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Benthic-Pelagic Microbial Interactions and Carbon Cycling in Clearwater Lakes

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Abstract
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This thesis focuses on the interactions among microbiota in clearwater lakes. Field sampling and field experiments were performed to evaluate interactions among microbiota and the importance of benthic versus pelagic microbiota in terms of biomass and production. In addition, carbon cycling in an oligotrophic clearwater lake was calculated.

Biomass and production of microbiota was clearly focused to the benthic habitat. During natural nutrient concentrations growth of heterotrophic bacteria (benthic and pelagic) was coupled to production of microphytobenthos in Lake Eckarfjärden, indicating interactions between autotrophic and heterotrophic microbiota in, as well as between, habitats. At increased nutrient concentrations, growth of heterotrophic bacteria was not correlated to microphytobenthos production. This was explained by less release of dissolved organic carbon (DOC) from microphytobenthos when they got access to more nutrients. Further investigations showed different scenarios in oligotrophic clearwater lakes following increased nutrient concentrations. The interactions between microbiota may be altered following increased nutrient concentrations and the microbial mat either positively or negatively affect the pelagic microbiota. The most striking result was that the expected shift towards dominance of pelagic primary production does not necessarily occur.

Major flows of carbon were identified between different habitats in the oligotrophic clearwater Lake Eckarfjärden, and the net result was that the benthic habitat provided carbon to the pelagial. High DOC concentrations in the lake together with low pelagic production are factors that would indicate net heterotrophy. Accordingly, the pelagial of Lake Eckarfjärden was net heterotrophic but when the benthic and littoral habitats were included in the calculations, the lake turned out to be net autotrophic.

In conclusion, the benthic microbiota contributed significantly to the total production in the investigated lakes and had a major role in the lake metabolism. Thus, this thesis emphasises the importance of benthic microbiota in shallow clearwater lakes.

Keywords: microphytobenthos, phytoplankton, heterotrophic bacteria, interactions, nutrients, carbon cycling, clearwater lakes

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To the memory of Peter Blomqvist

I will always be grateful to you
for introducing me to the joy of Limnology

List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.

I   Brunberg A-K., Nilsson E. and Blomqvist P. (2002) Characteristics of oligotrophic hardwater lakes in a postglacial land-rise area in mid-Sweden. Freshwater Biology 47: 1451-1462

II   Andersson E. and Brunberg A-K. Net autotrophy in an oligotrophic lake rich in dissolved organic carbon. (submitted)

III   Andersson E. and Brunberg A-K. Inorganic nutrient acquisition in a shallow clearwater lake - dominance of benthic primary producers. (submitted)

IV   Andersson E., Blomster E. and Brunberg A-K. Benthic-pelagic coupling in a shallow clearwater lake - effects of nutrient additions on plankton. (manuscript)

V   Andersson E. and Kumblad L. A carbon budget for an oligotrophic clearwater lake in mid-Sweden. (submitted)

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Contents

Introduction

Phytoplankton and heterotrophic bacterioplankton in lakes have been extensively studied throughout the years. About 90 % of published studies of heterotrophic bacterial and primary production concern the pelagic environment whereas benthic microbiota, i.e. microphytobenthos and benthic heterotrophic bacteria have been less frequently studied (Vadeboncoeur et al. 2002). Studies where benthic and pelagic microbiota have been investigated simultaneously are even scarcer. However, it has been shown that benthic microbiota often contribute substantially to the microbial production in lakes (e.g. Doremus & Clesceri 1982, Wetzel 1996). In shallow clearwater lakes, the light climate in the benthic habitat is often good enough for microphytobenthos to make a significant contribution to the total primary production (Hargrave 1969, Wetzel 1996). As a large part of the worlds lakes are small and shallow (Wetzel 1990), production of microphytobenthos in these lakes should not be disregarded. Furthermore, also in relatively deep lakes, microphytobenthos may add significant parts of the total primary production (Loeb & Reuter 1981, Heath 1988).

Interactions among microbiota

Close interactions occur between autotrophic and heterotrophic microbiota, between phytoplankton and heterotrophic bacterioplankton as well as between microphytobenthos and benthic heterotrophic bacteria. In nutrient poor lakes there is often a close competition between phytoplankton and heterotrophic bacterioplankton for inorganic nutrients. When bacteria have access to an energy source, they are assumed to win this competition as they are considered better competitors for inorganic nutrients (Currie & Calff 1984, Bratbak & Thingstad 1985). The phytoplankton community often responds to this inferiority by changing to mixotrophic species that can utilize bacteria as a food source (Bird & Kalff 1986, Isaksson et al. 1999). On the other hand, when bacteria are carbon limited they may depend on organic carbon exudates from phytoplankton for growth and thereby be coupled to phytoplankton production (Bell 1983, Coveney & Wetzel 1989). In the benthic habitat the organic carbon exudates from microphytobenthos are often high, and it has been proposed that the microbial loop plays a significant role

in the benthic community (Goto et al. 1999). Moreover, it has been shown that benthic heterotrophic bacterial production in microbial mats is enhanced during light, indicating a coupling to primary production (Neely & Wetzel 1995, Espeland et al. 2001, Rier & Stevenson 2002).

In addition to competition between autotrophic and heterotrophic microbiota, there is also competition between microbiota in the benthic and the pelagic habitats. When nutrients are limiting, benthic primary producers have an advantage compared to phytoplankton as they have access to nutrients from the sediments (Carlton & Wetzel 1988, Hagerthey & Kerfoot 1998). The access of nutrients from the water column is considered restricted for benthic microbiota due to a boundary layer through which nutrients slowly penetrate (Riber & Wetzel 1987). Thus, increased nutrient concentrations in the water column are supposed to favour phytoplankton, which increases in biomass. This will lead to lower light intensities reaching the benthic habitat and microphytobenthos may become light limited (Hansson 1988, Havens et al. 2001, Vadeboncoeur et al. 2001). Potentially there could also be a competition between bacterioplankton and benthic bacteria for e.g. organic carbon and nutrients. Benthic heterotrophic bacteria have access to carbon from sedimentation of organic material. Heterotrophic bacterioplankton, on the other hand, has first access to allochthonous carbon entering the lake through inlets.

Limiting nutrients for growth of microbiota

Different inorganic nutrients may be limiting for the growth of microbiota in lakes. Phosphorus is often put forward as the main limiting nutrient for the growth of both phytoplankton and heterotrophic bacterioplankton (Vollenweider 1976, Stockner & Shortreed 1985, Elser et al. 1995, Vadeboncoeur et al. 2003). However, phytoplankton growth may also be limited by the access of nitrogen (Blomqvist et al. 1993, Jansson et al. 1996, Camacho et al. 2003) and trace elements (Goldman 1972, Evans & Prepas 1997, Hyenstrand et al. 2001) and heterotrophic bacterioplankton growth may be limited by the access of carbon and nitrogen (Elser et al. 1995, Vrede et al. 1999, Blomqvist et al. 2001). Phosphorus, nitrogen as well as silica have been put forward as factors limiting growth of microphytobenthos (Fairchild et al. 1985, Carrick & Lowe 1988, Fairchild & Sherman 1992, Marks & Lowe 1993, Hillebrand & Kahlert 2001). One of the main factors limiting bacterial activity in sediments is the availability of organic carbon (vanDuyl & Kop 1990, Sander & Kalff 1993). Generally, nitrogen and phosphorus concentrations in sediments far exceed the concentrations in the pelagial and hence, these nutrients are less likely to restrict bacterial growth in sediments. However, in biofilms, a polysaccharid matrix embedding the

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microorganisms might restrict the exchange of nutrients between the biofilm and the surrounding environment. Thus, both nitrogen and phosphorus might limit the growth of benthic microbiota, heterotrophic as well as autotrophic. Since benthic and pelagic microbiota have access to different nutrient pools (in sediments and lake water, respectively), it is not necessarily the same inorganic nutrients that are limiting for growth in the two habitats. Accordingly, studies of periphyton and phytoplankton have shown different limiting nutrients in the benthic and pelagic habitats (Marks & Lowe 1993, Maberly et al. 2002).

In addition to nutrients, there are also many other factors that may play a significant role in determining the growth of microbiota. For instance, light is one of the main factors determining the growth of primary producers and heterotrophic bacterial production is often considered limited by temperature (Bell & Ahlgren 1987, Sander & Kalff 1993).

Carbon budgets for lakes

Lakes are considered ideal for whole-ecosystem studies due to their clear outer boundaries (Vadeboncoeur et al. 2002, Forbes [1887] 1991). Despite that, whole-ecosystem carbon budgets are scarce in the literature (Wetzel 2003) and more often partial budgets for discrete lake habitats are calculated. Most commonly pelagial budgets are constructed using the benthic and littoral habitat as sinks and sources for carbon (Kankaala et al. 1996, Camarero et al. 1999). However, both benthic and littoral microbiota can make a significant contribution to the total production in lakes (Doremus & Clesceri 1982, Wetzel 1996, Theil-Nielsen & Søndergaard 1999) and the carbon flow from these habitats upwards in the food chain may substantially influence the whole lake metabolism. Whole-lake carbon budgets with calculated flows of carbon may identify the most importance groups of organisms, and demonstrate couplings between organisms as well as between habitats. Moreover, carbon budgets can be used to evaluate whether lakes are net autotrophic or net heterotrophic systems. Already Salonen et al. (1983) and Tranvik (1989) showed that in many lakes, bacterial respiration exceeds primary production, i.e. net heterotrophic conditions. del Giorgio et al. (1997) showed that unproductive lakes (pp < 100 µg C L^{-1} day^{-1}) tend to be net heterotrophic and generally only clearwater lakes are considered net autotrophic (Schindler et al. 1972, Ochs et al. 1995). However, recently also some clearwater lakes have been shown to be net heterotrophic (Jonsson et al. 2003). Net heterotrophic lakes are supersaturated in CO_2 (Kling et al. 1992, Cole et al. 1994) and are net sources of carbon dioxide to the atmosphere. The assumption that only unproductive lakes (pp < 100 µg C L^{-1} day^{-1}) are net autotrophic, implies that a majority of lakes should be net hetero-

trophic, releasing CO_2 to the atmosphere and thus having an impact on the global carbon cycling. In net heterotrophic lakes there must be an import of allochthonous carbon, e.g. in the form of humic substances from the lake catchment. Hence, there are strong interactions between the lake ecosystem and the surrounding terrestrial ecosystems. Nevertheless, boundaries are needed when calculating different parts of the global carbon cycling, and lakes are relatively easy to identify and define as ecosystems.

Several recent studies have stressed the importance to, in addition to the pelagial, include the benthic and littoral habitats when evaluating lake metabolism and lake functioning (Schindler & Scheurell 2002, Vadeboncoeur et al. 2002, VanderZanden & Vadeboncoeur 2002, Sierszen et al. 2003). In partial budgets, interactions between microbiota may be overlooked. Moreover, as benthic and littoral microbiota may contribute significantly to lake production and lake respiration, a holistic view is important when evaluating lakes role in the global carbon cycling.

Aims of this thesis

This thesis focuses on the interactions among benthic and pelagic microbiota in lakes. Field studies and experiments were performed to evaluate the significance of benthic vs. pelagic microbiota in terms of biomass and production. Interactions between benthic and pelagic, autotrophic as well as heterotrophic, microbiota were evaluated during natural and increased nutrient concentrations. In addition, a carbon budget for a shallow clearwater lake was calculated, demonstrating the major paths of carbon on a whole-ecosystem level. The carbon budget calculations were also used to evaluate whether the lake was net autotrophic or net heterotrophic. The work in this thesis was performed in shallow clearwater lakes and for this lake type the following questions were addressed:

- How important is benthic compared to pelagic microbiota in terms of biomass and production? (addressed in paper I, II and V)
- Which are the interactions among microbiota (benthic and pelagic, autotrophic and heterotrophic)? (addressed in paper II and V)
- How are the interactions among microbiota altered at increased nutrient concentrations? (addressed in paper III and IV)
- Which are the major carbon flows in the lake ecosystem and what is the dominating process, primary production or respiration? (addressed in paper V)

Study site

Along the coast of central Sweden, new lakes are continuously formed due to the shoreline displacement in the area since the last glaciation, which ended some 8800 years ago (Ignatius et al. 1981). Many of the formed lakes are oligotrophic clearwater lakes. Paleoecological studies indicate that the oligotrophic stage of these lakes is ephemeral and that they develop towards brownwater systems with time (Brunberg & Blomqvist 2000, and references therein).

Earlier studies in this kind of lakes have focused on water chemistry, phytoplankton and the macroalgae *Chara* (Lundqvist 1925, Willén 1962, Forsberg 1965, Kleiven 1991). The lakes are small and shallow, with very soft sediments. A large part of the benthic habitats are covered by the macroalgae *Chara* and the lakes have been characterised as "Chara-lakes". The lakes have also been referred to as "bottomless" due to very high water content in the fluffy sediments. Lundqvist (1925) described the sediments as "cyanophyceaegyttja" and noticed that the sediments were covered with a thick microbial mat. Although no quantitative measurements were available, his conclusion was that the microbial community was heavily focused to the benthic habitat.

The lake water is very calcium rich (Forsberg 1965) due to calcareous soils that were transported into the area during the last glaciation. Phosphorus is prone to precipitate with calcium carbonates and thus the phosphorus concentrations in the water are low. The water chemistry is very special compared to other Swedish lakes (paper I). The lakes have very high pH, conductivity, alkalinity and total nitrogen concentrations while phosphorus concentrations are low, resulting in a high N: P ratio. They have unusually high concentrations of dissolved organic carbon (DOC) in combination with moderate watercolour, indicating that much of the DOC should have autochtonous origin.

This thesis is based on studies in the two oligotrophic clearwater Lakes Hällefjärd and Eckarfjärden, situated 5 and 6 m above sea level, which corresponds to an age of 780 and 930 years, respectively (*Figure 1*). Both lakes are shallow with a mean depth of 0.9 and 1.5 m, respectively. The water chemistry is similar for the lakes whereas phosphorus concentrations in the sediments are three times higher in Lake Eckarfjärden compared to in Lake Hällefjärd. The lakes also differ in the composition of the catchment area

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and theoretical residence time of the water. Lake Hällefjärd is surrounded by mires and has a retention time of 63 days, while Lake Eckarfjärden is surrounded by forest and has a theoretical retention time of 383 days (paper I).

Due to an unusual thick microbial mat in the benthic habitat, these lakes are good candidates to evaluate interactions between benthic and pelagic microbiota. Although the water chemistry is very special and the oligotrophic stage is ephemeral, many characters are the same as for other shallow oligotrophic lakes. Nutrient concentrations in the water are low, biomass of pelagic microbiota is low and biomass of benthic microbiota is high. Hence, interactions between microbiota in this kind of lake could be the same as in other shallow clearwater lakes.
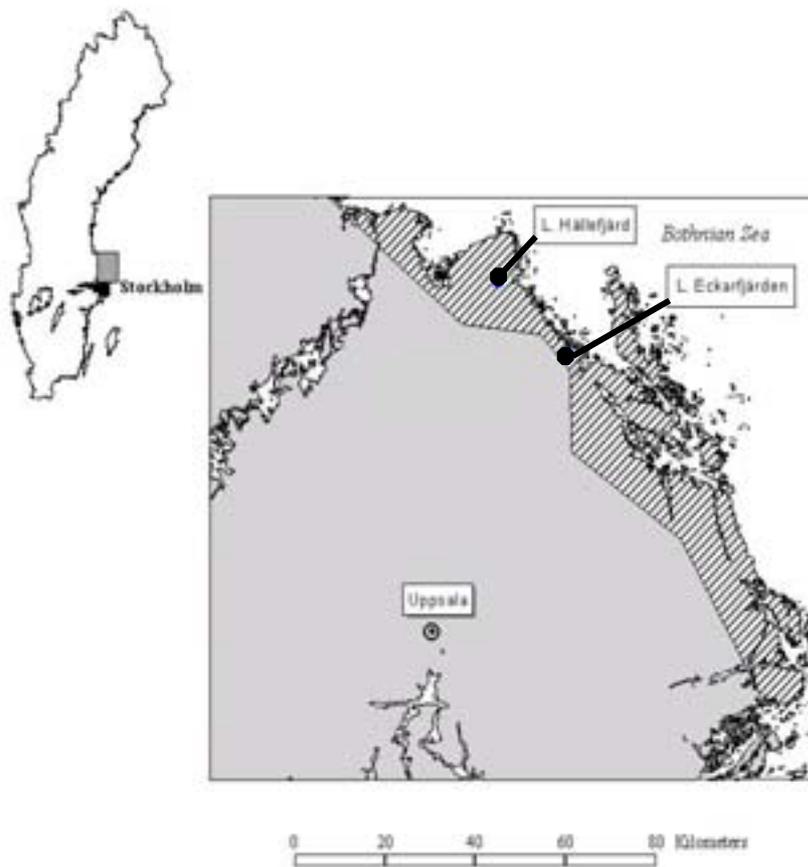

Figure 1. Map of the area along the east coast of Sweden where ephemeral oligotrophic clearwater lakes are formed. Lakes Hällefjärd and Eckarfjärden are studied in this thesis.

Methods

Biomass and production measurements

Integrated water samples (Blomqvist 1995) were taken for monitoring of biomass and production in the water. Biomass and production of pelagic microbiota were calculated for the mean depths of the lakes. From the sediments, the top 5 cm were used for analyses of biomass of microbiota and production of heterotrophic microbiota. Production of microphytobenthos was measured in the top 1 cm of the sediment.

Numbers and biovolume of heterotrophic bacteria were measured with epifluorescence microscopy after staining with acridine orange. Bacterial dry weight and carbon biomass were calculated according to Loferer-Krössbacher et al. (1998), and assuming that 50% of the dry weight was carbon.

Phytoplankton and microphytobenthos were counted and measured in an inverted phase-contrast microscope, after settling of the organisms in sedimentation chambers. Carbon biomass was calculated assuming a wet weight of 1 g cm^{-3} and using conversion factors for carbon content of different taxa according to Olrik et al. (1998). Phytoplankton was divided into autotrophic and mixotrophic phytoplankton according to Isaksson et al. (1999).

Heterotrophic bacterial production was measured by incorporation of ^{3}H-thymidine *in situ* according to Bell (1993) and Bell & Ahlgren (1987). Heterotrophic bacterial production per hour was multiplied with 24 to achieve the production per day.

Primary production was measured by incorporation of ^{14}C-sodium bicarbonate *in situ*. Phytoplankton production was measured in glass bottles at different depths and production of microphytobenthos was measured in Jönsson cores, which allows the radioactive tracer to percolate down in the sediment (Jönsson 1991). Primary production per hour was re-calculated to daily primary production by assuming a direct proportionality to light (Wetzel & Likens 1991).

Enclosure experiments

Two enclosure experiments were performed in Lake Eckarfjärden in order to elucidate interactions between microbiota at enhanced nutrient concentrations (paper III and IV).

During 2002, 10 transparent polyethylene tubes (1*1 m) were attached to wooden frames at 0.5 m depth. The mesocosms included both water and microbial mat. Concentrations of nitrogen and phosphorus in the water were manipulated and biomass and production of benthic as well as pelagic microbiota were monitored for 15 days.

During 2003, a total number of 9 polyethylene tubes and bags (0.4*0.4 m) were attached to wooden frames (0.5 m depth). Nitrogen and phosphorus were added to all the mesocosms and biomass of phytoplankton and heterotrophic bacterioplankton was monitored for 8 days. In order to elucidate the effect of the microbial mat on the plankton community, three tubes, which included both microbial mat and lake water, were compared to three bags that only contained lake water. The remaining three mesocosms were bags, which received a trace elements mixture in addition to nitrogen and phosphorus in order to elucidate whether the plankton community was limited by trace elements.

Carbon budget calculations

For carbon flow calculations, Lake Eckarfjärden was divided into three habitats (pelagic, benthic and littoral) and 19 functional groups. Data on biomass and production of biota were as far as possible taken from the lake. When this was not available, data from lakes as similar as possible to Lake Eckarfjärden were used. Biomass values in other units than carbon were recalculated using conversion factors from Kautsky (1995). Heterotrophic bacterial respiration was calculated assuming a growth efficiency of 25 % (delGiorgio et al. 1997). For other heterotrophic organisms, respiration was calculated from biomass using conversion factors (Kautsky 1995). Feeding preferences for different functional groups were obtained from the literature. Each functional group was assumed to feed on their potential food sources in proportion to the available biomass of each source. Consumption of carbon by bacteria was calculated as the sum of respiration and production. For fish the consumption was assumed to be 1.74 times the respiration (Kumblad et al submitted) and for all other consumers the consumption was assumed to be 3 times the respiration (Crisp 1971).

Results and discussion

Biomass and production of microbiota

Biomass and species composition

Biomass of microbiota was heavily focused to the benthic habitat in the shallow clearwater Lakes Hällefjärd and Eckarfjärden. During year 2000, the annual averages of biomass per unit lake area of microphytobenthos were 73 and 70 times higher than the biomass of phytoplankton in the two lakes, respectively (Table 1, Paper I). Likewise, the benthic heterotrophic biomass was 84 and 52 times higher than the heterotrophic bacterioplankton biomass (Table 1, Paper I). Lake Eckarfjärden was monitored also during 2001-2002 and then the relative contribution of the benthic microbiota to the total microbial biomass was even higher (paper II). All microbiota except benthic heterotrophic bacteria showed a pronounced seasonality, with high biomass in summer and low biomass during winter (*Figure 2*).

In the pelagic habitat, the biomass of heterotrophic bacterioplankton and phytoplankton were of similar size (paper II). In both lakes, about half of the phytoplankton community was composed of mixotrophic species belonging to the classes Chrysophyceae and Cryptophyceae (paper I and II).

Table 1. Biomass (mg C m^{-2}) of microbiota in the water column (mean depth) and surface sediments (0-5cm) in Lakes Hällefjärd and Eckarfjärden during year 2000. Values are given as annual average ± SD. Number of observations are stated within brackets.

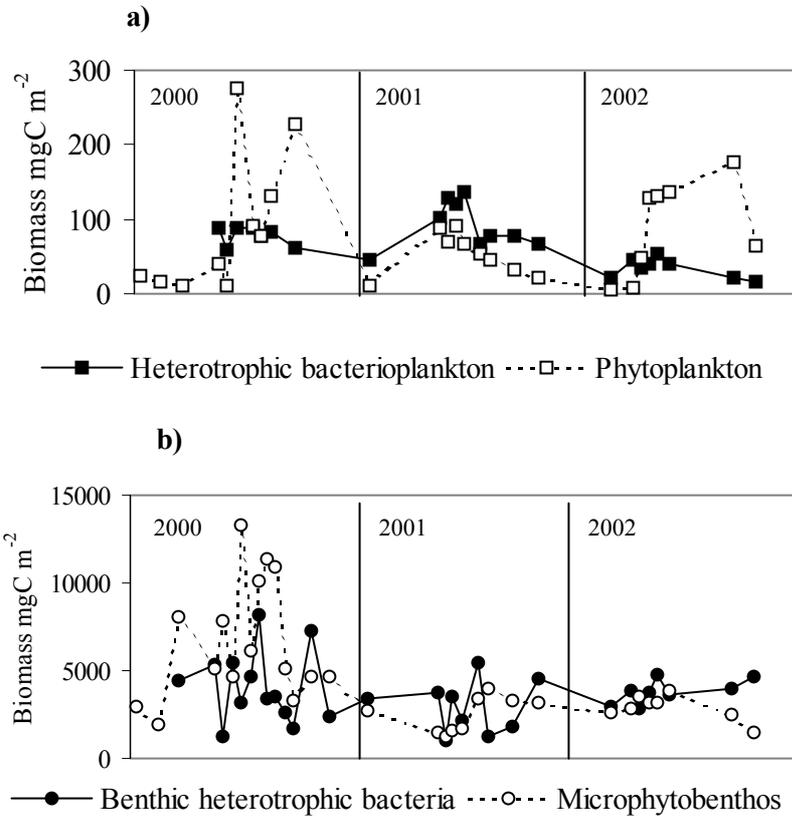| Lake	Hällefjärd	Eckarfjärden
	mg C m^{-2}	*mg C m^{-2}*
Planktonic microbiota		
Phytoplankton	58 ± 33 (15)	96 ± 79 (16)
Heterotrophic bacterioplankton	43 ± 23 (7)	79 ± 12 (7)
Benthic microbiota		
Microphytobenthos	4216 ± 2078 (15)	6741 ± 3402 (16)
Benthic heterotrophic bacteria	3624 ± 1830 (14)	4114 ± 2069 (13)

a)

b)

Figure 2. Biomass of microbiota in Lake Eckarfjärden during 2000-2002 in the water column (1.5 m, mean depth) and in the surface sediment (0-5 cm). Note the different scales on the axes in a and b.
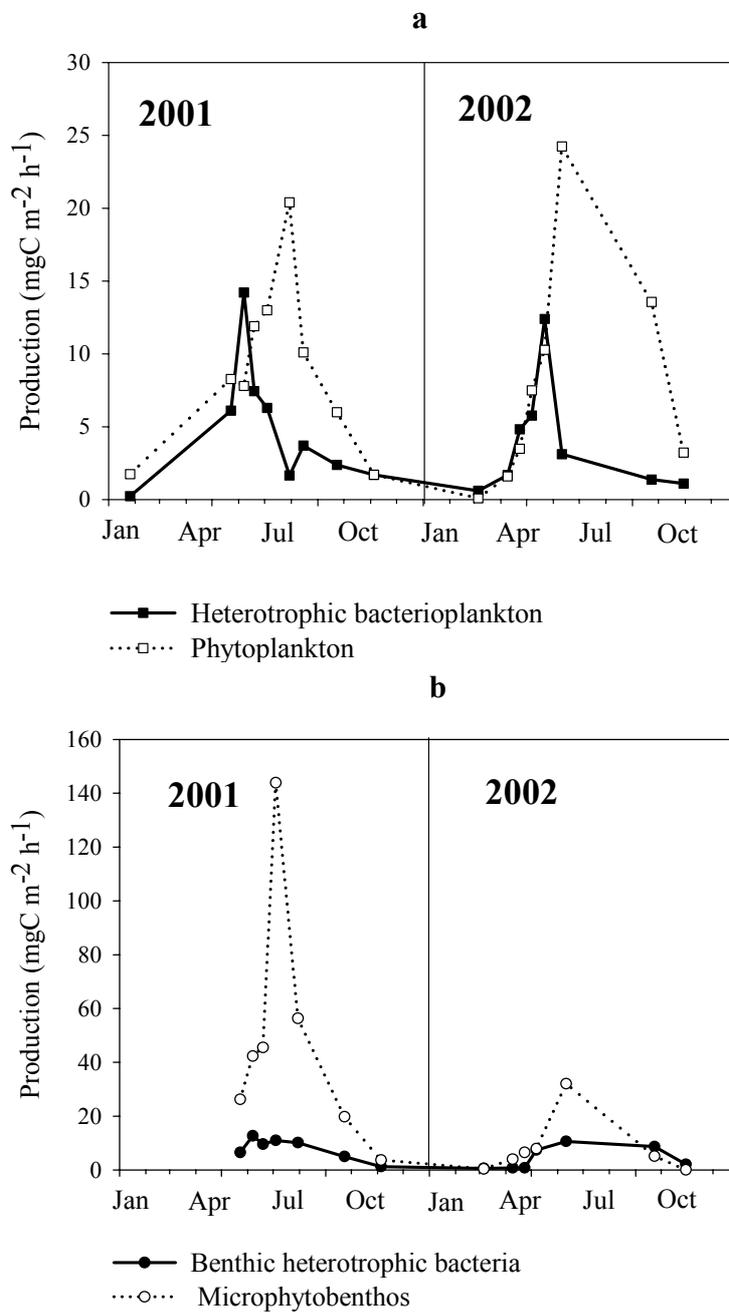
In the benthic habitat, both lakes had a remarkably thick microbial mat with green and red colours. Concentrations of chl *a* were high down to a depth of about 10-15 cm (paper I). The phototrophic microbiota in the mat were dominated by cyanobacteria, followed by diatoms and purple sulphur bacteria. The photosynthesising microphytobenthos is probably dependent on regular mixing of the microbial mat (resuspension, bioturbation, gas ebullition etc.) to reach layers where there is enough light for growth. Microphytobenthos is sensitive to low oxygen conditions (Peterson 1996). During the spring 2001, anoxic conditions were recorded in the water close to the bottom of Lake Eckarfjärden. This occasion was followed by a decrease in the biomass of microphytobenthos (*Figure 2*, paper II). This indicates that microphytobenthos suffered from oxygen stress and that oxygen during normal conditions is transported down in the microbial mat. The summer-biomass of microphytobenthos did not reach the same magnitude in 2001 and 2002 as in

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2000, which could indicate that the microphytobenthos community needed long time to fully recover after the anoxic period. Purple sulphur bacteria thrive on the boarder between oxic and anoxic conditions, as they are dependent on anoxia for their photosynthesis. They were usually recorded as a red band in the sediment, positioned at different depths during the year. Most commonly, purple sulphur bacteria were found at 2-3 cm depth in winter and at 5-8 cm depth in summer. During 2000 the biomass of microphytobenthos was higher than the biomass of benthic heterotrophic bacteria. However, due to the decrease in summer biomass of microphytobenthos after the anoxic conditions in spring 2001, the biomass of benthic heterotrophic bacteria was higher than that of microphytobenthos the following two years. Hence, the situation with dominance of autotrophic or heterotrophic microbiota may vary between years and change due to environmental disturbance.

Production

The production of microbiota, measured in lake Eckarfjärden 2001 and 2002, was heavily focused to the benthic habitat (paper II and V). The benthic production was about twice as high as the pelagic one. Primary production of microphytobenthos was 56 g C m^{-2} yr^{-1} compared to phytoplankton primary production of 24 g C m^{-2} yr^{-1}. The heterotrophic bacterial production was 44 and 25 g C m^{-2} yr^{-1} in the benthic and pelagic habitat, respectively. The production of all microbiota showed a clear seasonality with high summer values and low winter values (*Figure 3*).

The total annual primary production by microbiota was higher than the total annual heterotrophic bacterial production (paper II). In the benthic habitat, the production of microphytobenthos was higher than the production of heterotrophic bacterial production per day (paired t-test $p < 0.05$). In the pelagic habitat, production of phytoplankton per hour (mean 9 ± 7 mg C m^{-2} h^{-1}) was significantly higher than the production per hour of heterotrophic bacterioplankton (4 ± 4 mg C m^{-2} h^{-1}). However, after adjustment to light intensities and daylength primary production and heterotrophic bacterial production per day in the pelagial were of similar size.

a

b

Figure 3. Production of microbiota in Lake Eckarfjärden during 2001 and 2002 in the water column (1.5 m) and in the surface sediment (0-1 cm for microphytobenthos and 0-5 cm for benthic heterotrophic bacteria). Figure from paper II.

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Interactions among microbiota

At natural nutrient concentrations

During natural nutrient concentrations, there were strong indications that heterotrophic bacteria were carbon limited and dependent on primary producers for carbon exudates (paper II and V). Production of benthic heterotrophic bacteria was positively correlated to production of both phytoplankton ($R^2 = 0.794$, $p < 0.01$) and microphytobenthos ($R^2 = 0.642$, $p < 0.01$; paper II). In addition, the biomass of heterotrophic bacterioplankton was positively correlated to the production of microphytobenthos ($R^2 = 0.667$, $p < 0.01$). Carbon limitation of heterotrophic bacteria in Lake Eckarfjärden is rather surprising, considering the very high DOC concentrations in the lake (> 20 mg C L^{-1}). The high DOC concentration is combined with relatively low water colour, which implies that the organic carbon is of autochthonous origin. Autochtonous carbon has generally been considered a high quality carbon source for bacteria (Wetzel 1995). However, Tranvik and Bertilsson (2001) have shown that UV-light may transform autochtonous carbon to forms that are unavailable for bacterial growth. The shallowness of Lake Eckarfjärden, together with the clear water, may allow a large amount of UV-light to penetrate the water and transfer autochthonous carbon to forms that are unavailable for bacterial growth. Thus, heterotrophic bacteria could be dependent on newly released DOC from primary produces, which would explain the coupling between heterotrophic bacteria and primary producers. Co-variation and coupling between heterotrophic bacterioplankton and exudates from phytoplankton have been demonstrated in other studies (Bell 1983, Coveney & Wetzel 1989). In Lake Eckarfjärden, however, heterotrophic bacterioplankton biomass was positively correlated to microphytobenthos production, indicating that the bacterioplankton were depending on carbon exudates from benthic primary producers. Hence, interactions not only between autotrophic and heterotrophic microbiota, but also between microbiota in different habitats were found.

In the pelagic environment, phytoplankton is probably relying to a large extent on the consumption of heterotrophic bacteria (paper V). Half of the phytoplankton community was composed of mixotrophic species that can utilize bacteria (paper I and II). The ratio of photosynthesis to phagotrophy in mixotrophic phytoplankton is highly variable between different species and growth conditions (Sanders et al. 1990, Jones 1997). The dependence on bacterivory may be high and *in situ* measurements in humic oligotrophic Lake Örträsket showed that 2/3 of the carbon demand of the natural population of mixotrophic algae was met from utilizing bacteria (Jansson et al. 1999). As the light conditions in Lake Eckarfjärden are better than in the humic Lake Örträsket, the mixotrophic phytoplankton in Lake Eckarfjärden could be expected to rely on photosynthesis to a larger extent. Several stud-

ies however, have failed to show light effects on phagotrophy (Bird & Kalff 1986, Arenovski et al. 1995). Therefore, the light conditions may have less effect on the phagotrophy than the amount of available nutrients for photosynthesis. Consequently, the consumption of bacteria by mixotrophic phytoplankton in the oligotrophic Lake Eckarfjärden could be as high as in oligotrophic Lake Örträsket.

Summarising the situation at natural nutrient conditions, strong relationships between autotrophic and heterotrophic microbiota were demonstrated. Heterotrophic bacteria are most probably depending on carbon exudates from primary producers, and phytoplankton is most probably depending on heterotrophic bacteria as an extra nutrient source.

At increased nutrient concentrations

During 2002 and 2003, enclosure experiments were conducted in Lake Eckarfjärden to evaluate the effect of increased nutrient concentrations on the microbial community.

Increased nutrient concentrations are generally considered to increase phytoplankton biomass, which then reduces the light availability for benthic algae that become light limited (Hansson 1988, Havens et al. 2001, Vadeboncoeur et al. 2001). The enclosure experiment in 2002 was designed to evaluate the effect of increased concentrations of nitrogen and phosphorus on the biomass and production of benthic and pelagic microbiota in Lake Eckarfjärden (paper III). In contrast to other studies, increased nutrient concentrations (P and P+N) led to increased biomass of microphytobenthos whereas phytoplankton biomass remained roughly the same. The primary production was focused to the benthic habitat where 70 % of the total microbial primary production took place. Primary production of microphytobenthos was highest in mesocosms receiving nitrogen, suggesting nitrogen limitation. Also the heterotrophic bacterial production was focused to the benthic habitat (81% of total). Nutrient additions, especially nitrogen, had a negative effect on the heterotrophic bacteria, indicating interactions with the stimulated microphytobenthos. Heterotrophic bacterioplankton biomass decreased following nutrient additions, most in enclosures receiving nitrogen. Benthic heterotrophic bacteria had roughly the same biomass with or without nutrient additions, but their production was lower in enclosures receiving nitrogen.

At the increased nutrient concentrations in the enclosure experiment, the production of heterotrophic bacteria was not coupled to primary production. Contrarily, biomass of heterotrophic bacterioplankton and production of benthic heterotrophic bacteria were low when production of microphytobenthos was high. However, this does not necessarily contradict that heterotrophic bacteria depend on carbon exudates from primary producers. The DOC exudates from microphytobenthos may vary between 30-73 % of primary

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fixed carbon (Goto et al. 1999, Smith & Underwood 2000). It is reasonable to believe, that as much carbon as possible should be incorporated into biomass when inorganic nutrients are available. When nutrient-limited microphytobenthos gets access to inorganic nutrients, they may release less DOC, resulting in lower heterotrophic bacterial biomass and production, i.e. in accordance with the results from paper III.

The mixotrophic components of phytoplankton may have suffered from the decrease in heterotrophic bacterioplankton biomass following the nutrient additions. Accordingly, during the experiment the biomass of mixotrophic phytoplankton decreased and their relative contribution to the total phytoplankton community declined. The reason for the low response of autotrophic phytoplankton to nutrient additions is harder to explain. One reason could be allelopathic effects. Many phytoplankton species have been shown to produce allelopathic substances (Legrand et al. 2003), and also some benthic algae are capable of toxin production (Faust 1995, Mez et al. 1998). Moreover, although not present within the enclosures, large parts of the benthic habitat is covered with Chara, which is another organisms known to produce allelopathic substances that may suppress phytoplankton (Berger & Schagerl 2003). Influence of allelopathy in this lake thus cannot be excluded, although is less likely as an explanation to the lack of response by phytoplankton. The zooplankton biomass during 2002 was very low (Andersson et al. 2003), and therefore it does not seem likely that the zooplankton biomass increased to such size that it could suppress the phytoplankton community early in the experiment. Most probably, the lack of response by autotrophic phytoplankton was either due to limitation of trace elements or due to effective competition by microphytobenthos for the inorganic nutrients.

In order to further evaluate this, another enclosure experiment was performed in 2003 (paper IV). In this experiment, the microbial mat had a positive effect on the plankton community and both bacterioplankton and phytoplankton biomass was higher in enclosures including the microbial mat compared to in enclosures excluding the microbial mat. Trace elements, on the other hand, had minor effect on the pelagic microbiota. The enclosures including the microbial mat contained much higher biomass of heterotrophic bacteria in the water column already at the start of the experiment compared to enclosures excluding the microbial mat. This was probably due to mixing and/or upward migration of the benthic heterotrophic bacteria. The enclosures were left for one day after placing to allow the microbial mat to settle if disturbed during placing of the enclosures and this should have minimized the effect of mixing. The biomass of heterotrophic bacterioplankton continued to increase in all enclosures indicating that carbon was available. Mixotrophic phytoplankton biomass increased most in the enclosures containing microbial mat, and the increase was most probably due to high biomass of heterotrophic bacterioplankton. The autotrophic phytoplankton showed low response to

nutrient additions, indicating that heterotrophic bacterioplankton was superior to autotrophic phytoplankton in nutrient acquisition.

Alternative shifts in microbial interactions following increased nutrient concentrations

The effect of increased nutrient concentrations on the relationships between benthic and pelagic microbiota was different during 2002 and 2003. Stephen et al. (2004) also got different results in field experiments during two subsequent years. They explained this by varying starting conditions. In Lake Eckarfjärden, there was probably a difference in sensitivity of the microbial mat to mixing during the different years. During 2003 large amounts of benthic bacteria moved up in the water column at increased nutrient concentrations. This does not seem to be the case during 2002 when biomass of heterotrophic bacteria was low in the pelagial and continued to decline throughout the experiment. During some years, a crust of calcium carbonate has been observed on top of the microbial mat, and this could prevent resuspension of heterotrophic bacteria and nutrients. Other years the microbial mat should be prone to mixing due to the very fluffy sediments with high water content (98%).

At natural nutrient concentrations, heterotrophic bacteria were dependent on carbon exudates from primary producers, and phytoplankton was most probably dependent on heterotrophic bacterioplankton as an extra nutrient source (*Figure 4*). Increased nutrient concentrations can lead to two different scenarios. In the first scenario (occurred during 2002), the microbial mat negatively affects phytoplankton and heterotrophic bacterioplankton, whereas in the second scenario (occurred during 2003) the pelagic microbiota are stimulated by connection with the microbial mat. In the first scenario, a crust on top on the microbial mat prevents benthic heterotrophic bacteria to move upwards in the water column. Instead, added nutrients are utilized by microphytobenthos and interactions between microbiota decrease. When microphytobenthos gets access to limiting nutrients, DOC exudates may decrease. This leads to decreased heterotrophic bacterial biomass and thus also decreased possibilities for mixotrophic phytoplankton to feed on heterotrophic bacteria (*Figure 4*). In the second scenario, benthic heterotrophic bacteria are resuspended or migrate up in the water column and utilize the added nutrients. Then, interactions between microbiota remain as before nutrient additions and interactions between phytoplankton and heterotrophic bacteria become even stronger (*Figure 4*). One conclusion from this is that the starting conditions can heavily influence the outcome of an experiment. It is clear that the interactions between benthic and pelagic microbiota can be altered by nutrient additions. However, the expected shift towards pelagic production may not occur but the main production may remain in the benthic habitat.
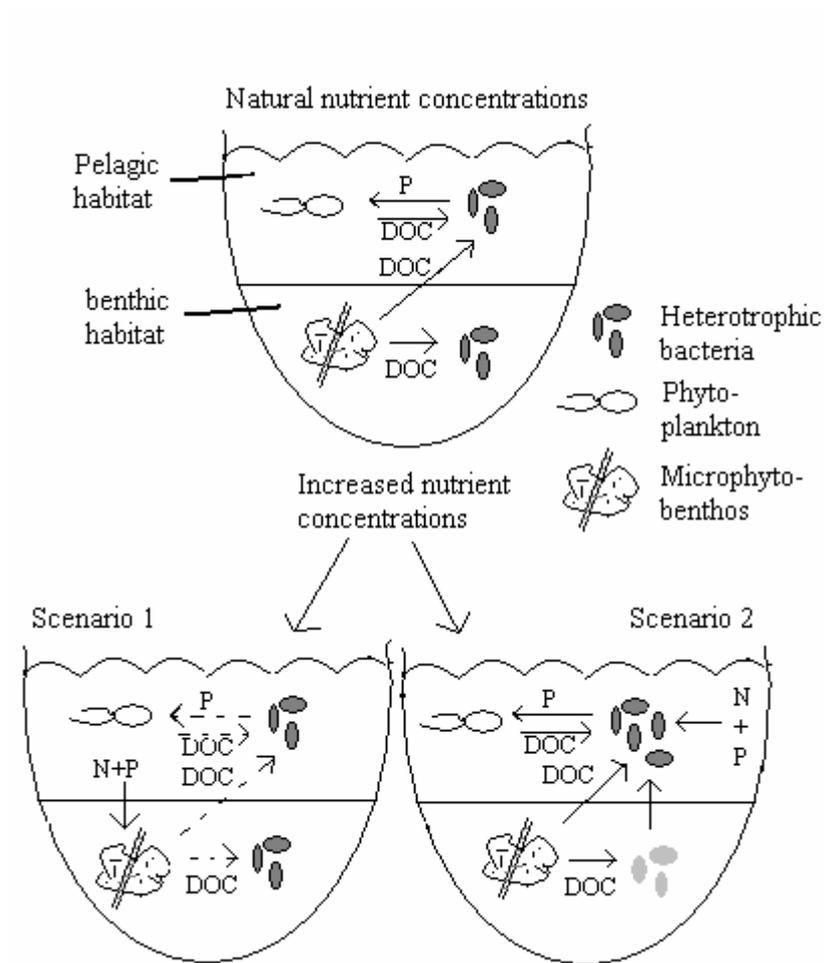
24

Figure 4. Proposed interactions among microbiota at natural nutrient concentrations, and two alternative scenarios following increased nutrient concentrations corresponding to the results from enclosure experiments during 2002 and 2003, respectively. Broken lines indicate decreased flows between microorganisms.

A carbon budget for Lake Eckarfjärden

Major flows of carbon

The benthic microbiota clearly dominated the base of the food web in Lake Eckarfjärden. A carbon budget for Lake Eckarfjärden (paper V) shows that both biomass and production of primary producers were focused to the benthic (58%) and littoral habitats (34%) and to a few functional groups (fig 5). Macrophytes, macroalgae, and microphytobenthos dominated the biomass and production of primary producers. Only 9 % of primary production was allocated to the pelagial. Respiration was focused to the benthic (60%) and pelagic (39%) habitats, and to heterotrophic bacterioplankton and benthic heterotrophic bacteria. Heterotrophic bacteria (benthic and pelagic) were also responsible for the majority of the annual consumption of carbon in the lake (82%). This situation where benthic and littoral microbiota contribute substantially to the total production in the lake ecosystem is in accordance with results from other studies (Doremus & Clesceri 1982, Wetzel 1996, Theil-Nielsen & Søndergaard 1999).

Only about 5% of the carbon fixed through primary production was directly consumed by higher organisms. Instead, most of the carbon was consumed in the form of DOC and POC. There were two major flows of carbon reaching the top predator piscivorous fish (P-fish, Fig 5). One was the consumption of microphytobenthos and macroalgae by benthic fauna, which were further channelled upwards in the food web by fish feeding on benthic fauna (B-fish) further to P-fish. The other large carbon flow was from DOC and POC that was utilized by benthic and pelagic heterotrophic bacteria, which in turn were consumed by mixotrophic phytoplankton. Mixotrophic phytoplankton was grazed by zooplankton and the carbon was further transported to fish feeding on zooplankton (Z-fish) to P fish. Hence, much of the carbon consumption by higher organisms had its origin in the benthic habitat.

A large part of the carbon produced in Lake Eckarfjärden was, in the budget calculations, not consumed but settled on the sediment. This corresponds well with measured sedimentation of 30 g C m^{-2} year^{-1} (Brunberg, unpublished). Also, field observations of un-decayed parts of Chara in the sediments indicate that a large part of the primary production is not fully utilized by consumers.

From the budget calculations, it is clear that the benthic microbiota plays a significant role for the whole-lake metabolism. There were major flows of carbon between habitats, and the benthic habitat provides the pelagial with carbon. Organisms in the pelagial feed directly or indirectly on the benthic habitat. Concurrently, the pelagial supports the benthic habitat with carbon in the form of sedimenting planktonic biota.
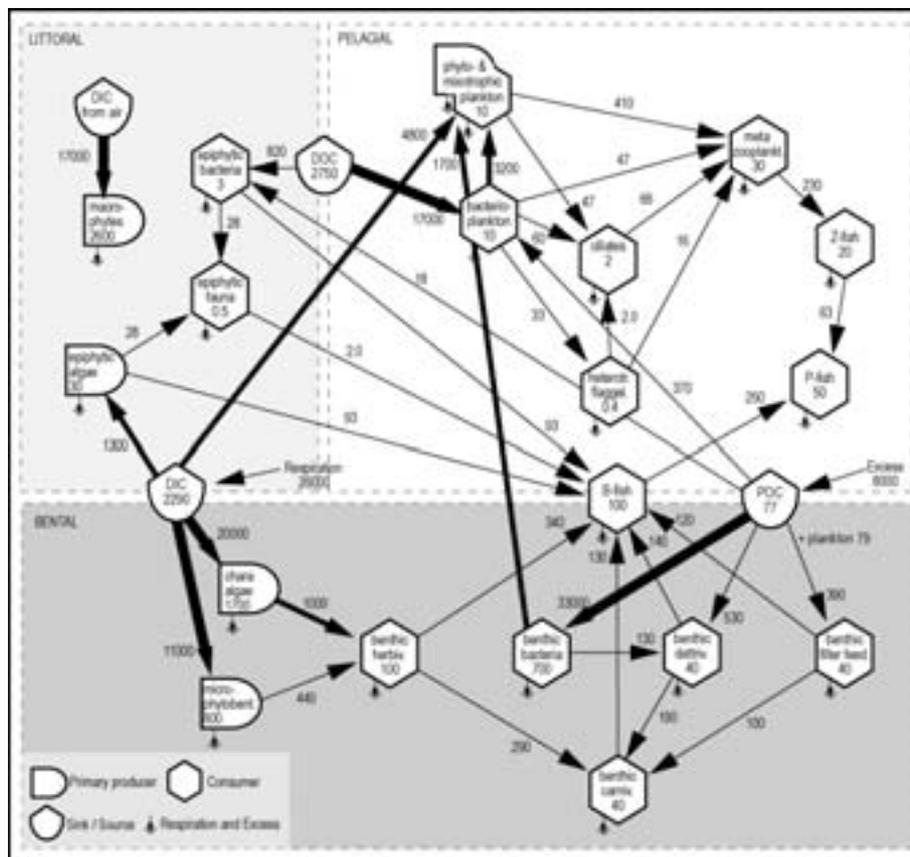
Figure 5. Calculated carbon flows in Lake Eckarfjärden. Numbers within symbols indicate total annual mean biomass (kg C) of the functional groups in the lake. Numbers on arrows indicate the annual flow of carbon (kg C) between different functional groups. Three different widths exist on the arrows and indicate the magnitude of the carbon flow. Not illustrated in the figure are the exchange of DIC with the atmosphere and the sedimentation of POC. Figure from paper V.

A net autotrophic system

Lake Eckarfjärden was calculated to be net autotrophic (paper II and V). This is further strengthened by CO_2 measurements in the lake in July and October 2002, showing under-saturation, during summer and autumn (paper II). Moreover, DOC concentrations measured in the spring 2002 were lower in the inlets than in the outlet, showing net production of DOC during springtime (paper II). DOC concentrations have also been measured in a monitoring program at 11 occasions evenly spread over the year 2002 (Swedish Nuclear Fuel and Waste Management CO., unpublished data). These measurements show that the import of DOC is less than the export on

an annual basis. The primary production in the pelagial of Lake Eckarfjärden was low, 55 μg C L^{-1} day^{-1}, and unproductive lakes (<100 μg C L^{-1} day^{-1}) tend to be net heterotrophic (delGiorgio et al. 1997). Moreover, DOC concentrations in the lake were very high (25 mg C L^{-1}) which would also indicate net heterotrophic conditions (Jansson et al. 2000). Accordingly, the pelagic habitat in Lake Eckarfjärden was net heterotrophic, but when the benthic and littoral habitats were included in the calculations, the lake turned out to be net autotrophic (paper V).

Conclusions

Overall, this thesis demonstrates that benthic microbiota may contribute significantly to the total microbial production in shallow clearwater lakes. Moreover, there are strong interactions between benthic and pelagic microbiota as well as between autotrophic and heterotrophic microbiota within habitats.

Both biomass and production of benthic microbiota were higher than the biomass and production of pelagic microbiota (paper I and II). The unusually thick (10-15 cm) microbial mats in these lakes are most probably sustained by mixing and resuspension, that allow the photosynthesising microbiota to reach layers were there is enough light for growth. The primary production can only occur in the uppermost millimetres where there is enough light. Hence, shallow clearwater lakes in general, also with thin and less impressive microbial mats, may have major parts of their primary production allocated to the benthic habitat.

In Lake Eckarfjärden, relationships between autotrophic and heterotrophic microbiota, within as well as between habitats, were demonstrated, indicating interactions among microbiota during natural nutrient concentrations. Further, this thesis shows that the interactions between microbiota may be altered following increased nutrient concentrations but the sensitivity to changes in interactions may vary between years (paper III and IV). Moreover, the expected shift towards pelagic production following increased nutrient concentrations in oligotrophic clearwater lakes does not necessarily occur.

Benthic production dominated the food web of the investigated clearwater Lake Eckarfjärden (paper V). Major flows of carbon were identified between habitats and the net result was that the benthic habitat provided carbon to the pelagial. In addition, I demonstrate that lakes with intense benthic primary production may be net autotrophic despite high DOC concentrations in the water column, which otherwise often results in net heterotrophy. The pelagial in Lake Eckarfjärden was net heterotrophic but when the benthic and littoral habitats were included in the calculations, the lake turned out to be net autotrophic. This emphasises the importance of a holistic view when studying lake metabolism.

Summarising the results, this thesis demonstrates that more studies of microbiota and whole lake status would benefit from including the benthic habitat.

Svensk sammanfattning (Swedish summary)

Mikroorganimser utgör basen i födoväven i sjöar. Mikroorganismer består dels av bakterier, dels av fotosyntetiserande organismer (alger och cyanobakterier, hädanefter refererade till som alger). Algerna utnyttjar i fotosyntesen solenergi och koldioxid för att bilda organiskt material. Bakterierna utnyttjar organiskt material som läcker ur alger eller som härrör från nedbrytning av organismer. Det organiska materialet kan antingen ha bildats i sjön eller runnit till sjön från omkringliggande områden. Mest studerade är mikrorganismerna i vattnet, växtplankton och bakterieplankton. Det finns dock även stora mängder alger och bakterier på bottnarna av sjöar, mikrofytobentos och bentiska bakterier, men dessa har studerats i mindre utsträckning.

Jag har undersökt förekomsten av alger och bakterier i såväl vattnet som på bottnarna i näringsfattiga klarvattensjöar längs Upplandskusten. Jag har studerat mängder och produktion av mikroorganismer, samt interaktioner mellan mikroorganismerna som lever på bottnen och i vattnet. Slutligen har jag utvärderat betydelsen av de bottenlevande och de vattenlevande mikroorganismerna i födoväven i en klarvattensjö.

Fokus av mikroorganismer till bottnarna i klarvattensjöar

Alger på bottnar av sjöar är ofta begränsade av solljus. I klarvattensjöar når solljuset ner till stora delar av bottnarna och mikrofytobentos har då en fördel jämfört med växtplankton i form av näringsämnen från sedimenten. I klarvattensjöar längs Upplandskusten fann jag låga halter växtplankton och bakterieplankton medan det fanns en tjock grön mikrobiell matta (10-15 cm) med mikrofytobentos och bentiska bakterier. Dessa sjöar beskrivs ibland som bottenlösa på grund av den mikrobiella mattan som bildare ett grönt fluffigt lager på bottnarna som man lätt sjunker igenom. Mikrofytobentos och bentiska bakterier hade högre produktion än växtplankton och bakterioplankton.

Respons på eutrofiering

Sjöar som har produktionen av mikroorganismer fokuserad till bottnarna är ofta känsliga för ökande näringskoncentrationer. Mer näring i vattenmassan leder ofta till mer växtplankton. När växtplanktonhalterna ökar minskar lju-

set som tränger ner till bottnarna och mikrofytobentos missgynnas. Produktionen förskjuts då från bottnarna till vattenmassan. Jag gjorde ett försök i Eckarfjärden 2002, där jag tillsatte kväve och fosfor och mätte halter och produktion av alger och bakterier, i såväl den mikrobiella mattan som i vattenmassan. I motsats till andra studier så gynnades de bottenlevande mikroorganismerna av den ökande näringshalten. Mikrofytobentos var överlägsna på att tillgodogöra sig den tillsatta näringen och det blev inget skifte till produktion i vattenmassan. I motsats till tidigare studier, visar denna alltså att produktionen kan bibehållas i den mikrobiella mattan även vid förhöjda näringshalter.

Mikroorganismer har effekt på det globala klimatet

Det fanns ungefär lika mycket alger som bakterier i sjöarna men algerna hade en större produktion än bakterierna. Detta är ovanligt i sjöar. Oftast är bakteriernas produktion högre än algernas. Eftersom bakterierna är beroende av organiskt material är sjöar där bakteriernas produktion är högre än algers beroende av inflöde av organiskt material (humusämnen) från omgivningarna. I Eckarfjärden däremot var produktionen av alger högre än bakterieproduktionen. När bakterierna tillgodogör sig organiskt material använder de syrgas och avger koldioxid. Alger däremot tar upp koldioxid och avger syrgas under fotosyntesen. När bakterierna avger mer koldioxid än vad algerna tar upp fungerar en sjö som en koldioxidkälla och bidrar till växthuseffekten. I Eckarfjärden däremot tog algerna upp mer koldioxid än vad bakterierna släppte ut och sjön fungerar som en koldioxidfälla.

Födoväven i klarvattensjöar

Födoväven i Eckarfjärden visar att mycket av den föda som fisk får i sig härstammar från mikroorganismernas produktion på bottnarna. Mikrofytobentos och bentiska bakterier äts av bottenlevande djur som i sin tur äts av fisk. Mängden mikroorganismer i vattenmassan var mycket lägre än på bottnarna och de vattenlevande mikroorganismerna bidrog också i mycket mindre utsträckning som föda för större organismer. Mikroorganismer i vattenmassan gynnas av att fiskar äter på bottnarna. Fiskarna transporterar då näringsämnen från bottnarna till vattenmassan. I vattnet avges en del av näringen i form av avföring och blir tillgänglig för mikroorganismerna i vattenmassan. Därför kan man säga att mikroorganismerna på botten är mycket viktiga för alla organismer i sjön. En stor del av den mikrobiella produktionen i Eckarfjärden åts dock inte av andra organismer utan lagrades som sediment på bottnen av sjön. Detta beror på att organiskt material inte bröts ner lika fort som det tillverkades av alger.

Sammanfattningsvis

Den här avhandlingen visar att mikroorganismer på bottnar av sjöar kan utgöra en stor del av det totala mikrobiella samhället i klarvattensjöar och ha en stor betydelse i födoväven. Algernas produktion var högre än bakteriernas. Vidare tog de fotosyntetiserande organismerna upp mer koldioxid än bakterierna släppte ut, vilket resulterar i att sjön fungerar som en koldioxidfälla. Organismerna på bottnarna och i vattenmassan interagerar med varandra och för att förstå hur sjöekosystem fungerar är det viktigt att inkludera alla organismer i sjön.

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