R-01-24

A preliminary carbon budget for two oligotrophic hardwater lakes in the Forsmark area, Sweden

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June 2001

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ISSN 1402-3091 SKB Rapport R-01-24

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This report concerns a study which was conducted for SKB. The conclusions and viewpoints presented in the report are those of the author(s) and do not necessarily coincide with those of the client.

Summary

The Swedish Nuclear Fuel and Waste Management Co (SKB) is responsible for management and disposal of Swedish radioactive waste. The company is planning to construct repositories that will keep radioactive waste away from humans for hundreds of thousands of years. In a safety assessment of the repositories hypothetical releases are used to evaluate the robustness of the repositories. It is important to know how the radioactive nuclides would react if they were released and by which way they could enter the living biota. SFR are responsible for the disposal of low radioactive waste and close to the nuclear plant in Forsmark there is a storage for low radioactive waste. At the moment this storage is located in the bedrock far below the sea level but due to landrise in the area it will in the future be located above sea level. Hence, it is of importance to know how the surface ecosystems in the area are functioning. A carbon budget for the aquatic ecosystem above SFR in Öresundsgrepen exist (Kumblad 1999), but it is also important to have a carbon budget for the surface systems in the Forsmark area since SFR in the future will be situated above sea level.

Carbon budgets can be used to get a picture of how an ecosystem functions. The carbon flow shows how carbon is transported through a food web from lower trophic levels, e.g. plants and bacteria to higher trophic levels such as fish. Oligotrophic hardwater lakes are the most important lakes in the Forsmark area. This report aims to give a picture of a potential flow of carbon through the ecosystem in two oligotrophic hardwater lakes, Lake Hällefjärd and Lake Eckarfjärden. Macrophytes, mainly *Chara*, were calculated to make up the largest part of the biomass and production in both lakes. Benthic bacteria and microphytobenthos (benthic photosynthesising microorganisms) were other large contributors to the production. Benthic bacteria were found responsible for a major part of respiration and, hence, consumption of carbon in the lakes. The biomass and production of biota were calculated to be concentrated to the light exposed soft-bottom community.

Unfortunately very few studies have been performed in oligotrophic hardwater lakes in Uppland and some of the values in the carbon budget are highly uncertain since they were calculated from literature data originating from other lake types. However, this estimate of the carbon flow, may serve as a basis for planning of future studies, of the function of the ecosystem in oligotrophic hardwater lakes.

Sammanfattning

Svensk Kärnbränslehantering AB (SKB) är ansvariga för hanteringen av svenskt radioaktivt bränsle och avfall. Det radioaktiva avfallet ska förvaras så att det är oåtkomligt för människor i hundratusentals år. Om radionuklider trots allt skulle komma ut i naturen är det viktigt att veta hur omkringliggande ekosystem fungerar så att riskanalyser för människor kan göras. SFR är ansvariga för lågradioaktivt avfall, och i Östersjön i närheten av kärnkraftverket i Forsmark, finns idag ett förvar för lågradioaktivt avfall. För tillfället befinner sig detta förvar under havsytan men genom landhöjningen i området kommer det i framtiden att befinna sig på land. Ytterligare förvar av kärnbränsle planeras men var dessa kommer att placeras är ännu inte bestämt.

De viktigaste sjöarna i Forsmarksområdet är de kalkoligotrofa sjöarna. Definitionen av en kalkoligotrof sjö är att den är kalkrik och näringsfattig. De kalkoligotrofa sjöarna i Uppland är relativt unga och har skapats genom landhöjningen som har pågått sedan den senaste istiden, vilken slutade för 8800 år sedan. På grund av de låga näringshalterna i vattnet är produktionen i vattenmassan låg. På bottnarna finns dock en stor biomassa av växter (makrofyter) och fotosyntetiserande mikroorganismer. Vissa av sjöarna är omgivna av myr medan andra är omgivna av skog. Tillrinningsområdets karaktär är sannolikt av stor betydelse för ekologin i sjöarna då tillrinnande vatten förändras med avseende på jonsammansättning när det passerar olika typer av ekosystem.

Denna rapport ger en bild av hur kol kan tänkas flöda mellan olika organismgrupper i två kalkoligotrofa sjöar i Forsmarksområdet; en omgiven av myrmark och en omgiven av skogsmark. Om radionuklider skulle komma ut i de kalkoligotrofa sjöarna är det mest troligt att de skulle komma in i näringskedjan via fotosyntetiserande mikroorganismer eller via bakterier.

I beräkningarna befanns makrofyter, främst *Chara*, vara de viktigaste primärproducenterna och deras produktion utgjorde mellan 78 och 80 % av den totala produktionen i sjöarna. Fotosyntetiserande mikroorganismer på bottnarna utgjorde en annan viktig del av primärproduktionen medan primärproduktionen i vattenmassan var försumbar.

Bakterieplanktons biomassa och produktion beräknades vara låga medan den bentiska bakteriebiomassan och produktionen var höga. Bentiska bakterier stod för en stor del av respirationen och därmed konsumtionen av organiskt kol i båda sjöarna.

Konsumtionen av organiskt kol var högre än produktionen av organiskt kol i sjöarna. Detta beror troligen på att sjöarna tillförs avsevärda mängder kol från omgivningarna. En annan orsak kan vara att produktionen i sjöarna undervärderats eller att konsumtionen övervärderats. Få studier har genomförts i de kalkoligotrofa sjöarna i Uppland och därför användes värden från liknande sjöar. Detta medför givetvis en risk att vissa organismgruppers produktion och konsumtion missbedömts. För att säkerställa denna kolbudget är det viktigt att fler studier av produktionen i de kalkoligotrofa sjöarna genomförs. Främst är det studier av mikrofytobentos biomassa och produktion som är önskvärda. Eftersom mätvärden från detta tjocka lager av mikrofytobentos saknas, och någon motsvarighet ej finns i andra sjöar, blir den uppskattade produktionen från litteraturdata mycket osäker. Sammanfattningsvis är detta en grov uppskattning av kolflödet i två kalkoligotrofa sjöar i Uppland. Dess huvudsakliga användning bör vara till att planera de studier som behövs för att med rimlig noggrannhet fastställa kolflödet i sjöarna så att pålitliga riskanalyser för radionuklider kan göras.

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1 Introduction

The Swedish Nuclear Fuel and Waste Management Co (SKB) is responsible for management and disposal of Swedish radioactive waste. The company is planning to construct deep repositories, which will keep the radioactive waste away from humans through hundreds of thousands of years. One of the possible sites for the repositories is the Forsmark area. Already, a storage for low and intermediate level radioactive waste, SFR, is situated near the nuclear plant in Forsmark. At the moment this storage is situated below the bottom of the sea. In the future, however, this area will rise and, around year 3500 AD, the land above the storage will be dry /Brydsten, 1999/. In case of a hypothetical release of radionuclides, it is important to understand how the surrounding ecosystems function to be able to make risk assessments for humans.

¹⁴C would by dose be the dominant radionuclide released from the SFR storage and, hence, it is important to know the flow of carbon through the ecosystems in the area. A carbon budget gives a picture of the importance of different organism groups and how carbon is transported from lower trophic levels to higher trophic levels in the food web. A carbon budget for the area above the SFR, the Öresundsgrepen, has been done /Kumblad, 1999/. However, in the future the SFR will be situated above sea level and the hence it is important to evaluate also ecosystems above sea level.

The Forsmark area is characterised by forested lowland with several short rivers of which Forsmarksån is by far the largest (40 km long, 375km² catchment area). Oligotrophic hardwater lakes constitute the most important lake type in the area today /Brunberg and Blomqvist, 1998/. These lakes are young and have been created by the shore displacement that has been going on since the last glaciation which terminated 8800 years ago /Ignatius et al., 1981/. In the future more lakes and new catchment areas will be formed in the area by the same process.

Two structurally different oligotrophic hardwater lake ecosystems of approximately the same age were chosen for carbon budget calculations; Lake Hällefjärd being surrounded by mire and Lake Eckarfjärden being surrounded by forest. The horizontal growth of mires around some lakes will most likely influence the ontogeny of the entire lake ecosystem /Brunberg and Blomqvist, 2000/. To illustrate potential differences between oligotrophic hardwater lakes surrounded by mire and those surrounded by forest in terms of flow of nutrients and energy through the systems, one representative of each type were chosen.

Very few studies of the limnology of these lakes have been carried out and consequently only limited amounts of data are available. The carbon budget is, as far as possible, based on biomass values and carbon flows between functional groups in the lakes. When data were lacking, biomass values from similar lakes were used.

2 Description of the area

The two oligotrophic hardwater lakes chosen for the budget calculations, Lake Hällefjärd and Lake Eckarfjärden, are situated in the province Uppland, central Sweden, close to the Baltic Sea. Since the depression during the last glaciation the area has been rising gradually and currently the land rise is about half a meter per century /Ignatius et al., 1981/. The bedrock mainly consists of granites and gneisses. The overlaying glacial and postglacial soils are calcium-rich till and glacial and post-glacial clay respectively, which results in surface waters being highly alkaline.

Lake Hällefjärd is a small lake with a total lake area of 0.05 km^2 (Table 2-1). It is situated in the county Tierp (60°30.6'N, 17°57.3'E) at 4 m above the sea level. The average depth is 0.9 m and the maximum depth is 1.5m. Lake Hällefjärd has a volume of 200 000 m³ and the theoretical residence time of the water is 63 days. The catchment area of the lake is 0.5 km^2 and is mainly made up by forest (77.3%) of which a small part, 3.6%, has recently been clear-cut. The lake is surrounded by mire, which constitutes 18.1% of the catchment area. *Phragmites* is covering a large part of the mire. There are no visible inlets to the lake. The northern part of the mire close to the outlet has been partly drained, but no effect of this drainage on the lake ecosystem has been discovered. Because of the low degree of anthropogenic influence, Lake Hällefjärd has been considered to have the highest value in different biological conservation surveys /Haglund, 1972; Länsstyrelsen i Uppsala län, 1987; Naturvårdsverket, 1999/. Both pool frog (*Rana leesonae*) and medicinal leech (*Hirudo medicinalis*), which are endangered species in Sweden are found in the lake. The mire contains many different species of rare herbs and a number of birds are stationary in the area.

Lake Eckarfjärden is larger than Lake Hällefjärd but still a small lake with an area of 0.23 km^2 (Table 2-1). It is situated 2 km East of Forsmark in the county Östhammar (60°22'N, 18°12'E) at 6 meters above the sea level. The average depths is 1.5 m and the maximum depth is 2.6 m. The volume of the lake is 350 000 m³ and the theoretical residence time of the water is 383 days. The catchment area is 1.51 km² and is dominated by forest which make up 73% /Brunberg and Blomqvist, 1998/. The lake makes up 15%, wetlands 7% and arable and pastureland 5% of the catchment area /Brunberg and Blomqvist, 1998/. The lake is surrounded by forest and not by mire as Lake Hälle-fjärd. However, the outlet passes through a small mire. The outlet has been subjected to drainage and the lake level has been slightly lowered. Otherwise there are no visible signs of human impact on the lake.

Table 2-1. Area, depth, volume, residence time and catchment area of Lake Hällefjärd and Lake Eckarfjärden.

	Lake area (km²)	Mean depth (m)	Max. depth (m)	Volume (m³)	Residence time (days)	Catchment area (km²)
Lake Hällefjärd	0.05	0.9	1.5	200 000	63	0.5
Lake Eckarfjärden	0.23	1.5	2.6	350 000	383	1.51

The sediments of both Lake Hällefjärd and Lake Eckarfjärden are very soft. These lakes are sometimes referred to as "bottomless" as there is no distinct border between the sediment and the lake water. The water content in the upper 0–5 cm layer is 97–98% in Lake Hällefjärd and 98% in Lake Eckarfjärden /Eva Nilsson, unpublished data/. The sediments are calcareous and rich in organic material of autochthonous origin /Brunberg and Blomqvist, 1999/. Stoneworths (Charophytes) and microphytobenthos (mainly cyanobacteria and diatoms) cover the sediments.

Water enters the lakes by direct precipitation, groundwater inflow and, in the case of Lake Eckarfjärden, through a very small tributary. The water in both Lake Hällefjärd and Lake Eckarfjärden has an oligotrophic character with low concentrations of phosphorous. The water in both lakes is moderately stained by humic substances. During 1999, water chemistry analyses were performed in Lake Hällefjärd and in January 2000 an ongoing sampling programme was started in both lakes. Some water chemistry parameters are presented in Table 2-2.

Table 2-2. Some abiotic factors from Lake Hällefjärd and Lake Eckarfjärden. Values of pH, conductivity, colour and alkalinity are mean values from sampling at 15 and 16 occasions, during 2000 for each lake respectively. /Eva Nilsson, unpublished data/.

	Lake Hällefjärd	Lake Eckarfjärden	
рН	8.0	8.2	
Conductivity (mS/m)	27	26	
Colour (mgPt/l)	77	83	
Alkalinity (mekv/l)	2.5	2.4	

The ionic composition of the water in the oligotrophic hardwater lakes is different from that of the average lake in Uppland /Forsberg, 1965/. The hardwater lakes contain at least 10 equivalent % more calcium than the standard composition measured by Rodhe /1949/. The ionic composition in Lake Hällefjärd was measured by Forsberg /1965/ and is presented in Table 2-3 together with the average composition for 27 oligotrophic hardwater lakes in Uppland. Lake Hällefjärd has a higher proportion of HCO₃ than the average hardwater lake in Uppland. No data on the ionic composition in Lake Eckarfjärden were available, but the ongoing sampling programme during 2000 will yield data on the ionic composition of both Lake Hällefjärd and Lake Eckarfjärden.

Table 2-3. Ionic composition in Lake Hällefjärd and a mean value for 27 hardwater lakes in Uppland /Forsberg,1965/. The values are given in equivalent %.

Location	Date	Са	Mg	Na	к	HCO ₃	SO₄	CI
Lake Hällefjärd	1961.04.23	89.0	6.6	3.4	1.0	89.5	8.1	2.4
Lake Hällefjärd	1962.08.12	87.2	5.8	6.1	0.9	85.2	10.4	4.4
Mean for 27 lakes	1960	73.3	14.1	7.2	1.6	63.9	28.7	7.4
Standard composition		63.5	17.4	15.7	3.4	73.9	16.0	10.1

During winter, the lakes in this area are covered with ice for 140–160 days from November to April /Eriksson, 1920/. In Eckarfjärden there is a low risk for oxygen deficiency below the ice /Brunberg and Blomqvist, 2000/. For Lake Hällefjärd no studies of oxygen deficiency has been made. However, preliminary studies of oxygen concentrations during 2000 did not show any oxygen deficiency this year.

Both lakes are shallow and have limited volumes of water, and hence the water warms up quickly during summer. In the summer of 2000 the temperature rose above 20°C in both lakes. The annual mean temperature in the area is 5.8°C. Because of the small depth it is unlikely that any thermoclines are formed.

3 Construction of the food web

In general terms, the carbon that flows through the organisms in a food web finally ends up in the organisms at the highest trophic levels in the system. By understanding the structure of the food web as well as the production, respiration and consumption of different organism groups it is possible to calculate the flow of carbon. In lakes, carbon is mobilised by two different processes at the base of the food web. First of all, organic carbon can be produced within the lakes by photosynthetic organisms (autochthonous carbon). Alternatively, carbon which enters the lake via the inflows, allochtonous organic carbon, can be incorporated into the food web by heterotrophic bacteria. Traditionally, lakes have been considered net autotrophic systems where the autochthonous primary production exceeds or equals the respiration. However, recent findings suggest that lakes may be net sources of CO_2 /Cole et al., 1994/ and that bacterial respiration of allochtonous carbon exceeds primary production in many lakes /del Giorgio et al., 1997/.

Photosynthetic organisms use carbon dioxide, nutrients and solar energy to produce organic carbon. Primary producers in lakes include phytoplankton, macrophytes, epiphytic algae and microphytobenthos. Bacteria use dissolved organic carbon (DOC) for their production and this carbon may be supplied from allochtonous or autochtonous sources. The bacteria in lakes are present in the pelagial, in the sediments and on macrophytes.

Zooplankton, benthic fauna and fish consume the carbon produced by primary producers and bacteria at the base of the food web. Animals that feed exclusively on autotrophs are termed herbivores. Some feed on other animals and are termed carnivores. Still others feed on both autotrophs and other animals and are called mixotrophs. When the consumers are foraging, some carbon is lost due to respiration, excudation, and sloppy feeding. The carbon that is lost in the food chain may be used again by autotrophs as well as by bacteria.

Carbon is transported from the primary producers in several steps. An animal eating an autotroph is a primary consumer. The animal feeding on the primary consumer is a secondary consumer, and so on. The autotrophs and consumers constitute different trophic levels in the food web, i.e. the primary producers are the first trophic level, the primary consumers are the second trophic level, the secondary consumers are the third trophic level, and so on. However, the food web is seldom simple and animals often forage at more than one trophic level.

In this study the organisms has been divided into functional groups mainly in accordance with Kumblad /1999/, who constructed a carbon budget for a nearby brackish water ecosystem in Öresundsgrepen. The organisms were divided on the basis of their food source and their function in the ecosystem. Below follows a list of the functional groups as well as a brief definition of the organisms included.

- Phytoplankton: pelagic microalgae and cyanobacteria.
- *Microphytobenthos:* microalgae and cyanobacteria on the bottom of the lakes.
- *Macrophytes:* macroalgae, higher plants, bryophytes and epiphytic algae.
- *Bacterioplankton:* pelagic heterotrophic bacteria.
- Zooplankton: pelagic animals.
- Benthic bacteria; heterotrophic bacteria in the sediments and on the bottom of lakes.
- *Benthic fauna:* invertebrate fauna in/on the sediment and associated to macrophytes.
- Fish.

The ecosystem of oligotrophic hardwater lakes may be divided into three characteristic habitats, the pelagic habitat, the emergent macrophyte habitat, and the light exposed soft-bottom habitat /Brunberg and Blomqvist, 1999/. Since the lakes are shallow, light reaches the entire bottom and there is no profundal zone. The division has been used in the calculations to determine in which habitat of the lake ecosystem production and consumption is highest. In this report calculations for the emergent macrophyte zone has not been included. *Sphagnum* makes up a large part of the emergent macrophyte zone and enters into the surrounding mire. It is difficult to determine were the emergent macrophyte zone has been included in the surrounding mire in the calculations. Higher organisms that move freely between the habitats (i.e. fish) were treated separately.

The benthic soft bottom habitat in the oligotrophic hardwater lakes is believed to be the most important part of the lake in terms of primary production /Brunberg and Blom-qvist, 1999/. The functional groups found in this habitat are microphytobenthos, macro-phytes, epiphytic bacteria, benthic fauna and benthic bacteria.

The pelagic habitat in hardwater lakes such as Lake Hällefjärd and Lake Eckarfjärden is probably not very productive, since most of the production in such lakes is believed to be allocated to the bottoms and the nutrient concentrations in the water are low /Brunberg and Blomqvist, 2000/. Functional groups in this habitat include phytoplankton, bacterioplankton and zooplankton.

Sphagnum and/or *Phragmites* dominate the emergent macrophyte zone in lakes in the Forsmark area. Mires often encircle the entire lakes, which is the case for Lake Hälle-fjärd. The mire forms a floating edge, a quagmire, into the lake and *Sphagnum* is the dominating species. *Sphagnum* is known to sieve the inflowing water to the lake and to function as a cation exchanger releasing hydrogen ions for other ions /e.g. Clymo, 1963; Clymo, 1964/. Water is probably entering the lake through the mire and if so, *Sphagnum* is most likely also important in determining how much organic carbon that reaches the lake. It is possible that the *Sphagnum* mire is releasing dissolved organic carbon (DOM) produced by *Sphagnum* but it is also possible that the bacterial microflora within the mire takes up the DOM in the passing water. Lake Eckarfjärden lacks surrounding mire. Instead the emergent macrophyte zone is dominated by *Phragmites*.

The higher trophic levels that can move freely between the habitats include fish and birds. Fish can feed both from the pelagic and the light exposed soft-bottom habitat. In this kind of oligotrophic lake, where most of the biomass is concentrated to the bottoms, it is reasonable to believe that fish are mainly foraging from the benthic community.

Macrophyte vegetation in lakes increases the amount of food for birds /Blindow, 1986/. Birds can feed either on the macrophytes, on the invertebrates living on the plants, or on fish. The concentration of invertebrates is high on *Chara* and since the bottoms of oligotrophic hardwater lakes usually are covered with *Chara*, they are regarded as good bird locations /Blindow, 1986/.

4 The carbon budget

4.1 Initial considerations and calculations

As far as possible, in the budget calculations presented below, values of biomass, production, respiration and consumption of organisms in Lake Hällefjärd and Lake Eckarfjärden, collected from the literature, were used. When values were not available, data from similar lakes were chosen. If possible, mean values of biomass for the entire year were used, but in most cases, only biomass values from summer studies were available. Biomass values in terms of wet or dry weight were converted to carbon using conversion factors for different groups of organisms obtained from Kautsky /1995 a/. In a majority of cases, only biomass values were available, and were used to calculate production, respiration and consumption according to Kautsky /1995 b/. Biomass and production of benthic bacteria were taken from Törnblom /1995/. Epiphytic algal biomass and production were assumed to be included in the macrophyte biomass and production. Data on fish biomass for Lake Eckarfjärden were available as catch per unit effort (CPUE) /Brunberg and Blomqvist, 1999/. These values were calculated to g carbon in the lake with a conversion factor of $33 \text{kg} \cdot \text{ha}^{-1}$ per 1 CPUE /Nyberg, personal communication/. Fish were assumed to contain 10% carbon. No data of fish biomass were available for Lake Hällefjärd. Instead, a mean value for six oligotrophic hardwater lakes in Uppland /Brunberg and Blomqvist, 1999/ was used.

When only summer values of production and respiration were available, they were corrected for the difference in solar radiation and temperature to get values representing the annual production and respiration. The primary production was assumed to be dependent on solar radiation and the calculation includes number of light days, which is the number of days when the relative insolation exceeds $5 \text{ MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. At 60°N, the latitude where Lakes Hällefjärd and Eckarfjärden are situated, the number of light days was estimated to 105 using data from the Baltic Sea /Kautsky and Kautsky, 1995/. This value was corrected by the authors for the reduction in insolation that the ice cover results in. However, such a reduction in light due to icecover in Lake Hällefjärd and Lake Eckarfjärden is not possible to calculate since no data are available of the thickness of the icecover during the winter season. Therefore, the number of light days in the Baltic Sea at the same latitude was assumed to be identical to the number of light days in lake Hällefjärd and Lake Eckarfjärden. The respiration of animals was compensated for temperature differences and the annual degree days were estimated to 2400°C at 60°N /Kautsky and Kautsky, 1995/.

Calculations for biomass, primary production, respiration and consumption

• biomass $(gC \cdot m^2) =$	dry weight · value for carbon content in the organism/Kautsky, 1995 a/,
• biomass Fish $(kgC \cdot m^{-2}) =$	CPUE \cdot 33kg \cdot ha ⁻¹ \cdot lake area \cdot 0.10,
• primary production $(gC \cdot m^{-2} \cdot year^{-1}) =$	biomass · conversion factor for primary production /Kautsky, 1995 b/ · annual light days,

- bacterial production $(gC \cdot lake^{-1} \cdot year^{-1}) = (30.16 \mu gC \cdot g_{sediment}^{-1}) \cdot days,$
- respiration $(gC \cdot m^{-2} \cdot year^{-1}) =$

biomass · conversion factor for respiration /Kautsky, 1995 b/ · degree days,

- consumption (benthic and pelagic bacteria) = production + respiration,
- consumption (zooplankton, benthic fauna and fish) = $3 \cdot \text{respiration}$.

Very few studies have been performed in the oligotrophic hardwater lakes and no data are available of how much dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and particulate organic carbon (POC) that reaches the lakes. However, to be able to calculate the amount of DOC, DIC and POC that reaches the lake, the flow of water and the ability of the mire to retain carbon must be known. No studies have been made of the water flow to Lake Hällefjärd or Lake Eckarfjärden and neither is the carbon retention of the mire known. Therefore, the amount of carbon reaching the lake from the emergent macrophyte community could not be calculated. However, a calculation was made of how much TOC that theoretically has to reach the lake with the inflowing water to balance the budget.

Since data on the carbon biomass, production, respiration and consumption for different functional groups only occasionally were available from Lake Hällefjärd and Lake Eckarfjärden and mostly taken from other lakes, a more detailed explanation of which values were used for the different functional groups is given below.

4.1.1 Macrophytes

Characeans, mainly *Chara aculeolata* but also *Chara aspera* and *Chara globularis* cover most of the bottom in Lake Hällefjärd /Forsberg, 1965/. Lake Eckarfjärden is also a *Chara* lake but there are no data available of the percentage cover of *Chara*. In both lakes Phragmites is also found but no data of biomass are available. Since no quantitative data were available for the biomass of the macrophytes in neither Lake Hällefjärd nor Lake Eckarfjärden, values from the *Chara* Lake Krankesjön in southern Sweden were used. In a study of the macrophyte cover in June to September 1989, the biomass of *Chara* was 478±115 g dry weight m⁻² and the biomass of *Potamogeton* was 73±10 g dry weight \cdot m⁻² /Blindow, 1992/. Together with the lake area of each lake these values were used to calculate the carbon biomass for the entire lakes. This gives a gross estimation of how large the biomass of macrophytes in the two lakes may be. Of course the biomass may differ between lakes and further studies are needed to confirm the large percentage of biomass and production that *Chara* was calculated to make up in this study.

Epiphytic algal biomass and production were assumed to be included in the macrophyte biomass and primary production.

4.1.2 Phytoplankton

Phytoplankton were studied in Hällefjärd during the summer 1999 /Halvarsson, 2001/. The biomass value used in this carbon budget is the mean value from six samplings during the summer 1999. Samples were taken 23 June, 7 and 20 July, 5 and 17 August and 9 September. The biomass values from Lake Hällefjärd were also used for Lake Eckarfjärden. Forsberg /1965/ noted that the phytoplankton biomass in Lake Sigge-forasjön in Uppland were of the same order of magnitude as those in the oligotrophic hardwater lake Långsjön. All the oligotrophic hardwater lakes seem to have a small phytoplankton biomass and they can probably be assumed to be of the same order of magnitude. Phytoplankton production was calculated with conversion factors from Kautsky /1995 b/.

4.1.3 Microphytobenthos

The biomass of microphytobenthos was studied in Lake Hällefjärd during 1999 /Halvarsson, 2001/. In that study, the biomass of microphytobenthos was generally found to be much larger than the biomass of phytoplankton (Figure 4-1) and the biomass increased considerably during the summer. No data were available of microphytobenthos biomass or production in Lake Eckarfjärden and on production in Lake Hällefjärd. Lundqvist /1925/ who studied the oligotrophic hardwater lakes claimed that the biomass of microphytobenthos was mainly made up by cyanobacteria and diatoms.

Since no data were available on the productivity of microalgae in the lakes, the calculations had to be based on literature data. The production of microphytobenthos has not been well studied in freshwater and, hence no good lake data were available for budget calculations. However, studies of marine microphytobenthos have shown that

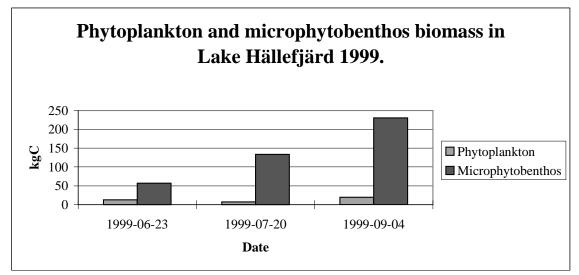


Figure 4-1 Biomass of microphytobenthos and phytoplankton in Lake Hällefjärd during 1999 /Halvarsson, 2001/. The microphytobenthos were sampled from the top 5 cm of the sediment and the biomass for the whole lake has been calculated by multiplication with the lake area.

the benthic primary production can exceed the primary production of the integrated water column both on shallow /Barranguet et al., 1996; Carmouze et al., 1998/ and on deep (14–40m) locations /Cahoon and Cooke, 1992/. In marine studies inorganic nutrients has been shown to limit for the growth of microphytobenthos /Nilsson et al., 1991/. If groundwater is entering the oligotrophic hardwater-lake there is probably a good source of inorganic nutrients to provide large production. Light may also be limiting for the growth of microphytobenthos but Sundbäck et al., /1996/ showed that the benthic communities seem to be adapted to low light intensities. In this carbon budget, production values for filamentous algae in the Baltic Sea /Kautsky, 1995 b/ were used. The result is in the same order of magnitude as when microphytobenthos values from the Danish Wadden Sea are used /Grøntdev, 1962/.

4.1.4 Epiphytic bacteria

No values were available for the biomass or production of epiphytic bacteria from Lake Hällefjärd or Lake Eckarfjärden. Neither were biomass values found for epiphytic bacteria from other *Chara* lakes. However, epiphytic bacterial biomass and production may be high. In Lake Dystrup in Denmark, with a 95% cover of macrophytes, the epiphytic bacterial biomass was 7-fold higher than the pelagic bacterial production /Theil-Nielsen and Søndergaard, 1995/. Since the bottom of both Lake Hällefjärd and Lake Eckarfjärden is covered with *Chara*, values from Lake Dystrup were assumed to be applicable even for Lake Hällefjärd and Lake Eckarfjärden. Biomass of 0.33 gC \cdot m⁻² were used and the production were assumed to be 7 times the pelagic bacterial production.

4.1.5 Bacterioplankton

No data were available on the biomass or production of bacterioplankton in either Lake Hällefjärd or Lake Eckarfjärden. Brunberg and Blomqvist /1999/ speculated that the bacterioplankton production should be of equal to or larger than the phytoplankton production, because dissolved organic carbon present in high concentrations in the lakes in the form of allochtonous substances. In some lakes, bacterioplankton are dependent on the phytoplankton for dissolved organic carbon but this is most likely not the case in the oligotrophic hardwater lakes where bacterioplankton may rely on humic substances as carbon source.

Values on bacterioplankton biomass were taken from Lake Njupfatet, an oligotrophic clearwater lake in northern part of Sweden /Vrede, 1997/. The production of bacteria was assumed to be of the same magnitude as the phytoplankton production in this study.

4.1.6 Benthic bacteria

No studies on benthic bacterial biomass or production in Lake Hällefjärd or Lake Eckarfjärden were available. The biomass of benthic bacteria is generally high and their activity is also high compared to that in the water column /Doremus and Clesceri, 1982/. The benthic bacterial biomass in sediments does not vary much between sediments, ranging between 10^8 and 10^{10} cells \cdot cm⁻³ in both marine and freshwater sediments /Schallenberg et al., 1989/. Also, the number of bacteria in the sediment varies little both within and between years /Boström et al., 1989/. No good correlation has been found between the bacterial biomass and the bacterial production /van Duyl and

Kop, 1990; Nilsson et al., 1991; Brunberg, 1993/. This may be due to the fact that a large amount of the bacteria are inactive /Boström and Törnblom, 1990/.

In the oligotrophic hardwater lakes the bacterial biomass and production may be small due to competition with the microphytobenthos for inorganic nutrients but they may also be favoured by the presence of microphytobenthos which provide them a readily available carbon source. The sediment of Lake Hällefjärd and Lake Eckarfjärden ought to be highly organogenic due to the large amount of microphytobenthos. Therefore, values of benthic bacterial biomass and production were taken from a study in Vallentunasjön, in which the sediments also are highly organogenic /Törnblom, 1995/. In that study, the bacterial biomass (2921 μ g C \cdot g_{sediment}⁻¹) was used to calculate the bacterial biomass in Lake Hällefjärd and Lake Eckarfjärden. The density of the sediment of Lake Hällefjärd and Lake Eckarfjärden. The density of the sediment of Lake Hällefjärd and Lake Eckarfjärden. A layer of 1 cm was used in the calculation of biomass and production. Also benthic bacterial production was estimated using data from the study of Törnblom /1995/.

4.1.7 Zooplankton

Since phytoplankton biomass and production in the oligotrophic hardwater lakes are generally low, the biomass and production of zooplankton should also be low (e.g. McCauley and Kalff, 1981/. No data were available on zooplankton biomass in lakes Hällefjärd an Eckarfjärden. Since zooplankton are feeding on phytoplankton, phytoplankton populations of equal size could be assumed to provide the same size of zooplankton populations. Of course there can be differences between different zooplankton populations and different species in their need of food. Zooplankton values from Siggeforasjön are available for the entire year, and since the phytoplankton population of Siggforasjön was of equal size as those in oligotrophic hardwater lakes, values from Lake Siggeforasjön were used in this carbon budget as a gross estimate. The mean value 77 μ g C \cdot 1⁻¹ from a study 1996 to 1997 in Lake Siggeforasjön /Lindström,1998/ was choosen for both Lake Hällefjärd and Lake Ecklarfjärden.

4.1.8 Benthic fauna

No studies were available on the biomass or composition of benthic fauna in the oligotrophic hardwater lakes in Uppland. However, Lundqvist /1925/ noted high amounts of Chironomid tubes in some of the oligotrophic hardwater lakes. In a study in Lake Krankesjön in southern Sweden the biomass of macroinvertebrates on *Chara*, *Potamogeton* and bare sediment was studied /Hargeby et al., 1994/. It was found that the invertebrate biomass was larger on *Chara*. *Chara* is usually not fed upon by benthic animals but provide a good substrate for benthic fauna which use the vegetation as a shelter from predators and they also feed on the epiphytic algae and bacteria /Blindow, 1986/. Values from Lake Krankesjön were used to calculate the biomass of benthic fauna in Lake Hällefjärd and Lake Eckarfjärden assuming that the whole lake area is covered with *Chara*. Since only macroinvertebrates were considered in this study it may have lead to an underestimation of the biomass, respiration and consumption of benthic fauna. In *Chara* lakes in northern Norway the densities of benthic fauna were studied and were found to range between 8–10g dry weight $\cdot m^{-2}$ /Fjeldsa, 1977/. Using this value would result in slightly higher biomass value for the lakes than using those from Lake Krankesjön. However, since data from Lake Krankesjön have been used for other groups of organisms it seems reasonable to use them also for benthic fauna.

4.1.9 Higher organisms

Gillnet fishing has been performed in Lake Eckarfjärden according to Swedish standards. Five species were found, Pike, Roach, Perch, Ruffe and Tench. The catch per unit effort (CPUE) was 47 individuals and 3.9kg. It is difficult to translate these values to g carbon in the lake. A conversion factor of 33 kg \cdot ha⁻¹ per 1kg CPUE was used /Nyberg, personal communication/. The fish biomass was calculated to be 296kg carbon in Lake Eckarfjärden. In Lake Hällefjärd gillnet fishing has not been done but a mean value for six oligotrophic hardwater lakes in the Forsmark area /Brunberg and Blomqvist, 1999/ were used and the biomass was estimated to be 29kg carbon in Lake Hällefjärd.

4.2 Calculated carbon biomass in habitats and motile biota.

In both Lakes Hällefjärd and Eckarfjärden the carbon biomass was calculated to be concentrated to the light exposed soft-bottom community (Figure 4-2, Tables 4-1 and 4-2). In lake Hällefjärd, the biomass of organisms in the light exposed soft-bottom community made up 99% of the total biomass, fish made up 1% and the biomass of pelagic organisms was negligible (Figure 4-2a). The distribution of carbon in Lake Eckarfjärden were almost identical to that in Lake Hällefjärd with the soft-bottom community making up 98%, fish 1% and the pelagial 1% of total biomass, respectively (Figure 4-2b).

4.3 Distribution of biomass and production of carbon among functional groups

Both in Lake Hällefjärd and Lake Eckarfjärden macrophytes was calculated to be the functional group that made up the largest part of the total biomass, more than 60% of the total biomass of biota in the lakes (Figure 4-3, Table 4-1 and Table 4-2). Benthic bacteria were calculated to make up about 20%, microphytobenthos between 4 and 7%, and benthic fauna 3%, respectively. The functional groups in the pelagial only made small contributions to the total biomass, in all cases below 1%.

The major primary producer in both lakes were submersed macrophytes, i.e. *Chara*, which were calculated to make up 78% of the production in Lake Hällefjärd and 74% of the production in lake Eckarfjärden (Figure 4-4). Benthic bacteria and microphytobenthos were calculated to make up the remaining parts of the production, whereas the pelagic production was negligible.

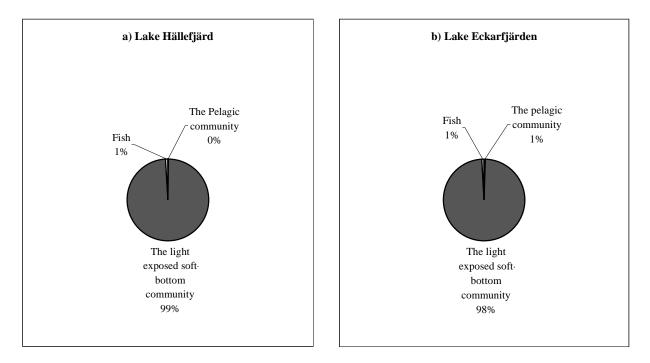


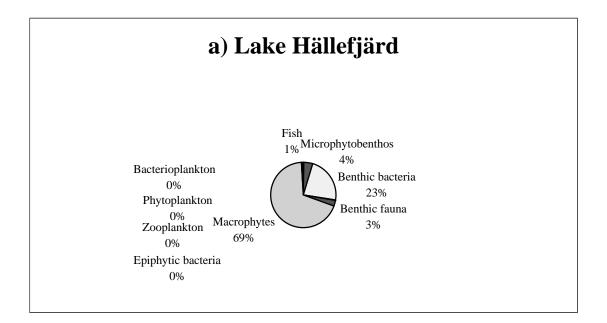
Figure 4-2. Distribution of biomass between the pelagic and light exposed soft-bottom community and fish in a) Lake Hällefjärd and b) Lake Eckarfjärden.

Functional groups	Biomass kgC	Prod 1000 kgC ∙ year ⁻¹	Respiration 1000 kgC · year⁻¹	Consump. 1000 kgC ∙ year¹	Sec. cons. 1000 kgC ∙ year¹	Source and location
Phytoplankton	10	0.1	_	_	_	1
Microphytobenthos	140	1.4	_	-	_	1
Macrophytes	2149	16.6	_	_	_	2
Bacterioplankton	1	0.1	0.1	0.2	0.1	3,4
Benthic bacteria	712	2.6	118	121	3	5
Epiphytic bacteria	4	0.7	0.7	3.4	2.7	6
Zooplankton	2	_	0.5	1.4	0.9	7
Benthic fauna	88	_	6	18	12	8
Fish	29		2	7	5	9
Total	3131	21	127	148	21	

Table 4-1. Biomass, production, respiration and consumption of different organism groups in Lake Hällefjärd.

Source and location:

- 1. Halvarsson, 2001; Lake Hällefjärd.
- 2. Blindow, 1992: Lake Krankesjön.
- 3. Vrede, 1997: Lake Njupfatet.
- 4. Brunberg and Blomqvist, 1999.
- 5. Törnblom, 1995: Lake Vallentunasjön.
- 6. Theil-Nielsen and Søndergaard, 1995: Lake Dystrup.
- 7. Lindström, 1998: Lake Siggeforasjön.
- 8. Hargeby et al., 1994: Lake Krankesjön.
- 9. Nyberg /personal comment/.



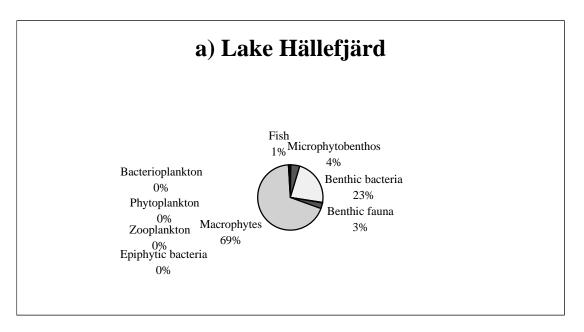


Figure 4-3. Carbon distribution among living organisms in a) Lake Hällefjärd and b) Lake Eckarfjärden.

Carbon respiration was calculated to be almost exclusively allocated to benthic bacteria in both lakes (Figure 4-5). The benthic bacteria were found to make up 92% and 91% of the total respiration in Lake Hällefjärd and Lake Eckarfjärden, respectively. Benthic fauna, fish and epiphytic bacteria made up 5, 2 and 1% of the total respiration, respectively. In Lake Eckarfjärden zooplankton made up 1% of the respiration.

Functional groups	Biomass kgC	Prod 1000 kgC · year¹	Respiration 1000 kgC year ⁻¹	Consump. 1000 kgC ∙ year¹	Sec. cons. 1000 kgC · year¹	Source and location
Phytoplankton	158	2	_	_	_	1
Microphytobenthos	2236	14	_	_	_	1
Macrophytes	20282	157	_	_	_	2
Bacterioplankton	10	2	2	3	2	3,4
Benthic bacteria	6718	25	1113	1138	25	5
Epiphytic bacteria			12	25	13	6
Zooplankton	27	-	7	22	15	7
Benthic fauna	832	_	57	171	114	8
Fish	296		23	70	47	9
Total	30559	200	1202	1404	156	

 Table 4-2. Biomass, production, respiration and consumption of different organism groups in Lake Eckarfjärden.

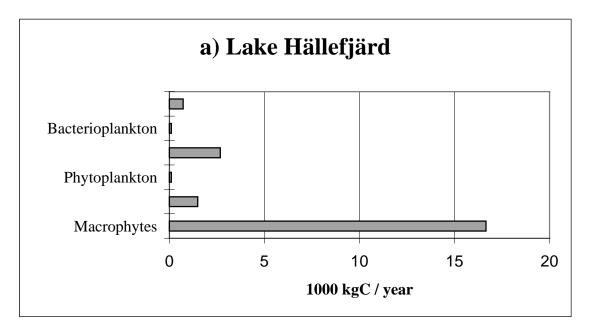
Source and location:

- 1. Halvarsson, 2001; Lake Hällefjärd.
- 2. Blindow, 1992: Lake Krankesjön.
- 3. Vrede, 1997: Lake Njupfatet.
- 4. Brunberg and Blomqvist, 1999.
- 5. Törnblom, 1995: Lake Vallentunasjön.
- 6. Theil-Nielsen and Søndergaard, 1995: Lake Dystrup.
- 7. Lindström, 1998: Lake Siggeforasjön.
- 8. Hargeby et al., 1994: Lake Krankesjön.
- 9. Nyberg /personal comment/.

Consumption of carbon was also dominated by the benthic bacteria which made up 81% of the total consumption in Lake Hällefjärd and 79% of the total consumption in Lake Eckarfjärden (Figure 4-6). Benthic fauna made up 12% and fish made up 5% of the total consumption in both lakes.

4.4 Flow of carbon

Carbon flows through the food web from the lowest and successively to higher trophic levels. In Figures 4-7 and 4-8 the calculated flow of carbon through the ecosystem in Lake Hällefjärd and Lake Eckarfjärden, respectively, is shown. Optimally also the DOC, DIC should be included in the carbon flow. However, these figures give a rough idea how the carbon may flow in the oligotrophic hardwater lakes in the Forsmark area. According to the calculations, the largest flow of carbon passes through the benthic fauna. A large part of carbon is transported from benthic fauna to fish. However, the fish population is not big enough to fully utilise the carbon produced by the benthic fauna.



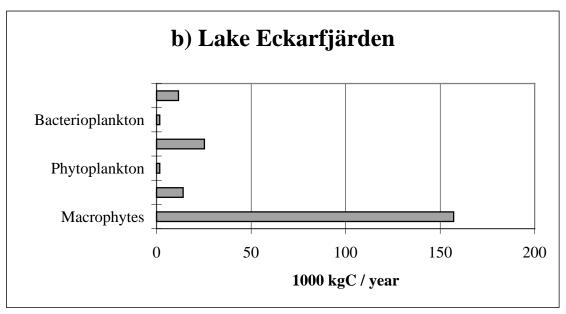
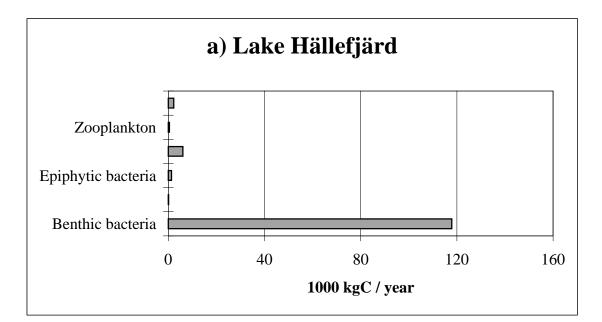


Figure 4-4. Production of carbon by photosynthesis and heterotrophic bacterial production in a) Lake Hällefjärd and in b) Lake Eckarfjärden.

The primary producers within the lakes can not supply enough C to support the calculated benthic bacterial consumption. There is a lack of $13.5 \cdot 10^3 \text{ kgC} \cdot \text{year}^{-1}$ and $132 \cdot 10^3 \text{ kgC} \cdot \text{year}^{-1}$ for Lake Hällefjärd and Lake Eckarfjärden, respectively. Calculations of the residence time and the volume of the lakes shows that the inflowing water would need to have concentration of $11,7 \text{ mgC} \cdot 1^{-1}$ and $396 \text{ mgC} \cdot 1^{-1}$ in Lake Hällefjärd and Lake Eckarfjärden, respectively. The large mire surrounding Lake Hällefjärd may produce carbon enough to balance the budget. Literature values of Sphagnum production vary between 50 and 300 gww $\cdot \text{m}^{-2} \text{ year}^{-1}$ /Wallén et al., 1988/. The mire surrounding Lake Hällefjärd is 90500 m² and, calculated with the values above, produce



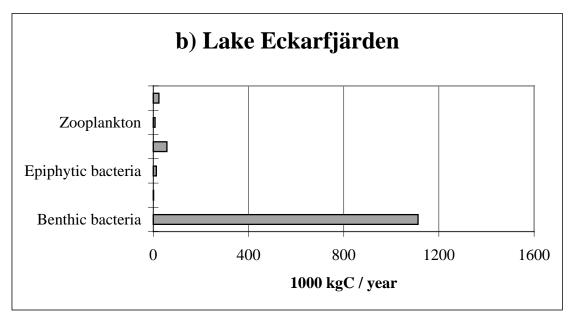
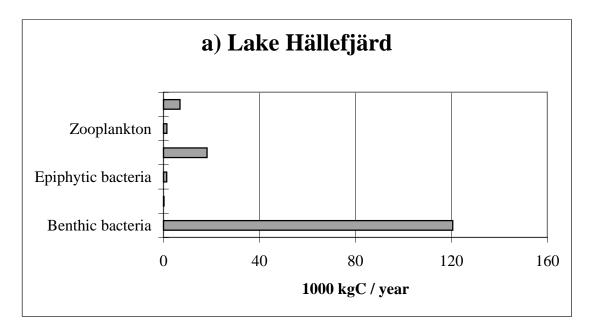


Figure 4-5. Respiration of C in a) Lake Hällefjärd and b) Lake Eckarfjärden.

between $4.5 \cdot 10^3$ and $27 \cdot 10^3$ gww · year⁻¹. Carbon most probably do not make up more than 10% of the wet weight and hence, calculated with these values, the *Sphagnum* do not produce the $13,5 \cdot 0^3$ kgC · year⁻¹ needed to balance the budget. However, the literature values of production refer to increase in biomass but during production large quantities of carbon may be produced that are not allocated to growth but are released as exudates. The exudates may be used by bacteria within the mire but can also be transported to the lake and may be a significant contribution of carbon source in the lake. It is unknown how much carbon that is transported from the mire to the lake.



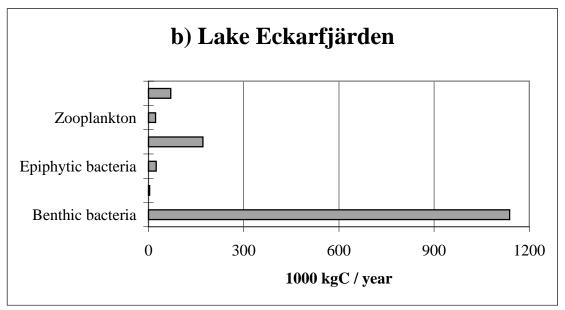


Figure 4-6. Consumption of organic carbon in a) Lake Hällefjärd and in b) Lake Eckarfjärden.

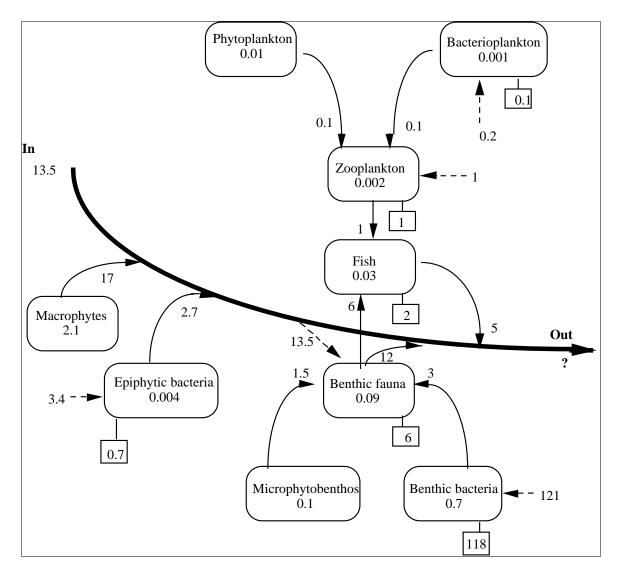


Figure 4-7. Annual carbon budget with calculated flow of carbon between organisms in Lake Hällefjärd. All values are in 10^3 kg $C \cdot year^{-1}$. Biomasses are given below the functional groups. The arrows between functional groups write primary production and secondary consumption that reaches the trophic levels above. Respiration is given in the small squares connected to the functional groups. Consumption not covered by the trophic levels below is indicated by dotted lines.

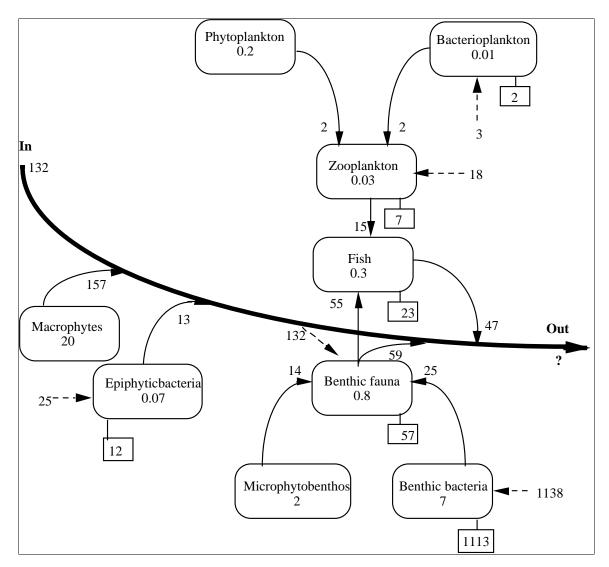


Figure 4-8. Annual carbon budget with flow of carbon between different organisms group in Lake Eckarfjärden. All values are in 10^3 kg C \cdot year⁻¹. Biomasses is given below the functional groups. Primary production and secondary consumption that reaches the trophic levels above is written by the arrows between functional groups. Respiration is given in the small squares connected to the functional groups. Consumption not covered by the trophic levels below is indicated by dotted lines.

5 Discussion

The carbon budget presented above gives a preliminary picture of how carbon may flow through the ecosystem of the two oligotrophic hardwater lakes Hällefjärd and Eckarfjärden, respectively. Unfortunately very few of the calculations have been based on actual data from the two lakes and the values presented are therefore very rough estimates. Nevertheless, they may be used to design further studies on the ecosystems.

A common characteristic to both lakes is that the production of C within the lakes was found to be much smaller than the consumption of C. One interpretation of this is that consumers in the systems may be dependent on allochtonous carbon. However, the carbon concentrations that would be needed in the incoming water to balance the budget are very high and it is reasonable to believe that the autochthonous production has been underestimated or that the consumption has been overestimated. The primary production of microphytobenthos is most probably much higher than calculated in this study. The thick layer of microphytobenthos found in the oligotrophic hardwater lakes is unique for this kind of lakes and, therefore, data from other lakes most likely are underestimates. Also production of epiphytic algae, which was assumed to be included in the macrophyte primary production, may contribute more carbon to the system. Few studies has been made of the epiphytic algal production but from a theoretical point of view it could be high, since macrophytes were abundant in the lakes and provide good substrates for growth of epiphytes. Also the bacterial production may be higher than estimated in this budget.

Since many of the biomass and production values are taken from other lakes than Lake Hällefjärd and Lake Eckarfjärden and then recalculated to fit the lakes, no evident differences between the lakes were found. A difference in carbon flow could otherwise be expected, since the lakes have different catchment areas and therefore the amount of carbon entering the lakes supposedly is of different magnitude. In future carbon budgets the non living fraction of carbon should preferably be integrated in the carbon budget to more easily determine if the lakes are dependent on allochtonous carbon or not. One of the keys to do this is that the flow of water through the mire is known. Further necessary knowledge includes values on the production and decay rates of *Chara* and values on the retention of carbon in the mire by bacteria and fungi. The flow of water through the mire is at the moment studied in co-operation with the Royal Institute of Technology (KTH) in Stockholm. Only about 15% of Sphagnum are supposed to decay /Clymo, 1987; Johnson and Damman, 1991/, but since the area covered by mire is large it can theoretically still contribute large amounts of carbon to the lake. However, the carbon produced in the mire is probably not enough to balance the budget for Lake Hällefjärd. The carbon needed to balance the budget for Lake Eckarfjärden is higher than the carbon needed for Lake Hällefjärd. At least in the case of Lake Eckarfjärden there must be another source of carbon than the mire that balance the budget and it is reasonable to believe that even Lake Hällefjärd has another source of carbon than the mire production.

It is also important to know how the water enters the lake because groundwater inflow is known to influence the biomass of microphytobenthos /Hagerthey and Kerffot, 1998/. The biomass of microphytobenthos often increases near spots of high inflow of groundwater and this may lead to a patchy distribution. It is therefore important to determine if there are discrete points of high groundwater inflow to a lake to be able to take representative samples when studying the production of the lakes.

The calculations show that carbon biomass as well as production of C in the lakes is concentrated to the benthic community and more studies are required to understand this community better. If radionuclides are released to oligotrophic hardwater lakes they would most probably enter the biota via the benthic community either by bacteria or microphytobenthos.

In conclusion this is a preliminary carbon budget for Lake Hällefjärd and Lake Eckarfjärden. It gives a gross picture of carbon flow in oligotrophic hardwater lakes but clearly shows that more studies are needed to accurately determine the carbon flow.

6 Acknowledgements

I would like to thank Ulrik Kautsky, Anna Brunberg, Peter Blomqvist and Don Pierson for valuable comments and suggestions on the construction of the carbon budget and manuscript.

7 References

Barranguet C, Plante-Cuny M R, Alivon E, 1996. Microphytobenthos production in the gulf of Fos, French Mediterranean coast. Hydrobiologia 333: 181–193.

Blindow I, 1986. Undervattensväxter viktiga i fågelsjöar. Fauna Och Flora 81: 233–244.

Blindow I, 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwater Biology 28: 15–27.

Boström B, Pettersson A-K, Ahlgren I, 1989. Seasonal dynamics of a cyanobacteriadominated microbial community in surface sediments of a shallow, eutrophic lake. Aquatic Sciences 51:153–178.

Boström B, Törnblom E, 1990. Bacterial production, heat production and ATP-turnover in shallow marine sediments. Thermochimica Acta 172: 147–156.

Brunberg A-K, 1993. *Microcystis* in lake sediments Its potential role in phosphorous exchange between sediments and lake water. PhD-thesis. Acta Universitatis Upsaliensis. Science 448.

Brunberg A-K, Blomqvist P, 1998. Vatten i Uppsala län 1997. Rapport nr 8/1998. Upplandsstiftelsen.

Brunberg A-K, Blomqvist P, 1999. Characteristics and ontogeny of oligotrophic hardwater lakes in the Forsmark area, central Sweden. SKB R-99-68, Swedish Nuclear Fuel and Waste Management Co.

Brunberg A-K, Blomqvist P, 2000. Post-glacial, land rise-induced formation and development of lakes in the Forsmark area, central Sweden. SKB TR-00-02, Swedish Nuclear Fuel and Waste Management Co.

Brydsten L, 1999. Shore level displacement in Öregrundsgrepen. SKB TR-99-16, Swedish Nuclear Fuel and Waste Management Co.

Cahoon L B, Cooke J E, 1992. Benthic microalgal production in Onslow Bay, North Carolina, USA. Marine Ecology Progress Serier 84: 185–196.

Carmouze J P, de Farias B, Bernardes M C, Kuroshima K N, 1998. Benthic influence on the metabolism of a shallow tropical lagoon (Lagoa da Barra, Brazil). Hydrobiologia 373/374: 89–100.

Clymo R S, 1963. Ion exchange in Sphagnum and its relation to bog ecology. Ann. Bot. N. S. 27: 309–324.

Clymo R S, 1964. The origin of acidity in Sphagnum bogs. Bryologist 67: 427–431.

Clymo R S, 1987. The ecology of peatlands. Sci. Prog. Oxf. 71: 593–614.

Cole J J, Caraco N F, Kling G W, Kratz T, 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265: 1568–1570.

del Giorgio P A, Cole J J, Cembleris A, 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385: 148–151.

Doremus C, Clesceri L S, 1982. Microbial metabolism in surface sediments and its role in the immobilization of phosphorous on oligotrophic lake sediments. Hydrobiologia 91: 261–268

Eriksson I V, 1920. Isläggning och islossning i Sveriges insjöar. Medd. fr. Statens Hydrologiska anstalt 1:2, 95 pp.

Fjeldsa J, 1977. Benthos densities in the littoral zone of some lakes in northern Norway. Fauna 30(4) 227–236.

Forsberg C, 1965. Environmental conditions of Swedish Charophytes. Symb. Bot. Ups. 18:4

Grøntved J, 1962. Preliminary report on the productivity of microbenthos and phytoplankton in the Danish Wadden Sea. – Meddr Kommn Danm. Fisk. og Havunders. (N:S.) 12: 347–378.

Hargeby A, Andersson G, Blindow I, Johansson S, 1994. Trophic web structure in a shallow eutrophic lake during a dominance from phytoplankton to submerged macro-phytes. Hydrobiologia 279/280: 83–90.

Hagerthey S E, Kerfoot W C, 1998. Groundwater flow influences the biomass and nutrient ratios of epibenthic algae in a north temperate seepage lake. Limnol. Oceanogr. 42(6) 1227–1242.

Haglund E, 1972. Naturvårdsinventering av Uppsala län del VIII. Tierps kommun, norra delen. Länsstyrelsen Uppsala Län.

Halvarsson E, 2001. Hällefjärd – en kalkoligotrof sjö I Norduppland, beskrivning av avrinningsområde, sjöekosystem och antropogen påverkan. Scripta Limnologica Upsaliensia 2001 B:11.

Ignatius H, Axelberg S, Niemistö L, Winterhalter B, 1981. Quaternary geology of the Baltic Sea. In: Voipio A (ed). The Baltic Sea. Elsevier Oceanography Series 30.

Johnson L C, Damman A W H, 1991. Species-controlled Sphagnum decay on Southern Swedish raised bog. Oikos 61: 234–242.

Kautsky U, 1995 a. Annual variation in carbon and nutrient stocks of Baltic coastal ecosystems. In : Ecosystem processes in coastal areas of Baltic Sea, Doctoral thesis at University of Stockholm, Depatment of Zoology.

Kautsky U, 1995 b. Seasonal dynamics of carbon and nutrient fluxes in Baltic coastal ecosystems. in: Ecosystem processes in coastal areas of Baltic Sea, Doctoral thesis at University of Stockholm, Depatment of Zoology.

Kautsky U, Kautsky H, 1995. Coastal productivity in the Baltic Sea. in: Ecosystem processes in coastal areas of Baltic Sea, Doctoral thesis at University of Stockholm, Depatment of Zoology.

Kumblad L, 1999. A carbon budget for the aquatic ecosystem above SFR in Öresundsgrepen. SKB R-99-40. SKB Swedish Nuclear Fuel and Waste Management Co.

Lindström E S, 1998. Bacterioplankton community composition in five lakes differing in trophic status and humic content. In: Temporal and spatial variation in the community composition of lake bacterioplankton. PhD-thesis. Acta Universitatis Upsaliensis 413.

Lundqvist G, 1925. Utvecklingshistoriska insjöstudier i Sydsverige. Akademisk avhandling. Stockholms högskola. Kungliga boktryckeriet P.A. Norstedt & Söner, Stockholm.

Länsstyrelsen i Uppsala Län, 1987. Naturvårdsprogram för Uppsala län. Värdefulla områden för naturvård och rörligt friluftsliv. Meddelande från planeringsavdelningen. 1987.2.

McCauley E, Kalff J, 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Can. J. Fish. Aquat. Sci. 38: 458–463.

Naturvårdsverket, 1999. Bedömningsgrunder för miljökvalitet. Sjöar och vattendrag. Rapport 4913. Naturvårdsverket, Stockholm.

Nilsson P, Jönsson B, Lindström-Swanberg I, Sundbäck K, 1991. Response of a marine shallow-water sediment system to an increased load of inorganic nutrients. Marine ecology progress series 71: 275–290.

Rodhe W, 1949. The ionic composition of lake waters. Verh. Int. Ver. Limnol. 10: 377–386.

Schallenberg M, Kalff J, Rasmussen J, 1989. Solutions to problems in enumerating sediment bacteria in direct counts. Appl. environ. Microbiol 55:1214–1219.

Sundbäck K, Carlsson L, Nilsson C, Jönsson B, Wulff A, Odmark S, 1996. Response of benthic microbial mats to drifting green algal mats. Aquatic microbial ecology 10:195–208.

Theil-Nielsen J, Søndergaard M, 1995. Production of epiphytic bacteria and bacterioplankton in three shallow lakes. Oikos 86:283–292.

Törnblom E, 1995. Bacterial production and total community metabolism in sediments of a eutrophic lake. In: Microbial activity and biomass in aquatic surface sediments a community level approach. PhD-thesis. Acta Universitatis Upsaliensis 153.

van Duyl F C, Kop A J, 1990. Seasonal patterns of bacterial production and biomass in intertidal sediments of the western Dutch Wadden Sea. Marine ecology progress series 59: 249–261.

Vrede K, 1997. Bacterioplankton production and biomass in two lakes of different trophic status, responses to inorganic nutrients, organic carbon, and other planktonic biota. PhD-thesis. Comprehensive Summaries of Uppsala Dissertations from the faculty of Science and Technology 282.

Wallén B, Falkengren-Grerup U, Malmer N, 1988. Biomass, productivity and relative rate of photosynthesis of Sphagnum at different water levels on a South Swedish peat bog. Holarctiv Ecology 11:70–76.