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Habitat distribution, water chemistry, and biomass and production of pelagic and benthic microbiota in Lake Eckarfjärden, Forsmark

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November 2002

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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 authors and do not necessarily coincide with those of the client.

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## Abstract

This report describes the habitat distribution, water chemistry, biomass and production of microbiota in the oligotrophic hardwater Lake Eckarfjärden (60°22' N, 18°12' E) during 2000 and 2001. Ephemeral oligotrophic hardwater lakes represent the most common lake type in the Forsmark area. These lakes are continuously formed by isolation of bays of the Baltic Sea due to the land-rise that has been going on in the area since the termination of the last glaciation, some 10,000 years ago. Due to easily weathered, calcium rich, soils in the area, the newly formed lakes initially become oligotrophic and highly alkaline. After about 1,000–1,500 years, the calcium concentrations decrease and the lakes turn brown-water systems.

Regarding water chemistry, Lake Eckarfjärden turned out to be unusual compared to other lakes in Sweden and elsewhere. The water was very alkaline and rich in dissolved salts (mean alkalinity: 2.4 mekv/l). Concentrations of organic carbon (mean TOC: 24.8 mg/l) and total nitrogen (mean TN: 1,360 µgN/l) were very high, while concentrations of phosphorous were low (mean TP: 16 µgP/l).

Three main habitats were identified in the lake ecosystem; an emergent vegetation habitat, an illuminated soft-sediment habitat, and a pelagic habitat. The illuminated soft-sediment habitat seemed to dominate the system in several ways: The biomass of microbiota was heavily focused to a 10–15 cm microbial mat covering the bottom. The top 5 cm of this mat was dominated by microphytobenthos ( $4,940 \pm 3,350 \text{ mgC/m}^2$ ), mainly cyanobacteria. Heterotrophic bacteria also made up a substantial part of the microbial mat ( $3,570 \pm 1,810 \text{ mgC/m}^2$ ). In contrast, the biomass of microbiota in the pelagic habitat was low and the community was dominated by heterotrophic organisms.

Our results indicate that the microbial mat has an important role in the lake metabolism, governing the turnover of DOC and N, as well as the immobilisation of P. However, at anoxic conditions, large amounts of inorganic nitrogen and phosphorus can be released from the illuminated soft-sediment habitat, which implies that there is not a final deposition of substances in the microbial mat.

Another important conclusion of this study is that, since oligotrophic hardwater lakes are very different from lakes in general, data from other lakes should not uncritically be used for modelling of future events in the lakes of the Forsmark area.

## Sammanfattning

I Forsmarksområdet utgör de kalkoligotrofa sjöarna den viktigaste sjötypen. Sjöarna bildas genom att havsvikar avsnörs till följd av den landhöjning som pågår i området sedan den senaste istiden. Berggrunden i området är sur men jordarterna är mycket kalkrika vilket leder till att vattnet i sjöarna blir mycket kalkrikt och näringsfattigt. Efter cirka 1 000–1 500 år har kalkhalten i de omkringliggande jordarterna minskat på grund av urlakning och sjöarna övergår till brunvattenkaraktär.

Denna rapport beskriver habitatutbredning, vattenkemi, biomassor och primärproduktion av mikrobiota i den kalkoligotrofa sjön Eckarfjärden (Svenskt sjönummer 669723-163205, 60°22' N, 18°12' E). Under år 2000 och 2001 skedde provtagning för vattenkemi och biomassor en gång per månad under vinterhalvåret och varannan vecka under sommarhalvåret. Den areella utbredningen av olika huvudhabitat kartlades under sommaren 2001 då även preliminära mätningar av primärproduktionen hos mikrobiota utfördes.

Tre huvudhabitat identifierades; ett strandnära makrofytdominerat habitat, den fria vattenmassan (pelagialen), samt ett solbelyst mjukbottenhabitat. Biomassan av mikrobiota i sjön var starkt fokuserad till de solbelysta mjukbottnarna där det fanns en tjock (10–15 cm) mikrobiell matta. De översta 5 cm av denna matta dominerades av mikrofytobentos (4 940 ± 3 350 mgC/m<sup>2</sup>) som till största del utgjordes av cyanobakterier. Även heterotrofa bakterier utgjorde en viktig beståndsdel i den mikrobiella mattan (3 570 ± 1 810 mgC/m<sup>2</sup>). Biomassan av mikrobiota i pelagialen var låg och organism-samhället dominerades främst av heterotrofa organismer.

Med avseende på vattenkemi representerar Eckarfjärden en mycket ovanlig sjötyp såväl i Sverige som globalt. Alkaliniteten och salthalten var mycket höga (medelvärde alkaliniet: 2,4 mekv/l). Koncentrationerna av kväve var höga (medelvärde total-N: 1 360 µgN/l) medan koncentrationerna av fosfor var låga (medelvärde total-P: 16 µgP/l), vilket resulterade i en mycket hög kväve/fosfor-kvot (medelvärde 98). Koncentrationen av organiskt kol var mycket hög (medelvärde 24,8 mg/l) medan vattenfärgen var relativt låg (absorbans 420 nm, medelvärde 0,16), vilket indikerar att det lösta organiska kolet kan vara producerat i sjön.

Undersökningarna i Eckarfjärden indikerar att den mikrobiella mattan har en dominerande roll i ekosystemets struktur och funktion i denna typ av sjö, såväl vad gäller koloch kväveomsättning som fosforretention. Under syrgasfria förhållanden under vintern 2001 frigjordes stora mängder inorganiskt kväve och fosfat till vattenmassan. Detta antyder att det inte sker en slutgiltig deposition i den mikrobiella mattan. Ämnen som bundits upp där kan under vissa omständigheter frigöras i systemet igen.

Sammanfattningsvis kan sägas att kalkoligotrofa sjöar är mycket ovanliga med avseende på såväl vattenkemi som den osedvanligt höga biomassan av mikrobiota i den mikrobiella mattan. Därför bör inte resultat från undersökningar i kalkoligotrofa sjöar utan vidare appliceras på andra sjötyper. Inte heller bör data från andra sjötyper okritiskt användas vid modellering av framtida händelser i kalkoligotrofa sjöar i Uppland.

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## 1 Introduction

SKB (The Swedish Nuclear Fuel and Waste Management Company) 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 the biosphere through hundreds of thousands of years. A total of three sites have been selected for studies of their suitability for storage of the nuclear waste, Forsmark and Tierp in the province of Uppland, and Oskarshamn in the province of Småland, all in the southern part of Sweden. Site descriptions will include the bedrock and overlying geological layers, as well as the terrestrial, wetland, lake, and river ecosystems of the drainage areas, which potentially may become affected by the installation. Also coastal ecosystems to which the water drains will be included. One important question to be addressed is: in the case of a leakage from the containers with the nuclear waste, are there any biological processes which in the long-term perspective may lead to an accumulation of radioactive compounds to such an extent that it may become harmful for the organisms? In aquatic ecosystems, special focus is given to the formation and diagenesis of sediments and to the ontogeny of coastal bays to lakes and wetlands. The studies presented in this paper concern the conditions in the dominant existing lake type in the Forsmark area, the oligotrophic hardwater lake.

A majority of the lake basins in Scandinavia were formed by glacial activities during and after the Pleistocene. Along the coastal areas of the Baltic Sea, and particularly in its northern parts, new lakes continue to be formed because the land is still rising after the last glaciation, which ended some 8,800 years ago /Ignatius et al, 1981/. Such land-rise induced formation of lakes also occurs in some other parts of the northern hemisphere that were recently glaciated /Hutchinson, 1975; Engstrom et al, 2000/. In the Forsmark area, current shoreline displacement amounts to approximately 60 centimeters per century /Påsse, 1996/. Since the coast today is rather shallow, a considerable land area with at least 14 larger and numerous small lake basins will be formed there during the coming five millennia /Brydsten, 1999/.

A characteristic of heavily glaciated areas world-wide is that most young geological layers have been lost due to the tremendous physical stress during and after the glaciation. As a result, the bedrock in such areas is dominated by the Precambrian shield and covered by soils originating from this acidic and nutrient-poor geological material /e.g. Bush, 2000/. The lakes are typically oligotrophic and have a low content of dissolved salts. Recent studies indicate that during their entire ontogeny, the lake ecosystems stay oligotrophic, and progressively become more acidic, to finally end up as fens or bogs /e.g. Engstrom et al, 2000/.

In terms of water chemistry, the lakes formed due to post-glacial land-rise processes along the coast of the province of Uppland in central Sweden do not conform to the oligotrophic, soft-water character described above. Rather, lakes in this area show an array of different characteristics and at least three main types of lakes can be distinguished: oligotrophic hardwater lakes, naturally highly eutrophic lakes, and alkaline humic lakes /Brunberg and Blomqvist, 2000/. One reason for this diversity of lakes formed by isolation of bays from the Baltic Sea is that the granite/gneiss bedrock is covered by very calcium-rich soils in the form of till and glacial and post-glacial clays. These soils originate to a large extent from the Cambrosilurian bedrock located at the bottom of the nearby SW part of the Bothnian Sea. The soils are easily weathered and contribute large amounts of dissolved salts, including nutrients such as phosphorus and nitrogen, to the surface waters. In the area of interest for construction of the storage for nuclear waste at Forsmark, which was isolated from the Baltic rather recently, the dominant lake type is the oligotrophic hardwater lake /Brunberg and Blomqvist, 2000/.

Paleoecological studies of the oligotrophic hardwater lakes indicate that the oligotrophic stage is ephemeral, lasting 1,000-1,500 years /Brunberg and Blomqvist, 2000, and references therein/. Later, as mires develop in the catchment and often close to the lakes, they evolve into brownwater systems and in the long run their basins are closed by mires /Ingmar, 1963/. Based on existing data about these lakes /Brunberg and Blomqvist, 2000/ suggested that the oligotrophic hardwater lakes can be characterised by the presence of three main habitats: i) a *Phragmites*-dominated emergent macrophyte zone which successively is invaded by *Sphagnum* and turned into a floating-edge mire; ii) a light-exposed soft-sediment habitat with a very high water content in the upper sediment layers and partly overgrown by Chara meadows; and iii) a pelagic zone with a poor plankton community. Earlier investigations /Lundkvist, 1925; Willén, 1962; Forsberg, 1965; Kleiven, 1991/ show that the lakes are small and shallow (less than 2-3 m deep), and contain very soft sediments and submerged vegetation of stoneworts (Chara spp.). Their water chemistry is characterised by high conductivity, high alkalinity and low concentrations of nutrients. Phytoplankton biomass is low and dominated by chrysophytes and dinoflagellates. /Lundqvist, 1925/ characterised the sediments as "cyanophycée-gyttja" and claimed that the microbial community (including autotrophs as well as heterotrophs) in these lakes is mainly confined to the sediments. Since cyanobacteria are absent from the water column, the cyanophyceègyttja is most likely of benthic origin. In a study of two oligotrophic hardwater lakes on the Hållnäs peninsula near Forsmark, L Eckarfjärden and L Hällefjärd, /Brunberg et al, 2002a/, verified that with respect to water chemistry, this lake type is rare in a national as well as in an international perspective. They also showed that, in terms of biomass, microbiota were highly focused to the illuminated sediment habitat, while the pelagic habitat was characterised by low biomasses of phytoplankton and heterotrophic bacterioplankton. In terms of chlorophyll, the thickness of the microbial mat on the bottoms was found to vary between 10 and 15 centimeters. This microphytobenthos community was dominated by non-nitrogen-fixing cyanobacteria, but purple sulphur bacteria also made up a substantial part. The biomass of heterotrophic bacteria in the sediments was also high, only slightly lower than that of microphytobenthos. The phytoplankton community was dominated by mixotrophic flagellates, and bacterioplankton biomass was high, indicating that ingestion of bacteria may be an important means of nourishment for phytoplankton.

The aim of this paper is to describe the area distribution of main habitats in the lake and the structure and basic function of two of the three main habitats in the lake, the pelagic and the illuminated soft sediment zones. Focus is given to the water chemistry and biomasses of autotrophic and heterotrophic microbiota. Preliminary data from measurements of autotrophic production of microbiota are also presented.

## 2 Methods

### 2.1 The study site

Lake Eckarfjärden (Swedish Lake number 669723-163205) is located 2 km south of Forsmark, along the coast of the province of Uppland, Sweden (60°22' N, 18°12' E). It has an altitude of 6 m above sea level, which corresponds to an age of about 930 years /Brydsten, 1999/. The lake is small and very shallow /Brunberg and Blomqvist, 1998/, and its catchment is dominated by mature coniferous forest (Table 2-1). Apart from the deposition of airborne pollutants, anthropogenic impact on the ecosystem is minimal /Franzén, 2002/.

Catchment data		Lake morphometry	
Total area (km <sup>2</sup> )	1.51	Lake area (km <sup>2</sup> )	0.23
Forest (%)	73	Maximum depth (m)	2.6
Wetland (%)	7	Mean depth (m)	1.5
Pastures (%)	5	Volume (Mm <sup>3</sup> )	0.35
Eckarfjärden (%)	15	Theoretical water residence time (days)	383

Table 2-1. Some characteristics of Lake Eckarfjärden and its catchment.

#### 2.2 Habitat distribution

Delineation of the main habitats within the lake was carried out using GPS and DGPS (Garmin GPS 12XL coupled to DGPS), by following the outer edge of the emergent and/or floating leaved vegetation by boat. The shore-line was taken from the topographic map. The fact that the sediments in the deeper parts of the lake had already been monitored for microphytobenthos, and that such organisms were found to be abundant at all depths /Brunberg et al, 2002a/, made further delineation (e.g. of the profundal zone) unnecessary.

### 2.3 Sampling

Samples of water chemistry, plankton, microphytobenthos and sediment bacteria were taken at monthly or shorter intervals during the period January 2000–November 2001. Samples for the analysis of water chemistry and plankton were taken with a tube sampler at 15 sites and pooled in a bucket from which subsamples were drawn. Samples for chemical analysis were brought unpreserved to the laboratory. Samples for dissolved oxygen were taken with a Ruttner sampler from surface and bottom water, immediately fixed and later analysed using Winkler methodology according to Swedish Standards /SLU, 2001a/. Samples for the analysis of bacterioplankton were preserved with formaldehyde (final concentration 4%), and those for the analysis of phytoplankton were preserved with acidified Lugol's solution according to /Olrik et al, 1998/.

Samples of microphytobenthos and heterotrophic bacteria in the sediments were taken with a tube sampler at a station located in the deepest part of the lake. The upper 0-5 cm

layer was transferred into plastic jars and brought to the laboratory where two sub-samples, one for microphytobenthos and one for heterotrophic bacteria, were taken and preserved with formaldehyde (final concentration 2% and 4%, respectively). On 14 August 2000, three additional 15 cm deep sediment cores were taken and stratified in the field into 1 cm layers for the analysis of chlorophyll *a*.

#### 2.4 Water chemistry and biota

Water colour, pH, alkalinity, conductivity, molybdate-reactive phosphorus, ammoniumnitrogen and dissolved oxygen were measured within 24 h. The remaining water was kept frozen until analysis. When no other reference is given, the analyses were carried out according to European and/or Swedish standard methods /SLU, 2001a/.

Total phosphorus and molybdate reactive phosphorus were analysed according to /Menzel and Corwin, 1965/ and /Murphy and Riley, 1962/, respectively. Residual phosphorous (organic phosphorous and precipitated phosphorous) was calculated as the subtraction of molybdate reactive phosphorous from total phosphorous. NH<sub>4</sub>-N, NO<sub>2</sub>+NO<sub>3</sub>-N and Kjeldahl-N were analysed according to /Chaney and Marbach, 1962/, /Wood et al, 1967/ and /Jönsson, 1966/, respectively. During 2000, Total N was calculated as the sum of NO<sub>2</sub>+NO<sub>3</sub>-N and Kjeldahl-N, whereas during 2001 it was measured according to Swedish standard methods /SLU, 2001a/. Organic nitrogen (residual nitrogen) was calculated as the subtraction of NO<sub>2</sub>+NO<sub>3</sub>-N and NH<sub>4</sub>-N from total nitrogen. TOC (unfiltered lake water) and DOC (water filtered through pre-ignited Whatman GF/F filters) were analysed by combustion and IR detection of the resulting carbon dioxide using a Shimadzu TOC 5000 carbon analyser. Water colour was measured spectrophotometrically on filtered water at 420 nm, using a 5 cm quartz cuvette.

Species composition and carbon biomass of planktonic microbiota (phytoplankton, heterotrophic nanoflagellates and ciliates) were determined using an inverted phase-contrast microscope, after overnight sedimentation of the organisms in 10 ml of water /Olrik et al, 1998/. The biomass of phytoplankton was divided into two groups, autotrophs and mixotrophs. The characterisation of autotrophic and mixotrophic phytoplankton, and heterotrophic nanoflagellates, was carried out according to /Jansson et al, 1996/ with modifications according to /Isaksson et al, 1999/.

Species composition and carbon biomass of microphytobenthos were determined in the same way as for phytoplankton, with the exception that sediment samples were diluted with water (1:200) and counted in 1 ml chambers. Chlorophyll biomass of microphytobenthos was analysed according to /ISO, 1992/, using 1 g wet sediment and including correction for degradation products.

Heterotrophic bacterioplankton and sediment bacteria were counted and measured with an epifluorescence microscope. Sediment samples were first sonicated (1 minute, 100 W); the other samples directly stained with acridine orange and filtered through 0.2  $\mu$ m polycarbonate filters. A total of 100 to 400 cells in 40 fields were counted for each sample, and the total bacterial biovolume was estimated by sorting the cells into different size classes. Bacterial dry weight and carbon content was calculated according to /Loferer-Krössbacher et al, 1998/, using the formula DW = 435 \cdot V^{0.86}, and assuming that 50% of the dry weight was carbon.

# 2.5 Tests of measurements of primary production in water and sediments

Primary production was measured at 9 occasions in the pelagic zone (January-November) and at 7 occasions in the soft sediment zone (May–November). Primary production in the water was measured in situ by <sup>14</sup>C-incorporation into biota in 60 ml glass bottles at the depths 5, 25, 50, 100 and 150 cm. Two light incubations were made at each depth, and a dark incubation was made at the top and at the bottom. One ml of 5  $\mu$ Ci/ml of <sup>14</sup>C were added to the bottles, which were incubated between 10:00 am and 14:00 pm. The incubations were stopped with 0.5 ml 37% formaldehyde. A sub-sample of 3 ml were bubbled over night with HCl before treated with 10 ml scintillation cocktail (Optiphase Hisafe2) and counted in a scintillation counter. The primary production in the sediment was also measured by <sup>14</sup>C-incorporation. The sediments were incubated in situ in Jönsson cores where the radioactive tracer is percolated down into the sediment /Jönsson, 1991/. The volume of the cores were 39 ml, (diameter 42 mm), and 1 ml of 5 µCi/ml were added to each core. Three light incubations and two dark incubations were made at 150 cm depth, between 11 am and 13 pm. After the incubation a sub sample of the top cm was taken from each core. This sub sample was thoroughly mixed before triplicate samples of 0.2 ml were withdrawn. HCl was added and the samples were dried at 40°C in an oven for about 2 hours before 0.5 ml of the organic solvent, Biolute-S, was added. The samples were treated with the organic solvent for about 24 hours before the scintillation cocktail (Optiphase Hisafe2) was added.

The results from the primary production measurements using the <sup>14</sup>carbon-incorporation method may be interpreted as estimates of something between gross and net photosynthesis. However, during long incubations the primary production approaches net production /Ahlgren, 1970/. Incubations for primary production were four hours for phytoplankton and two hours for microphytobenthos. Four hours can be considered as relatively long incubations and, hence, the primary production estimates have been interpreted as net primary production and no further conversions have been made.

Primary production over the day was roughly calculated by the following formula:

Primary production  $(mgC^*m^{-2}*day^{-1}) = (I_{day}/I_{sampling}) * pp_{hour}$ 

Where:

I <sub>day</sub>	=	solar radiation in PAR for the entire day of sampling taken from Norr Malma station (59°25'N, 18°15'E),
I <sub>sampling</sub>	=	solar radiation in PAR for the actual sampling period taken from Norr Malma station (59°25'N, 18°15'E),

 $pp_{hour}$  = primary production in mgC\*m<sup>-2</sup>\*h<sup>-1</sup>, for the sampling period.

This calculation of primary production for the entire day may be an overestimate since the light intensities are lower during the late afternoon and early morning than during the day. However, at least some phytoplankton are able to move upwards in the water column to compensate for lower light intensities.

### 2.6 Statistical analyses

To establish the rarity of Lake Eckarfjärden in terms of water chemistry, chemical data were compared to those representing 4111 randomly sampled lakes (3.9% of the Swedish lake population) during autumn 1995, obtained in the Swedish National Surface Water Survey 1995 /Wilander et al, 1998/.

Differences in biomass between biota in the open water and surface sediments as well as differences in water chemistry, plankton, and microphytobenthos between the two years were determined using Wilcoxon's signed rank test /Campbell, 1974/.

## 3 Results

#### 3.1 Water chemistry

All measurements of water chemistry are presented in Appendix 1.

The measurements of water temperature revealed that there was no thermal stratification of the system during summer, since surface and bottom temperatures in most cases were identical during the entire ice-free season. In winter, water temperatures were lower (close to 0°C) immediately under the ice than at the bottom, indicating the normal inverse thermal stratification. Heating of the system took place very rapidly during early spring and already in the middle of May temperatures around 15°C were found during both years. Maximum temperatures of 20°C were reached in August both years.

The water was rich in salts, as reflected by the high conductivity values (range 20–35 mS/m; mean 26.5 mS/m). Maximum values were recorded during winter under the ice, and there was a gradual decrease throughout the summer with minimum values recorded August 2000 and September 2001, respectively (Figure 3-1). The alkalinity was very high (range  $1.7-3.2 \text{ meq } \text{L}^{-1}$ ; mean 2.4 meq  $\text{L}^{-1}$ ) and followed the same seasonal pattern as conductivity. Calcium was by far the dominant cation in the water and bicarbonate the dominant anion. The pH-values were generally high (range 7.6–8.5; mean 8.1) and showed an opposite seasonal variation compared to alkalinity and major constituents, with minimum values of 7.6 and 7.7 recorded in winter under the ice during 2000 and 2001, respectively. Maximum values of 8.5 and 8.3, respectively, were recorded during late summer both years. Regarding conductivity, alkalinity, and pH-values there were no significant differences between the years (Wilcoxon's signed rank test p>0.05).



Figure 3-1. Conductivity in Lake Eckarfjärden during 2000 and 2001.

The concentrations of total phosphorus were relatively low, ranging between 8 and 48  $\mu$ g P L<sup>-1</sup> with an average of 16  $\mu$ g P L<sup>-1</sup>. Maximum concentrations were recorded in May 2000 (25  $\mu$ g P L<sup>-1</sup>) and, particularly, under the ice in March 2001 (Figure 3-2). There were no statistically significant differences between the years (Wilcoxon's signed rank test p>0.05). With the exception of the situation under the ice in March 2001, total-phosphorus was strongly dominated by residual phosphorus (range 8–28  $\mu$ g P L<sup>-1</sup>; mean 13  $\mu$ g P L<sup>-1</sup>). The concentrations of soluble reactive phosphorus (SRP) were usually low (range 0–20  $\mu$ g P L<sup>-1</sup>; mean 1.8  $\mu$ g P L<sup>-1</sup>), below or close to the detection limit of the method (2  $\mu$ g P L<sup>-1</sup>). However, at the maximum in March 2001 (Figure 3-2), concentrations of SRP (20  $\mu$ g P L<sup>-1</sup>) were almost as high as those of residual phosphorus (28  $\mu$ g P L<sup>-1</sup>).

The concentrations of total N were high and showed moderate seasonal variation (range 950–1,940  $\mu$ g N L<sup>-1</sup>; mean 1,360  $\mu$ g N L<sup>-1</sup>), with maximum values under the ice in late winter both years. There was a slight, but statistically significant (Wilcoxon's signed rank test p < 0.005) difference between the years, with lower values during 2001 than during 2000 (Figure 3-3). Most of the nitrogen was included in the organic (residual) fraction (Figure 3-3), with the exception of the situation under the ice in winter 2001, when inorganic nitrogen dominated and organic N decreased to very low values. In accordance with the situation regarding total-N, the concentrations of organic nitrogen were significantly (p<0.005) lower during 2001 than during 2000. The concentrations of total inorganic nitrogen (TIN) showed a conspicuous seasonal variation (Figure 3-4) being high during winter and low during summer (range  $15-1,580 \mu g N L^{-1}$ , mean 240  $\mu$ g N L<sup>-1</sup>). There was a significant (p<0.005) difference between years but in contrast to the situation regarding total-N and organic-N, the concentrations were higher in 2001 than in 2000. Ammonium-N usually dominated the TIN, except in March 2001, when NO<sub>3</sub>+NO<sub>2</sub>-N dominated (Figure 3-4). Hence, most of the large difference in concentrations of TIN between the two winters was due to a huge increase in the concentrations of NO<sub>3</sub>+NO<sub>2</sub>-N in March 2001. As a result of the high concentrations



*Figure 3-2.* Total phosphorus and the share of molybdate-reactive phosphorus ( $PO_4$ -P) in Lake Eckarfjärden during 2000 and 2001.



*Figure 3-3.* Total nitrogen and the share of organic nitrogen in Lake Eckarfjärden during 2000 amd 2001.



*Figure 3-4.* Total inorganic nitrogen (TIN) and the share of  $\sum NO_2 + NO_3$  in Lake Eckarfjärden during 2000 and 2001.

of total-N and the low concentrations of total-P, the ratio between these two elements in the water was usually very high (range 35–174; mean 98). The lowest value coincided with the high concentrations of phosphorus measured in March 2001. The concentrations of silica in the water, measured during 2001 only, were generally high (range 1.5–3.6; mean 2.8) but showed a conspicuous decrease during spring. The concentrations of dissolved oxygen were usually high (Figure 3-5) and both the surface and the bottom water were slightly oversaturated with dissolved oxygen during most of the open-water season. Minima were recorded during winter under the ice, with a major difference between years. In the winter of 2000, dissolved oxygen concentrations in the bottom water decreased to moderate levels (6 mg  $O_2/l$ ), whereas in the winter of 2001 they decreased to very low values (0.2 mg  $O_2/l$ ).

The concentrations of total organic carbon (TOC) were extremely high and showed little seasonal variation (range 20–31 mg C/l; mean 24.8 mg C/l). The concentrations of particulate organic carbon were always very low and, hence, the TOC was almost exclusively made up by dissolved organic carbon (DOC). Both the concentrations of TOC and DOC were significantly (Wilcoxon's signed rank test p<0.005) slightly higher in 2001 than in 2000. The highest values were recorded around the time of the maxima of phosphorus and inorganic nitrogen in the winter of 2001. The watercolour,





*Figure 3-5.* Dissolved oxygen in a) surface waters and in b) water close to the bottom in Lake Eckarfjärden during 2000 and 2001.

as indicated by absorbance at 420 nm, was low ranging from 0.08–0.26 (mean 0.16). There was a tendency for higher values in spring and autumn and lower values in the summer but the trend was weak. As a result of the extremely high concentrations of TOC and the low water colour, the ratio between these two factors in the water was usually very high (range 93–300; mean 169), indicating that most of the TOC was made up of uncoloured substances.

The chemical rarity of Lake Eckarfjärden, in comparison with data from 4,111 randomly chosen lakes sampled within the National Swedish Lake Monitoring Programme and using autumn data only, is evident from Table 3-1. With respect to alkalinity, conductivity, pH, concentrations of total-N, concentrations of NH<sub>4</sub>-N, total-N/total-P ratio, TOC/absorbance ratio and concentrations of TOC (and DOC), the lake belong to the upper 10 percentile. Contrastingly, with respect to the concentrations of total-P, concentrations of NO<sub>3</sub>+NO<sub>2</sub>-N, and water colour (absorbance at 420 nm) the lake come close to the median lake in the population and, with respect to concentrations of SRP, the lake falls within the bottom 10 percentile.

Table 3-1. Mean values for Lake Eckarfjärden (n=6) and percentiles within National Swedish Lake Monitoring Programme.

parameter	min	10	25	50	75	90	max	Eckar- fjärden
рН	4.01	6.06	6.53	6.82	7.09	7.4	9.46	8.1
Kond	0.42	1.73	2.55	4.23	8.65	13.8	3460	24.8
Alk	-0.215	0.03	0.085	0.153	0.284	0.679	5.045	2.4
Tot-P	3	6	8	11	17	26	910	14
PO <sub>4</sub> -P	1	2	2	3	4	7,5	320	1
Tot-N	42	234	338	524	807,5	1128	7356	1305
NH <sub>4</sub> -N	1	5	7	13	27	61	1345	140
NO <sub>2</sub> +NO <sub>3</sub>	1	4	9	23	52	112	2948	15
тос	0.3	2.9	5	7.5	10.7	15.2	88.5	24.6
Abs	0	0.021	0.047	0.092	0.177	0.287	2.11	0.154
TOC/Abs	14	44	54	77	117	178	1100	177
TN/TP	1	22	31	44	64	93	367	103

#### 3.2 Area distribution of main habitats in the lake

The ecosystem of Lake Eckarfjärden can be characterised by three major habitats, an emergent macrophyte habitat following the shoreline, and a pelagic habitat overlying an illuminated benthic habitat (Figure 3-6). The latter is almost exclusively dominated by very soft sediments covered by a thick mat of photosynthetic microbiota and meadows of stoneworths (Chara spp.), and elodeids were also present. In terms of area, the pelagic and illuminated sediment habitats were somewhat larger (130,000 m<sup>2</sup>, 56.5% of the total lake area) than the emergent macrophyte habitat (100,000 m<sup>2</sup>, 43.5% of the total lake area). The total length of the shoreline of Lake Eckarfjärden was calculated to 2,700 meters. Along 400 meters (15%) of the shoreline, the open water habitat connected directly to the shore and so did more or less also the soft sediment habitat.



Figure 3-6. Habitat distribution in the ecosystem of Lake Eckarfjärden.

# 3.3 Biomass and community composition of pelagic and benthic microbiota

All measurements of the biomass of different groups of biota are presented in Appendix 2.

The phytoplankton community was dominated by mixotrophic flagellates, mostly chrysophytes, followed by autotrophic non-flagellates, mostly non-nitrogen-fixing cyanobacteria (Table 3-2). With respect to seasonal dynamics, the phytoplankton community showed a pronounced seasonality with maxima during the ice-free season and minima under the ice in winter (Figure 3-7). Mixotrophic flagellates dominated in early summer and autotrophic non-flagellates dominated during late summer and autumn. There was a significant (Wilcoxon's signed rank test p<0.01) difference between the years with lower phytoplankton biomass during 2001 than during 2000 and this difference was valid for both the dominant groups of organisms.

The biomass of bacterioplankton exceeded that of phytoplankton by 36% and in contrast to phytoplankton (Table 3-2), these organisms did not show any pronounced seasonality. Neither were there any differences between years in terms of bacterioplankton biomass. However, bacterioplankton showed one pronounced maximum in late winter/early spring of 2001, when biomass was some three times higher than during the rest of the studied period (Figure 3-8).

The biomasses of heterotrophic nanoflagellates and planktonic ciliates were low compared to the biomass of bacterioplankton and phytoplankton (Table 3-2).

Table 3-2. Biomass (mgC m<sup>-2</sup>) of biota in the open water and surface sediments (the upper 0–5 cm) of Lake Eckarfjärden during the period January 2000– November 2001. Values given are annual averages  $\pm$  standard derivation. Number of observations is 26 unless stated within brackets after the numbers.

Parameter	average±sd mgC*m <sup>-2</sup>
Planktonic biota	
Total phytoplankton	77 ± 67
Autotrophic non-flagellates	28 ± 34
Autotrophic flagellates	3 ± 2
Mixotrophic flagellates	$43 \pm 49$
Bacterioplankton Heterotrophic flagellates Ciliates	105 ± 52 (20) 2 ± 1 13 ± 11
Benthic biota Total microphytobenthos Autotrophic non-flagellates Purple sulphur bacteria Heterotrophic bacteria	<b>4,942 ± 3,348</b> 4,505 ± 2,795 437 ± 687 <b>3,570 ± 1,811</b> (25)



**Figure 3-7.** Phytoplankton biomass and the relative contribution of different important groups of organisms in Lake Eckarfjärden during 2000 and 2001. Svavelbakt = purple sulphur bacteria, mf = mixotrophic flagellates, hf = heterotrophic flagellates, af = autotrophic flagellates, anf = autotrophic non flagellates.



Figure 3-8. Bacterioplankton biomass in Lake Eckarfjärden during 2000 and 2001.

The biomass of microphytobenthos was almost exclusively made up of non-nitrogenfixing cyanobacteria (mostly colony-forming Chroococcales, but also Oscillatoriales of the genus *Komvophoron*). Purple sulphur bacteria and diatoms (pennate forms) were occasionally of some importance, and a few green algae were also found in the samples (Figure 3-9). There was no evident seasonality in the biomass of microphytobenthos, but the biomass was significantly higher during 2000 than 2001 (Wilcoxon's signed rank test p<0.005). This result was valid for cyanobacteria as well as diatoms but not for purple sulphur bacteria (no difference between years).



*Figure 3-9.* Biomass of microphytobenthos and the relative contribution of different important groups of organisms in Lake Eckarfjärden during 2000 and 2001.

The biomass of heterotrophic bacteria in the sediments was slightly (28%) lower than that of microphytobenthos (Table 3-2). The heterotrophic bacterial community showed a high variability over time but no evident seasonal pattern (Figure 3-10). Neither was there any significant difference between the years. In contrast to the situation for heterotrophic bacterioplankton, there was neither any maximum in the late winter of 2001.

The biomasses per unit lake area of autotrophic as well as of heterotrophic microbiota were much higher (Wilcoxon's signed rank test, p < 0.005) in the illuminated soft-sediment habitat than in the water column above (Table 3-2). Calculated from the long-term averages, the biomass of total microphytobenthos was 64 times higher than the biomass of phytoplankton in the lake. The corresponding value for the benthic biomass of heterotrophic bacteria was that it was 34 times higher than the bacterio-plankton biomass.

The thickness of the "microbial mat" measured as the concentration of chlorophyll a in the sediments of Lake Eckarfjärden varied between 10 and 15 cm at the three stations (0.1, 0.5, and 2 meters water depth, Appendix 3). Calculated as an average for the three stations, the biomass of microphytobenthos was maximal in the 2–4 centimeter layer and decreased successively down to 15 centimeters depth in the sediments (Figure 3-11). Notably, the concentration of chlorophyll a was still relatively high at 15 centimeters depth.



Figure 3-10. Biomass of benthic bacteria in Lake Eckarfjärden during 2000 and 2001.



*Figure 3-11.* Mean biomass of microphytobenthos measured as chla in a depth profile in sediments of Lake Eckarfjärden. At each depth triplicates were measured.

#### 3.4 Measurements of primary production in water and sediments

The integrated primary production in the 1.5 m water column (mean depth of Lake Eckarfjärden) varied between 1.7 and 20.4 mgC  $*m^2 *h^{-1}$  (mean 8.5 mgC  $*m^2 *h^{-1}$ ; sd 5.7) with the lowest values under the ice and in late autumn, and the highest values in the summer (Figure 3-12). The daily pelagic primary production varied between 9 and 170 mgC m<sup>-2</sup> day<sup>-1</sup>. The primary production of microphytobenthos was some 5 times larger than the planktonic primary production and varied between 3.6 and 144 mgC  $*m^2 *h^{-1}$  (Figure 3-12). The primary production of microphytobenthos was on average 48.2 mgC  $*m^2 *h^{-1}$  (sd 10.0) and showed a conspicuous maximum in early July. The maximum value in early July coincided with high insolation. Other summer values of primary production were measured on comparably cloudy days and the primary production was also lower. The benthic primary production, roughly calculated from the insolation, was 1,470 mgC m<sup>-2</sup> day<sup>-1</sup> on the 4 July. Other days the benthic primary production was more moderate, 20–580 mgC m<sup>-2</sup> day<sup>-1</sup>.



#### Primary production in Lake Eckarfjärden

*Figure 3-12. Primary production of phytoplankton and microphytobenthos in Lake Eckarfjärden during 2000 and 2001.* 

## 4 Discussion

Altogether, our results show that Lake Eckarfjärden has unusual water chemistry, the water being high in salts and very alkaline. Concentrations of nitrogen and organic carbon are very high, while concentrations of phosphorus are low. They also show that oxygen-free conditions during winter may trigger off considerable amounts of inorganic phosphorus and nitrogen from the sediments. In terms of biomass and production, microbiota in the system are heavily focused to the illuminated soft sediment habitat, while the pelagic habitat is characterised by a scarcity of organisms.

From the comparison with the National Lake Monitoring data it is evident that Lake Eckarfjärden represents a rare type of lake within the total population of 105,000 lakes in Sweden. /Brunberg and Blomqvist, 2000/ use the name ephemeral, oligotrophic hardwater lake to describe the lake type. In Sweden, oligotrophic hardwater lakes are principally found in areas where the bedrock and/or soils are calcareous, i.e. in the provinces of Uppland, Skåne and Gotland, and all these areas are naturally poor in lakes. Oligotrophic hardwater lakes, often termed Chara-lakes because of the presence of stoneworths, are relatively common in calcareous areas world-wide /Hutchinson, 1975; Wetzel, 2001/. What makes the lakes in Uppland very unusual is that the calcareous compounds are restricted to the soils, while the bedrock is composed by granites and gneisses. This is most likely the reason why the lakes undergo a rather rapid ontogeny towards brownwater systems, wetlands, and finally pine bogs /Ingmar, 1963; Brunberg and Blomqvist, 2000/. /Brunberg et al, 2002a/ argues that the combination of oligotrophic hardwater conditions in an area of land-rise also makes the lakes extremely unusual in a wider perspective. Although similar lakes may exist in North America /cf Wetzel, 2001/ the normal situation seems to be that lakes born in land-rise areas develop into oligotrophic softwater lakes /e.g. Engstrom et al, 2000/. In Europe, land-rise areas are currently situated almost exclusively in Sweden and Finland and, from analysis of the Finnish literature /Maristo, 1941; Cedercreutz, 1947; Lindholm, 1991/, very few similar lakes seem to exist in Finland. Hence, we believe that the ephemeral oligotrophic hardwater lakes are very rare not only in Scandinavia but also globally. The rarity of the lakes in the Forsmark area is of great importance in the context of the site investigations to be performed by SKB. Data from these lakes should not be used for generalisations about lakes in other areas of Sweden. Neither should data from other lakes uncritically be used to model potential events in the Forsmark lakes.

The chemical characteristics of Lake Eckarfjärden include high concentrations of all major ions in the water, but particularly those of calcium and bicarbonate. The conductivity, alkalinity, and the pH-values were very high, and these parameters showed a pronounced seasonal variation. In the case of conductivity and alkalinity maxima were recorded during winter and minima during summer, while the opposite was true for the pH-values. We interpret this as an indication that during periods of high rates of photosynthesis (i.e. during summer, see below), there is considerable precipitation of lime on biota in the sediments and this affects the concentrations of salts in the water /cf also Brunberg et al, 2002a,b/. That precipitation of CaCO<sub>3</sub> is of great

importance in the system was also evident from visual inspection of the colour of the microbial mat on the bottoms, which changed from dark green to yellowish white during early summer.

The presence of a thick microbial mat and the precipitation of lime on the bottoms may be important keys for the understanding of the metabolism of nutrients in the lake. The concentrations of total-N in the lake water were generally very high, while the concentrations of total-P were low, typical of oligotrophic lakes. This results in very high N:P ratios and, presumably, a pronounced limitation of production by phosphorus during the open water period. The fact that nitrogen-fixing cyanobacteria neither were found in the microphytobenthos nor in the phytoplankton, strengthens this conclusion. /Brunberg et al, 2002a/ suggested that the initial mechanism leading to a low concentration of phosphorus in the water is uptake by the benthic biota, primarily autotrophs. The high photosynthetic activity of these autotrophs during the open water season, indicated by high pH-values during summer, may result in precipitation of CaCO<sub>3</sub>. When phosphorus is released at decomposition (e.g. during winter), it may adsorb to or precipitate with the CaCO<sub>3</sub> particles in the sediments and be successively further transferred in sediment diagenetic processes.

Notably, with the exception of the situation under the ice and especially in March 2001, both phosphorus and nitrogen predominantly occurred in residual/organically bound form and these fractions, as well as the DOC, did not show any major seasonal variations. However, this was not the case with the inorganic fractions of nitrogen and phosphorus, which showed a conspicuous seasonal variation and where a considerable difference between the years also was recorded. During the winter of 2000 when the water was relatively high in dissolved oxygen, the concentrations of inorganic nitrogen (principally NH<sub>4</sub>-N) in the water increased to 700  $\mu$ g N L<sup>-1</sup>, while the concentrations of SRP remained below detection. During the winter of 2001 when the water was very low in dissolved oxygen, the concentrations of inorganic nitrogen in the water increased to 1,600  $\mu$ g N L<sup>-1</sup> and nitrogen occurred both in the form of NO<sub>3</sub>+N O<sub>2</sub>-N and NH<sub>4</sub>-N. Concomitantly, the concentrations of SRP increased to relatively high levels. Hence, under oxic conditions, decomposition processes in the sediments result in the release of NH<sub>4</sub>-N but not of inorganic phosphorus to the overlying water. At anoxia, both phosphate and NH<sub>4</sub>-N are released, and part of the NH<sub>4</sub>-N is transferred to NO<sub>3</sub>+NO<sub>2</sub>-N in the overlying water. Since the result of decomposition processes alone should be release of both phosphorus and nitrogen, we conclude that there must be other processes involved which lead to a retention of phosphorus in the sediments at oxic conditions. /Brunberg et al, 2002a/, using data from two lakes (Eckarfjärden and Hällefjärd) measured during 2000, suggested that there is a continuous supply of nitrogen in the form of NH<sub>4</sub>-N from the underlying sediments to the microbial mat throughout the year. As long as the activity of benthic microbiota is high (i.e. during summer), this nitrogen is assimilated into biota and not released to the water. They also argued that the presence of large amounts of non-nitrogen-fixing cyanobacteria on the sediments is indicative of a continuous supply of nitrogen, since these organisms are favoured by a supply of nitrogen in the form of NH<sub>4</sub>-N /Vincent et al, 1993; Blomqvist et al, 1994; Hyenstrand, 1999/. /Brunberg et al, 2002a/ attributed the lack of release of phosphorus from the sediments at oxic conditions to adsorption to, or co-precipitation of phosphorus with, CaCO<sub>3</sub> particles formed during periods of high photosynthetic activity (i.e. during summer). If this reasoning is correct, there must be other processes involved in the release of phosphorus during anoxic conditions, e.g. redox-sensitive microbial and

chemical processes /Boström et al, 1988; Gächter and Meyer, 1993/. In the context of future studies of the oligotrophic hardwater lakes by SKB, events such as the ones described above may be of great interest to study more in detail, since it can not be concluded that there is a final retention of all substances deposited in the sediments.

A striking feature of Lake Eckarfjärden, also discussed by /Brunberg et al, 2002a/, is the extremely high concentrations of DOC in the water. Concentrations of DOC around 20 mg C  $L^{-1}$  are almost twice as high as that in the river water that leaves Sweden to the Baltic Sea /SLU, 2001b/, and are normally coupled to a very high water colour and a short retention time of the water. Since the water in Lake Eckarfjärden has moderate colour and a relatively long retention time in the basin, /Brunberg et al, 2002a/ concluded that the DOC must have been produced within the lake. They also concluded that the high concentrations of DOC in the water most likely originate from the illuminated soft-sediment habitat. A high production of biota in this very thick layer may well result in a release of large amounts of DOC and DON to the overlaying shallow water.

Another interesting result from the water chemistry studies is the fact that nitrification of NH<sub>4</sub>-N formed under the ice in winter was higher in 2001 than 2000. Thus, when the water was low in dissolved oxygen and high in phosphate more nitrate was formed than when dissolved oxygen was abundant but phosphate concentrations were low. This indicates that the nitrifying bacteria were phosphorous-limited in 2000, and such a result certainly merits further investigations. It is also very interesting to note that both phytoplankton and microphytobenthos seemed to be highly affected by the presumed nitrification-denitrification "event" during the winter of 2001. The biomass of both these groups were significantly lower during the summer after the event than during the previous year. This may be taken as another sign of the key importance of processes in the illuminated soft sediment habitat to the metabolism of the entire lake ecosystem. Future studies should therefore include measurements of chemical and biological transformations of nutrients at the sediment (microbial mat) – water interface.

The studies of the habitat distribution within the lake show that by area, the three main habitats are of relatively similar size. Since the ecosystem of the emergent macrophyte habitat was not included in the studies, the following discussion will mainly concern the relationship between the pelagic and illuminated soft sediment habitats. However, it should be noted that the growth of macrophytes (principally *Phragmites*) was relatively sparse in large areas of the emergent macrophyte habitat, and that the microbial mat on the bottom also was developed in such areas.

Our studies of autotrophic and heterotrophic microbiota clearly show that in terms of biomass, these organisms are focused to the illuminated soft-sediment habitat. Biomasses of microphytobenthos and benthic heterotrophic bacteria were 64 and 34 times higher, respectively, than the biomasses of phytoplankton and heterotrophic bacterioplankton in the water column above. Since the biomass estimates of the benthic organisms originated from the uppermost 5 centimeters of the microbial mat, which extended at least down to 15 centimeters, the true difference should be even greater. That the microbial mat on the sediments of Lake Eckarfjärden may be considered unusually thick is evident also from the fact that the chlorophyll biomass on the sediments is approximately one order of magnitude higher than values reported from other lakes /i.e. Hansson, 1989; Björk-Ramberg and Ånell, 1985; Hagertey and Kerfoot, 1998; Franzén, 2002/.

In terms of biomass, the benthic community of microorganisms was dominated by microphytobenthos. The community composition of the microphytobenthos, showed pronounced dominance of non-nitrogen-fixing cyanobacteria, with diatoms and purple sulphur bacteria as other important constituents. This indicates that autotrophic processes are of great importance for the carbon mobilisation in this habitat, since these organisms most likely are predominantly autotrophic i.e. rely on photosynthesis for mobilisation of energy /Jansson et al, 1996; Isaksson et al, 1999/. Contrastingly, the phytoplankton community was usually dominated by mixotrophic flagellates, which can acquire nutrients from ingestion of bacterioplankton and energy from photosynthesis. Furthermore, the biomass of phytoplankton was on average lower than that of bacterioplankton and there were only few occasions during the summer when phytoplankton biomass exceeded bacterioplankton biomass. From these observations, the fact that the concentrations of DOC in the water were extremely high, and the fact that there are clear indications that phosphorus may limit the production of biota in both habitats due to precipitation with CaCO<sub>3</sub>, we would like to propose a simple model for the functioning of the system. Assuming that light is not limiting for photosynthesis of biota during the open water season, which there is little reason to believe due to the shallowness of the system and clarity of the water, primary production will be focused to the bottoms where concentrations of nutrients are higher than in the open water. Assuming that nitrogen is not limiting to production on the bottoms but that phosphorus occasionally becomes limiting due to precipitation by CaCO<sub>3</sub>, the high concentrations of DOC in the water may be explained by exudation from the autotrophs on the bottoms at periods of nutrient limitation. If nutrients are limiting and energy supply is high, formation of cellular constituents will be limited and carbon will be released from the algal cells /Reynolds, 1984 p 133, and references therein/. Such a release may explain the very high concentrations of DOC and relatively low water colour in the lake. Another potential source of the high concentrations of DOC in the water would be death and decomposition of biota during winter, particularly under anoxic conditions.

The reasoning about primary production being focused to the bottoms (cf Introduction) is supported by our measurements. The maximum primary production of microphytobenthos in the beginning of July was high (above 1,000 mgC m<sup>-2</sup> day<sup>-1</sup>) compared to other lake studies /i.e. Gruendling, 1971; Björk-Ramberg and Ånell, 1985; Heat, 1988/. The other summer values were comparably low, which can be explained by lower solar radiation during these days. Since only one day had this high primary production, more values are needed to achieve a reliable value of primary production on a yearly basis for Lake Eckarfjärden. However, the primary production can potentially be very high and, hence, the primary production can have a larger influence than suggested in a carbon budget for Lake Eckarfjärden /Nilsson, 2001/.

The high concentrations of uncoloured DOC and low concentrations of nutrients (especially P) in the water may also explain the dominance of bacterioplankton over phytoplankton and the dominance of mixotrophs in the phytoplankton community. In systems where bacterioplankton have access to an external carbon, they will outcompete phytoplankton for inorganic nutrients. Phytoplankton responds to this competition by changes in the community structure towards mixotrophic flagellates, which can ingest bacteria /e.g. Blomqvist et al, 2001 and references therein/. Although our data are not sufficient to draw any firm conclusions, it may be suggested that the same reasoning can be applied to Lake Eckarfjärden, but with the sediments as "external" carbon source to the pelagic community. This suggested model certainly merits further investigation. In the context of the investigations to be performed by SKB, inorganic carbon fixation on

the bottoms, and subsequent release of organic compounds from biota may be of major importance for the understanding of the transport of radioactive compounds through the lake basins.

In conclusion, our study indicates that the dominant habitat in this kind of lake is the illuminated soft-bottom, which initially covers most of the lake basin. The activity of biota in the thick microbial mat, which potentially may govern the turnover of dissolved organic carbon and nitrogen, as well as the immobilisation of phosphorus in the system, makes these lakes extremely unusual in Sweden as well as globally.

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## Appendix 1

#### Water chemistry of Lake Eckarfjärden 2000 and 2001.

Date	PH	Conductivity	Alkalinity	Temperature	Temperature
		(mS/m)	(mekv/l)	(°C)	(°C)
2000-01-11	7.9	28	2.8	0	2
2000-02-15	7.6	35	3.2	-	-
2000-03-21	7.9	33	2.9	3.5	3.5
2000-05-19	8.3	27	2.3	16	16
2000-06-02	8.4	26	2.1	15	_
2000-06-19	8.4	24	1.9	18	18
2000-07-03	8.4	23	2.0	18	18
2000-07-17	8.4	23	1.7	16	_
2000-07-31	8.2	23	_	19	19
2000-08-14	8.3	22	2.6	_	-
2000-08-29	8.3	25	1.9	20	20
2000-09-12	8.5	25	2.4	14	14
2000-09-25	8.2	25	2.5	_	-
2000-10-27	7.9	27	2.6	8	8
2000-11-25	7.9	27	2.6	5	5
2001-01-26	7.7	33	2.9	1	4
2001-03-06	8.2	33	3.1	0.5	3.5
2001-04-02	7.8	30	2.9	3.5	4
2001-05-04	8.1	28	2.6	12	12
2001-05-23	8.2	28	2.7	14	13
2001-06-07	8.3	27	2.6	18	18
2001-06-19	8.2	26	2.4	18	18
2001-07-04	8.2	26	2.3	-	-
2001-07-30	7.9	-	2.0	_	_
2001-08-15	8.3	23	2.1	20	19
2001-09-24	8.3	20	2.0	13	13
2001-11-25	8.2	25	2.2	4	4
Mean	8.1	26.5	2.4	11.7	11.6
Stdev	0.23	3.68	0.40	7.0	6.6
No of observations	27	26	26	22	20
Minimum value	7.6	20	1.7	0	2
Maximum value	8.5	35	3.2	20	20

Date	Colour 420 nm	DOC (mg/l)	TOC (mg/l)	POC (mg/l)	TOC/Abs
2000-01-11	0.183	22.4	22.7	0.3	124
2000-02-15	0.104	24.6	23.3	0	23
2000-03-21	0.193	21.2	21.3	0.1	110
2000-05-19	0.176	20.4	21.7	1.3	123
2000-06-02	0.137	21.3	21.8	0.5	159
2000-06-19	0.139	22.4	22.7	0.3	163
2000-07-03	0.132	23.0	23.8	0.8	180
2000-07-17	0.078	23.5	23.4	0	300
2000-07-31	0.124	_	_	_	_
2000-08-14	0.156	25.3	25.2	0	162
2000-08-29	0.105	25.7	25.1	0	239
2000-09-12	0.261	25.4	24.4	0	93
2000-09-25	0.170	25.5	24.6	0	144
2000-10-27	0.142	24.1	23.7	0	167
2000-11-25	0.128	23.7	22.4	0	175
2001-01-26	0.209	27.5	28.6	1.1	137
2001-03-06	0.227	28.4	29.6	1.2	130
2001-04-02	0.210	31.1	32.5	1.4	154
2001-05-04	0.207	23.1	23.8	0.7	115
2001-05-23	0.179	23.1	23.5	0.4	131
2001-06-07	0.158	23.6	24.8	1.2	157
2001-06-19	0.154	_	_	_	_
2001-07-04	0.122	26.2	25.7	0	211
2001-07-30	-	24.7	26.0	1.3	-
2001-08-15	-	26.1	26.6	0.5	-
2001-09-24	0.091	25.6	25.6	0	281
2001-11-25	0.132	25.4	26.7	1.3	202
Mean	0.157	24.5	24.8	0.3	169
Stdev	0.045	2.4	2.6	0.8	54
No of observations	0.25	25	25	25	23
Minimum value	0.091	20.4	21.3	0	9
Maximum value	0.227	31.1	32.5	1.4	281

Date	NH₄-N (µgN/I)	∑NO₂+NO₃ (µgN/I)	TIN (µgN/I)	Organic nitrogen (µgN/I)	Total nitroge (µgN/I)
2000-01-11	516	37	554	1,324	1,877
2000-02-15	624	57	681	1,256	1,937
2000-03-21	_	40	_	1,580	1,620
2000-05-19	21	16	37	1,219	1,256
2000-06-02	8	7	15	1,262	1,277
2000-06-19	9	4	14	1,391	1,404
2000-07-03	10	4	15	1,390	1,404
2000-07-17	19	7	25	1,531	1,557
2000-08-14	10	2	13	1,480	1,492
2000-08-29	17	16	32	1,413	1,446
2000-09-12	19	7	26	1,411	1,437
2000-09-25	34	8	42	1,416	1,458
2000-10-27	162	18	180	1,188	1,368
2000-11-25	353	40	393	817	1,210
2001-01-26	602	134	736	1,005	1,741
2001-03-06	600	984	1584	118	1,702
2001-04-02	586	5	617	646	1,263
2001-05-04	186	43	229	724	953
2001-05-23	34	223	257	720	977
2001-06-07	177	3	180	800	980
2001-06-19	85	_	_	_	_
2001-07-04	28	3	31	1,055	1,086
2001-07-30	60	11	72	1,135	1,207
2001-08-15	66	8	74	1,004	1,078
2001-09-24	44	5	49	1,078	1,127
2001-11-25	230	15	245	984	1,229
Mean	179	70	239	1,072	1,363
Stdev	222	197	354	409	271
No of observations	25	25	24	25	25
Minimum value	8	2	13	118	953
Maximum value	624	984	1584	1,580	1,937

Date	PO <sub>4</sub> -P	Residual	Tot-P	TN/TP	Si
	(µgP/I)	µllosphorous (µgP/l)	(µgP/I)	(µgP/I)	Mekv/l
2000-01-11	2	12	14	134	_
2000-02-15	1.5	10	12	161	_
2000-03-21	1.5	11	13	125	_
2000-05-19	2	23	25	50	-
2000-06-02	1	21	22	58	-
2000-06-19	<1	20	21	67	-
2000-07-03	<1	18	18	78	-
2000-07-17	1.5	11	13	120	-
2000-08-14	<1	14	15	99	_
2000-08-29	<1	13	14	103	-
2000-09-12	2	11	13	111	-
2000-09-25	1.5	10	11	133	-
2000-10-27	<1	12	13	105	-
2000-11-25	<1	21	21	57	-
2001-01-26	1	9	10	174	3.3
2001-03-06	20	28	48	35	3.6
2001-04-02	<1	9	10	126	3.5
2001-05-04	<1	8	8	119	2.8
2001-05-23	1	14	15	65	1.9
2001-06-07	1.5	10	11	89	1.5
2001-06-19	1.5	_	-	-	_
2001-07-04	1.5	10	11	99	2.0
2001-07-30	-	17	17	71	3.1
2001-08-15	<1	15	16	67	3.1
2001-09-24	<1	10	9	125	3.4
2001-11-25	<1	15	14	88	3.2
Mean	1.8	13	15.8	98	2.8
Stdev	4.0	5.2	8.0	35	0.7
No of observations	25	25	25	25	11
Minimum value	0	8	8	35	1.5
Maximum value	20	28	48	174	3.6

Date	O <sub>2</sub> surface	O <sub>2</sub> bottom	O <sub>2</sub> surface	O <sub>2</sub> bottom
	Mg O <sub>2</sub> /I	mg O <sub>2</sub> /I	% saturation	% saturation
2000-01-11	11.0	5.9	75	42
2000-03-21	5.4	6.0	54	45
2000-05-19	11.8	12.0	120	121
2000-06-02	10.5	10.5	104	104
2000-06-19	10.5	10.6	111	113
2000-07-03	9.7	9.6	103	102
2000-07-17	9.1	-	93	-
2000-08-14	9.1	9.8	_	_
2000-08-29	12.9	13.1	142	145
2000-09-12	10.0	9.9	97	97
2000-09-25	14.2	14.2	132	132
2000-10-27	10.1	10.1	84	84
2000-11-25	11.3	10.7	86	86
2001-01-26	19.3	2.5	136	19
2001-03-06	3.1	0.2	22	2
2001-04-02	2.5	1.9	19	14
2001-05-04	15.9	15.8	148	147
2001-05-23	16.2	16.6	157	157
2001-06-07	15.5	15.3	163	162
2001-06-19	14.8	15.3	157	161
2001-08-15	16.4	16.0	181	172
2001-09-24	15.0	15.3	143	145
2001-11-25	17.2	17.0	138	137
Mean	11.8	10.3	112	104
Stdev	4.3	5.4	43.6	52.7
No of observations	23	22	22	21
Minimum value	2.5	0.2	19	2
Maximum value	19.3	17	181	172

Date	Ca	Na	Mg	К	HCO3	CI	SO4
••••	mekv/l	mekv/l	mekv/l	mekv/l	Mmol/I	mekv/l	mekv/
2000-01-11	-	_	-	-	2.8	_	-
2000-02-15	2.5	0.44	0.35	0.07	3.2	0.32	0.29
2000-03-21	-	-	-	_	2.9	-	_
2000-05-19	-	-	-	-	2.3	-	-
2000-06-02	-	-	-	-	2.1	-	_
2000-06-19	-	-	-	_	1.9	-	_
2000-07-03	1.8	0.34	0.28	0.05	2.0	0.24	0.23
2000-07-17	-	_	-	-	1.7	-	_
2000-07-31	_	_	_	_	2.6	_	_
2000-08-29	1.9	0.37	0.28	0.06	1.9	0.23	0.21
2000-09-12	_	_	_	_	2.4	_	_
2000-09-25	_	_	_	_	2.5	_	_
2000-10-27	_	_	_	_	2.6	_	_
2000-11-25	2.4	0.30	0.27	0.06	2.6	0.17	0.09
2001-01-26	_	_	_	_	2.9	_	_
2001-03-06	_	_	_	_	3.1	_	_
2001-04-02	_	_	_	_	2.9	_	_
2001-05-04	_	_	_	_	2.7	_	_
2001-05-23	_	_	_	_	2.7	_	_
2001-06-07	_	_	_	_	2.6	_	_
2001-06-19	_	_	_	_	2.4	_	_
2001-07-04	_	_	_	_	2.4	_	_
2001-07-30	_	_	_	_	2.0	_	_
2001-08-15	_	_	_	_	2.2	_	_
2001-09-24	_	_	_	_	2.1	_	_
2001-11-25	_	_	_	-	2.2	_	_
Mean	2.2	0.36	0.29	0.06	2.5	0.24	0.20
Stdev	0.33	0.058	0.035	0.007	0.4	0.062	0.083
No of observations	4	4	4	4	26	4	4
Minimum values	1.8	0.30	0.27	0.05	1.7	0.17	0.09
Maximum value	2.5	0 44	0 35	0.07	29	0 32	A 29

#### Biomass of microbiota.

Date	Autotrophic non flagellates	Autotrophic flagellates	Heterotrophic flagellates	Mixotrophic flagellates	Total
2000-01-11	13	2	0	1	16
2000-02-15	1	2	0	9	11
2000-03-21	6	0	1	6	13
2000-05-19	6	5	0	16	27
2000-06-02	29	2	0	52	82
2000-06-19	29	3	1	152	185
2000-07-03	22	3	1	87	113
2000-07-17	15	4	1	40	60
2000-07-31	31	1	2	19	53
2000-08-14	48	1	1	36	87
2000-08-29	42	3	2	38	85
2000-09-12	24	2	1	17	43
2000-09-25	110	2	1	40	152
2000-10-27	13	3	1	10	27
2000-11-25	6	2	2	5	16
2001-01-26	2	2	1	2	7
2001-03-06	1	1	0	4	6
2001-05-04	1	4	2	29	37
2001-05-23	6	2	5	46	59
2001-06-07	10	1	1	34	46
2001-06-19	10	1	2	48	61
2001-07-04	11	1	2	30	44
2001-07-30	22	1	1	12	36
2001-08-15	21	2	1	6	30
2001-09-24	8	3	1	10	21
2001-11-25	3	4	1	6	14
Mean	19	2	1	29	51
Stdev	22	1	1	32	45
No of observations	26	26	26	26	26

Table 1. Phytoplankton biomasses in Lake Eckarfjärden during 2000 and 2001. Values are in ugC\*L<sup>-1</sup>.

Date	Cyano- bacteria	Chryso- phyceae	Bacillario- phyceae	Chloro- phyceae	Crypto- phyceae	Dino- phyceae	Eugleno- phyceae
2000-01-11	8	1	3	2	2	0	0
2000-02-15	0	7	0	0	2	2	0
2000-03-21	6	3	0	0	1	3	0
2000-05-19	0	13	5	1	5	3	0
2000-06-02	26	31	2	1	2	4	16
2000-06-19	27	131	0	2	4	17	4
2000-07-03	17	12	0	4	4	6	69
2000-07-17	9	6	3	3	4	5	29
2000-07-31	22	7	2	7	2	3	9
2000-08-14	37	4	0	11	3	9	23
2000-08-29	34	8	0	9	5	27	2
2000-09-12	19	5	0	4	3	11	0
2000-09-25	106	8	1	3	3	28	3
2000-10-27	9	7	1	3	4	3	0
2000-11-25	2	3	0	5	3	1	1
2001-01-26	1	2	0	0	3	1	0
2001-03-06	0	3	0	0	1	1	0
2001-05-04	0	22	1	1	6	3	4
2001-05-23	2	20	2	2	6	7	19
2001-06-07	3	14	2	5	2	18	2
2001-06-19	4	17	1	5	3	30	0
2001-07-04	9	12	0	2	3	17	1
2001-07-30	20	10	1	2	1	2	0
2001-08-15	15	6	1	4	2	0	0
2001-09-24	5	10	1	2	4	0	0
2001-11-25	0	6	2	1	5	0	0
Mean	15	14	1	3	3	8	7
Stdev	22	25	1	3	1	9	15
No of observations	26	26	26	26	26	26	26

Table 2. Phytoplankton biomasses during 2000 and 2001. Values are in  $ugC^*L^{-1}$ .

Date	Autotrophic non flagellates	Autotrophic flagellates	Heterotrophic flagellates	Mixotrophic flagellates	Total
2000-01-11	20	3	0	2	24
2000-02-15	1	2	0	13	17
2000-03-21	9	1	1	9	20
2000-05-19	9	7	1	24	40
2000-06-02	43	3	1	77	123
2000-06-19	43	4	2	228	277
2000-07-03	32	4	2	130	169
2000-07-17	23	6	1	60	90
2000-07-31	47	1	2	28	79
2000-08-14	72	2	2	55	130
2000-08-29	63	5	3	57	127
2000-09-12	36	2	2	25	65
2000-09-25	165	3	2	60	229
2000-10-27	19	5	2	15	41
2000-11-25	9	4	3	7	24
2001-01-26	2	4	1	4	10
2001-03-06	1	2	0	7	9
2001-05-04	3	6	2	44	55
2001-05-23	9	3	7	68	88
2001-06-07	15	1	1	50	68
2001-06-19	15	1	3	72	92
2001-07-04	17	2	3	46	66
2001-07-30	34	1	1	18	53
2001-08-15	31	3	1	9	44
2001-09-24	12	5	1	14	32
2001-11-25	5	7	1	9	21
Mean	28	3	2	43	77
Stdev	34	2	1	49	67
No of observations	26	26	26	26	26

Table 3. Phytoplankton in Lake Ecakrfjärden during 2000 and 2001. Values are in mgC\*m<sup>-2</sup>.

Date	Cyano- bacteria	Chryso- phyceae	Bacillario- phyceae	Chloro- phyceae	Crypto- phyceae	Dino- phyceae	Eugleno- phyceae
2000-01-11	12	1	4	3	3	1	0
2000-02-15	0	11	0	1	3	3	0
2000-03-21	9	4	0	0	2	5	0
2000-05-19	0	19	8	2	8	4	0
2000-06-02	39	47	2	2	3	6	24
2000-06-19	40	197	0	3	6	25	6
2000-07-03	26	18	0	7	6	8	103
2000-07-17	13	9	5	5	6	7	44
2000-07-31	34	10	3	11	4	5	14
2000-08-14	56	6	0	16	4	14	35
2000-08-29	50	12	0	13	8	41	3
2000-09-12	29	8	1	6	4	16	1
2000-09-25	159	13	1	5	4	42	4
2000-10-27	13	10	2	4	7	5	0
2000-11-25	4	4	1	7	5	2	1
2001-01-26	2	3	0	0	4	0	0
2001-03-06	0	5	0	0	2	2	0
2001-05-04	0	33	2	1	8	5	6
2001-05-23	4	29	3	3	9	11	28
2001-06-07	5	20	4	7	2	27	3
2001-06-19	6	26	2	8	4	45	1
2001-07-04	13	18	1	3	4	26	2
2001-07-30	30	15	1	2	2	2	1
2001-08-15	23	9	2	6	4	0	0
2001-09-24	8	14	2	2	5	0	0
2001-11-25	0	9	3	2	7	0	0
Mean	22	21	2	5	5	12	11
Stdev	32	37	2	4	2	14	22
No of observations	26	26	26	26	26	26	26

Table 4. Phytoplankton in Lake Eckarfjärden. Values are given in mgC\*m<sup>-2</sup>.

Date	Autotrophic non flagellates	Purple sulphur bacteria	Total
2000-01-11	3,003	0	3,003
2000-02-15	1,891	0	1,891
2000-03-21	8,048	37	8,085
2000-05-19	5,183	19	5,131
2000-06-02	6,591	1,135	7,796
2000-06-19	4,575	121	4,696
2000-07-03	11,504	1,813	13,317
2000-07-17	5,899	214	6,113
2000-07-31	8,696	1,423	10,119
2000-08-14	9,587	1,748	11,336
2000-08-29	8,878	2,046	10,924
2000-09-12	4,895	167	5,062
2000-09-25	3,024	223	3,248
2000-10-27	4,621	0	4,621
2000-11-25	4,690	0	4,690
2001-01-26	2,683	36	2,719
2001-03-06	3,695	23	3,718
2001-05-04	1,645	341	1,986
2001-05-23	1,335	107	1,443
2001-06-07	1,081	199	1,281
2001-06-19	1,619	6	1,624
2001-07-04	1,697	34	1,731
2001-07-30	1,826	1,621	3,446
2001-08-15	3,956	40	3,996
2001-09-24	3,287	6	3,293
2001-11-25	3,216	6	3,222
Mean	4,505	437	4,942
Stdev	2,795	687	3,348
No of observations	26	26	26

Table 5. Microphytobenthos in the top 5 cm of the "sediment" of Lake Eckarfjärden 2000 and 2001. Values are in mgC\*m<sup>-2</sup>.

Date	Cyano- phyceae	Bacillario- phyceae	Chloro- phyceae	Konjugato- phyceae	Purple sulphur bacteria	Total
2000-01-11	2,712	290	0	0	0	3,003
2000-02-15	1,568	324	0	0	0	1,891
2000-03-21	7,147	899	2	0	37	8,085
2000-05-19	3,763	1,350	0	0	19	5,131
2000-06-02	4,850	1,741	71	0	1,135	7,796
2000-06-19	4,094	481	0	0	1,221	4,696
2000-07-03	9,500	2,004	0	0	1,813	13,317
2000-07-17	5,169	731	0	0	214	6,113
2000-07-31	5,725	2,971	0	0	1,423	10,119
2000-08-14	7,190	2,398	0	0	1,748	11,336
2000-08-29	8,118	759	0	0	2,046	10,924
2000-09-12	4,110	785	0	0	167	5,062
2000-09-25	2,785	240	0	0	223	3,248
2000-10-27	4,547	74	0	0	0	4,621
2000-11-25	4,133	556	1	0	0	4,690
2001-01-26	2,655	29	0	0	36	2,719
2001-03-06	3,616	76	2	0	23	3,718
2001-05-04	1,519	125	0	0	341	1,986
2001-05-23	915	420	0	2	107	1,443
2001-06-07	898	184	0	0	199	1,281
2001-06-19	1,525	93	0	0	6	1,624
2001-07-04	1,540	158	0	0	34	1,731
2001-07-30	1,631	195	0	0	1,621	3,446
2001-08-15	3,832	121	2	0	40	3,996
2001-09-24	3,229	58	0	0	6	3,293
2001-11-25	3,151	65	0	0	6	3,222
Mean	3,843	659	0	3	437	4,942
Stdev	2,259	795	0	14	687	3,348
No of observations	26	26	26	26	26	26

Table 6. Biomass of microphytobenthos in the top 5 cm of the "sediment" in mgC/m<sup>2</sup> in Lake Eckarfjärden 2000 and 2001.

Date	Bacterio-	Bacterio-	Benthic	Ciliates	Ciliates
	(µgC/I)	(mgC/m2)	(mgC/m2)	(µgC/I)	(mgC/m2)
2000-01-11	-	_	-	5	8
2000-02-15	-	-	_	3	4
2000-03-21	_	-	4,440	3	5
2000-05-19	59	89	5,294	23	34
2000-06-02	40	60	1,261	18	27
2000-06-19	59	89	5,510	22	33
2000-07-03	-	_	3,205	8	12
2000-07-17	58	88	4,699	6	10
2000-07-31	53	79	8,212	8	13
2000-08-14	55	83	3,353	6	9
2000-08-29	-	_	3,533	13	19
2000-09-12	_	_	2,559	3	5
2000-09-25	42	62	1,739	24	36
2000-10-27	-	_	7,269	24	36
2000-11-25	-	_	2,413	11	16
2001-01-26	41	92	3,398	2	3
2001-03-06	74	111	3,132	2	3
2001-04-02	164	246	3,528	_	-
2001-05-04	160	240	2,182	3	5
2001-05-23	68	102	3,732	1	2
2001-06-07	86	129	1,021	10	15
2001-06-19	80	119	3,557	4	6
2001-07-04	91	137	2,191	11	16
2001-07-17	58	86	-	-	4
2001-07-30	45	67	5,411	3	-
2001-08-15	51	77	1,253	2	3
2001-09-24	52	79	1,798	3	5
2001-11-25	44	67	4,571	1	1
Mean	69	105	3,570	8	13
Stdev	35	52	1,811	8	11
No of observations	20	20	25	26	26

#### Table 7. Biomasses of bacteria and ciliates.

Sediments depth (cm)	Station 0 m	Station 0.5 m	Station 2 m	Mean	Stdev
0–1	86	95	116	99	15
1–2	105	116	289	170	103
2–3	111	165	203	160	46
3–4	187	163	156	168	16
4–5	108	99	156	121	31
5–6	153	109	143	135	23
6–7	118	92	130	113	19
7–8	126	87	109	107	19
8–9	112	77	79	89	20
9–10	120	73	66	86	29
10–11	146	64	61	91	48
11–12	167	53	66	95	63
12–13	143	49	67	86	50
13–14	97	35	45	59	33
14–15	62	35	29	42	17
Total	1.842	1.311	1,716	1,623	277

Concentrations of ChI *a* in depth profiles of the sediment in Lake Eckarfjärden below the water depths 0 m, 0.5 m, and 2 m.