Alpine lakes receive only little organic matter from the terrestrial environment due to the low terrestrial productivity and thus have very clear water with low nutrient concentrations, low organic carbon concentrations and high light penetration.



Figure 2. The locations of the study sites and pictures of typical lakes and lake water for each site. The four Abisko lakes are situated in the northernmost area.

Photos: Jenny Ask.

Eleven additional lakes situated in a natural climate gradient were studied during the summer of 2006 and 2007. These lakes, together with the original four lakes, spanned an altitude range of 772 m (993 – 221 m a.s.l.) along a north-southeast gradient from 68° to 63° Northern Latitude. The altitudinal range corresponded to a 15°C difference in midsummer (June – July) water temperature (7.5 – 22.5°C) and a 6.5°C difference in mean annual (1961 – 1999) air temperature (-4.5 – 2°C). Due to the warmer temperature, lakes at lower altitudes had a longer ice-free season (~170 days) than lakes at higher altitudes (~90 days). These climatic prerequisites drive the terrestrial primary production and export of DOC, resulting in low DOC concentrations at the cold end of the gradient and high DOC concentrations at the warm end. I will refer to this gradient as the DOC gradient.

Methods

The four lakes in the Abisko region were sampled on five occasions during the summer of 2005 (**I**) and Lake Almberga was also sampled once a month during the winter season of 2005/2006 (**II**). The additional eleven lakes were only measured once during midsummer (June or July) in 2006 or 2007, and midsummer values from the four Abisko lakes were also included in the gradient studies (**III**, **IV**). The same sampling protocol was followed for all lakes if not stated otherwise. Water samples representative for the whole water volume were taken for standardized analyses of DOC, nitrogen, phosphorous, absorbance and bacterial production (**I-IV**). To get an independent measure of the light availability in the lakes we measured the PAR at several depths from the surface to the greatest depth of the lake. From the light-depth relationship we calculated the light extinction coefficient (k_d). We also measured pelagic primary production (**I-IV**), respiration (**I**, **II**, **IV**) and $p\text{CO}_2$ (**IV**). Soft bottom benthic primary production (**I-IV**) and respiration (**I**, **II**, **IV**) were measured by collecting intact sediment cores from 5 or 6 different depths and incubating the cores with or without a dark outer cover. The cores were incubated at the depth of collection for ca 24 hours. Respiration (R) was calculated as the production of dissolved inorganic carbon (DIC) in the dark cores over the incubation period ($R \triangleq \Delta\text{DIC}_{\text{dark}}$) whereas gross primary production (GPP) was calculated as the difference in DIC change between the light and dark cores over the incubation period. Net ecosystem production, which determines the net metabolic balance, was calculated as $\text{NEP} = \text{GPP} - R = \Delta\text{DIC}_{\text{light}}$. In the four Abisko lakes artificial stone discs were placed out during the summer of 2006 for estimation of epilithic algal growth and of primary production and

respiration in the near-shore stony area (**I**, **III**, **IV**). Benthic bacterial production was measured at 3 (shallow, deep and intermediate) depths (**I**, **III**) and the method is described in paper **I**.

Stable carbon isotopes ($\delta^{13}\text{C}$) were used in order to determine the origin of carbon used for bacterial respiration (**I**, **II**). Values of $\delta^{13}\text{C}$ was measured on the DIC increase during incubation of water or a sediment core in dark respiration bottles or tubes. A Keeling plot (Karlsson *et al.* 2007) was used to determine the isotopic signal of respired CO_2 . Values were then compared to those of benthic algae or of a terrestrial signal.

All production values are given in ' $\text{mg C m}^{-2} \text{d}^{-1}$ ', which means that we have calculated a whole-lake mean for each type of production based on depth-volume-area relationships in each lake. From the measured values of primary production and bacterial production we calculated the basal productivity, or energy mobilization (**I**, **III**). Basal production, or energy mobilization, is the sum of primary production (PP) and bacterial production based on terrestrial organic carbon (BP_{allo}), i.e. the "production of new biomass" ($\text{PP} + \text{BP}_{\text{allo}}$). Primary production and bacterial production on allochthonous organic carbon are considered production of new biomass (Fig. 1) since these processes are introducing organic carbon into the foodweb that otherwise would have been unavailable for higher trophic levels.

Results and discussion

Autotrophic basal production

All four lakes in the Abisko region were very similar with respect to production (**I**), in spite of the fact that two of the lakes are situated in the alpine birch forest belt and the other two in the alpine heath belt (i.e. below and above the tree-line). There were some minor differences regarding DOC and nutrient concentrations between the lakes due to their different locations, although values were generally low and all four lakes are considered as clear-water oligotrophic lakes (table 1 in paper **I**). The only clear difference between the lakes was that the two lakes above the tree-line had significantly lower pelagic and epilithic primary production than the other two, following the trend of nitrogen concentration in the lake water. Nitrogen is often suggested to be the limiting nutrient for pelagic primary production in northern Swedish lakes (Bergström & Jansson 2006). The most striking similarity between the lakes was that the whole-lake production was completely dominated by benthic primary production throughout the summer season (Fig. 2 and Appendix B in paper **I**). Benthic primary production decreased with depth in all lakes, likely as a consequence

of the decreasing light (**I**). The dominance of benthic primary production and its decrease with depth has also been shown in other studies in the Abisko area (Björk-Ramberg 1983).

Pelagic primary production was very low compared to benthic primary production in the four Abisko lakes (Fig. 2 and Appendix B in paper **I**), and only contributed ca 7 % to whole-lake production. Our assumption was that pelagic primary production would increase in the DOC gradient due to the simultaneous increase in nutrients (**III**), which however was not the case (**III**, **IV**). Although the correlation between pelagic primary production and nutrients is well established in other studies we failed to see this. In fact, pelagic primary production was not correlated to any of the environmental variables measured. The possible reason for this result is that any positive effect following an increase in nutrients was cancelled out by the concomitant increase in light extinction (Jones 1992). In the lakes with the highest DOC, light as well as pelagic primary production was more or less absent below 1 – 2 meters, i.e. below the thermocline. This explanation is supported by comparing only epilimnion values which shows that brown-water lakes indeed displayed higher values of pelagic primary production than the clear-water alpine lakes (J. Ask unpubl. data).

For benthic primary production there was a clear decreasing trend in the DOC gradient (Fig. 3, **III**, **IV**). Benthic primary production is not thought to be limited by nutrients, with the exception of extremely high alpine lakes where nutrients are scarce in the sediments as well (Hansson 1992), and our data support this notion. We even found that benthic primary production was negatively correlated with nutrients (**III**, Karlsson *et al.* 2009). This is however not a causal relationship since nutrients are unlikely to have a negative effect on primary production, but an indirect effect of the simultaneous increase of nutrients and light extinction. Benthic algae are attached to the lake bottom and can not escape a decreasing light in the same manner as can phytoplankton (being part of the circulating water mass). Light availability at the lake bottom is however not only a function of water colour (measured by light extinction or absorbance) but also of lake morphometry. Indeed, benthic primary production was best explained by combining light extinction and mean depth of the lakes in a multiple regression analysis (**IV**). A shallow lake with clear water is thus expected to have very high benthic productivity whereas a brown deep lake is expected to have very low benthic productivity, with all possible combinations in between with varying values of productivities.

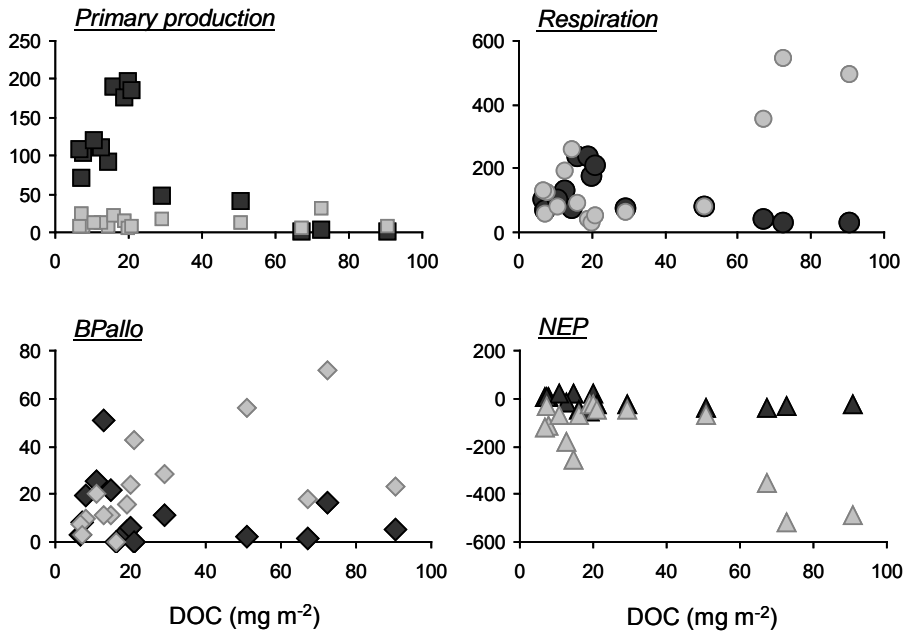


Figure 3. Some of the major results from this thesis showing the primary production, respiration, bacterial production on allochthonous organic carbon (BP_{allo}) and net ecosystem production (NEP) in benthic (dark grey symbols) and pelagic (light grey symbols) habitats in relation to lake water concentrations of dissolved organic carbon (DOC). Units on the y-axis are in 'mg C m⁻² d⁻¹'.

Heterotrophic basal production

Pelagic bacterial production (both BP_{allo} (Fig. 3) and total) increased in the DOC gradient (III, and unpublished), although only slightly and less than expected from earlier studies in the same type of gradient (Karlsson *et al.* 2005). This might be because of seasonal variations since only one sample was taken from each lake in the gradient. Pelagic bacterial production has been shown to vary quite much over the season at least in brown-water lakes due to varying qualities of the imported carbon, whereas it is quite stable in clear-water alpine lakes (I).

Benthic bacterial production decreased with depth in all four Abisko lakes, similar to but not as drastic as the benthic primary production (I). Benthic bacteria are often dependent on benthic algae as a source of carbon due to their close proximity in the microbial matrix on benthic substrates (Carr *et al.* 2005). For instance, benthic bacterial production often responds to light in the same way as benthic primary production (Scott *et al.* 2008). What also changed with depth was the source of organic carbon used for

bacterial growth. At shallow depths the benthic primary production was high enough to support about 90% of the benthic bacterial production, i.e. BP_{allo} was only about 10% of the total measured bacterial production (Fig. 3 in paper **I**). BP_{allo} increased with depth and was about 50% of the total measured bacterial production at the largest depths (Fig. 3 in paper **I**). The allochthonous source of organic carbon for benthic bacteria is likely a mixture of settling organic carbon of pelagic and terrestrial origin. Stable carbon isotope analyses support this calculation and reveal that a majority of the carbon respired in shallow sediments was derived from benthic algae, not only in summer (**I**) but also during winter (**II**). The carbon signal of the respired DIC (**II**) and that of the sediment (**I, II**) became more similar to the pelagic signal with depth.

On a whole lake scale, BP_{allo} in the benthic habitat was the second most important type of production in the four Abisko lakes (**I**). There was no clear trend for BP_{allo} in the DOC gradient (Fig. 3), although the highest values were found in Lake Almerga, Abisko (J. Ask unpubl. data). The contribution of total pelagic ($PP + BP_{\text{allo}}$) and total bacterial (pelagic + benthic) basal production to whole-lake production increased in the DOC gradient (**III**). This switch from benthic and autotrophic dominated systems in clear-water lakes to pelagic and heterotrophic dominated systems in brow-water lakes was mainly driven by the drastic decline in benthic primary production (**III**).

Whole-lake metabolic balance

Production of biomass was concentrated to the benthic habitats of clear-water lakes but the opposite was true for respiration (**I**). Pelagic respiration was equal to or slightly higher than benthic respiration (Fig. 3) but since the benthic respiration was balanced by an equally high benthic primary production the lakes were net heterotrophic (negative NEP values, **I**). Furthermore, benthic respiration decreased whereas pelagic respiration increased in the DOC gradient (Fig. 3, **IV**). Benthic respiration decreased in the same manner as benthic primary production (**IV**), showing that the benthic habitat was more or less in metabolic balance throughout the gradient. Since most of the dark respiration is assumed to be by heterotrophic bacteria this result indicates a tight coupling between benthic algae and benthic bacteria. In the pelagic habitat, on the other hand, respiration increased in the DOC gradient not at all following the pattern of pelagic primary production (**IV**). It can therefore be assumed that pelagic bacteria to a large extent depended on import of terrestrial organic carbon whereas benthic bacteria used the carbon produced by benthic algae, both for growth and respiration. Although this thesis does not provide any direct evidence for this, allochthonous organic carbon was shown to subsidize

respiration (**IV**) but was apparently not as available for benthic bacteria as it was for pelagic bacteria.

Respiration is the process where CO_2 is produced from an organic carbon source whereas primary production consumes CO_2 when producing organic carbon. Since CO_2 is one of the most important greenhouse gases in the atmosphere, the in-lake processes of respiration and primary production connect the lake to the atmosphere. And since respiration often is subsidized by terrestrially derived organic carbon (**IV**), respiration is also an in-lake process which forms a link between terrestrial systems and the atmosphere (Cole *et al.* 1994). Total respiration increased in the DOC gradient mainly due to the increase in pelagic respiration, whereas total primary production decreased mainly due to the decreasing benthic primary production. Since the benthic habitat was more or less in metabolic balance throughout the DOC gradient the increasing net heterotrophy along the gradient was mainly a result of increased respiration of allochthonous organic carbon in the pelagic habitat. The increasing net heterotrophy along the DOC gradient was also reflected in the increasing $p\text{CO}_2$ of the lakes (**IV**).

Lake Almberga is covered by ice for about 7 months and during this time the DIC concentration increased due to continuous respiration and no or low primary production (**II**). Winter respiration was quite low on an annual scale (26%, **II**); nevertheless this seldom studied process revealed some very interesting patterns. Respiration in Lake Almberga (as well as in the other three Abisko lakes) was dominated by pelagic respiration throughout the summer (**I**). Although total respiration decreased during the winter, there was a drastic shift from dominance of pelagic to a dominance of benthic respiration (**II**). As much as 80% of the winter respiration was due to benthic respiration, and about half of the carbon respired was from carbon produced by benthic algae the previous summer (**II**). This may not seem to add up since the benthic habitat of Lake Almberga was in metabolic balance during the summer, but 13% (i.e. half of the winter respiration which was 26% of total respiration) has to be considered to lie within the margin of error. Nevertheless, much of the carbon respired during winter is from carbon produced by algae the previous summer, and not from external sources as often suggested. The results obtained in Lake Almberga indicate that differences in net heterotrophy between brown- and clear-water lakes should be pronounced on an annual scale due to respiration of allochthonous organic carbon in brown-water lakes during winter (Striegl *et al.* 2001), while winter respiration in clear-water lakes was fuelled by autochthonous organic carbon.

Concluding remarks

In this thesis I present results showing that an increased input of DOC may significantly alter the metabolic processes of lakes via two distinct pathways. First, whole-lake primary production decreases in the DOC gradient due to the strong correlation between benthic primary production and light availability. Pelagic production could not compensate for the loss of benthic primary production, resulting in a decrease of whole-lake production. This conclusion could not have been drawn from a pelagic perspective alone. Second, lakes become more heterotrophic in a gradient of increasing DOC which is mainly caused by a simultaneous increase in pelagic respiration. Net heterotrophy, and subsequent release rates of CO₂ to the atmosphere, will therefore depend on terrestrial export of DOC which determines the respiration of this carbon in the lake water column.

Acknowledgements

Financial support for this thesis was given by the Swedish Research Council (VR) and Kempe Foundation to Mats Jansson, and by Abisko Scientific Research Station to Jenny Ask. The thesis is also a contribution from the strong research environment, Lake Ecosystem Response to Environmental Change (LEREC), financed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS).

Sammanfattning (Swedish summary)

Primärproduktion i sjöar är den process där vattenlevande växter använder ljusenergi och näring för att omvandla vatten och koldioxid till biomassa. I många typer av sjöar är alger de viktigaste primärproducenterna, och alger återfinns antingen som frilevande i den öppna vattenmassan (fytoplankton) eller som fastsittande (perifyton). Perifyton delas in i olika grupper beroende på underlaget de växer på; epifyton (på andra alger), epipelon (på sediment), epipsammon (på sand), epixylon (på trä) och epilithon (på sten). Fytoplankton är betydligt mer studerade än perifyton och sjöars trofiska status (d.v.s. hur produktiva de är på basnivå) beskrivs ofta med sambandet mellan mängden fytoplankton (ofta mätt som klorofyll eller primärproduktion) och näringshalten i vattnet. Sjöar med hög näringshalt i vattnet har hög primärproduktion av fytoplankton och detta samband har lett till slutsatsen att sjöar med låg näringshalt är lågproduktiva. Men det är sällan så enkelt. De flesta av världens sjöar är små och relativt grunda med

relativt klart vatten vilket innebär att en stor del av sjöars botten nås av ljus och därmed utgör ett lämpligt habitat även för perifyton, även kallade bentiska alger. Bentiska alger tas sällan med i bedömningen av sjöars produktivitet men studier visar att den bentiska primärproduktionen kan vara flera gånger högre än den pelagiala (fria vattenmassan). Detta gäller framförallt i klarvattensjöar, d.v.s. sjöar med låg näringshalt och låg pelagisk primärproduktion som i vanliga fall skulle klassas som lågproduktiva. Bentiska alger som lever på botten av sjöar har tillgång till de höga näringshalter som finns lagrade i sedimentet men eftersom de är fastsittande är de i stort behov av klart vatten så att ljuset kan tränga ner. Bentiska alger är alltså ljusbegränsade vilket innebär att så länge inget hindrar ljus från att komma ner till botten så växer algerna. De främsta orsakerna till skuggning av bentiska alger är hög primärproduktion av fytoplankton eller ett stort inflöde av ljusabsorberande ämnen från den terrestra omgivningen (t.ex. terrestert organiskt kol). Många sjöar i Sverige är starkt påverkade av högt inflöde av terrestert organiskt kol och är därför mer eller mindre bruna, vilket är en effekt av att terrestert organiskt kol till stor del består av brunfärgade ljusabsorberande humusämnen. I dessa sjöar är primärproduktionen låg. Istället spelar bakterier en stor roll för basproduktionen eftersom de kan utnyttja det terrestra kolet för tillväxt. Primärproduktion är en process som bildar syrgas och använder koldioxid medan respiration (alla organismer respirerar) använder syrgas och bildar koldioxid. Bakterier står för en stor del av den totala respirationen i sjöar och om de har tillgång till en extra kolkälla (som terrestert organsikt kol) innebär det att respirationen kommer att vara högre än primärproduktionen. När så är fallet kommer sjöar att släppa ut koldioxid till atmosfären, och därmed utgöra en potentiellt viktig del av den terrestra kolcykeln. I min avhandling har jag undersökt primärproduktion, bakterieproduktion och respiration i de bentiska och pelagiska habitatet i sjöar. Jag har använt mig av klara fjällsjöar och bruna skogssjöar (Figur 2) för att kunna visa på vilken typ av basproduktion som är viktig i dessa olika typer av sjöar.

Det jag har kommit fram till (sammanfattas i Figur 3) är att klara fjällsjöar är produktiva men i motsats till den vanliga uppfattningen om en produktiv sjö, så sker i stort sett all produktion på botten. Den mesta av denna bentiska produktion sker via alger, men även bentiska bakterier är av betydelse. Trots den höga bentiska primärproduktionen så var dessa sjöar nettoheterotrofa, vilket innebär att respirationen var högre än primärproduktionen. Respirationen var koncentrerad till det pelagiala habitatet. Klara fjällsjöar har därför en hög produktion av biomassa i det bentiska habitatet och hög koldioxidproduktion i det pelagiala habitatet. Trots att inflödet av terrestert kol var litet i dessa sjöar så var det tillräckligt stort för att upprätthålla hög respiration i det pelagiska habitatet. De bruna skogssjöarna var annorlunda jämfört med de klara fjällsjöarna. Eftersom de

är bruna så når inte ljuset ner mer än till 1-2 meter vilket resulterade i en i stort sett obefintlig bentisk primärproduktion. Även den bentiska bakterieproduktionen minskade medan den pelagiska produktionen (både av fytoplankton och av bakterier) var i stort sett oförändrad. Det som däremot ökade mest med ökande inflöde av terrestert kol var den pelagiska respirationen. Alltså avger bruna sjöar betydligt mer koldioxid till atmosfären än vad klara sjöar gör, och de har en betydligt lägre produktion av biomassa. I ett klimatförändringsperspektiv kan det antas att klara fjällsjöar mer och mer kan komma att likna skogssjöar eftersom en ökande temperatur antagligen leder till ökad terrester produktivitet (t.ex. att trädgränsen förflyttas uppåt). Om så skulle vara fallet, d.v.s. att klara fjällsjöarna blir brunare, så kan det få stora konsekvenser för dessa sjöekosystem, t.ex. att deras basproduktion minskar och att de avger mer koldioxid till atmosfären.

References

- Algesten G, Sobek S, Bergström AK, Jonsson A, Tranvik LJ, Jansson M (2005) Contribution of sediment respiration to summer CO₂ emission from low productive boreal and subarctic lakes. *Microbial Ecology*, **50**, 529-535.
- Algesten G, Sobek S, Bergström AK, Ågren A, Tranvik LJ, Jansson M (2004) Role of lakes for organic carbon cycling in the boreal zone. *Global Change Biology*, **10**, 141-147.
- Andersson E, Kumblad L (2006) A carbon budget for an oligotrophic clearwater lake in mid-Sweden. *Aquatic Sciences*, **68**, 52-64.
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Marine Ecology-Progress Series*, **10**, 257-263.
- Baines SB, Pace ML (1991) The Production of Dissolved Organic Matter by Phytoplankton and Its Importance to Bacteria - Patterns across Marine and Fresh-Water Systems. *Limnology and Oceanography*, **36**, 1078-1090.
- Battin TJ, Luysaert S, Kaplan LA, Aufdenkampe AK, Richter A, Tranvik LJ (2009) The boundless carbon cycle. *Nature Geoscience*, **2**, 598-600.
- Baulch HM, Schindler DW, Turner MA, Findlay DL, Paterson MJ, Vinebrooke RD (2005) Effects of warming on benthic communities in a boreal lake: Implications of climate change. *Limnology and Oceanography*, **50**, 1377-1392.
- Berggren M, Laudon H, Jansson M (2009a) Aging of allochthonous organic carbon regulates bacterial production in unproductive boreal lakes. *Limnology and Oceanography*, **54**, 1333-1342.
- Berggren M, Laudon H, Jansson M (2009b) Hydrological Control of Organic Carbon Support for Bacterial Growth in Boreal Headwater Streams. *Microbial Ecology*, **57**, 170-178.
- Bergström AK, Jansson M (2006) Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. *Global Change Biology*, **12**, 635-643.
- Biddanda B, Ogdahl M, Cotner J (2001) Dominance of bacterial metabolism in oligotrophic relative to eutrophic waters. *Limnology and Oceanography*, **46**, 730-739.
- Björk-Ramberg S (1983) Production of epipellic algae before and during fertilization in a subarctic lake. *Holarctic Ecology*, **6**, 349-355.
- Björk-Ramberg S (1984) Species composition and biomass of an epipellic algal community in a subarctic lake before and during lake fertilization. *Holarctic Ecology*, **7**, 195-201.

- Björk-Ramberg S, Ånell C (1985) Production and chlorophyll concentration of epilithic algae in fertilized and nonfertilized subarctic lakes. *Hydrobiologia*, **126**, 213-219.
- Blomqvist P, Jansson M, Drakare S, Bergström AK, Brydsten L (2001) Effects of additions of DOC on pelagic biota in a clearwater system: Results from a whole lake experiment in northern Sweden. *Microbial Ecology*, **42**, 383-394.
- Blumenshine SC, Vadeboncoeur Y, Lodge DM, Cottingham KL, Knight SE (1997) Benthic-pelagic links: responses of benthos to water-column nutrient enrichment. *Journal Of The North American Benthological Society*, **16**, 466-479.
- Bonilla S, Villeneuve V, Vincent WF (2005) Benthic and planktonic algal communities in a high arctic lake: Pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology*, **41**, 1120-1130.
- Brunberg AK, Nilsson E, Blomqvist P (2002) Characteristics of oligotrophic hardwater lakes in a postglacial land-rise area in mid-Sweden. *Freshwater Biology*, **47**, 1451-1462.
- Carpenter SR, Cole JJ, Kitchell JF, Pace ML (1998) Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography*, **43**, 73-80.
- Carr GM, Morin A, Chambers PA (2005) Bacteria and algae in stream periphyton along a nutrient gradient. *Freshwater Biology*, **50**, 1337-1350.
- Cole JJ, Caraco NF, Kling GW, Kratz TK (1994) Carbon-Dioxide Supersaturation in the Surface Waters of Lakes. *Science*, **265**, 1568-1570.
- Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: A cross-system overview. *Marine Ecology-Progress Series*, **43**, 1-10.
- Cole JJ, Likens GE, Strayer DL (1982) Photosynthetically produced dissolved organic carbon: An important carbon source for planktonic bacteria. *Limnology and Oceanography*, **27**, 1080-1090.
- Cole JJ, Prairie YT, Caraco NF, *et al.* (2007) Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems*, **10**, 171-184.
- Davison IR (1991) Environmental-Effects on Algal Photosynthesis - Temperature. *Journal of Phycology*, **27**, 2-8.
- del Giorgio PA, Cole JJ, Caraco NF, Peters RH (1999) Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology*, **80**, 1422-1431.
- den Heyer C, Kalff J (1998) Organic matter mineralization rates in sediments: A within- and among-lake study. *Limnology and Oceanography*, **43**, 695-705.

- DeNicola DM (1996) Periphyton responses to temperature at different ecological levels. In: *Algal ecology: Freshwater benthic ecosystems* (eds Stevenson RJ, Bothwell ML, Lowe RL). Academic Press, San Diego.
- Downing JA, Prairie YT, Cole JJ, *et al.* (2006) The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, **51**, 2388-2397.
- Elser JJ, Andersen T, Baron JS, *et al.* (2009) Shifts in Lake N:P Stoichiometry and Nutrient Limitation Driven by Atmospheric Nitrogen Deposition. *Science*, **326**, 835-837.
- Enell M, Löfgren S (1988) Phosphorus in interstitial water: Methods and dynamics. *Hydrobiologia*, **170**, 103-132.
- Findlay S, Meyer JL, Risley R (1986) Benthic Bacterial Biomass and Production in 2 Blackwater Rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1271-1276.
- Fischer H, Pusch M (2001) Comparison of bacterial production in sediments, epiphyton and the pelagic zone of a lowland river. *Freshwater Biology*, **46**, 1335-1348.
- Graneli W (1978) Sediment Oxygen-Uptake in South Swedish Lakes. *Oikos*, **30**, 7-16.
- Graneli W, Lindell M, Tranvik L (1996) Photo-oxidative production of dissolved inorganic carbon in lakes of different humic content. *Limnology and Oceanography*, **41**, 698-706.
- Haecky P, Andersson A (1999) Primary and bacterial production in sea ice in the northern Baltic Sea. *Aquatic Microbial Ecology*, **20**, 107-118.
- Haglund AL, Törnblom E, Boström B, Tranvik L (2002) Large differences in the fraction of active bacteria in plankton, sediments, and biofilm. *Microbial Ecology*, **43**, 232-241.
- Hanson PC, Bade DL, Carpenter SR, Kratz TK (2003) Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography*, **48**, 1112-1119.
- Hansson LA (1992) Factors regulating periphytic algal biomass. *Limnology and Oceanography*, **37**, 322-328.
- Harris GP, Piccinin BB (1977) Photosynthesis by Natural Phytoplankton Populations. *Archiv Fur Hydrobiologie*, **80**, 405-457.
- Hessen DO (1985) The relation between bacterial carbon and dissolved humic compounds in oligotrophic lakes. *Fems Microbiology Ecology*, **31**, 215-223.
- Hessen DO, Andersen T, Lyche A (1990) Carbon Metabolism in a Humic Lake - Pool Sizes and Cycling through Zooplankton. *Limnology and Oceanography*, **35**, 84-99.
- Hillebrand H, Kahlert M (2002) Effect of grazing and water column nutrient supply on biomass and nutrient content of sediment microalgae. *Aquatic Botany*, **72**, 143-159.

- Hope D, Billet MF, Cresser MS (1994) A review of the export of carbon in river water: fluxes and processes. *Env. Pollut.*, **84**, 301-324.
- Jansson M (1980) Role of benthic algae in transport of nitrogen from sediment to lake water in a shallow clearwater lake. *Archiv Fur Hydrobiologie*, **89**, 101-109.
- Jansson M, Bergström AK, Blomqvist P, Drakare S (2000) Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in lakes. *Ecology*, **81**, 3250-3255.
- Jansson M, Bergström AK, Drakare S, Blomqvist P (2001) Nutrient limitation of bacterioplankton and phytoplankton in humic lakes in northern Sweden. *Freshwater Biology*, **46**, 653-666.
- Jansson M, Blomqvist P, Jonsson A, Bergström AK (1996) Nutrient limitation of bacterioplankton, autotrophic and mixotrophic phytoplankton, and heterotrophic nanoflagellates in Lake Ortrasket. *Limnology and Oceanography*, **41**, 1552-1559.
- Jansson M, Persson L, De Roos AM, Jones RI, Tranvik LJ (2007) Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends in Ecology & Evolution*, **22**, 316-322.
- Jones RI (1992) The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia*, **229**, 73-91.
- Jonsson A, Karlsson J, Jansson M (2003) Sources of carbon dioxide supersaturation in clearwater and humic lakes in northern Sweden. *Ecosystems*, **6**, 224-235.
- Kalff J (2002) *Limnology: Inland water ecosystems*. Prentice-Hall, Upper Saddle River, New Jersey 07458 USA.
- Karlsson J, Byström P, Ask J, Ask P, Persson L, Jansson M (2009) Light limitation of nutrient-poor lake ecosystems. *Nature*, **460**, 506-U580.
- Karlsson J, Jansson M, Jonsson A (2007) Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. *Limnology and Oceanography*, **52**, 603-608.
- Karlsson J, Jonsson A, Jansson M (2001) Bacterioplankton production in lakes along an altitude gradient in the subarctic north of Sweden. *Microbial Ecology*, **42**, 372-382.
- Karlsson J, Jonsson A, Jansson M (2005) Productivity of high-latitude lakes: climate effect inferred from altitude gradient. *Global Change Biology*, **11**, 710-715.
- Karlsson J, Jonsson A, Meili M, Jansson M (2003) Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. *Limnology and Oceanography*, **48**, 269-276.
- Kling GW, Kipphut GW, Miller MC (1991) Arctic Lakes and Streams as Gas Conduits to the Atmosphere - Implications for Tundra Carbon Budgets. *Science*, **251**, 298-301.

- Kling GW, Kipphut GW, Miller MC (1992) The Flux of Co₂ and Ch₄ from Lakes and Rivers in Arctic Alaska. *Hydrobiologia*, **240**, 23-36.
- Kortelainen P, Rantakari M, Huttunen JT, *et al.* (2006) Sediment respiration and lake trophic state are important predictors of large CO₂ evasion from small boreal lakes. *Global Change Biology*, **12**, 1554-1567.
- Lampert W (1978) Release of dissolved organic carbon by grazing zooplankton. *Limnology and Oceanography*, **23**, 831-834.
- Laudon H, Köhler S, Buffam I (2004) Seasonal TOC export from seven boreal catchments in northern Sweden. *Aquatic Sciences*, **66**, 223-230.
- Lauster GH, Hanson PC, Kratz TK (2006) Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 1130-1141.
- Lennon JT (2004) Experimental evidence that terrestrial carbon subsidies increase CO₂ flux from lake ecosystems. *Oecologia*, **138**, 584-591.
- Liboriussen L, Jeppesen E (2003) Temporal dynamics in epipelagic, pelagic and epiphytic algal production in a clear and a turbid shallow lake. *Freshwater Biol*, **48**, 418-431.
- McKnight DM, Aiken GR (1998) Sources and age of aquatic humus. In: *Aquatic Humic Substances -Ecology and Biogeochemistry* (eds Hessen DO, Tranvik L). Springer-Verlag, Berlin.
- O'brien WJ, Hershey AE, Hobbie JE, *et al.* (1992) Control Mechanisms of Arctic Lake Ecosystems - a Limnocorral Experiment. *Hydrobiologia*, **240**, 143-188.
- Pace ML, Cole JJ (2000) Effects of whole-lake manipulations of nutrient loading and food web structure on planktonic respiration. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 487-496.
- Pace ML, Prairie YT (2005) Respiration in lakes. In: *Respiration in aquatic ecosystems* (eds Del Giorgio PA, Williams PJ). Oxford University Press.
- Prairie YT, Bird DF, Cole JJ (2002) The summer metabolic balance in the epilimnion of southeastern Quebec lakes. *Limnology and Oceanography*, **47**, 316-321.
- Reynolds CS (2008) A changing paradigm of pelagic food webs. *International Review Of Hydrobiology*, **93**, 517-531.
- Rier ST, Stevenson RJ (2002) Effects of light, dissolved organic carbon, and inorganic nutrients on the relationship between algae and heterotrophic bacteria in stream periphyton. *Hydrobiologia*, **489**, 179-184.
- Riera JL, Schindler JE, Kratz TK (1999) Seasonal dynamics of carbon dioxide and methane in two clear-water lakes and two bog lakes in northern Wisconsin, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 265-274.
- Roberts BJ, Howarth RW (2006) Nutrient and light availability regulate the relative contribution of autotrophs and heterotrophs to respiration in

- freshwater pelagic ecosystems. *Limnology and Oceanography*, **51**, 288-298.
- Roehm CL, Prairie YT, del Giorgio PA (2009) The pCO₂ dynamics in lakes in the boreal region of northern Quebec, Canada. *Global Biogeochemical Cycles*, **23**, GB3013.
- Salonen K (1981) The ecosystem of oligotrophic Lake Pääjärvi. 2. Bacterioplankton. *Int. Ver. Theor. Angew. Limnol. Verh.*, **21**, 448-453.
- Sand-Jensen K, Borum J (1991) Interactions among Phytoplankton, Periphyton, and Macrophytes in Temperate Fresh-Waters and Estuaries. *Aquatic Botany*, **41**, 137-175.
- Schallenberg M, Kalff J (1993) The Ecology of Sediment Bacteria in Lakes and Comparisons with Other Aquatic Ecosystems. *Ecology*, **74**, 919-934.
- Schindler DW (1977) Evolution of phosphorus limitation in lakes. *Science*, **195**, 260-262.
- Scott JT, Back JA, Taylo JM, King RS (2008) Does nutrient enrichment decouple algal-bacterial production in periphyton? *Journal Of The North American Benthological Society*, **27**, 332-344.
- Sorsa K (1979) Primary Production of Epipellic Algae in Lake Suomunjarvi, Finnish North Karelia. *Annales Botanici Fennici*, **16**, 351-366.
- Stanley DW (1976) A Carbon Flow Model of Epipellic Algal Productivity in Alaskan Tundra Ponds. *Ecology*, **57**, 1034-1042.
- Stets EG, Striegl RG, Aiken GR, Rosenberry DO, Winter TC (2009) Hydrologic support of carbon dioxide flux revealed by whole-lake carbon budgets. *Journal of Geophysical Research-Biogeosciences*, **114**, 14.
- Striegl RG, Kortelainen P, Chanton JP, Wickland KP, Bugna GC, Rantakari M (2001) Carbon dioxide partial pressure and C-13 content of north temperate and boreal lakes at spring ice melt. *Limnology and Oceanography*, **46**, 941-945.
- Tranvik LJ (1988) Availability of Dissolved Organic-Carbon for Planktonic Bacteria in Oligotrophic Lakes of Differing Humic Content. *Microbial Ecology*, **16**, 311-322.
- Tranvik LJ (1989) Bacterioplankton Growth, Grazing Mortality and Quantitative Relationship to Primary Production in a Humic and a Clearwater Lake. *Journal of Plankton Research*, **11**, 985-1000.
- Vadeboncoeur Y, Jeppesen E, Vander Zanden MJ, Schierup HH, Christoffersen K, Lodge DM (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography*, **48**, 1408-1418.
- Vadeboncoeur Y, Kalff J, Christoffersen K, Jeppesen E (2006) Substratum as a driver of variation in periphyton chlorophyll and productivity in lakes. *Journal Of The North American Benthological Society*, **25**, 379-392.
- Vadeboncoeur Y, Lodge DM (2000) Periphyton production on wood and sediment: substratum-specific response to laboratory and whole-lake

- nutrient manipulations. *Journal Of The North American Benthological Society*, **19**, 68-81.
- Vadeboncoeur Y, Lodge DM, Carpenter SR (2001) Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. *Ecology*, **82**, 1065-1077.
- Vadeboncoeur Y, Vander Zanden MJ, Lodge DM (2002) Putting the lake back together: Reintegrating benthic pathways into lake food web models. *Bioscience*, **52**, 44-54.
- Vadstein O (2000) Heterotrophic, planktonic bacteria and cycling of phosphorus: Phosphorus requirements, competitive ability, and food web interactions. In: *Advances in Microbial Ecology* Vol. 16 (ed Schink B), pp. 115-167. Kluwer Academic/Plenum Publishers.
- Van de Bogert MC, Carpenter SR, Cole JJ, Pace ML (2007) Assessing pelagic and benthic metabolism using free water measurements. *Limnology and Oceanography-Methods*, **5**, 145-155.
- Welch HE, Kalff J (1974) Benthic Photosynthesis and Respiration in Char Lake. *Journal of Fisheries Research Board of Canada*, **31**, 609-620.
- Wetzel RG (2001) *Limnology. Lake and River Ecosystems*. Academic Press, San Diego.
- White PA, Kalff J, Rasmussen JB, Gasol JM (1991) The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microbial Ecology*, **21**, 99-118.

Tack!

Nu har jag varit vid Umeå Universitet i typ 10 år (!) och jag har haft den osannolika turen att jag och många av mina bästa vänner från studietiden har följts åt även som doktorander. Man (läs jag) kan lätt bli sentimental för mindre... Det känns omöjligt att sammanfatta 10 år, så jag tänker att "less is more"!

Men för den här avhandlingen vill jag börja med att tacka mina två handledare, Jan Karlsson och Mats Jansson. Jag måste säga att jag är så otroligt glad över att ha fått jobba med er, jag har verkligen uppskattat den öppna och avslappnade, men samtidigt utmanande och uppmuntrande atmosfären. Janne, det finns inte så många som har din positiva inställning; det finns ingen utmaning som är för stor, inget problem som inte går att lösa och ingen ryggsäck som är för tung. Mats, du är som en hel uppslagsbok och din känsla för sammanhang och din förmåga att få till en text är nästintill magiska. Ni är otroliga inspirationskällor och jag hade inte kunnat ha bättre handledare.

Tack Anki, Anders, Jan, Martin och övriga i gruppen för all hjälp, trevliga samtal och diskussioner och för att det är en så härlig stämning på jobbet.

Tack Lennart, Pelle och alla andra i, som jag ser det, min "extra-grupp" för att ni är så bra (och då menar jag inte bara forskningsmässigt)!

Tack alla ni uppe i Abisko för roligt umgänge och för hjälp på alla möjliga sätt och för att ni har gjort alla fältsånger så trevliga. Ett speciellt tack till Thomas Westin för alla konstiga prylar du har fått bygga och alla båtar mm du har fått släpa, till Annika Kristoffersson för all hjälp med data, till ANS för organisation och till CIRC (Reiner) för de fina labben. Ett stort tack till alla ni som har slitit så hårt i fält; Marina Becher, Klockar Jenny Nääs, Andreas Karlsson, Stina Eriksson och Jenny Lundh.

Thanks everyone involved in LEREC for all the nice workshops, dinners and discussions!

Tack alla studenter för att ni har lyckats genomföra alla mer eller mindre omöjliga projekt. Tack till lärarkollegor, till alla administratörer för hjälp med dessa omöjliga blanketter mm, till datateknikerna för hjälp med alla jobbiga data-problem och till ledningen för att EMG är en så bra arbetsplats.

Karin och Kristin (jag säger bara Kronlund...), när även ni är färdiga och vi är arbetslösa (?) så kanske vi måste åka till lerfallet för att se vad vi missade (fast det kan aldrig slå det vi inte missade). Kram kram! En stor kram även till Magnus, Lotta, Gunnar och alla andra underbara kompisar för allt roligt på och kanske framförallt utanför jobbet. Kram till alla doktorander och icke-doktorander för att det är så trevligt på jobbet! Kram

till keramikgruppen för välbehövd avkoppling utanför jobbet. Tack Cissi och Bettan (med familjer) för allt roligt sedan väldigt länge, och kram på er för att ni ser till att jag som liten biolog-nörd inte helt tappar världsuppfattningen.

Kram till Lasse och Kerstin för allt stöd och för att ni alltid har fått mig att känna mig som en del även i er familj.

En stor kram till hela tjocka släkten, som inte alls är särskilt "tjock" utan faktiskt precis så lagom att det går att träffa i stort sett alla när man är på besök, och som alltid varit en stor del i mitt liv.

Mamma och pappa, tack för att ni är så himla bra! Tack för ert enorma stöd, för att ni alltid trott på mig, för alla små uppmuntrningar i rätt riktning, för alla utflykter, upptäcktsfärder och naturupplevelser som ni har tagit mig med på. Syster Karin, jag säger det alltför sällan men jag är en väldigt stolt storasyster och jag är otroligt imponerad av allt du gör! Kram på er!

Och till sist min egen lilla familj, Per och Orvar (min lilla solstråle), vilken tur att jag har er! Puss puss på er!