Carbon metabolism in clear-water and brown-water lakes

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LIST OF PAPERS

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


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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 (CO₂) 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.

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 CO₂ 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, CO₂, 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).
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). Epipelon (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 epipelon 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 epipelic production. Grazing has, to my knowledge, not been shown to strongly regulate epipelic production although it is an important structuring factor for epilithic production (Hillebrand & Kahlert 2002). Epipelon and epipelic 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 & Kumbalad 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 CO₂ 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 CO₂ (pCO₂) (Cole et al. 1994) and using pCO₂ can be biased by external inputs of CO₂-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 pCO₂ 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 CO₂ 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 pCO₂ 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 CO$_2$ 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 CO$_2$ from lakes to the atmosphere is often based on summer values, but lakes may be an even greater source of CO$_2$ to the atmosphere on an annual scale due to insignificant primary production during the winter. High CO$_2$ 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 CO$_2$ accumulation has been explained by the concentration of DOC in the lake water (Striegl et al. 2001). The carbon sources responsible for CO$_2$ 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 pCO_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 ΔDIC 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 NEP = GPP – R = ΔDIC 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 (δ¹³C) were used in order to determine the origin of carbon used for bacterial respiration (I, II). Values of δ¹³C 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 CO₂. Values were then compared to those of benthic algae or of a terrestrial signal.

All production values are given in 'mg C m⁻² 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” (PP + BP_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 Almberga, Abisko (J. Ask unpubl. data). The contribution of total pelagic ($PP + BP_{allo}$) 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 $p$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.

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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 primärproducnterna, 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

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 bottnen. Den mesta av denna bentiska produktion sker via alger, men även bentiska bakterier är av betydelse. Trots den höga bentiska primärraproduktionen så var dessa sjöar nettoheterotrofa, vilket innebär att respirationen var högre än primärraproduktionen. Respirationen var koncentrerad till det pelagala habitatet. Klara fjällsjöar har därför en hög produktion av biomassa i det bentiska habitatet och hög koldioxidproduktion i det pelagala 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 när inte ljuset ner mer än till 1-2 meter vilket resulterade i en i stort sett obeintlig 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 biomass. 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.
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