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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.

Abstract

This is the first part of a report characterising the lakes of Uppsala county, with special emphasis on the coastal lakes in the Forsmark area. The aim of the study is to characterise different main types of lakes within the Forsmark area and to create a basis for prediction of their ontogeny, that can be used also for new lakes which due to shoreline displacement will be formed during the next 10 000 years. Areas where future research is needed to fully understand the functioning of the lake ecosystems and their ontogeny should also be identified. This first part of the study identifies and describes one of the most common lake types in the area, the oligotrophic hardwater lake.

The geology in the catchments of the Forsmark area includes a bedrock dominated by granites and gneisses, covered by calcareous glacial till and postglacial clay. The catchments are dominated by forest, and the oligotrophic hardwater lakes are to a large extent surrounded by mires. Inflow as well as outflow of water is often diffuse, via the surrounding mire. The lakes are small and shallow, with nutrient poor and highly alkaline water. Three key habitats have been identified within the lakes; i) the pelagic zone, characterised by low production of biota, ii) the presumably moderately productive emergent macrophyte zone, dominated by *Sphagnum* and *Phragmites*, and iii) the light-exposed soft-bottom zone with *Chara* meadows and an unusually rich and presumably highly productive microbial sediment community.

The oligotrophic hardwater lakes have their origin as depressions in the bottom of the Baltic Sea, which are successively transported upwards due to the land-rise process in the area. As the basins are isolated from the sea, a gradual change from a brackish to freshwater conditions occur. When the lakes have become completely isolated, the oligotrophic hardwater stage follows, due to inflow of carbonate-rich and well-buffered groundwater. In the next successional stage, *Sphagnum* mosses start to colonise the littoral, and a mire is formed around the lake. In later stages of succession, *Sphagnum* becomes more and more dominant in the system, which successively turns acidic. The final stage of the ontogeny is likely to be a raised bog ecosystem with an autonomous hydrological functioning.

A tentative model for a mature hardwater lake has been created, indicating how and where substances from the drainage area may be accumulated in the system. Depending on the (unknown) hydrology of the lake basin, accumulation of substances can either take place in the *Sphagnum* littoral, in the illuminated soft-bottom sediments or in both these habitats. Processes in the open water will be of less importance in the system, since production of organisms in that habitat is most likely low. However, fish may act as a pump for nutrients and organic matter between the soft-bottom and the open water habitats, thereby disturbing the accumulation of substances in the sediments.

In conclusion, several pieces are lacking to complete the picture of the structure and functioning of the ecosystem in the oligotrophic hardwater lakes of the Forsmark area. Research directed towards the understanding of the lakes as a trap for contaminants should be focused on the hydrology of the basin and on the basal production in two of the key habitats; the mire/floating littoral system and the “microbial mat” in the light-exposed soft bottom areas.

Sammanfattning

Detta är en delrapport i ett arbete vars syfte är att beskriva Uppsala läns sjöar, med speciell tonvikt på förhållandena i Forsmarksområdets sjöar. De senare har definierats som sjöar tillhöriga avrinningsområdena 54/55 samt 55 i det indelningssystem som utarbetats av SMHI.

Med hjälp av kalciumkarbonathalterna i tillrinningsområdenas ytliga morän har sjöarna i Forsmarksområdet delats upp ytterligare, varvid två huvudtyper av sjöar har identifierats. Den viktigaste av dessa båda sjötyper, den kalkoligotrofa (kalkrika och näringsfattiga) sjön, beskrivs i denna delrapport utifrån befintlig kunskap om ekosystemets struktur och funktion.

Syftet med studien som helhet är att skapa ett underlag för bedömning av de vanligaste sjötyperna i Forsmarksområdet och deras utveckling i samband med avsnörningsprocesser från Östersjön och naturligt åldrande. Materialet ska på sikt användas för att söka förutsäga om sjöekosystemen kan komma att fungera som en fälla för radionuklider som eventuellt kan avges från befintligt och planerat lager för radioaktivt avfall i området (SFR) och i så fall var i ekosystemet en eventuell upplagring av radioaktivt material kan komma att ske.

Geologin i Forsmarkssjöarnas avrinningsområden karaktäriseras av en berggrund dominerad av sura bergarter, främst graniter och gnejser. Ovanpå liggande jordar, däremot, är starkt basiska från kambrosilurkalk som blandats in i moränen och från postglaciala leravlagringar som avsatts som sediment i Östersjöns olika utvecklingsstadier. Vegetationen i avrinningsområdena domineras av barrskog och myrmarker och de flesta av sjöarna omges av myrar.

Den kalkoligotrofa sjötypen är dominerande i Forsmarksområdet och även flera av de brunvattenssjöar som finns har genomgått ett kalkoligotroft stadium. De kalkoligotrofa sjöarna saknar ofta synliga inlopp och även utloppet är ofta delvist dolt i den omgivande myren. Sjöarnas vattenkemi kännetecknas av näringsfattigdom, hög alkalinitet och höga koncentrationer av baskatjoner, särskilt kalciumjoner. Vattenfärgen är måttlig men ökar i samband med sjöarnas åldrande. Utifrån biologiska data har tre nyckelbiotoper kunnat identifieras i sjöekosystemen: 1) den fria vattenmassan, vilken kännetecknas av låg biologisk produktion; 2) den vindskyddade strandnära zonen (litoralen), dominerad av vitmossa och bladvass som bildar ett gungfly och som sannolikt är måttligt produktiv, samt 3) de solbelysta mjukbottnarna som kännetecknas av kransalger samt en ovanligt tjock ”mikrobiell matta” av bland annat cyanobakterier och kiselalger. Denna senare biotop är med stor sannolikhet den mest produktiva i sjöekosystemet.

Viktiga skeenden som styr de kalkoligotrofa sjöarnas ontogeni börjar redan innan avsnörningen från Östersjön skett, i havsvikar med ett vattendjup på två till tre meter. I detta stadium börjar bladvass och andra vattenväxter kolonisera de grundare strandnära områdena medan mattor av kransalger breder ut sig på bottnarna. När vikarna med tiden helt avsnörs från havet börjar det kalkoligotrofa stadiet, vilket kännetecknas av utfällningar av kalk och medfällda näringsämnen, främst fosfor, på de solbelysta mjukbottnarna. Utfällningarna leder till låga koncentrationer av näringsämnen i vattenmassan och en därtill hörande låg produktion av organismer. Något senare börjar de strandnära växterna att koloniseras av vitmossor. Detta är början till bildandet av en myr runt sjöarna. I ett

mognare stadium omges hela sjöbäckenet av myren, vilken därmed börjar påverka vattenkemin i hela ekosystemet genom tillförsel av syra och färgat organiskt material. Myrens ytterkant, den egentliga skyddade litoralzonen i sjön, är oftast av gungflykaraktär och är troligen inte tillgänglig för högre biota (t ex bottenfauna och fisk) från andra delar av sjöekosystemet. I takt med att myren/litoralen sluter sig ökar betydelsen av denna nyckelbiotop för hela sjöekosystemet som övergår från kalkoligotrofi till ett stadium karaktäriserat av betydligt surare vatten som är starkt färgat av löst organiskt material. Slutstadiet i utvecklingen är sannolikt en tallmosse, med ett mer eller mindre separat hydrologiskt system baserat på regnvattentillförsel.

Den kalkoligotrofa sjöns funktion som en fälla för material från tillrinningsområdet är sannolikt mest komplex i det stadium när myren just slutit sig runt sjön. En hypotetisk modell för hur systemet då fungerar har upprättats. Modellen ger två valmöjligheter vad gäller den gungflyartade myrlitoralens funktion. Den ena förutsätter att djupare grundvatten penetrerar myrlitoralen, som då fungerar som en biologisk sil för olika ämnen. Den andra baseras på att myren är ett eget, huvudsakligen regnvattenmatat hydrologiskt system. I båda fallen är näringsflödet från litoralen till övriga delar av sjöekosystemet mycket begränsat. De solbelysta mjukbottnarna intar därmed en nyckelposition i sjöekosystemets funktion som fälla för inflödande substanser. Den biogent inducerade utfällningen av kalk och näringsämnen torde leda till stark ackumulation av olika oorganiska och organiska substanser. Denna filtrering av inflödande vatten, genom såväl litoral som mjukbotten, förklarar den mycket låga produktionen i den fria vattenmassan. Fisk kan dock fungera som en slags biologisk pump av energi och näringsämnen från sedimenten till den fria vattenmassan.

Sammantaget kan sägas att den modell som beskrivs i hög grad baseras på författarnas intuition och kunskap om funktionen hos sjöekosystem i allmänhet, eftersom fakta om de aktuella sjöarna i området i hög grad saknas. Framtida forskning med syfte att klarlägga sjöarnas funktion som en fälla för olika substanser från tillrinnande vatten bör fokuseras på funktionen hos och balansen mellan de olika nyckelbiotoperna, särskilt myr-litoralen och de solbelysta mjukbottnarnas mikrobiella matta. Det är även av största vikt att utreda de hydrologiska förhållandena i systemet.

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1 Introduction

Lake basins may be formed in many different ways, often related to catastrophic events in the history of earth. Lakes appear wherever a threshold is formed, which obstructs the passage of runoff water. Hutchinson /1975/ defined eleven main classes and characterised totally 76 sub-classes of lake basins, based on the processes involved in their formation. The lake basins that are found in Sweden include *e.g.* tectonic basins, basins formed by glacial activity, by fluviatile action and by meteorite impact as well as man-made dams.

Immediately after the formation of the lakes, an ontogenic process starts, where the basins ultimately are filled out with sediments, thereby developing towards extinction of the lakes. Depending on the environmental conditions they may be converted either to a final stage of bog or to forest /Wetzel, 1983/. Seen in a broader geological perspective, however, the lakes and the sediments collected within the basins are only short resting stages for the material transported by the river systems from the continents to the sea. Water is the transporting medium for this large-scale erosion of the continents.

One of the most common types of lake basins that can be found in Sweden are the ones that have been formed by glacial activities during and after the Pleistocene glaciations. Along the coastal areas new lakes are still continuously formed as the land is rising from the depression that occurred during the last glaciation period which terminated about 8800 years ago /Ignatius *et al*, 1981/.

The storage for low activity radioactive waste, SFR is located nearby the nuclear power plant at Forsmark. SFR is below the present sea bottom. In the future, however, this area will rise and become situated on land, *i.e.* the storage will be situated below a land area instead of below the sea /Brydsten, 1999/. Due to the formation of the new land area, the hydrological conditions will be subject to substantial alterations, affecting groundwater as well as surface waters. Regarding the surface waters, new catchments will develop, and within these catchments both rivers and lakes will be formed.

The Swedish Nuclear Fuel and Waste Management Co. (SKB) is responsible for the management and disposal of Swedish radioactive waste, most of which originates from the nuclear power plants. The used nuclear fuel is also planned to be stored in deep geological repositories. The purpose of the repositories is to keep the radioactive material separated from man and environment for hundreds of thousands of years. During this time span drastic changes in geology, hydrology, climate and other environmental conditions will occur.

The aim of this study is to summarise the information about the lakes which are present within the Forsmark area today. Data from these lakes constitute the basis for a prediction of the characteristics and ontogeny of the lake systems in the future, including also the new lakes which will be formed during the next 10 000 years. The prediction will be included in the safety analysis for the low-level repository SFR in the SAFE project. The present report is the first part of the study, including a general description of all lakes in Uppsala county, and of the lakes in the Forsmark region in particular. The main emphasis in the report has then been put on describing the characteristics and ontogeny of one of the most common lake types in the Forsmark area; the oligotrophic hardwater lakes (*Chara* lakes).

2 Material and methods

2.1 Area description

Uppsala county has an area of 7000 km^2. The bedrock in this area is dominated by granites and gneisses and the geological history includes several periods of total glaciation; the last ice period terminating about 12 000 years ago. When the ice was retreating and melting the entire province turned the bottom of the Ancylus Lake and the Litorina Sea (which later developed into the Baltic Sea) and which covered large parts of South Sweden and Finland. The land which was depressed by the ice has gradually been rising during postglacial time, and still the elevation amounts to about half a meter per century /Ignatius *et al*, 1981/. The landscape of the province can be characterised as a lowland crossed by several eskers (another remnant of the ice cover). Only small parts of the area elevates more than 50 m over the sea level. In some areas in the northern part of the province peat-land is dominating. Due to the substantial changes of the landscape during and after the latest ice period, many of the lakes are, from a geological perspective, to be regarded as young. In fact, the land rise is still continuously creating new lakes along the coast, as bays of the Baltic Sea are isolated.

The glacial and postglacial soils overlaying the bedrock consists of calcium-rich till and clay, and as a consequence the surface waters in general are naturally well buffered and relatively nutrient rich. The land use includes a relatively high portion of farmland (22% of the total area), concentrated to the central and southwestern parts. The vegetation is dominated by coniferous forest and mires which constitute 58% of the total area, alternating with farmland in a mosaic pattern. The largest town in the province is Uppsala (about 100 000 inhabitants 1993), hosting two large universities but lacking large industries. In the forested northern part of the province mining and iron industries were developed during the 17th century, and the demand for water in the industry processes led to substantial human impact on the freshwater systems in this area. Nowadays this industry has almost completely been closed down, but the profound changes in the water systems persist in form of several man-made lakes and diversion of water in new directions.

The area has a transition between a continental and a maritime climate. According to the Swedish Meteorological and Hydrological Institute (SMHI), the average (1961–1990) annual precipitation is 544 mm and the average temperature is 5.8 °C. The area is covered by snow for about 100 days and the lakes by ice for 140–160 days from November 20 to April 20 /Eriksson, 1920/. The area-specific runoff is 6–7 $l\ s^{-1}\ km^{-2}$ (SMHI). Eight larger river systems or parts of larger river systems can be identified within Uppsala county /SMHI, 1985/. Five of these rivers have their outlet to the Baltic Sea at the Swedish East coast. The other three enters Lake Mälaren, which in turn has the outlet to The Baltic Proper.

2.2 The total lake material

A large data set concerning all lakes (> 3 hectares) in the province of Uppsala has been thoroughly described by Brunberg and Blomqvist /1998/. A condensed version aimed at analysing the anthropogenic threats to the lakes and their catchments is presented in Brunberg and Blomqvist /in prep./. These two materials create the basis for the present evaluation of environmental conditions in and ontogeny of coastal lakes in the Forsmark area. When the data set for Brunberg and Blomqvist /1998/ was gathered, during the years 1982–1997, emphasis was put on to make the basic descriptive material about the lakes as complete as possible regarding each essential parameter. In this evaluation we have principally used those parameters which were available for more than 50% of the lakes as a basis to initially describe the conditions in all lakes in the province and in the subset lakes in the Forsmark area, respectively. Parameters which were only available for a limited number of lakes have been used to discuss potential characteristics of the coastal lakes. Thus, the basic descriptive material includes the following parameters (Table 2-1):

Table 2-1. Basic parameters used to characterise the catchments and lakes in the province of Uppsala.

Catchment parameters	Lake parameters
Area (km^2)	Total area (km^2)
Forest (% of area)	Average depth (m)
Wetland (% of area)	Maximum depth (m)
Farmland (% of area)	Volume (Mm^3)
Lakes (% of area)	Turnover time (days)
Other types of land (% of area)	Lowering of lake water level
	Water colour
	Alkalinity
	Nutrient status (based on tot-P concentrations)
	Oxygen conditions (predicted winter oxygen deficiency)
	Fish fauna

2.3 Identification of and subdivision of coastal lakes in the Forsmark area

In their division of Sweden into major river catchments and residual catchments, SMHI /1985/ identified 17 units, which partly or in their entirety are located in the province of Uppsala. Brunberg and Blomqvist /1998/ further divided these units into 269 sub-units. The coastal area includes five major river catchments (terminology according to SMHI, 1985): 53 River Dalälven, 54 River Tämnarån, 55 River Forsmarksån, 56 River Olandsån, and 57 River Skeboån. Between these river catchments there are another 5 residual catchments which at least partly are located in the province and which drain directly to the coast. The remaining catchment units of the county all drain to Lake Mälaren, the outlet of which is termed 61 River Norrström.

The coastal lakes of the Forsmark area were defined as those belonging to the Swedish major catchment units 54/55 “Between River Tämnarån and River Forsmarksån” and 55 River Forsmarksån (Figure 3-1). River Tämnarån, in the north, was delineated from the material because of its character as a lowland river draining plains heavily dominated by clay and to a large extent exploited for agriculture. Furthermore, River Tämnarån has very few lakes, and they are located far from the outlet to the Bothnian Sea. The southern border was set to River Olandsån which is also heavily affected by agriculture and drainage and in which the few remaining lakes are also located very far from the coast. One of the lakes in catchment no 54/55, Lake Strömaren, was also omitted from the defined coastal lakes. The reason is that this lake, which has a separate outlet river to the Bothnian Sea, was considered to be situated too far from the coast. Thus, the "Forsmark area" altogether includes 42 of the sub-units described by Brunberg and Blomqvist /1998/.

3 Results

3.1 The lakes of the Forsmark region and their deviations from the average lake in Uppsala county

The lakes which are situated in the Forsmark area (as delimited above) differ in several aspects from the lakes of Uppsala county in general (Table 3-1). Because of their location close to the Baltic coast in a lowland area they are generally younger than the inland, *i.e.* more elevated, lakes. In addition they are situated in an area where the soil is mainly till, which means that the land use in the catchments is not so intense as in the catchments which have been formed on the post-glacial clay. This is reflected in the percentage of wetland and farmland, where the Forsmark lake catchments have a higher percentage of

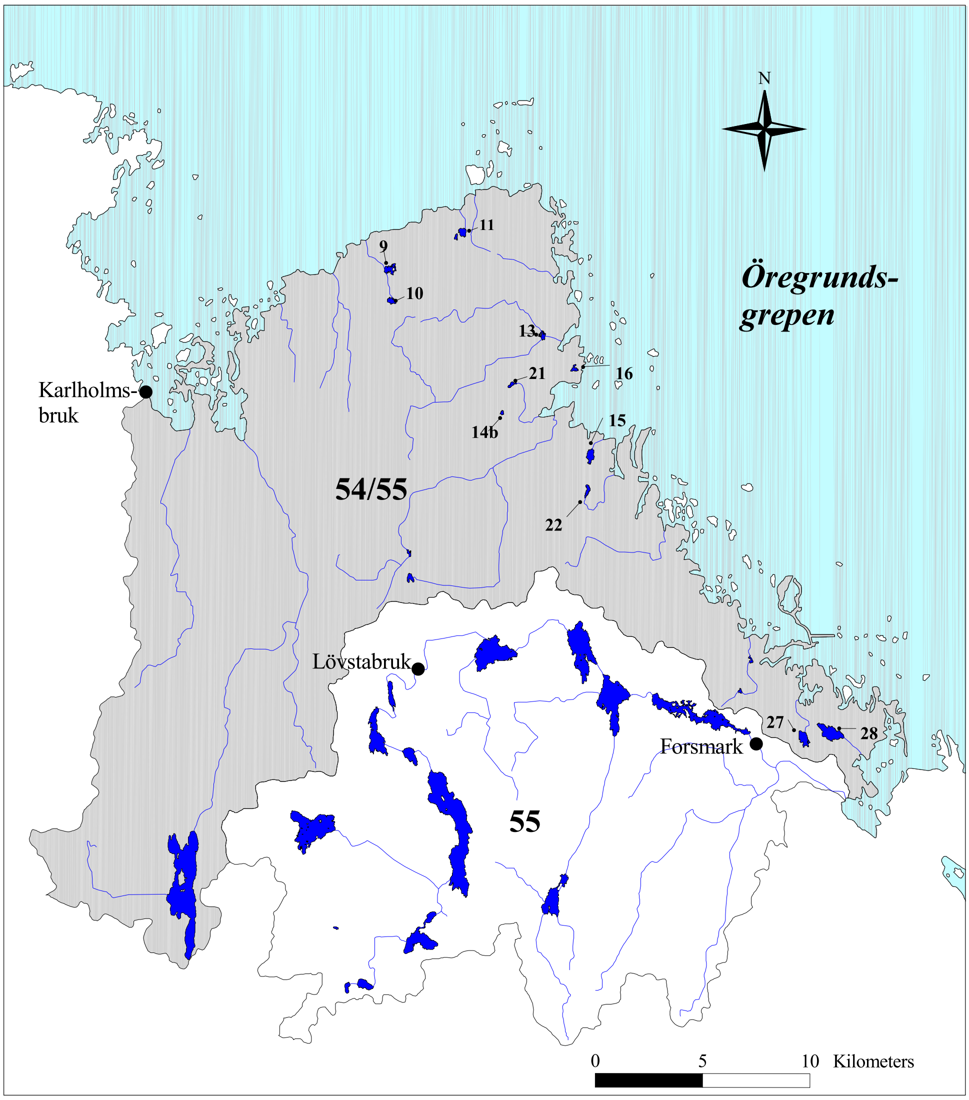

Figure 3-1. *Map showing the "Forsmark area" with the SMHI catchments no 54/55 "Between River Tämnarån and River Forsmarksån" and 55 "River Forsmarksån". Lakes indicated by numbers refer to the oligotrophic hardwater systems discussed in the text (cf Table 3-2). Permission: The National Land Survey of Sweden. Register number 507-96-1524.*

Table 3-1. Lake and catchment data from the Forsmark area, compared to corresponding values for all lakes in Uppsala county. Classification of lake chemistry according to SNV /1990/ and Brunberg and Blomqvist /1998/. Tot-P: 1= very nutrient poor, 2= nutrient poor, 3=moderately nutrient rich, 4=nutrient rich, 5=very nutrient rich. Water colour: 1=no or negligible colour, 2=slightly coloured, 3=moderately coloured, 4=substantially coloured, 5=strongly coloured water. Buffer capacity: 1=very good, 2=good, 3=weak, 4=very weak, 5=no or negligible buffer capacity. Oxygen conditions: 1=small risk for low concentration of O_2, 2=risk for <5 mg O_2/l, 3= risk for <1 mg O_2/l, 4=risk for anoxic conditions.

	Catch-ment area km^2	forest %	wetland %	farmland %	lake %	other %	Lake area km^2	Average depth m	Max depth m	Volume Mm^3	Water renewal time, days	Lowering of water level, m	Oxygen condi-tions	Nutrient status (tot-P)	Water colour	Buffer capacity
Lakes within the Forsmark area:																
Average	59.1	69	20	4	6	0	0.81	1.35	2.3	1.45	129	0.3	2.5	2.7	4.0	1.3
Median	15	69	20	2	6	0	0.21	1.15	2.2	0.35	65	0.3	2	3	4	1
Max	285	87	46	20	17	1	4.25	2.8	4	7.77	383	1	4	4	5	2
Min	0.22	50	5	0	0	0	0.02	0.5	0.9	002	1	0	1	2	2	1
N obs	29	29	29	29	29	29	30	22	23	22	21	25	22	21	25	24
All lakes in Uppsala county:																
Average	54.3	72	11	10	6	1	1.04	1.98	3.8	2.35	263	0.75	2.6	3.5	4.0	1.3
Median	9.9	74	8	5	5	0	0.25	1.5	2.6	0.38	91	0.5	2	3	4	1
Max	707	95	55	74	24	69	36.74	22	52	47.8	6954	3	4	5	5	5
Min	0.22	14	0	0	0	0	0.01	0.4	0.9	0.01	1	0	1	2	1	1
N obs	142	142	142	142	142	142	141	119	122	119	117	111	107	105	131	121

wetland but lower percentage of farmland. Less influence from agriculture activities is also reflected in that these lakes have not been subject to drainage and lowering of the water level to the same extent as the average (or median) lake of the county. However, several of the lakes of River Forsmarksån (catchment no 55) have been strongly affected by another kind of anthropogenic activity, *i.e.* construction of dams and water regulation. The iron works at Forsmark, dating back to the 17th century, used the river system for water supply to the workshops for more than 200 years. Nowadays this industry has almost completely been closed down. However, as the natural thresholds of the lakes in several cases have been removed since long time ago, the dam constructions are still needed to keep the water levels in the lakes on a "natural" level. Nevertheless, the regulation of the water levels has stopped, and the drainage areas have to a large extent remained in a natural state of wetland.

Other characteristics of the Forsmark lakes are that they are smaller, shallower and have smaller volume of water than the lakes of Uppsala county in general, and the renewal time of their water is shorter. It should also be noted that the shallowness is to a larger extent of natural origin than for the other lakes in the county, which is shown by the data on lowering of the lakes. Considering all the lakes of the county, the average lowering of the lake water levels caused by drainage of land is 0.75 m, while the corresponding value for the lakes of the Forsmark area is 0.28 m.

The water chemistry does not differ much between the two groups of lakes, when comparing them classified according to the recommendations by the Swedish Environmental Protection Agency (Table 3-1). Slightly less nutrient rich conditions is shown for the Forsmark lakes if compared as average values. The water colour is very similar to the lakes in the county in general and indicates a substantial amount of dissolved organic substances in the lake water. The alkalinity is also similar to the lakes in the county in general. However, if a class sorting out waters with "extremely good" buffering capacity is added to the classification system, the lakes of the Forsmark area clearly become separated from the other lakes of the county by their higher concentrations of bicarbonate (HCO_3^-) ions.

In conclusion, the lakes of the Forsmark area are small and shallow, and the renewal time of the water is short. They are very well buffered and their nutrient status is classified as moderately rich. The water has a substantial colour, indicating a relatively high concentration of dissolved organic substances within the lakes.

3.2 Characteristic lake types within the Forsmark region

The environmental conditions within the drainage area, and thereby the quality of the inflowing water, is one of the most important factors determining the character of the lake ecosystem. Therefore, when distinguishing between different lake types in the Forsmark area, we decided to use the composition of the soils within the drainage area, as this affects the leakage of different substances to the lakes. A very detailed investigation of the calcium content in the soils of northern Uppland /Gillberg, 1967/ was found to be suitable for this purpose. Using this information, the lakes within the selected area (catchments 54/55 and 55) could be divided into two different categories, one group draining areas with less than 6% and another group draining areas with more than 20% of calcareous matter in the fine grain fraction of the till (area weighed mean values from a depth of 0.5–1.0 m). Only two lake catchments fell outside these two main groups, taking an intermediate position. These two lakes are situated very close to the nuclear power plant at Forsmark and have been severely affected by the human activities in the area. No chemical or biological information is available from the lakes, of which one is nearly overgrown and the other partly has been filled out during construction work. They were thus omitted from this description of lakes in the Forsmark area. The lakes which had drainage areas rich of calcareous matter were defined as oligotrophic hardwater lakes, which corresponds to the more commonly used name "*Chara* lakes". This type of lakes is described in detail below. The lakes with less calcareous material within the catchments were characterised as brownwater lakes, and will be described in a following report.

3.3 Description and characterisation of oligotrophic hardwater lakes (*Chara* lakes)

The literature regarding the ecosystem structure and functioning of the oligotrophic hardwater lakes of the Forsmark area is very restricted. Some studies of *Chara* lakes from different areas of Sweden and Europe are available, often concentrated on the ecology of the *Charales*. The following presentation is based on the few data that have been found (referred to in the text when used), together with conclusions drawn from visits to the lakes as well as from general models for the functioning of lakes.

The coastal Forsmark area that was selected for the purpose of this lake characterisation includes ten of the lakes, which were described in Brunberg and Blomqvist /1998/. In addition, one small lake, Lake Hällefjärd, has been subject to a limnological investigation during 1999 /Halvarsson, in prep/. Thus Lake Hällefjärd has also been included in the data set that we have used for description and characterisation of the lakes within the area (Table 3-2). Additional data from other lakes in the area have in some cases been used for parameters which were not included in Brunberg and Blomqvist /1998/. Several small lakes or bays of the Baltic in different stages of isolation from the sea are also situated in the area, but data about these were almost completely lacking. In the following text, data about the drainage areas will be referred to by the numbers of the catchments as given by SMHI /1985/ and sub-catchments as given by Brunberg and Blomqvist /1998/. All these lakes have sub-catchments situated within catchment no 54/55 "Between River Tämnarån and River Forsmarksån" (Figure 3-1).

Table 3-2. Oligotrophic hardwater lakes in the Forsmark area. Catchment no according to SMHI /1985/, no of sub-catchment according to Brunberg and Blomqvist /1998/.

Catchment	Sub-catchment	Lake name	Coordinates for outlet x, y
54/55	9	Själsjön	671868, 161246
54/55	10	Degertrusket	671742, 161218
54/55	11	Storfjärden (Hållen)	672061, 161612
54/55	13	Storfjärden (Slada)	671560, 161997
54/55	14b*	Hällefjärd	671219, 161796
54/55	15	Dalarna	671408, 162145
54/55	16	Käringsjön	671341, 161859
54/55	21	Västersjön (Stora Hållsjön)	671041, 162215
54/55	22	Strönningsvik	670809, 162181
54/55	27	Eckarfjärden	669723, 163205
54/55	28	Fiskarfjärden	669681, 163407

* L. Hällefjärd is a sub-catchment of 54/55:14 (Vedlösaområdet) in Brunberg and Blomqvist /1998/.

3.3.1 The drainage area

The drainage areas of the oligotrophic hardwater lakes in the Forsmark area are generally very small (Table 3-3). Only one catchment (Lake Storfjärden, Slada) has a size which is very close to the average size (54 km^2) of lake catchments in Uppsala county. The other lakes have catchments with areas less than 5 km^2. The geology includes an acidic bedrock dominated by granites and gneisses, covered by calcareous glacial till and in minor areas postglacial clay (coinciding with agriculture areas). The high content of lime in the till originates from the cambrosilurian area in the Bothnian Sea.

Table 3-3. Characteristics of the catchments of oligotrophic hardwater lakes in the Forsmark area.

Catchment		Area	Forest	Wetland	Farmland	Lakes	Other land use
		km^2	%	%	%	%	%
54/55: 9	Själsjön	4.83	80	15	2	3	0
54/55: 10	Degertrusket	2.66	78	16	3	3	0
54/55: 11	Storfjärden (Hållen)	2.11	79	15	0	6	0
54/55: 13	Storfjärden (Slada)	54.80	69	11	20	0	0
54/55: 14b	Hällefjärd	0.60	-	-	-	-	-
54/55: 15	Västersjön (St Hållsjön)	0.22	59	23	4	14	0
54/55: 16	Dalarna	0.36	70	19	0	11	0
54/55: 21	Käringsjön	1.85	83	6	1	10	0
54/55: 22	Strönningsvik	0.65	57	28	3	12	0
54/55: 27	Eckarfjärden	1.51	73	7	5	15	0
54/55: 28	Fiskarfjärden	2.70	60	22	1	17	0
Average		6.57	70.8	16.2	3.9	9.1	0
Median		1.85	71.5	15.5	2.5	10.5	0
Max		54.80	83	28	20	17	0
Min		0.22	57	6	0	0	0
N obs		11	10	10	10	10	10

The vegetation of the catchments is dominated by forest and wetlands, which on average together cover 87% of the area (Table 3-3). The proportion of farmland is generally lower than in other catchments of Uppsala county, while the percentage of wetland is higher. The only exception from this is Lake Storfjärden (Slada), which has a relatively high proportion (20%) of farmland within the catchment. The oligotrophic hardwater lakes constitute on average 9% of the catchment area, which is a larger portion than in other catchments in the county. Other lakes upstream in the catchments are always lacking. The differences in elevation within the catchments are often small, especially in the riparian zone. Visible inlets as well as outlets are often more or less lacking, unless the catchments have been subject to drainage projects. Thus, a major part of the water transported through the catchments is more or less filtered through the surrounding wetlands before entering the lakes.

3.3.2 The riparian zone

Most of the oligotrophic hardwater lakes in the Forsmark area are, as stated above, to a large extent surrounded by mires, which in the outermost part form floating mats constituting the littoral zone of the lake. These surrounding mire systems have been subject to a large number of inventories, especially concerning their vegetation /references in Brunberg and Blomqvist, 1998/, while studies of functional aspects are lacking. The mires often have a mixed character with components of pine bog, poor fen, rich fen, extremely rich fen and, at the edge of the lake, *Phragmites*-populated floating *Sphagnum*-mats. The bottom layer of the pine bog is dominated by *Sphagnum*, and in the field layer *Ledum palustre*, *Rubus chamemorus*, and *Eriophorum vaginatum* are important components. The poor fen also has *Sphagnum* as a dominant constituent of the bottom layer, and a field layer with *Rhyncospora alba*, *Scheuchzeria palustris*, *Carex rostrata*, and *C. lasiocarpa*. Rich fens, interspersed with components of extremely rich fens, often dominate the mires. The bottom layer in these fens is dominated by a variety of brown coloured mosses. Important constituents of the field layer are *Parnassia palustris*, *Primula farinosa*, *Dactylorhiza incarnata*, *Epipactis palustris*, *Liparis loeserii*, and *Dactylorhiza traunsteineri*.

From the point of view of functioning of the combined mire-lake ecosystem, at least four potentially important observations can be made. First of all, the strongly variable character of the surrounding mire-littoral system indicates interesting differences in hydrology and water chemistry between its components. However, as far as the authors know, no studies of these parameters, or of the ecology of the mire-littoral from a functional point of view, have been undertaken in the area. Secondly, it is also evident that the horizontal growth of the surrounding mire is an important part of the ontogeny of the entire lake ecosystem towards a mire, but neither in this case are there any quantitative studies available from the lakes of the county. Thirdly, a characteristic of this kind of lake, which indeed requires further attention, is the compact character of the littoral zone. This almost closed, often floating, three-dimensional littoral system, dominated by *Sphagnum* (which in turn to some extent is colonised by *Phragmites*), most likely minimises the access to the system for larger lake biota (*e.g.* fish and benthic fauna). This lack of access for larger lake biota to the highly productive littoral zone is most likely a major difference between lakes surrounded by mires and other lake types in which the littoral is of great importance for growth and reproduction of many animals. Finally, for many of the lakes it is also evident that the drainage of the system is "diffuse" through the mire. It is not until the edge of the mire is reached that the outlet becomes visible. This filtration of the outflowing water must have considerable impact on the water quality as biologically active compounds must be efficiently retained in the mire.

In conclusion, there is a great need for quantitative and functional studies of couplings between the various ecological units of the mire-littoral-water system.

3.3.3 Lake morphometry

Chara lakes are in general very shallow. The oligotrophic hardwater lakes in the Forsmark area have an average depth of 1 meter (Table 3-4), while the average depth for all lakes in the county is 2 meters. The oligotrophic hardwater lakes within the Forsmark area also have small areas, compared to the other lakes in the county, although this is not a character that can be applied for *Chara* lakes in general.

Due to the small size and shallowness, the lakes also have a small water volume and consequently a short renewal time of the water (Table 3-4). In some of the lakes, which have not yet been enough separated from the sea level, the hydrological conditions also include intrusions of water from the Baltic sea during low pressure weather conditions which creates a high sea level.

Table 3-4. Lake morphometry for oligotrophic hardwater lakes in the Forsmark area.

Lake	Area, km²	Average depth, m	Maximum depth, m	Volume, Mm³	Water renewal time, days	Lowering of water level, m
Själsjön	0.07	-	-	-	-	0.8
Degertrusket	0.07	-	-	-	-	0.4
Storfjärden (Hållen)	0.11	0.6	1.1	0.066	47	0.3
Storfjärden (Slada)	0.03	1.2	2.2	0.036	1.2	0.4
Hällefjärd	0.05	0.9	1.5	0.022	63	-
Dalarna	0.07	0.5	1.3	0.035	301	0
Käringsjön	0.04	0.6	0.9	0.024	138	0
Västersjön	0.19	1.9	3.2	0.361	331	0
Strönningsvik	0.08	1.0	1.7	0.080	229	0
Eckarfjärden	0.23	1.5	2.6	0.345	383	0.3
Fiskarfjärden	0.61	0.7	2.0	0.427	251	0
Average	0.14	1.0	1.8	0.155	194	0.22
Median	0.07	0.9	1.7	0.066	229	0.15
Max	0.61	1.9	3.2	0.427	383	0.75
Min	0.03	0.5	0.9	0.022	1.2	0
N obs	11	9	9	9	9	10

Some of the oligotrophic hardwater lakes have been subject to drainage projects and lowering of the water level. However, both the frequency and the extent of these projects are less than for the other lakes in the county.

3.3.4 Sediment characteristics

Oligotrophic hardwater lakes are often characterised as “bottomless“, *i.e.* there is no distinct border between the very soft sediment and the lake water. The calcareous and highly organogenic sediment is of autochtonous origin, with minor contribution of mineral particles. It has been characterised as “algal gyttja“ or “cyanophycée gyttja“ /Lundqvist, 1925/. Paleo-ecological studies of the sediments were also performed by Jonsson /1973/ in several lakes in the Forsmark area, including Lakes Storfjärden (Slada), Hällefjärd, Västersjön (Stora Hållsjön) and Strönningsvik in catchment 54/55, and Lake Vikasjön in catchment 55 (Forsmarksån). These lakes of catchment 54/55 are all included in the oligotrophic hardwater lakes of the Forsmark area defined in Table 3-2, while Lake Vikasjön since long time ago have passed the calcareous hardwater lake stage. Lake Vikasjön, which nowadays is elevated 29 m over the sea level, was earlier a part of a large lake that initially was formed when the area of Florarna was isolated from the Baltic /Ingmar, 1963/. This former lake, which nowadays is a mire, has a threshold situated 27 m over the sea level /Jonsson, 1973/. The sediments of Lake Vikasjön show a nice paleo-ecological record of the different stages in the ontogeny of the lake since the separation from the sea approximately 4000–5000 years ago. Sedimentation rates, estimated from unpublished data from T. Ingmar (pers.com.) roughly corresponds to 1–1.5 mm of sediment per year during the oligotrophic hardwater stage and 1 mm/year during the following brownwater stage. The oligotrophic hardwater phase of Lake Vikasjön, as indicated by a layer of cyanophycée gyttja, corresponds to a time period of one millennium. The sediments of the oligotrophic hardwater lakes in the Forsmark area, which presently are in the oligotrophic hardwater phase, are of two types, depending of how much mineral particles that are transported to the lake. The typical cyanophycée gyttja is reddish-brown, gelatinous and almost free from mineral particles, except for precipitated $CaCO_3$ which in some cases may add a greyish colour to the sediment ("lime gyttja"). Lakes where mineral particles from the drainage area are mixed into the sediments have a green or bluegreen non-gelatinous surface sediment. This is the case when the inflowing water reaches the lake by visible inlets instead of being filtered through the riparian zone from diffuse sources.

In conclusion, the very few and often old investigations of the sediments of the oligotrophic hardwater lakes, describe a very characteristic and unusual type of sediments. Already Lundqvist /1925/ stated that the microbial activity in these lake ecosystems are focused to the soft bottoms, where different microorganisms "luxuriate" (op.cit.). These sediments thus should be subject to further investigations, using modern techniques for dating, chemical characterisation, identification of microorganisms, measuring of biological and chemical processes etc., in order to quantify different processes and flow of materials through the systems. This is probably a key to the understanding of the oligotrophic hardwater lake metabolism and ontogeny.

3.3.5 Water chemistry

The *Chara* lakes are chemically characterised as hard-water lakes, distinguished from soft-water lakes by their high conductivity and richness of calcium and magnesium dissolved in the water. Hard-water lakes occur all over the world, in areas of alkaline sedimentary rocks. These rocks are easily weathered and yield alkaline water rich in calcium and many other elements, *e.g.* micro-nutrients for the biota. However, due to both chemically and biologically induced interactions in the lake water, the amounts of nutrients (*e.g.* phosphorus) transported to the lakes may be effectively reduced by precipitation of calcium-rich particulate matter. This restricts the production of organisms in the lake that not have access, directly or indirectly, to the sediments as a nutrient source. Nitrogen, on the other hand, tends to be present in relatively high concentrations in the water, due to the combination of high input but low biotic utilisation /Wetzel, 1983/.

Forsberg /1965/ compared the ionic composition of *Chara* lakes in Sweden with the "standard composition" of fresh water lakes /Rodhe, 1949/, and concluded that as a rule the *Chara* lakes contained more calcium in relation to conductivity than would be expected from the standard composition while concentrations of other cations consequently were lower (Table 3-5). He also concluded that bicarbonate was the dominant anion in most of the lakes (bicarbonate group) but noted that in approximately 10% of the lakes sulphate was the dominant anion (sulphate group). The dominance of sulphate was explained by that the samples from the actual lakes were taken after a year of low precipitation, which may have caused low groundwater level and thereby oxidation of sulphur in the soils, followed by increased transport/wash-out of sulphate when the water levels increased again. The lakes from the Forsmark area that was included in Forsberg's investigation (Lakes Hällefjärd, Strönningsvik and Romsmaren) all belonged to the "bicarbonate group" of *Chara* lakes.

The oligotrophic hardwater lakes of the Forsmark region, as characterised in Brunberg and Blomqvist /1998/, all show the typical hard-water lake chemistry (Table 3-6), although the principal source of the salinity is not the bedrock but the glacial till and postglacial deposits constituting the soils in the area (*cf.* above). The lakes have low or moderately high phosphorus concentrations (<12.5 and 12.5–25 µg P/l, respectively). The alkalinity is very high; all the lakes have "very good buffer capacity" according to the classification system proposed by the Swedish Environmental Protection Board /NV,

Table 3-5. The ionic composition of *Chara* lakes in Uppland (equiv. %, average values), compared to the standard composition according to Rodhe /1949/. From Forsberg /1965/.

Water	Ca	Mg	Na	K	HCO_3	SO_4	Cl
Chara lakes of "bicarbonate group"	79.1	10.9	8.3	1.7	71.9	22.7	5.4
Chara lakes of "sulphate group"	73.3	16.0	8.8	1.9	37.2	55.4	7.4
Standard composition	63.5	17.4	15.7	3.4	73.9	16.0	10.1

1999/. This is similar to the vast majority of the lakes in Uppsala county. However, the classification system does not distinguish between higher levels of alkalinity. The limit for "very good buffer capacity", which is set to >0.20 meq/l, is in fact far below the alkalinity values that can be found in these lakes, varying between 1.35 and 4.21 meq/l in our data set. The water colour is varying, which reflects the varying conditions in the lakes, but also that the data set is very limited. In average, though, the oligotrophic hardwater lakes have slightly lower values compared to the lakes in Uppsala county in general, but still a "moderate" (25–60 mg Pt/l) to "significant" (60–100 mg Pt/l) water colour.

Table 3-6. Water chemistry classification for oligotrophic hardwater lakes in the Forsmark area. Data from Brunberg and Blomqvist /1998/, partly re-classified according to new recommendations from the Swedish Environmental Protection Agency /Naturvårdsverket, 1999/.

Lake	Total P µg P/l	Alkalinity meq/l	Water colour mg Pt/l	Oxygen conditions
	1 = ≤12.5 2 = 12.5-25 3 = 25-50 4 = 50-100 5 = >100	1 = >0.20 2 = 0.10-0.20 3 = 0.05-0.10 4 = 0.02-0.05 5 = ≤0.02l	1 = ≤10 2 = 10-25 3 = 25-60 4 = 60-100 5 = >100	1 = small risk for low O_2 concentration during winter 2 = risk for <5 mg O_2/l 3 = risk for <1 mg O_2/l 4 = risk for anoxic conditions
Själsjön	-	1	5	-
Degertrusket	-	-	-	-
Storfjärden (Hållen)	2	1	4	4
Storfjärden (Slada)	-	1	4	4
Hällefjärd	1	1	3	
Dalarna	3	1	4	4
Käringsjön	2	1	3	3
Västersjön	2	1	2	-
Stönningsvik	2	1	4	2
Eckarfjärden	2	1	3	1
Fiskarfjärden	3	1	3	4
Average	2.1	1.0	3.5	3.1
Median	2.0	1.0	3.5	4.0
Max	3	1	5	4
Min	1	1	2	1
N obs	8	10	10	7

An investigation of winter oxygen conditions in the lakes of Uppsala county showed that the oligotrophic hardwater lakes often experience oxygen deficit during the winter period /Sonesten, 1989/. This is not a surprising result, considering the shallowness and small water volume of these lakes. Poor oxygen conditions frequently occur during winter in many of the lakes in Uppsala county. In many cases this is caused by the extensive drainage of land, including lowering of the water levels in the lakes. Regarding the oligotrophic hardwater lakes, however, the shallowness is often natural, and the poor oxygen conditions are typical of aged systems. Depletion of dissolved oxygen is of course a threat to all oxygen respiring organisms, and strong effects may be seen on *e.g.* the structure of the fish community (*cf* 3.3.6 Water biology, *Fish*).

3.3.6 Water biology

Limnologists traditionally recognize three different main habitats in lakes, the open water or pelagial zone, the littoral zone: bottom areas with photosynthesizing plants, and the profundal zone: the deeper parts of the bottom area which lack photosynthesising plants /*cf* Blomqvist and Brunberg, 1999, and references therein/. The upper part of the littoral zone is often further divided into the wind-sheltered "emergent macrophyte habitat" and the wind-exposed habitat, two sub-units with some common characteristics but with fundamentally different ecosystem structure. In deeper areas of many lakes, a more or less pronounced ecotone between the littoral and profundal zones, "the light-exposed soft-bottom zone", can also be identified. This zone is characterised by the presence of photosynthesising plants in the form of submersed macrophytes and a microflora dominated by cyanobacteria and algae. Thus, in total five major elements (in the following termed key habitats) can be identified in the ecosystem of a lake, all contributing to the total biodiversity of the system. Of these five key habitats, the pelagic zone can be found in all types of lakes since the presence of open water is part of the definition of lakes, delimiting them from wetlands which are covered by emergent vegetation. A more or less well-developed littoral zone is also a natural constituent of all lakes but those damaged by water-level regulations. The kind of upper littoral zone referred to as wind-exposed littoral is a habitat exclusively found in large lakes. The wind-sheltered habitat, on the other hand, is found both in small and large lakes although in the latter case usually restricted to sheltered bays and other calm areas along the shore-line. A well developed light-exposed soft-bottom zone is typically found in lakes with a relatively clear water in which light is allowed to penetrate to deeper parts of the bottom.

Since oligotrophic hardwater lakes in general, and those of the province of Uppsala in particular, are small, shallow, and have relatively clear water (*cf.* above) a typical oligotrophic hardwater lake can be characterised as having three distinguishable key habitats, the open water, the emergent macrophyte zone, and the light-exposed soft-bottom zone. The other key habitats, the profundal zone and the wind-exposed littoral zone are missing. Understanding of processes regulating the ecological functioning and biodiversity of oligotrophic hardwater lakes must thus be focused on the balance between the three key habitats. Therefore, in the following presentation, knowledge of each key habitat and its major constituents will be presented. Fish, which are present in all three habitats and are able to move between them, will be treated separately.

The pelagic zone

There are very few studies of the phytoplankton communities in lakes of the Forsmark area and those that have been performed mainly concern phytoplankton community biomass and composition. Kleiven /1991/ studied environmental conditions and phytoplankton in some *Chara* lakes in the province of Uppland and included three lakes in the

Forsmark area in that study: Lakes Hällefjärd, Käringsjön, and Strönningsvik. The lakes were sampled just once, in September 1984 (two lakes) and 1985 (Strönningsvik). Phytoplankton total biomasses were low, 113, 815, and 451 µg wet weight/l, respectively, indicating oligotrophic conditions in the systems /Rosén, 1981; Brettum, 1989/. In all three lakes, chrysophytes dominated the community and accounted for approximately 50 (42–62) % of the biomass. Green algae was the second most important group in two lakes, and Cryptophytes in the third lake. Dinoflagellates and diatoms made up most of the remaining biomass, while cyanobacteria were less important despite the time of the year. Kleiven (op. cit.) also reviewed the scarce literature on phytoplankton biomass and community composition in *Chara* lakes in general and concluded that low phytoplankton standing stock seems to be a common feature to most *Chara* lakes as does also the dominance of chrysophytes.

At least three theories have been put forward to explain the suggested low primary production and biomass of phytoplankton in *Chara* lakes /for references see Kleiven, 1991/.

The first theory states that since *Chara* lakes often are shallow and have clear water, which results in high light intensities in the open water, phytoplankton may be subject to photoinhibition and in more severe cases photooxidise and die. There seems to be little evidence supporting this hypothesis and in the case of the lakes in the Forsmark area, which all have a relatively brownish water (*cf.* water chemistry above) the theory seems rather unlikely to fit although measurements of light intensity are lacking.

A second theory put forward by many researchers is that different charophytes, particularly of the genus *Chara*, control the open water system by allelopathy. This theory was the subject of Kleiven's /1991/ studies from which she concluded that although allelopathic compounds certainly were produced by the charophytes, could be extracted into aqueous solution, and were inhibitory to the growth of a test organism, there was no release of these compounds from intact *Chara* grown in the laboratory. Thus, the theory about allelopathic control remains to be verified *in situ*.

The third, and most likely, theory is based on the scarcity of certain inorganic nutrients in the open water. It particularly concerns phosphorus and certain essential inorganic micronutrients, especially iron and manganese, which have been shown to form highly insoluble compounds and precipitate from the trophogenic zone /Wetzel, 1972/. Thus, the most likely reason for the low production of phytoplankton is shortage of available nutrients (especially P) in the open water. The low success of cyanobacteria, especially nitrogen-fixing species, in hardwater lakes has been suggested to be due to low levels of sodium /Ward and Wetzel, 1975/. However, in this context it is also interesting to note that concentrations of available iron in hardwater lakes are low. Hyenstrand /1999/ performed enclosure experiments in nearby Lake Erken (some 60 km from the Forsmark area) in which he added P, N, and Fe to experimental enclosures *in situ* and found that iron additions, together with P and N, significantly stimulated the growth of nitrogen-fixing cyanobacteria.

Data on bacterioplankton biomass and production from *Chara* lakes in the Forsmark area are totally lacking. From a theoretical point of view /*e.g.* Jansson *et al*, 1996; 1999/ it can be hypothesised that bacterioplankton production should be at least as important as phytoplankton production in mobilising carbon at the base of the pelagic food web in the *Chara* lakes of the Forsmark region. Even more likely, bacterioplankton production should probably exceed phytoplankton production. Two observations are supporting this theory: First of all, concentrations of allochtonous organic carbon in the lakes must be relatively high, as indicated by the measurements of water colour (*cf.* water chemistry above), which provides bacterioplankton with an external carbon source and makes them independent of carbon derived from phytoplankton. Secondly, concentrations of phosphorus are low (*cf.* water chemistry above), which is believed to favour bacterioplankton because of their small size which gives them a competitive advantage over larger organisms regarding rates of nutrient uptake.

Studies of the zooplankton community or of the nektonic invertebrates of the *Chara* lakes in the Forsmark region are, as far as we have found, lacking. However, from a theoretical standpoint, zooplankton biomasses should be low /McCauley and Kalff, 1981/, but exceed those of phytoplankton (in the range equal to or twice the biomass of phytoplankton). Furthermore, both the number of species and abundance of nektonic invertebrates are most likely low, due to the presence of fish in all the lakes (see below).

In conclusion, the pelagic zone of *Chara* lakes in the Forsmark area is characterised by low concentrations of inorganic nutrients, especially P, which results in that phytoplankton standing stock and production is also low. Crysophytes are generally the dominating phytoplankton group, while cyanobacteria have little success, which may be explained by lack of Fe. Bacterioplankton can be hypothesized to play an important role in the production process at the base of the food web, since they have access to organic carbon derived from external sources, but their production is also most likely low, limited by P rather than by organic carbon or nitrogen. As a result of the low primary production and supposed low bacterioplankton production, zooplankton biomasses and production are most likely low. Since the lakes contain fish, nektonic invertebrates most likely play an insignificant role in the pelagic ecosystem. Altogether, the pelagic zone of the *Chara* lakes is likely to be the least productive of the three key habitats in the system.

The emergent macrophyte zone

As discussed in the section about the riparian zone (above), there is a more or less continuous shift from a surrounding complex mire system with many different subunits to an often floating outer edge, which constitutes the sheltered littoral zone of the lake. Studies that deal with this floating mat littoral from a functional perspective are virtually lacking, at least in the limnology literature. Thus, the conclusions presented at the end of this section must be regarded as highly speculative.

The macroflora of the littoral zone (*i.e.* mostly the floating outer edge of the mire) of the lakes in the Forsmark area is characterised by two species: *Sphagnum* in the bottom layer and *Phragmites* in the field layer. Quantitative data on the biomass and production of these organisms are as far as known lacking from the Forsmark area. The floating character of the system is caused by the mire vascular plants having air-filled roots or rhizomes (aerenchyma). When such organisms colonise soft-bottom sediments they often loose their attachment to the bottom and become floating. The colonisation of the floating plants by *Sphagnum* is then a secondary process /Rydin *et al*, 1999/. *Sphagnum* mosses grow upwards through an apical meristem and decay below this meristem (Rydin *et al*, 1999). In dense stands, light has been measured to penetrate only 1–2 cm into the moss cover /Clymo and Hayward, 1982/.

Functionally, it is well known that *Sphagnum* and associated encroaching vegetation acts as a cation exchanger sieving off material from the inflowing water /*e.g.* Clymo, 1963; 1964/, releasing hydrogen ions in exchange for other cations. As the mire-littoral vegetation circumscribes the lake basin, the buffering capacity of the water is successively reduced. Thus, the development of a mire around the original basin most likely has profound influences on the entire lake ecosystem and *Sphagnum* must be considered as one of the key species in the lake. It is also noteworthy that, since the *Sphagnum* often completely encircles the lake, all water entering the system must at least be filtered once (during the passage towards the outlet), sometimes twice (during the inflow and outflow phases, respectively).

Finally, it is noteworthy that neither *Sphagnum* nor *Phragmites* is considered to be eaten by any aquatic herbivores, in the case of *Sphagnum* in fact not by any herbivore at all /*cf* Rydin *et al*, 1999/.

There has been no studies on any of these groups of organisms in the sheltered littoral zone of the lakes in the Forsmark area. Neither is it possible to speculate regarding their importance from studies in other parts of the world. Because of the closed character of the system, with dense stands of *Spahgnum* underlying *Phragmites*, it may be hypothesized that the microflora in the water is not especially well developed due to shading (*cf*. above). The habitat is rich in organic matter, which implicates that decomposers, both bacteria and fungi, may be very important producers of organic carbon for higher trophic levels.

As far as the authors know, there has been no studies of the benthic fauna in the sheltered, *Sphagnum*-dominated littoral in the lakes of the Forsmark area, and data about benthic fauna in such habitats are very scarce. The compact structure of the almost closed, often floating, sheltered littoral should from a theoretical point of view most likely result in that the access to the system for larger benthic fauna is minimal (*e.g.* insect larvae, crustaceans, and molluscs).

In conclusion, the sheltered, *Sphagnum*-dominated, littoral zone of the oligotrophic hardwater lakes in the Forsmark area is most likely a key to the functioning and ontogeny of the entire lake ecosystem. One of the most important characteristics is probably that *Sphagnum* and associated plants act as cation exchangers, sieving the water passing through the lake basin at least once (during the passage to the outlet). Within the littoral habitat and besides *Sphagnum* and other macrophytes, bacteria and fungi presumably are important mobilisers of carbon energy at the base of the food web. Whether or not this system is important in providing food for higher trophic levels via short food chains, is an intriguing question that merits further investigation (see also section on fish, below).

The light-exposed soft-bottom zone

The stoneworths, *Charales*, is the most well studied of all groups of organisms in the oligotrophic hardwater lakes /*e.g.* Iversen, 1929; Hasslow, 1931; Forsberg, 1965; Blindow, 1988, 1992a, 1992b; van der Berg, 1999/. These submersed macroalgae strongly dominate parts of the light-exposed soft-bottom sediments and the characteristic *Chara* meadows have given rise to the name "*Chara* lakes", originating from the lake classification system by Almqvist /1929/. Totally 33 species of *Charales* have been found in Sweden, many of which are rare and thus included in the Swedish "red list" of endangered species /Aronsson *et al*, 1995/. Most species live exclusively in freshwater, several are restricted to brackish water, while a few species, *e.g. Chara tomentosa* L and *C. aspera* Deth. ex Willdenow, are able to grow in both types of water. For example, the dominance of *Chara* in the coastal oligotrophic hardwater lakes begins long before the lake basins have become isolated from the sea, as evidenced by the fact that these organisms are dominant in wind-sheltered, basin-shaped, bays of the Baltic already when the water depth is around 2 meters /*e.g.* Forsberg, 1965/. Such shallow bays of the Baltic are also believed to be of very high importance for fish reproduction, and many freshwater species present in the Baltic estuaries *e.g.* pike (*Esox lucius*), bream (*Abramis brama*), ide (*Leuciscus idus*), and perch (*Perca fluviatilis*) seem to rely on these bays for their spawning (Blomqvist, pers. obs.). As the basins successively become isolated from the sea, the charophytes successively adapt to live in less and less saline water and often remain dominant. General studies of *Chara* in the lakes in the Forsmark area have been performed by *e.g.* Forsberg /1965/ and Gamfeldt /1998/, both investigating the distribution of species in relation to different environmental conditions. Both studies have confirmed the general features of the environments where *Charales* thrive, *i.e.* high alkalinity and low phosphorus concentrations in lake water. However, the oligotrophic hardwater lakes in the Forsmark area seem to differ from *Chara* lakes in general by a slightly higher water colour (*cf* Water chemistry).

Belonging to the algae, the *Charales* have a more simple cell organisation than other macrophytes /*cf* Häusler, 1982/. They attach to the substrate, mainly soft bottoms, by rizoids which also are used for uptake of nutrients from the surficial sediments. The rizoids are able to withstand high levels of H_2S within the sediments. The stoneworths reproduce both sexually and asexually. Some species are dioecious and are often found as only one sex in a lake, and some species are mostly found as sterile. Vegetative growth thus is important for colonisation and survival, and many species are of perennial character, surviving also under the ice during winter /Hutchinson, 1975/. Species of the *Charales*, especially the genus *Chara*, are often restricted to highly calcareous water. The capability to use HCO^{3-} in photosynthesis, as an alternative to CO_2, allow them to grow in waters with high pH. This process involves also the precipitation and incrustation of calcium carbonate, which functions as a stabilising component surrounding the cells, corresponding to cellulose in higher plants. The high alkalinity and calcium precipitation also co-precipitates phosphorus, thus reducing the availability of this plant nutrient in the lake water. *Charales* has also been reported to decompose at a slow rate, from which follows that the retention of nutrients incorporated in them may be long /Pereyra-Ramos, 1981/. The occurrence of *Chara* species mainly in nutrient poor environments have been subject to several studies. Forsberg /1964/ found that higher concentrations of phosphorus was toxic to *Chara globularis* in laboratory experiments. However, later investigations /Blindow, 1988; Simons *et al*, 1994/ have not been able to confirm that increasing phosphorus concentrations cause a decline of *Chara* species. Instead, reduced light availability has been put forward as the most limiting factor when nutrient levels and thereby growth of other organisms (*e.g.* phytoplankton) increase (van der Berg 1999, and references therein).

Earlier studies also reported the presence of *Charales* as effectively reducing mosquitos, as the aquatic larvae were inhibited by different species of *Chara*. However, no convincing evidence was found that the *Chara* itself was reducing the insects; the co-variation of *Chara* and absence of mosquitos in nature probably was due to other factors, *e.g.* the alkalinity of the lake water /Hutchinson, 1975/.

Kleiven /1991/, studying the *Chara* lakes of Uppland, also addressed the question of whether or not *Charales* perform some type of allelopathic control of organisms in their environment, but in this case of other photosynthesising plants in *Chara* lakes. As discussed above (The pelagic zone) she concluded that although toxic compounds were found in charophytes they did not seem to be released during the growth season of plants in the lakes in general. She furthermore concluded that statements of allelopathy of charophytes, based mainly on laboratory studies, probably lack ecological relevance.

Recent studies of the ecology of stoneworths has been focused on the shifts between different photosynthesising organisms due to changed nutrient status of lakes /Hargeby *et al*, 1994; Blindow *et al*, 1998; van der Berg, 1999/. Stoneworth meadows are considered advantageous in lake management due to their stabilising effect on the sediments, and their role as food for ducks. They also provide an excellent three-dimensional environment protecting other organisms from predation and providing substrate for scrapers that feed on the microbial biofim of the plants. For example, *Chara* meadows have been found to favour cladoceran abundance /Hutchinson, 1975/. Gastropods, gammarids, isopods and some chironomid species are also abundant in dense *Chara* meadows /van der Berg, 1999/. Hargeby *et al* /1994/ compared macroinvertebrate communities from stands of *Chara tomentosa* and *Potamogeton pectinatus* within the same lake, and found higher total biomass in the *Chara* stands. This was explained by the differencies in plant morphology and life cycle between the two macrophytes. *C. tomentosa* had more dense stands and more complex structure, offering a larger substrate area and better shelter against predation. In addition, *C. tomentosa* overwinter with green parts, thus offering a more permanent habitat, which benefits slow colonisers like snails and crustaceans.

There are few, if any quantitative studies of the benthic fauna of the illuminated soft-bottom sediments of the lakes in the Forsmark area. However, Lundqvist /1925/ noted high amounts of chironomid tubes from large species that were formed by calcareous material of the sediments in some oligotrophic hardwater lakes, indicating a benthic fauna characteristic of most lakes in the Swedish lowlands.

Lundqvist /1925/ also noted that the soft-bottom microflora was dominated by cyanobacteria and diatoms, and that these organisms "luxuriate" on such bottoms in *Chara* lakes. He also concluded that the primary production by microorganisms in such lakes is concentrated to the surface sediments while the production in the open water is comparatively very restricted. This explains how the oligotrophic hardwater lakes may deposit "cyanophycée gyttja" despite that cyanobacteria is a negligible fraction of the pelagic phytoplankton. Apart from this very old observation of an unusually rich soft-bottom microflora, studies of this part of the habitat are virtually lacking. Preliminary investigations in Lake Hällefjärd /Halvarsson, in prep./ indicate high biomasses of non-nitrogen-fixing cyanobacteria and diatoms in an unusually thick microbial mat (10–20 cm) on top of the surface sediments. However, the most striking visual observation on the sediment cores taken during 1999 was a red colour extending down to 10–20 cm depth, originating from highly abundant phototrophic sulphur bacteria, presumably of the genus *Chromatium*. These purple sulphur bacteria have been subject to many studies during this century and their metabolism is well known /for references to reviews, see *e.g.* Wetzel, 1983, p. 325/. They are usually found at the borderline between oxic and anoxic conditions and, since they have the ability to swim /Häusler, 1982/, they often form distinct maxima in the water column. Purple sulphur bacteria use hydrogen sulfide or thiosulphate and oxidises that to sulphate in the photosynthetic reduction of carbon dioxide. Their presence in the surface sediments of Lake Hällefjärd, especially during late winter, indicates poor oxygen conditions in this shallow lake ecosystem as a whole and a continuous supply of reduced sulphur compounds from the sediments. Their presence and patchy distribution throughout the sediments during summer indicate anoxic microclimates in which hydrogen sulphide is produced. This is in accordance with earlier reports of very high concentrations of free H_2S in close connection to the rizoids of *Chara* /Hutchinson, 1975/.

As far as the authors have found, there have been no studies of biomass and production of neither heterotrophic bacteria nor fungi in the light-exposed soft-bottom zone. From a theoretical point of view a high biomass and production of either or both of these groups may be expected. The reason is that the soft-bottom zone can be expected to have high amounts of organic material produced both inside this habitat (*e.g.* by the *Charales*) and in the surrounding mire-littoral system (*e.g.* by *Sphagnum*).

In conclusion, the hitherto performed studies of the light-exposed soft-bottom zone of oligotrophic hardwater lakes have mostly been focused on the wax and wane of the *Charales*. However, from the sparse literature, the light-exposed soft bottom zone appears to be another key to the functioning of oligotrophic hardwater lakes. The habitat is characterised by a high standing stock of submersed macrophytes, mostly *Charales*. Most of the production of microbiota (photosynthetic as well as non-photosynthetic) is most likely concentrated to this zone which includes a very diverse microbial community with components of cyanobacteria, algae, phototrophic sulphur bacteria, heterotrophic bacteria and probably also fungi. In comparison with other lakes, the oligotrophic hardwater lakes seem to have an unusually thick microbial mat on top of the soft sediments. This microbial mat most likely serves as a sieve for incoming groundwater, reducing the concentrations of biologically active substances to a minimum, which is another mechanism that may help to explain the poorly developed ecosystem of the open water habitat. However, there are virtually no studies of the soft-bottom ecosystem from a functional point of view.

Fish

Of the totally 11 lakes in the Forsmark area, 6 have been subject to standardised survey gill-net fishing /Nyberg, 1999/. Fish was caught in all lakes (Table 3-7). The average catch (catch per unit effort, CPUE) was 3.6 kg in terms of biomass and 36 individuals in terms of abundance. The average number of species found was 3.7. In total for all 6 lakes, 6 species were encountered; roach (*Rutilus rutilus*), Crucian carp (*Carassius carassius*), tench (*Tinca tinca*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), and pike (*Esox lucius*). Crucian carp dominated in terms of numbers and/or biomass in four of the lakes. In the two other lakes, roach and perch were dominant. The other three species were less abundant in the lakes in which they occurred, pike and ruffe being found in three lakes and tench in one lake. In one of the lakes in which Crucian carp dominated it was also the only fish caught.

From the abundance, biomass and species distribution of fishes it seems as if the lake material can be divided into two classes; one class in which Crucian carp evidently was the most important species (four of the lakes), and one class in which perch and roach dominated and in which the diversity of the fish community was higher (two of the lakes). Analysing the morphometry characteristics of the lakes in each class (Table 3-7), it seems as if the lakes in which Crucian carp dominated were smaller and more shallow, both in terms of average and maximum depth, than the lakes with a more diverse fish fauna.

In comparison with data from the entire fish survey /Nyberg, 1999/, including 81 lakes in the province of Uppsala, the oligotrophic hardwater lakes have a lower abundance of fish (36 compared to 81 individuals per gill net), almost exactly the same biomass of fish (3.6 kg in both cases) and a lower diversity in the fish community (3.7 compared to 5.8 species encountered). Furthermore, it seems as if Crucian carp was more abundant in the oligotrophic hardwater lakes than in lakes of the county in general. The reason is most likely that these generally small and shallow lakes have very poor oxygen conditions during winter, which favours Crucian carp and disfavours other fish species, predators as well as competitors to the Crucian carp. In the deeper lakes, where oxygen conditions are better, also other fish species are able to survive during winter, and this disfavours the Crucian carp. The Crucian carp is thus an excellent bioindicator of severe oxygen deficiency (*cf* Table 3-7). At a first stage of poor oxygen conditions, when other fish species are still present, it often develops dominance in terms of biomass (*i.e.* large individuals like in Lake Storfjärden, Hållen). Later, at more severe oxygen defiency, when other fishes disappear, the Crucian carp population is characterised by large numbers of small individuals (dwarfs). Migration of fish from the Baltic Sea, and use of some of these oligotrophic hardwater lakes for spawning and first summer growth of the juveniles, or for feeding on the Crucian carps, may complicate the picture.

Table 3-7. Data from standardised survey gillnet fishing in oligotrophic hardwater lakes of the Forsmark area. Pi=pike, Ro=roach, Pe=perch, Cr=Crucian carp, Ru=ruffe, Te=tench. Oxygen conditions: See Table 3-6 for explanation of the numbers.

Lake	Elevation	Lake area	Lake depth		Oxygen conditions	Fish species	No of species	CPUE		Av. weight of Cr
	m.a.s.l.	km^2	average	max				no of ind.	kg	kg
Storfjärden (Hållen)	6	0.11	0.6	1.1	4	Pi, Ro, Pe, Cr	4	18	2.2	0.39
Dalarna	0.6	0.07	0.5	1.3	4	Ro, Pe, Cr, Ru	4	35	7.8	0.35
Käringsjön	5	0.04	0.6	0.9	3	Cr	1	26	0.32	0.01
Västersjön (St Hållsjön)	4	0.19	1.9	3.2	–	Pi, Ro, Pe, Cr, Ru	5	76	3.4	0.76
Strönningsvik	6	0.08	1.0	1.7	2	Ro, Pe, Cr	3	14	3.9	0.32
Eckarfjärden	6	0.23	1.5	2.6	1	Pi, Ro, Pe, Ru, Te	5	47	3.9	
Själsjön	9	0.07			–	–	–	–	–	–
Degertrusket	10	0.07			–	–	–	–	–	–
Storfjärden (Slada)	0.4	0.03	1.2	2.2	4	–	–	–	–	–
Hällefjärd			–		–	–	–	–	–	–
Fiskarfjärden	0	0.61	0.7	2.0	4	–	–	–	–	–
Average	**4.70**	**0.15**	**1.0**	**1.9**	**3.1**		**3.7**	**36**	**3.6**	
Median	**5.50**	**0.08**	**0.9**	**1.9**	**4.0**		**4.0**	**31**	**3.7**	
N obs	**10**	**10**	**8**	**8**	**7**		**6**	**6**	**6**	
Max	**10**	**0.61**	**1.9**	**3.2**	**4**		**5**	**76**	**7.8**	
Min	**0**	**0.03**	**0.5**	**0.9**	**1**		**1**	**14**	**0.32**	

In conclusion, the oligotrophic hardwater lakes have a fish community less rich in individuals and number of species than the average lake of the county, while the biomass of fish is still high. Crucian carp is a very important fish in most of the oligotrophic hardwater lakes and particularly the small and shallow ones, indicating severe oxygen deficiency in the water during winter.

4 Discussion

4.1 Ontogeny of the oligotrophic hardwater lakes in the Forsmark area

The oligotrophic hardwater lakes in the Forsmark area can from at least two points of view be regarded as being of an ephemeral nature. First of all, like all lakes, they are successively being filled with material from the drainage area and material produced in the lake basin itself, the final stage being a wetland forest or a bog. Secondly, the oligotrophic hardwater stage is also of ephemeral nature. The reason for the latter is to be sought among two processes both involved in the ageing of the lake basin; one coupled to the fact that it is only the glacial till and postglacial clays – not the bedrock in the area – that contains large amounts of carbonates and associated cations, and the other coupled to the fact that the hydrological and climatic conditions in the area – as well as in large parts of the Boreal forest zone in general – promotes growth of *Sphagnum* and subsequent accumulation of organic material in the form of peat /*cf.* Rydin *et al*, 1999/.

Without taking into consideration the effects of formation of a mire around the lake, the characteristic hardwater character of the lakes in the Forsmark area would be of ephemeral nature. The reason is that the exceedingly high concentrations of bicarbonates and cations, principally calcium, typically found at an early stage after the isolation of the lake basin from the Baltic Sea originates from the carbonaceous glacial and post-glacial soils of the catchment basin /Ingmar and Moreborg, 1976/. As long as these soils were bottom sediments of the Baltic Sea, there was little if any weathering of the systems. When isolated from the Baltic Sea and as the groundwater level descended, weathering of the soils began and this gave rise to large amounts of dissolved substances in the water. However, the underlying bedrock is typically acidic and the storage of carbonates and base cations, being restricted to the soils, must be considered as a finite source of ions which can and will be depleted in a relatively short geological perspective. The most important factors regulating the duration of the hardwater-stage in such systems must be the thickness and composition of the soils in a particular catchment, the acidity of the rainwater and amount of precipitation in the area, and to some extent also the groundwater level in the particular catchment (since very little weathering will take place below the lowest groundwater level). Regardless of the duration of the hard-water stage, it is evident that the system will sooner or later reach a point when the precipitation of $CaCO_3$, in the lake water will no longer take place. At that point, there will neither be any co-precipitation of important plant micronutrients (*e.g.* P) or essential trace elements (*e.g.* Fe, Mn). Instead, these elements, and especially P, will contribute to the production of organisms in the system and there will be a rapid change towards eutrophic conditions /*cf.* also Wetzel, 1983, p. 736/. This change towards more eutrophic conditions will in turn lead to increases in amounts of sedimenting organic matter (*i.e.* increased infilling), increased decomposition rates at least until anoxic conditions are reached, and enhanced nutrient recycling. Thus, from the point of view of geology alone, an expected pathway for an oligotrophic hardwater lake in the Forsmark area would be towards a eutrophic lake and then further towards a *Phragmites*-dominated reed swamp, a fen, and finally to a forest /*e.g.* Wetzel, 1983, p. 741/. However, there seems to be very few, if any, lakes or previous lakes in the Forsmark and nearby areas that conform to this picture, except those heavily affected by man via drainage of land and/or subsequent use of the soils in the catchment for agricultural purposes /*cf.* also Brunberg and Blomqvist, 1998/.

A more likely ontogeny of the hardwater-lakes in the Forsmark area is that towards a reed swamp, a fen, and finally a bog ecosystem /*e.g.* Wetzel, 1983, p. 741/. This idea is supported by the fact that large parts of the two principal catchments in the Forsmark area (54/55 and 55, respectively) consist of mires today (8 and 17%, respectively; *cf.* Brunberg and Blomqvist 1998). It is also supported by the fact that the riparian zone of most existing oligotrophic hard-water lakes in the area to a great extent is dominated by mires (*cf.* above).

To fully understand the ontogeny of a hardwater lake into a mire and finally to a bog, it is necessary to start the analysis by looking at the origin of the major biological components of the systems, respectively, and at what stage they colonize the basin:

All lakes in the Forsmark area, as well as all other lakes below the highest shore-line of the Baltic Sea (and its previous lake and sea stages), have their origin as depressions in the bottom of these large aquatic systems. As the land-rise proceeds, these areas are successively transported upwards to become shallow bays along the coast (Figure 4-1). Somewhere along this initial part of the ontogeny, inflow of freshwater in the form of ground- or surface water from the epicontinental aquifere begins and the system is slowly changing from a brackish to a freshwater stage. In those coastal basins which later will become lakes, there is a "threshold" in the mouth to the main part of the coastal basin. This threshold allows settling fine material to accumulate in the deepest part of the basin. At this stage, when the depth of the water is lower than 2–3 meters, different *Charales* (*e.g. Chara tomentosa*) colonises the illuminated soft-bottom sediments kept in the basin by the threshold /*cf.* Forsberg, 1965/. Along the shore, *Phragmites* and other aquatic vascular plants also begin to colonise the system and a wind-sheltered littoral zone is developed. In both these habitats, the colonisation by plants reduce the bottom currents and this results in increased sedimentation of both course and fine detritus. Thus, two of the major components of the oligotrophic hardwater lakes – the *Chara* meadows and the *Phragmites* littoral – start to develop already when the basin is a brackish water system along the coast (Figure 4-1 A). Since the glacial till and postglacial marine and freshwater sediments in the Forsmark area are rich in carbonates and associated cations the acidic rainwater falling in the catchment will be neutralized and the water entering the bay from the catchment will thus be rich in dissolved substances and well buffered. The residence of this water in the bay will be highly fluctuating as the passage of major weather systems (*i.e.* high- and low-pressures) generates currents that pump coastal water in and out of the bay. As a result of these changes in origin and quality of the bay water, the pelagic ecosystem may sometimes contain large amounts of phytoplankton and sometimes be extremely clear. Thus, the importance of the pelagic zone in the production and metabolism of carbon in the bay may vary substantially. As the basin successively becomes isolated from the Baltic Sea, the influence of the brackish coastal water decreases and so does the salinity of the system. In recently isolated lake basins which lack major tributaries (which seems to be one prerequisite for an oligotrophic hardwater lake to be formed), two components of the hardwater lake ecosystem are already present. The inflowing groundwater, still very rich in carbonates and well buffered, now becomes the only source of water to the system. It is probably at this stage that precipitation of $CaCO_3$ and co-precipitation of P, Fe, and Mn becomes pronounced. The importance of the pelagic ecosystem in the lake thus diminishes due to lack of inorganic nutrients in the water, and an oligotrophic clearwater system, in which the major components are the illuminated soft-bottom zone and the *Phragmites*-dominated sheltered littoral zone, establishes (Figure 4-1 B). During the proceeding succession towards a more mature oligotrophic hardwater lake stage, *Sphagnum* mosses start to colonise the macrophytes of the sheltered littoral. This is the beginning to the formation of a mire around the lake. As the growth of *Sphagnum* in an outward direction proceeds and organic accumulation underneath these plants increases, a mire/floating-mat littoral zone is successively

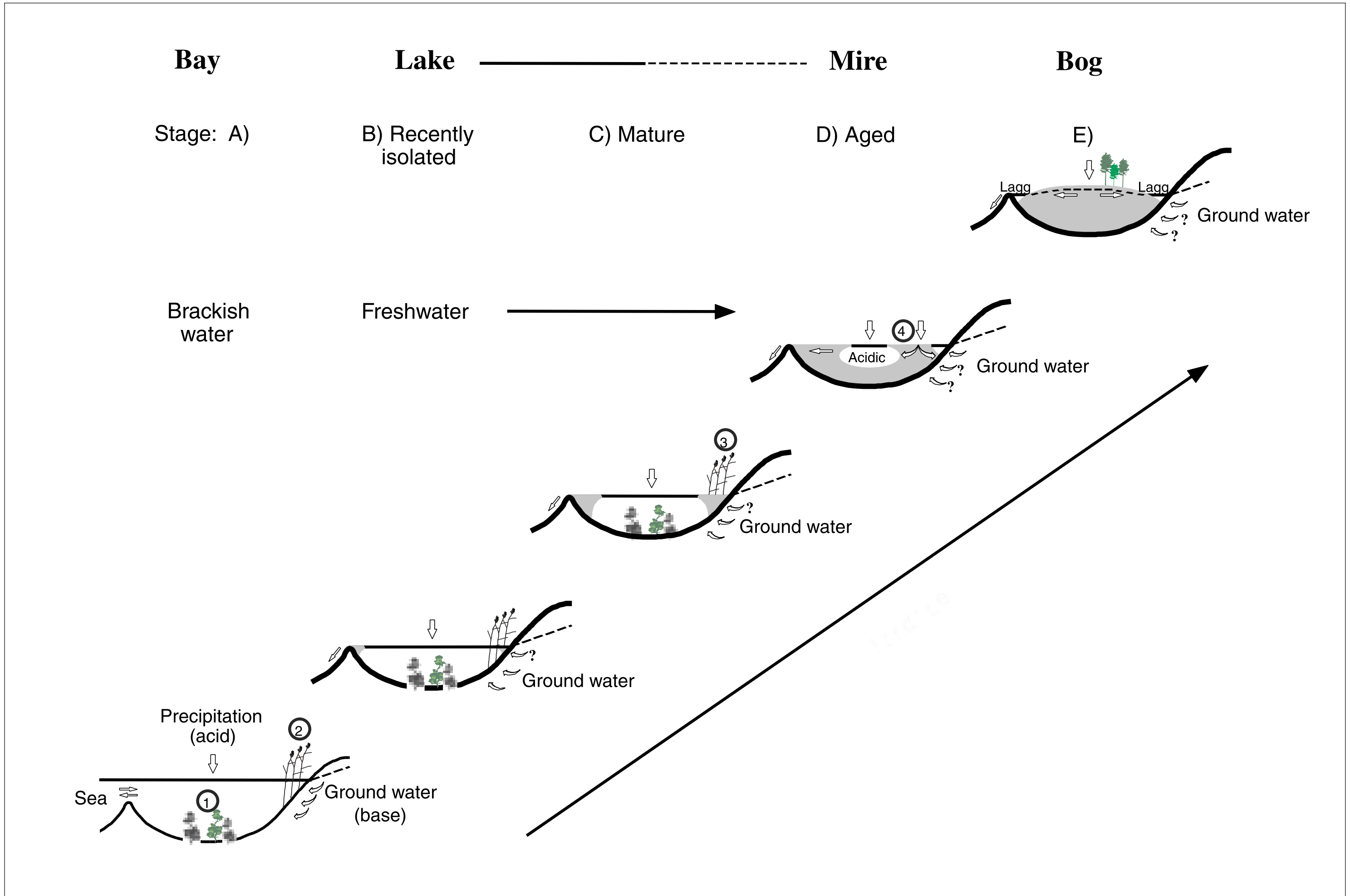

Figure 4-1 A-E. *Suggested ontogeny of the oligotrophic hardwater lakes in the Forsmark area. The numbers in the figure represent different major components of the ecosystem: 1 =* *Chara* meadow. *2 =* *Phragmites* littoral, 3 = mire/floating-mat littoral, 4 = *Sphagnum* littoral.

developed. The importance of this mire-littoral in altering the groundwater flow and/or chemistry of the inflowing water is virtually unknown, but two hypotheses, both including the importance of *Sphagnum*, may be formulated. A first hypothesis, "the sieve theory", is that due to the well-known function of *Sphagnum* as a cation exchanger, trading hydrogen ions from organic acids for base cations /*e.g.* Clymo, 1963; 1964; Rydin *et al*, 1999/, the part of the inflowing groundwater that passes through this zone will be efficiently sieved off from Ca and Mg, less well buffered due to neutralisation of the acids, and more brownish from organic compounds than the water which passed the littoral zone during the previous lake stage. An alternative hypothesis, "the dike theory", is that due to the formation of peat underneath the growing part of the *Sphagnum*-mire, a new hydrological system is created which is fuelled by rainwater and which creates a flow of water out of the system, preventing the calcareous groundwater from entering that habitat /*i.e.* the raised bog type of hydrological system, Moore and Bellamy, 1974; Rydin *et al*, 1999/. Most likely, both of these processes are important to the metabolism of the system. Thus, the invasion of the sheltered littoral by *Sphagnum* should, at least theoretically, have a profound effect on the functioning of the lake ecosystem (Figure 4-1 C), which still has two major key habitats both allocated to the bottom area. In a later stage of succession, the accumulation of organic detritus in the lake basin completely covers the previous illuminated soft-bottom area (Figure 4-1 D). At this stage, the *Sphagnum* littoral alone dominates the metabolism of the system, while the previous soft-bottom habitat has been lost through sedimentation of peat. The whole system; the mire-littoral as well as the open water, is now acidic /*cf*. Rydin *et al*, 1999/ due to one of the two hypothetical reasons presented above and accumulation of peat is accentuated. The final stage of this line of ontogeny, the raised bog ecosystem (Figure 4-1 E), most certainly represents an autonomous hydrological system which is almost exclusively fed by precipitation on the surface of the bog and which, through the capillary capacity of the *Sphagnum* necromass, is characterised by a raised groundwater surface in the bog and an outflow of water to the surrounding ecosystems. In this situation, material from the groundwater in the catchment area is transported through the surrounding lagg /Moore and Bellamy, 1974; Wetzel, 1983; Rydin *et al*, 1999/.

4.2 The oligotrophic hardwater lakes in the Forsmark area - a synthesis of the ecosystem functioning

From what has been said about ontogeny of the oligotrophic hardwater lakes towards a mire above, it is evident that the hydrology of the basin is a key to the understanding of the functioning and as far as we have found there are virtually no studies at all on the hydrological functioning of seepage lakes. It is also evident that the most complex and diverse stage in the ecosystem development is that of the mature, oligotrophic hardwater lake (Figure 4-1 C). In this stage, at the beginning of the formation of a mire around the basin, the functioning of the ecosystem as a trap for nutrients and particles from the drainage area is most likely maximal and may serve as a hypothetical model for how substances entering the system can be accumulated in different parts.

As discussed above, the existing hardwater lakes in the Forsmark area can be characterised by the presence of three main key habitats: the sheltered littoral zone, the light-exposed soft-bottom sediments, and the open water. In relatively mature systems, the two former habitats are well developed, and there is reason to believe that both these components may have great influence on the quality of the inflowing water before it reaches the pelagic zone. The open-water habitat, on the other hand, is most likely of little importance to the production and turnover of carbon and nutrients in the system in this as well as in all other stages of succession. The reason for the low importance of the pelagial is that the hardwater lakes typically have very limited drainage areas, in most cases lacking visible inlets. As a consequence, most of the inflow is "diffuse", *i.e.* in the form of groundwater, and this inflow passes through one or the other of the two bottom habitats. Thus, any water entering the pelagic zone of the lakes has been slowly prefiltered through a biological sieve, and thereby most likely cleared from biologically active substances.

A tentative model for the functioning of the mature hardwater lake based on current knowledge can then be formulated as follows (Figure 4-2):

All groundwater entering the mire-lake basin system contains large amounts of carbonates and associated cations. We assume this is the major source of inorganic nutrients for the producers (*i.e.* heterotrophic bacteria, fungi, cyanobacteria, algae and higher plants) at the basis of the food chain in the different key habitats.

Water entering the edge of the mire-sheltered littoral complex may be efficiently filtered by the *Sphagnum* and its necromass, which act as cation exchangers replacing Ca^{2+} and Mg^{2+} by H^+ and add coloured organic substances (humic compounds) to the water ("the sieve theory"). Alternatively, this water is diverged along the outer edge of the mire and does not enter the lake basin, or enters the lake basin after passage under the peat layer ("the dike theory"). This alternative either results in that the mire should be regarded as acting as a separate hydrological unit fed by rainwater, adding low amounts of acidic, heavily stained and soft water to the pelagic zone (the idea of a bog), i) which then is compensated for by more inflow of groundwater in the soft-botton area or ii) while the turnover time of the water in the lake basin gets longer because water is diverted around the system. Thus, from a basal production point of view, the *Sphagnum* littoral may either be regarded as a separate, autonomous, slowly growing unit receiving nutrients primarily from rainwater, or as an efficient sieve retaining a major share of the nutrients entering the mire-littoral part of the basin. The production system inside the *Sphagnum*-littoral seems likely to rely on carbon primarily produced by *Sphagnum* and macrophytes in the field layer above. It is most likely characterised by a very low primary production inside the habitat (*e.g.* by cyanobacteria and algae) because of the shading from the plants above. The large amounts of organic material produced in the habitat should favour production of bacteria and fungi but, this production is probably restricted because of anoxic conditions which favours accumulation of peat. It seems also likely that very little basal production is linked further on to higher trophic levels because a) very few, if any, animals are known to feed directly on *Sphagnum* and b) the closed three-dimensional character of the system probably limits the access for aquatic animals such as benthic macrofauna and fish. However, the system will certainly contribute with dissolved allochtonous organic matter to the pelagic zone. By reducing the available light, this organic material will also interfere with the primary production in both the pelagic and soft-bottom habitats.

Water entering the basin through the soft-bottom habitat will pass through an unusually thick microbial mat including autotrophic as well as heterotrophic components. These organisms will sieve off biologically active substances from the water and production will be high because of the relative fertility of the groundwater, which is rich in nutrients from the drainage area. High primary production because of favourable light conditions will lead to elevated pH-values during the growth season and this will result in precipitation of $CaCO_3$ and co-precipitation of important plant nutrients, especially P but also Fe and Mn, in the surface layer of the sediment. Growth of *Chara*, which deposits $CaCO_3$ inside the cells, also leads to trapping of nutrients in the system and subsequent deposition in the sediments as the charophytes die. These biologically mediated processes, rather than chemistry alone, are probably responsible for the oligotrophic hardwater character of the system. However, data to show this are virtually lacking. Very little is

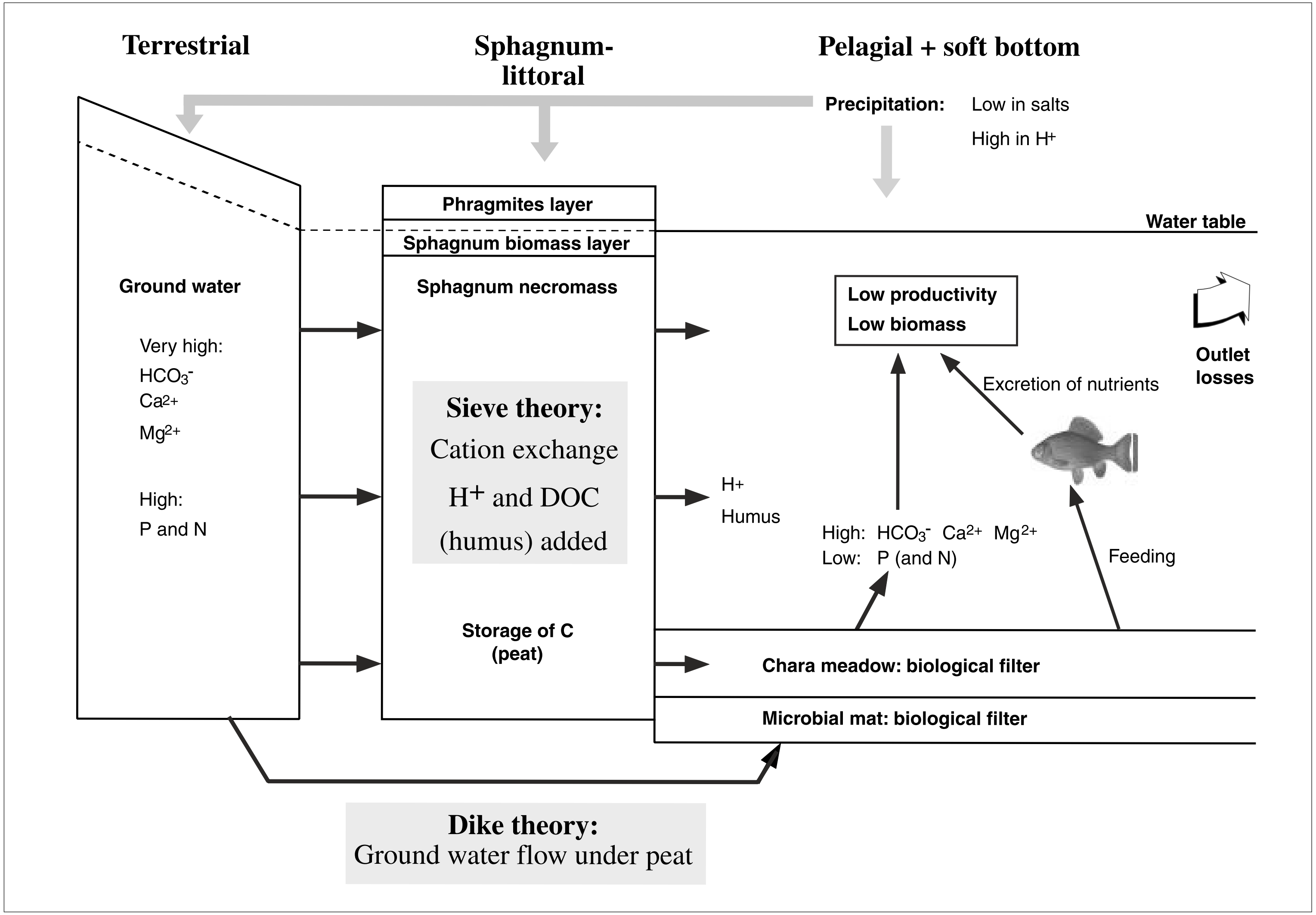

Figure 4-2. *A tentative model for the functioning of the mature oligotrophic hardwater lake.*

also known about the proportions between major basal producers in the system, although it may be hypothesised that primary producers (microflora) could be important compared to bacteria and fungi, because the inflowing water contains large amounts of inorganic nutrients and less organic material from the thin soils in the young terrestrial system on the infiltration area in the catchment (*i.e.* the area that contributes to the deep groundwater). An intriguing question is the role of photosynthetic sulphur bacteria in the systems but, apart from their effect on the sulphur cycle (*i.e.* production of SO_4), virtually nothing is known about their role in the habitat. The interactions within the light-exposed softbottom zone ecosystem are very poorly known. Benthic fauna is known to be rich on submersed macrophytes such as charophytes and the productive microbial mat should favour development of a rich fauna too, but this remains to be proved. It is known that Crucian carp is often dominant in the system and that biomass of fish is at least as high as in the average lake in the area /*i.e.* high compared to may other parts of Sweden, Nyberg, 1999/. The omnivorous Crucian carp may act as a pump for nutrients and organic matter between this habitat and the open water.

The low primary production in the pelagic zone is relatively well documented, and this low production is assumed to be the result of trapping of important nutrients in the other two habitats. An alternative hypothesis that needs to be tested is that: because of high availability of organic matter derived from the soft-bottom habitat and from the mire-littoral system, bacterioplankton outcompetes phytoplankton for avialable nutrients. An indication that bacterioplankton production could be substantial is that chrysophytes almost always dominate the phytoplankton community. These organisms avoid competition with bacterioplankton for inorganic nutrients by ingestion of bacteria /Isaksson, 1998; Isaksson *et al*, 1999/. Interactions with higher trophic levels are poorly investigated but evidently the Crucian carp, as well as other fishes if present, may be suggested to have a key role in the transport of substances between the habitats.

4.3 Need for further research

In this report, we have formulated a tentative model of the functioning and ontogeny of the oligotrophic hardwater lakes in the Forsmark area. We have identified some key pieces of this large jigsaw puzzle, which has compartments from many different disciplines, *e.g.* geology, geography, hydrology and several sub-disciplines of biology and ecology. However, it is evident that several pieces are still missing. We have tried to fill in the missing information with “educated guesses”, in some cases giving alternative theories of how the ecosystem is functioning during different stages of the ontogeny. Some areas where more research is urgently needed include:

– Studies on the hydrology of the system. This is essential for the basic understanding of the functioning of the lake as a biological system.

– Studies on the mire–floating littoral system, from the point of view of the functioning of *Sphagnum* as a sink for cations and as a source of acidity, organic matter and plant nutrients. This is badly needed to understand the role and relative importance of this unit. Studies on grazing on *Sphagnum* by animals and on utilisation of *Sphagnum* derivatives for bacterial and fungal production are also needed.

– Studies of the light-exposed soft bottom area regarding the role of primary producers vs photosynthetic sulphur bacteria, heterotrophic bacteria, and fungi. This is needed in order to understand the suggested key role of this habitat as a trap for material entering the lake basin. Studies on benthic fauna and fish are also important to understand the interactions in the community.

– The pelagic ecosystem requires less attention, but the relationship between primary production and bacterioplankton production needs to be examined and quantitative relationships between phyto- and zooplankton needs to be determined.

Altogether, the research directed towards the understanding of the hardwater lakes as a trap for contaminants should be focused on the hydrology of the basin and the basal production in the key (benthic) habitats.

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Glossary

allelopathic	påverkan från en levande växt på andra organismer i närmiljön
allochtonous organic carbon	organiskt kol som ej producerats i, utan tillförts, sjön
autotroph	primärproducent, har förmåga till fotosyntes
bream (*Abramis brama*)	braxen
Carex lasiocarpa	trådstarr
Carex rostrata	flaskstarr
Chara	ett släkte av kransalger
Chara aspera Deth. ex Willdenow	en art av kransalger
Chara globularis	en art av kransalger
Chara tomentosa L	sträfse (en art av kransalger)
Charales	kransalger
chrysophytes	guldalger (Chrysophyceae)
Cladocera	hinnkräftor
Crucian carp (*Carassius carassius*)	ruda
cryptophytes	rekylalger (Cryptophyceae)
cyanobacteria	cyanobakterier, “blågröna alger” (Cyanophyceae)
Dactylorhiza incarnata	ängsnycklar
Dactylorhiza traunsteineri	sumpnycklar
diatoms	kiselalger (Bacillariophyceae)
dinoflagellates	dinoflagellater (Dinophyceae)
Epipactis palustris	kärrknipprot
Eriophorum vaginatum	tuvull
Gammarids	sötvattensmärlor
Gastropods	snäckor
green algae	grönalger (Chlorophyceae)
heterotroph	konsument, utan förmåga till fotosyntes
ide (*Leuciscus idus*)	id
invertebrates	ryggradslösa djur
Isopods	gråsuggor

lake ontogeny	sjöars åldrande/successiva utveckling
Ledum palustre	skvattram
Liparis loeserii	gulyxne
macrophyte	större vattenväxt (ej mikroskopisk, ofta kärlväxt)
nectonic	simmande (organismer)
oligotrophic	näringsfattig
oligotrophic hardwater lakes	kalkoligotrofa sjöar
Parnassia palustris	slåtterblomma
perch (*Perca fluviatilis*)	abborre
Phragmites australis	bladvass
pike (*Esox lucius*)	gädda
Potamogeton pectinatus	borstnate
Primula farinosa	majviva
riparian zone	strandzon
Rhyncospora alba	vitag
roach (*Rutilus rutilus)*	mört
Rubus chamemorus	hjortron
ruffe (*Gymnocephalus cernua*)	gärs
Scheuchzeria palustris	kallgräs
Sphagnum	vitmossa
stoneworths	kransalger
tench (*Tinca tinca)*	sutare
trophogenic zone	det övre vattenskiktet i en sjö där fotosyntes försiggår