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Post-glacial, land rise-induced formation and development of lakes in the Forsmark area, central Sweden

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Abstract

This report describes 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 have also been identified.

Three main types of lake ecosystems could be identified:

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. In later stages of the lake ontogeny, *Sphagnum* becomes more and more dominant in the system, which successively turns acidic. The final stage is likely to be a raised bog ecosystem with an autonomous hydrological functioning.

The brownwater lakes are typically found within the main part of the River Forsmarksån and are characterised by a high flow-through of water from the upper parts of the drainage area, which are dominated by mires. Their lake water is highly stained by allochtonous organic carbon imported from the catchment area. Also in this lake type a *Sphagnum*-littoral successively develops, and in a mature lake three key habitats can be identified; i) the pelagic zone, most likely the dominant habitat in terms of production of organisms and in which bacterioplankton dominates the mobilisation of energy while phytoplankton are restricted by low light availability, ii) the emergent macrophyte zone, and iii) the profundal zone. Due to the characteristically short water renewal time, sedimentation processes are of relatively small importance and most of the carbon imported and produced is lost through the outlet. Production at higher trophic levels (*e.g.* benthic fauna and fish) within the brownwater lake type is very limited.

The deep eutrophic lakes are characterised by a limited drainage area, a large lake volume and a slow turnover time of the water. All five key habitats that optimally can be found in lakes are represented in this lake type: i) the pelagial, ii) the emergent macrophyte dominated littoral zone, iii) the wind-exposed littoral zone, iv) the light-exposed soft-bottom zone and, v) the profundal zone. Traditionally, the pelagial has been regarded as the dominant habitat in terms of mobilisation of carbon energy in the system. However, the productivity in the littoral habitats together may be equally important to the pelagial. As a result of the long turnover time of the water, most of the production of carbon is retained within the lake basin and sedimentation to the profundal zone is the main retention process.

Using information about the three main lake types, the characteristics and ontogeny of new lake basins isolated from the Baltic Sea due to the land rise are prognostisised. "Lake no 4" which will be isolated from the Baltic Sea about 4 900 years from now in the area of the low level repository SFR, will probably initially develop an oligotrophic hardwater ecosystem and later in the ontogeny switch to brownwater characteristics.

To evaluate the functioning of these ecosystems as a trap for contaminants, future research should focus on the hydrology of the lake basins and the basal production in the key habitats, *i.e.* the light-exposed soft bottoms of the oligotrophic hardwater lakes and the mire-littoral system of both lake types.

Sammanfattning

Denna rapport beskriver Uppsala läns sjöar, med speciell tonvikt på Forsmarksområdet. Det senare har definierats som avrinningsområdena 54/55 samt 55 i SMHI's indelningssystem. Syftet med studien som helhet är att identifiera de vanligaste sjötyperna i Forsmarksområdet och deras utveckling i samband med avsnörningsprocesser från Östersjön och naturligt åldrande. Materialet skall på sikt användas för att söka förutsäga om sjöekosystemen kan komma att fungera som en fälla för radionukleider som avges från befintligt och planerat lager för radioaktivt avfall i området och i så fall var i ekosystemet en sådan upplagring av radioaktivt material kan komma att ske. Tre huvudtyper av sjöar har identifierats och beskrivs utifrån befintlig kunskap om ekosystemens struktur och funktion:

Den kalkoligotrofa sjötypen är dominerande i Forsmarksområdet och även flera av de brunvattenssjöar som finns har genomgått ett kalkoligotroft stadium. De kalkoligotrofa sjöarna omgärdas vanligen av myr och saknar ofta synliga inlopp såväl som utlopp. Sjöarna är små och grunda, och vattenkemin kännetecknas av näringsfattiga förhållanden och hög alkalinitet. Tre nyckelbiotoper identifieras: 1) den fria vattenmassan (pelagialen), vilken kännetecknas av låg biologisk produktion; 2) den vindskyddade strandnära zonen (litoralen), dominerad av vitmossa och bladvass och som sannolikt är måttligt produktiv, samt 3) de solbelysta mjukbottnarna som kännetecknas av kransalger samt en ovanligt tjock ”mikrobiell matta” av bl a cyanobakterier och kiselalger. Denna senare biotop är med stor sannolikhet den mest produktiva i sjöekosystemet. I takt med att myrenlitoralen sluter sig ökar betydelsen av denna nyckelbiotop och sjön övergår till ett stadium karaktäriserat av betydligt surare vatten, starkt färgat av löst organiskt material. Slutstadiet i utvecklingen är sannolikt en tallmosse, med ett mer eller mindre separat hydrologiskt system baserat på regnvattentillförsel.

Brunvattensjöarna finns främst i Forsmarksåns avrinningsområde och karaktäriseras av en mycket hög vattenomsättning, varigenom starkt färgat, humusrikt vatten från de övre delarna av avrinningsområdet snabbt spolas genom systemet. Även här finns tre nyckelbiotoper: 1) pelagialen, som troligen har den högsta produktionen av de tre biotoperna, och där produktionen domineras av heterotrofa bakterier medan fytoplanktonproduktionen begränsas av dåliga ljusförhållanden i det bruna vattnet, 2) den vindskyddade litoralen, även här dominerad av vitmossa och bladvass, samt 3) profundala bottnar, där ljustillgången ej är tillräcklig för primärproduktion. På grund av den snabba vattenomsättningen är sedimentationen i sjöbäckenet liten; det mesta av produktionen transporteras vidare nedströms i systemet. En relativt liten andel av basproduktionen i sjön förs vidare till högre nivåer i systemet (ex bottenfauna och fisk).

De djupa eutrofa sjöarna slutligen, karaktäriseras av ett relativt litet tillrinningsområde och stor sjövolym, vilket tillsammans resulterar i lång omsättningstid. I dessa stora sjöar finns alla de fem möjliga nyckelbiotoperna representerade: 1) pelagial, 2) vindskyddad litoral, 3) vindexponerad litoral, 4) solbelysta mjukbottnar och 5) profundal. Vanligen betraktas pelagialen som den dominerande biotopen med avseende på produktion, men den sammanlagda produktionen i de tre litorala biotoperna kan troligen uppnå en motsvarande nivå. På grund av det långsamma vattenutbytet fungerar sjöarna som sedimentationsbassänger och mycket av det material som produceras kvarhålls i sjön.

Med hjälp av ovanstående information prognosticeras sjöekosystemens utveckling i de nya bäcken som i framtiden kommer att isoleras från Östersjön. Speciellt intressant i detta sammanhang är den blivande ”Sjö nr 4”, som är belägen i samma avrinningsområde som förvaret för lågaktivt avfall i Forsmark. Denna sjö, som kommer att isoleras om ca 4 900 år, kommer troligen initialt att genomgå ett kalkoligotroft stadium och därefter utvecklas till brunvattensjö.

För att kunna utvärdera de olika sjöekosystemens funktion som fälla eller genomflödeslokal för kontaminerande ämnen, är det av största vikt att fylla i de kunskapsluckor som finns framför allt rörande de kalkoligotrofa sjöarna. Framtida forskning bör fokuseras på funktionen hos och balansen mellan de olika nyckelbiotoperna, särskilt *Sphagnum*-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 terminating about 8 800 years ago (Ignatius *et al.* 1981).

The nuclear power plant at Forsmark is located in such a land rise area. A storage for low activity radioactive waste is also located in the area, 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. The report includes a general description of all lakes in Uppsala County, and of the lakes in the Forsmark area in particular. Three main types of lake ecosystems are identified. 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.

A glossary is included as an appendix to the report, translating limnological scientific terms as well as English and Latin names of organisms to Swedish.

2 Material and methods

2.1 Area description

Uppsala County has an area of 7 000 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 elevate 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 $\mathrm{l\ s^{-1}\ km^{-2}}$ (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 & Blomqvist (1998). A condensed version aimed at analysing the anthropogenic threats to the lakes and their catchments is presented in Brunberg & Blomqvist (manuscript). 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 of 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 1):

Table 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 & 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 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 & 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 2). 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 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 2). 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 was added to the classification system, the lakes of the Forsmark area would 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.

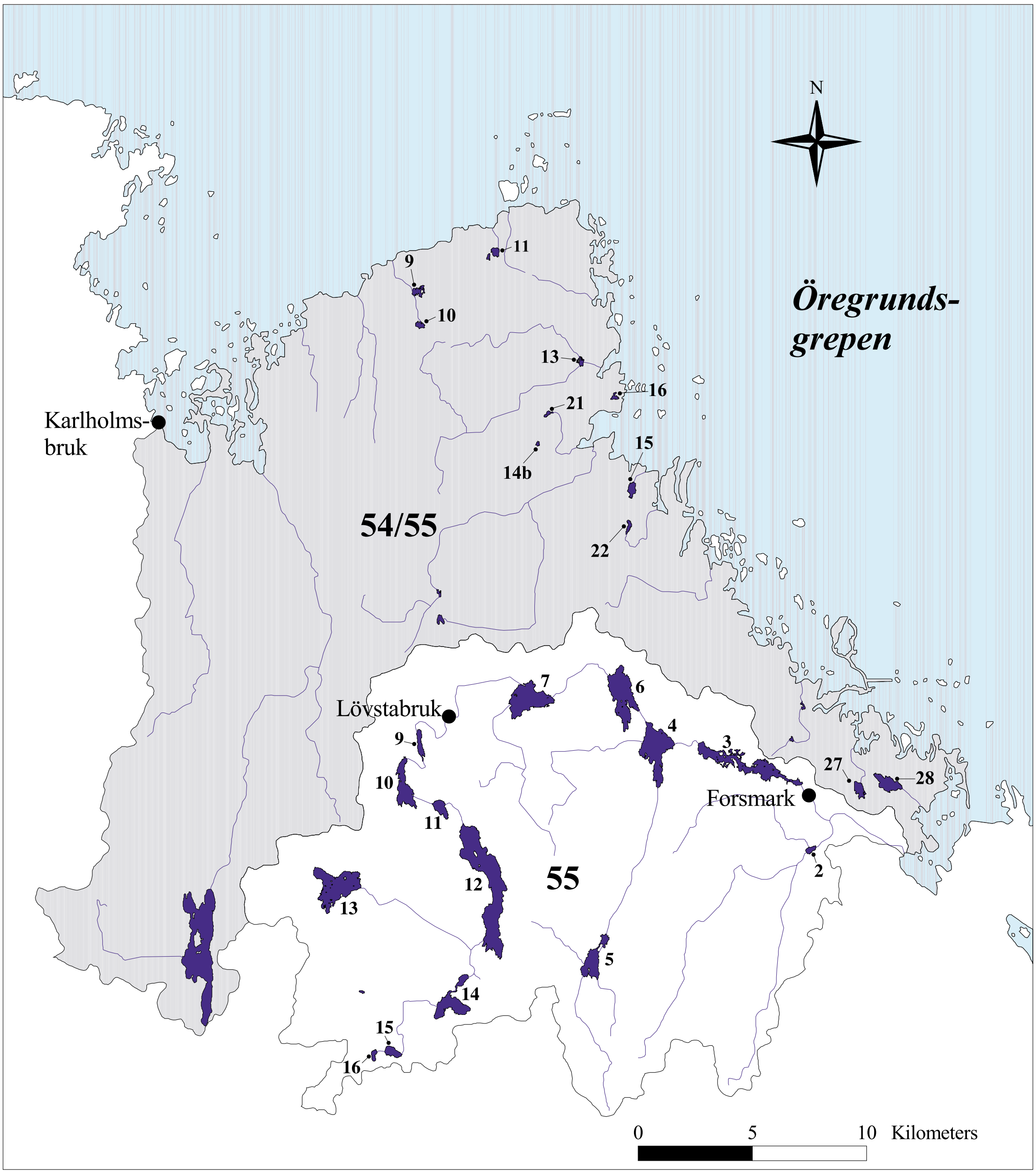

Figure 1. *Map showing the "Forsmark area" with the SMHI catchments no 54/55 "Between River Tämnarån and River Forsmarksån" and 55 "River Forsmarksån". Lakes indicated by numbers refer to the oligotrophic hardwater lakes (54/55) and the brownwater lakes (55), respectively, which are discussed in the text (cf Table 3 and 9). Permission: The National Land Survey of Sweden. Register number 507-96-1524.*

Table 2. 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 & 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.

	Catchment 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	0.02	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	6 954	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

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 (3.4).

The lakes with less calcareous material within the catchments were characterised as brownwater lakes. These lakes are, with two exceptions, found within the drainage area of River Forsmarksån. Situated mostly within the main river of this water system, the lakes are characterised by high water flow and thus very large influence from the upstream water system. The lakes within River Forsmarksån were chosen as the typical representatives of brownwater flow-through lakes and are described in detail in Chapter 3.5.

3.3 Other important lake types in the nearby coastal region not represented in the Forsmark area

Although oligotrophic hardwater lakes and brownwater lakes dominate the coastal region of the Forsmark area, the formation of other lake types due to the land rise during the coming millennia can not be excluded. Analysing the kind of lakes present in adjacent coastal regions, and particularly in the South, it is evident that also large, comparatively deep, and naturally highly eutrophic lakes must be considered as a type that may emerge. This kind of lakes are found in the area of Norrtälje, situated some 60 km from Forsmark. At least two lakes, Lake Erken and Lake Limmaren, have been well studied during the past decades and the former belongs to the most well studied lakes in the world. Data from these two lakes have been summarised and used to formulate a tentative model for the ecosystem functioning in this kind of lakes in general. Although the statistical basis for this model is weaker than for those of the hardwater and brownwater lakes, respectively, this is by far compensated for by the much larger amount of information about the conditions in the system.

3.4 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 that were described in Brunberg & 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 been included in the data set that we have used for description and characterisation of the lakes within the area (Table 3). Additional data from other oligotrophic hardwater lakes in the area have in some cases been used for parameters, which were not included in Brunberg & Blomqvist (1998). Several small lakes or bays of the Baltic Sea 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 & Blomqvist (1998). All these lakes have sub-catchments situated within catchment no 54/55 "Between River Tämnarån and River Forsmarksån" (Figure 1).

Table 3. Oligotrophic hardwater lakes in the Forsmark area. Catchment no according to SMHI (1985), no of sub-catchment according to Brunberg & Blomqvist (1998). Coordinates according to the Swedish National Grid System (RT 90, 2.5 gon W).

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 & Blomqvist (1998).

3.4.1 The drainage area

The drainage areas of the oligotrophic hardwater lakes in the Forsmark area are generally very small (Table 4). Only one catchment (Lake Storfjärden, Slada) has a large size (54.8 km^2); the other lakes have catchments with areas less than 5 km^2. The geology includes a 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 kambrosilurian area in the Bothnian Sea.

The vegetation of the catchments is dominated by forest and wetlands which for the median lake together cover 87% of the area (Table 4). The proportion of farmland is generally lower than in other catchments of Uppsala County, while the percentage of wetland is higher (*cf* Table 2). One exception from this is Lake Storfjärden, which has a relatively high proportion (20%) of farmland within the catchment. The oligotrophic hardwater lakes constitute 10% of the catchment area (median value), 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.

Table 4. Characteristics of the catchments of oligotrophic hardwater lakes in the Forsmark area.

Catchment	Area km^2	Forest %	Wetland %	Farmland %	Lakes %	Other land use %
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

3.4.2 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 & 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 compartments. 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 probably are 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.

3.4.3 Lake morphometry

Chara lakes are in general very shallow. The oligotrophic hardwater lakes in the Forsmark area have a depth of 0.9 meter (median value, Table 5), while the corresponding average depth for all lakes in the county is 1.5 meters (Table 2). 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 a wider perspective.

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 5). 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.

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.

Table 5. Lake morphometry for oligotrophic hardwater lakes in the Forsmark area.

Lake	Area km^2	Average depth m	Maximum depth m	Volume Mm^3	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

3.4.4 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, while Lake Vikasjön since long time ago have passed the oligotrophic 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 Sea (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 4 000–5 000 years ago. Sedimentation rates, estimated from unpublished data (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 is 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.

3.4.5 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 6). 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 ground water 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 were 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 & Blomqvist (1998), all show the typical hard-water lake chemistry (Table 7), 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). Most of 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 1999). This is similar to the vast majority of the lakes in Uppsala County.

Table 6. 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

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. As a median, 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.

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).

Table 7. Water chemistry classification for oligotrophic hardwater lakes in the Forsmark area. Data from Brunberg & 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=≤0.02	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

3.4.6 Water biology

Limnologists traditionally recognise three different main habitats in lakes, the open water or pelagial zone, the littoral zone: bottom areas with photosynthesising plants, and the profundal zone: the deeper parts of the bottom area which lack photosynthesising plants (*cf* Blomqvist & 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 shoreline. A well developed light-exposed soft-bottom zone is typically found in lakes with 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 & 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 & 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 (*cf* Fish 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 hypothesised 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 fish are present in the lakes, 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 & 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 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 have 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 *Sphagnum* underlying *Phragmites*, it may be hypothesised 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 mobilises 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 (*cf* 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.* 1996). 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 Sea already when the water depth is around 2 meters (*e.g.* Forsberg 1965). Such shallow bays of the Baltic Sea 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 the 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 rhizoid 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 were 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 mosquitoes, 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 mosquitoes 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* excreted some type of allelopathic control of organisms in their environment, but in this case of other photosynthesising plants in *Chara* lakes. As discussed above (*cf* 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 biofilm 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 differences 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 cyanobacteria and diatoms dominated the soft-bottom microflora, 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 rhizoid 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 inflowing groundwater, reducing the concentrations of biologically active substances of the lake water 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 8). 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 8), 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 8). 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.

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.

Table 8. Data from standardised survey gillnet fishing in oligotrophic hardwater lakes of the Forsmark area. Oxygen conditions: See Table 7 for explanations of the numbers. Pi=pike, Ro=roach, Pe=perch, Cr=Crucian carp, Ru=ruffe, Te=tench.

Lake	Elevation m.a.s.l.	Lake area km²	Lake depth average	max	Oxygen conditions	Fish species	No of species	CPUE no of ind.	kg	Av. weight of Cr, 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 (Stora 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	

3.4.7 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 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 & Moreborg 1976). As long as these soils were bottom sediments of the 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 granites and gneisses and the storage of carbonates and base cations, being restricted to the soils, must be considered as a finite source of ions which 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 & 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 & 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 colonise the basin:

All lakes in the Forsmark area, as well as all other lakes below the highest shoreline 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 2). Somewhere along this initial part of the ontogeny, inflow of freshwater in the form of ground- or surface water from the epicontinental aquifer 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 reduces the bottom currents resulting 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 2A). Since the glacial till and postglacial marine and

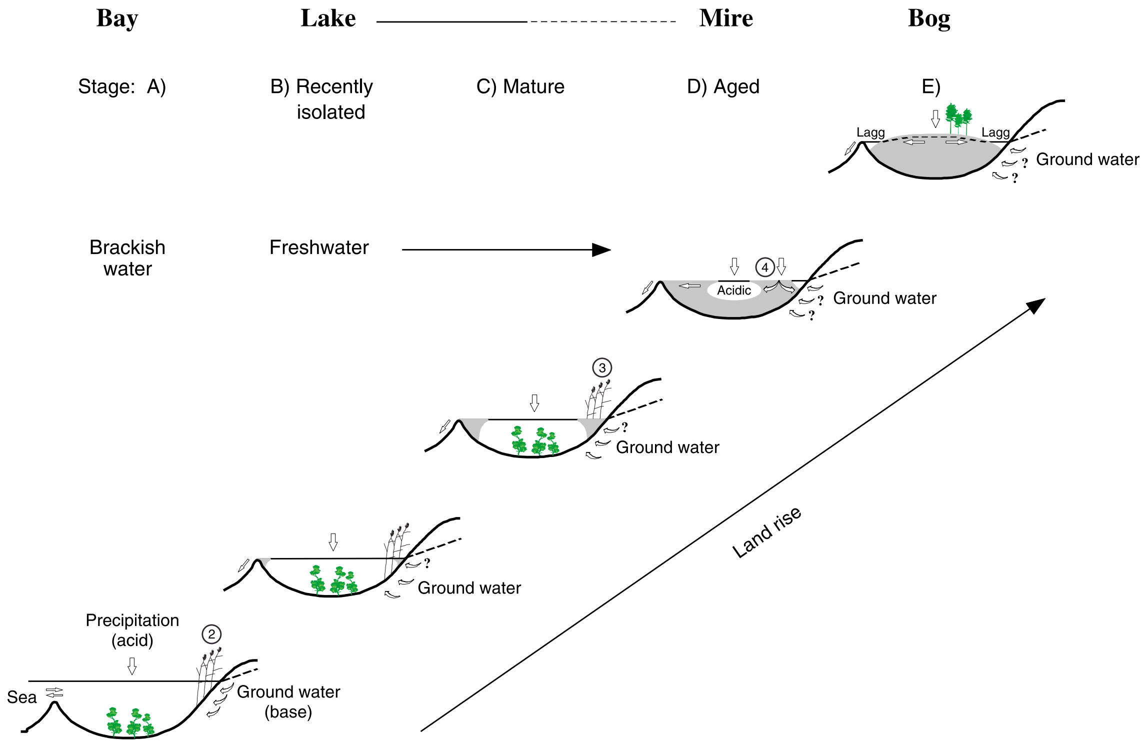

Figure 2 A-E. *Suggested ontogeny of the oligotrophic hardwater lakes in the Forsmark area. The numbers in the figure represent different major components of the ecosystem: 1 = Chara meadow, 2 = Phragmites littoral, 3 = mire/floating-mat littoral, 4 = Sphagnum littoral.*

freshwater sediments in the Forsmark area are rich in carbonates and associated cations the acidic rainwater falling in the catchment will be neutralised 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), the inflowing groundwater, still very rich in carbonates and well buffered, 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 2B). 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 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 fueled 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 & 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 2C), 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 2D). 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 2E), 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 & Bellamy 1974; Wetzel 1983; Rydin *et al.* 1999).

3.4.8 The oligotrophic hardwater lakes in the Forsmark area –a synthesis of the ecosystem functioning

From what has been said above about the 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 2C). 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 3):

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 web 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”). The latter “dike theory” may result 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), which is compensated for by more inflow of groundwater in the soft-bottom area; alternatively 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 in the microbial mat 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 also known about the proportions between major basal producers in

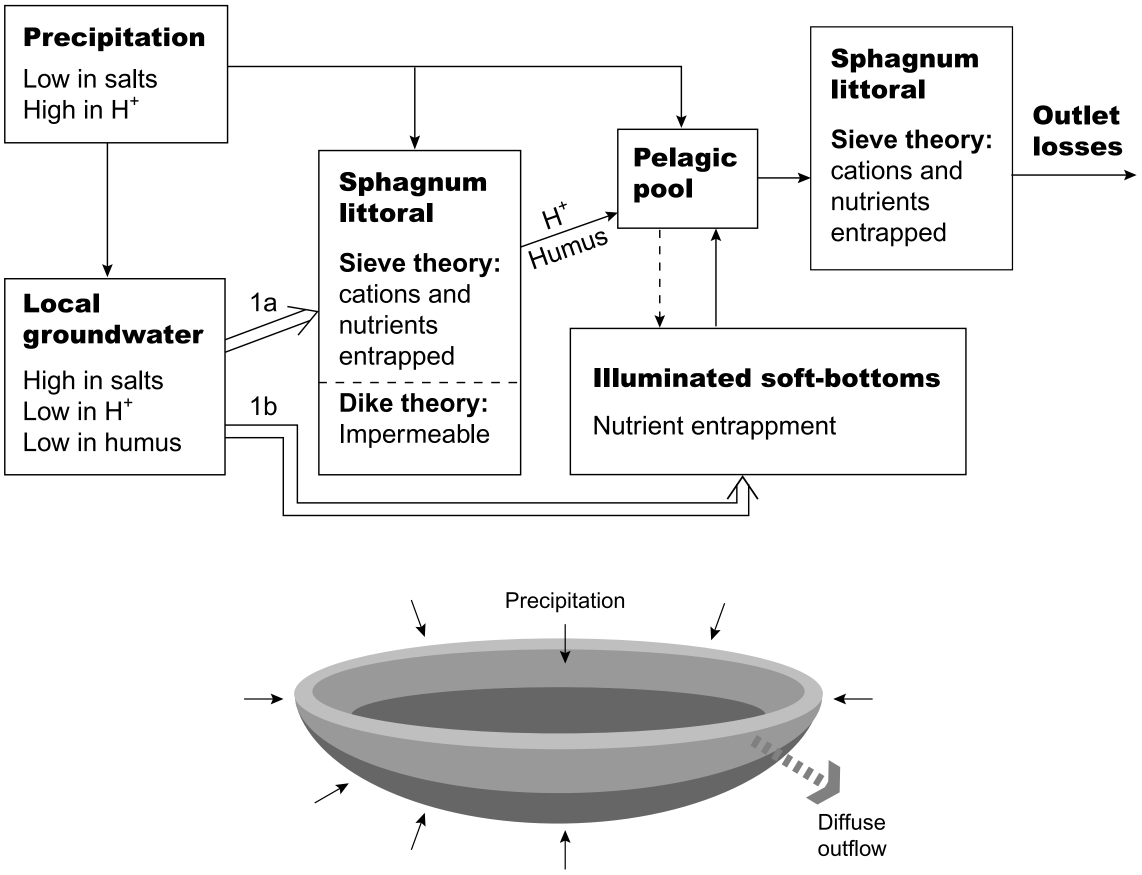

Figure 3. A tentative model for the functioning of the mature oligotrophic hardwater lake.

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 ecosystem on the infiltration areas of 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 available 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.

3.5 Description and characterisation of the brownwater lakes

Brownwater lakes are characteristic compartments of the boreal forest zone. The colour of the water originates from large amounts of dissolved organic material in the form of humus which are transported from the soils of the drainage area to lakes and streams, and these compounds have a substantial influence on the ecosystem functioning.

Most of the brownwater lakes within the Forsmark area form a long chain in the main river, Forsmarksån (Catchment no 55, Figure 1). The exceptions are Lake Fälaren (55:13), the outlet of which forms a branch in the uppermost part of the system, and two larger tributaries, from Lake Fågelfjärden (55:2) and Lake Älgsjön (55:5) respectively, that enters the main river in the lower parts of the catchment. In the following description, information regarding all lakes of the River Forsmarksån larger than 3 hectares (Table 9) is included. Data of the totally 14 lake catchments are referred to by the lake name and/or by the numbers of the catchments as given by SMHI (1985) and sub-catchments as given by Brunberg & Blomqvist (1998).

Table 9. Brownwater flow-through lakes in the Forsmark area. Catchment according to SMHI (1985), no of sub-catchment according to Brunberg & Blomqvist (1998). Coordinates according to the Swedish National Grid System (RT 90, 2.5 gon W).

Catchment	Sub-catchment	Lake name	Coordinates for outlet x, y	Elevation above sea level, m
55	2	Fågelfjärden	669445, 163016	4
55	3	Bruksdammen	669718, 162946	12.4
55	4	Södra Åsjön	669896, 162395	12.4
55	5	Älgsjön	669066, 162096	22.7
55	6	Norra Åsjön	670047, 162237	12.4
55	7	Skälsjön	670108, 161862	13.3
55	9	Ensjön	669972, 161263	28
55	10	Åkerbysjön	669828, 161229	28.6
55	11	Lissvass	669635, 161328	28.6
55	12	Finnsjön	669564, 161462	28.6
55	13	Fälaren	669267, 161021	32
55	14	Vikasjön-Själsjön	668882, 161498	28.6
55	15	Stora Agnsjön	668545, 161201	30.1
55	16	Lilla Agnsjön	668551, 161100	32

3.5.1 The drainage area

By median size (Table 10), the drainage areas of the lakes in River Forsmarksån are much larger than those of the lakes in Uppsala county in general (*cf* Table 2). However, there is a considerable variation in size among the lake sub-catchments. This is due to the fact that all lakes but Lakes Fälaren, Älgsjön and, Fågelfjärden form a chain within the main river, thus successively adding the lakes together in an increasing catchment.

The geology in the area includes a bedrock dominated by granites and gneisses, covered by glacial till and in some lower parts also by postglacial clay. As in most parts of Uppsala County, the vegetation is dominated by forest, which covers 64% (median value) of the area (Table 10). The most striking difference in the vegetation of this area, compared to the surrounding parts of Uppsala County, is the large contribution of wetland (median 26%). The upper parts of the River Forsmarksån catchment include a very large mire complex, Florarna, which is unique for this part of Sweden and considered to be of great value for nature conservation purposes (Ingmar 1953, Gustafsson & Löfroth 1986, Länsstyrelsen i Uppsala län 1987). The proportion of farmland is generally lower than in other parts of Uppsala County. The difference in elevation of land naturally divides the River Forsmarksån into two parts; one above and one below the 13 meter high waterfalls at Lövstabruk, respectively (Table 9). The upstream lakes are situated on a level of 28 m or more above the sea level. The chain of Lakes Ensjön-Åkerbysjön-Lissvass-Finnsjön-Skälsjön-Vikasjön is, from a geological and topographical point of view, compartments of one former large lake, *i.e.* the remnants of the ancient lake which initially was formed when the area was isolated from the sea (Jonsson 1973). The natural falls of the river at Lövstabruk has been used by man during centuries, providing energy for the iron workshops which were located there, and the upstream water system has been regulated (amplitude ca 1 m) for this and other purposes. Two lakes, which originally belonged to the River Fyrisån water system west of River Forsmarksån, Lakes Lilla and Stora Agnsjön, have been transferred via ditching to River Forsmarksån. This man-made alteration of the hydrology was performed in order to

Table 10. Characteristics of the catchments of brownwater flow-through lakes in the Forsmark area.

Catchment	Area km²	Forest %	Wetland %	Farmland %	Lakes %	Other land use %
55:2 Fågelfjärden	65.7	74	6	20	0	0
55:3 Bruksdammen	285	67	21	6	6	0
55:4 Södra Åsjön	268	68	20	6	6	0
55:5 Älgsjön	31.6	78	5	14	3	0
55:6 Norra Åsjön	198	64	25	4	7	0
55:7 Skälsjön	181	65	25	4	6	0
55:9 Ensjön	128	59	32	2	7	0
55:10 Åkerbysjön	119	58	32	2	8	0
55:11 Lissvass	107	57	33	2	8	0
55:12 Finnsjön	104	57	33	2	8	0
55:13 Fälaren	21.0	59	31	0	10	0
55:14 Vikasjön-Skälsjön	45.3	50	46	1	3	0
55:15 Stora Agnsjön	6.0	69	26	0	5	0
55:16 Lilla Agnsjön	4.8	73	25	0	2	0
Average	111.7	64.1	25.7	4.5	5.6	0
Median	105.5	64.5	25.5	2.0	6.0	0
Max	285	78	46	20	10	0
Min	4.8	50	5	0	0	0
N obs	14	14	14	14	14	14

increase the water flow and the storage capacity of the system. The regulations of the water levels in the upper parts of River Forsmarksån have now ceased, and the iron works at Lövstabruk have been closed down. However, the natural thresholds of the lakes were destroyed during the industry era, and the water level of the five nearest lakes upstream Lövstabruk is nowadays held by remnants of a dam construction (Pierreslutan) at the outlet of Lake Ensjön.

3.5.2 The riparian zone

The upper parts of River Forsmarksån, situated upstream of Lövstabruk, drain a wetland area of unusual size in this region. Within the area different forms of peatland form a mosaic pattern of *e.g.* swamp forest, bogs and rich or moderately rich fens. Thus, the riparian zones of the lakes in this area are to a large extent peatland, often in the form of mires, which are frequently flooded at high water flows. *Phragmites australis* (common reed) is often a dominating compartment of the flora along the lake shores, especially around the in- and outlet streams, sometimes with a transition within the riparian zone to a fen with *Equisetum* (horsetail) and various *Carex* (sedge) species.

In contrast to the situation in the smaller oligotrophic hardwater lakes described in Chapter 3.4, the outer edge of the mire surrounding the brownwater lakes of Florarna seldom forms a floating mat. The characteristic floating-mat littoral with *Sphagnum* colonising the aerenchyma of higher plants is formed only in the smallest lakes, while in the larger lakes emergent aquatic plants, mostly *Phragmites*, grow in the sediments and form a border between the mire and the open water. The reason to this difference is most likely that in the large lakes, the outer edge of the mire is frequently disturbed by waves, which affect the plants both physically and chemically; the latter by spraying ion-rich water onto them which they have problems to withstand (Ingmar pers. com.). Nevertheless, it is evident that growth of the mire is one reason for the successive closure of the lake basins in the area, which are all partly surrounded by mire, and are what is left of the large ancient lake which has closed due to the growth of the mire.

The pronounced dominance of *Phragmites* around large parts of the shore of all the lakes in the chain Finnsjön-Lissvass-Åkerbysjön-Ensjön, however, is probably the result of the regulation of the water level which took place between 1600 and 1954 (Ingmar pers. com.). Also the riparian zones of the lakes downstream Lövstabruk have been affected by water-level regulations in a similar manner, the dam being located to Forsmarks Bruk. At high water levels in the regulated systems, the helophytes were drowned or became light limited and died off. Also the mire-littoral was flooded with ion-rich water which resulted in that the *Sphagnum*-biomass died. Aberration of the underlying peat then followed down to a depth where the wave-action no longer affected the system. The resulting "plain" was then colonised by *Phragmites* forming an atypical and man-made littoral zone around the lakes.

The normal situation, however, is most likely to be that the lakes should be surrounded by mires with an outer border of less dense *Phragmites* and without a floating-mat outer edge. Later, as the size of the lakes is reduced by the growth of the mire, a floating-mat littoral may develop. Hence, with the exception of that the large lakes at the beginning of their ontogeny develop differently compared to small lakes, the conclusions regarding the potential importance of the surrounding mire to the lake ecosystem metabolism outlined for the oligotrophic hardwater lakes in Chapter 3.4, also seem valid for the brownwater lakes.

3.5.3 Lake morphometry

The median surface area of the brownwater lakes of the River Forsmarksån (Table 11), is four times larger than that of the lakes in Uppsala county in general (0.25 km^2), and much larger than that of the oligotrophic hardwater lakes in the adjacent area (0.07 km^2). By comparison of medians, the average depth is identical to that of the lakes of the county in general (1.5 m) but larger than that of the oligotrophic hardwater lakes (0.9 m). Hence, the brownwater lakes also hold a larger volume of water than both the median lake of the county and the adjacent oligotrophic hardwater lakes. However, despite their greater volume, and because of their much larger drainage areas, the brownwater lakes of River Forsmarksån have a shorter median water renewal time (31 days) than the other two categories of lakes (91 days for all lakes in the county and 240 days for the oligotrophic hardwater lakes). The short water renewal time reflects the fact that the main river passes through most of the lakes.

The human impact on the lakes in terms of lowering of the water level is, by comparison of median values, smaller than that on other lakes in the county (median 0.5 m lowering). Instead, the water levels have in several cases been elevated by construction of dams during the period when the lakes were utilised as water reservoirs. However, the natural thresholds were in many cases destroyed when the dams were constructed, and as the dams have been removed or destroyed the lakes have been lowered. As a consequence, man-made dam constructions are needed to protect and preserve the large wetland system of Florarna. The original water levels of the lakes have to be assessed from very old sources of documentation, before the industry started to develop in the 17th century. When the water regulation stopped in the 1950'ies, negotiations were

Table 11. Lake morphometry of brownwater flow-through lakes in the Forsmark area.

Lake	Area, km^2	Average depth, m	Maximum depth, m	Volume, Mm^3	Water renewal time, days	Lowering of water level, m
Fågelfjärden	0.12	–	–	–	–	0.6
Bruksdammen	2.06	–	–	–	–	–
Södra Åsjön	1.98	2.3	3.8	4.554	28	–
Älgsjön	1.17	0.6	1.2	0.702	38	1.0
Norra Åsjön	1.77	2.1	4.0	3.717	31	–
Skälsjön	1.83	0.8	1.5	1.464	14	0.5
Ensjön	0.34	0.5	1.4	0.170	2	0.3
Åkerbysjön	1.11	0.9	2.2	0.999	14	0.3
Lissvass	0.35	0.7	1.2	0.245	3	0.3
Finnsjön	4.09	1.9	3.4	7.771	123	0.3
Fälaren	2.05	1.5	2.6	3.075	249	0.7
Vikasjön-Skälsjön	1.04	–	3.3	–	–	0.3
Stora Agnsjön	0.24	2.8	3.7	0.672	190	0
Lilla Agnsjön	0.09	2.1	2.7	0.189	65	0
Average	1.30	1.5	2.6	2.142	69	0.39
Median	1.14	1.5	2.7	0.999	31	0.30
Max	4.09	2.8	4.0	7.771	249	1.0
Min	0.09	0.5	1.2	0.170	2	0
N obs	14	11	12	11	11	11

performed during several decades between representatives from different groups of interest in the area (mainly nature conservation vs forestry) regarding the appropriate water levels to keep or restore in the upper parts of the river system. An important dam for that purpose is now being constructed at the outlet of Lake Ensjön.

3.5.4 Sediment characteristics

There are few investigations made on surface sediments from the lakes in the River Forsmarksån. Results from occasional investigations by limnology students from Uppsala University (Appelberg *et al.* 1976, Conover *et al.* 1976, Danielsson *et al.* 1976, King *et al.* 1976) show that the lake sediments have a brown colour and are organogenic, with high C/N and C/P quotients. This indicates a characteristic "dy" sediment with large contribution of allochtonous material (*i.e.* material that has not been produced within the lake). The lakes are situated in an area with strong influence from wetlands producing organic compounds (humus) that are transported to the lakes. Some of the lakes have substantial autochtonous production of higher vegetation (*e.g. Phragmites*) within the lake, which also contributes with organic matter to the sediments. One of the lakes (Lake Skälsjön) has been subject to pollution by nutrients from municipal sewage from the village of Lövstabruk. Due to the construction of a modern wastewater treatment plant, the influence of the sewage water is today very low. Furthermore, due to the high flow of water through the system pollutants did not to any greater extent accumulate in the recipient.

Paleoecological studies of the sediments of Lake Vikasjön show that this lake passed through an oligotrophic hardwater stage after the isolation from the Baltic Sea, during which "cyanophycée-gyttja" was settled. This corresponds to the present situation in the oligotrophic hardwater lakes along the coast (*cf* 3.4). This stage lasted for about 1 000 years. Later the sediment switched to dy character, due to the influence of humic compounds from the surrounding mires which were developed in the drainage area. Most of the lakes in the upper parts of River Forsmarksån have the same or at least a similar historical record in the sediments. In contrast, the lakes which are situated below the 13 m falls at Lövstabruk have not passed any oligotrophic hardwater stage. Instead they developed to brownwater lakes more or less directly after the isolation, depositing dy sediments at the lake bottoms. Sedimentation rates, estimated from unpublished data from Lake Vikasjön (T Ingmar pers. com.) roughly corresponds to 1–1.5 mm of sediment per year during the oligotrophic hardwater stage and 1 mm per year during the following brownwater stage.

3.5.5 Water chemistry

Due to the successive flow of water from lake to lake in the main river system, and due to that the large upper compartments of the catchment have similar vegetation and soil types, the water chemistry shows small variations in different parts of River Forsmarksån. Except from some branching within the upper wetland part of the river system, only two of the lakes (Lakes Älgsjön and Fågelfjärden) are situated in tributaries. Both these tributaries add substantially to the total catchment area of the river, at Lake Södra Åsjön and downstream Lake Bruksdammen, respectively. These two tributaries drain areas located at a height above sea level similar to that of the main river. Other new areas that successively are added to the catchment in lower parts of the drainage basin are relatively small, and their contribution to the chemical composition of the water is thus also small. The similarities in water chemistry are evident when comparing the ionic composition (Table 12) of the water in the upper part (Lake Vikasjön) with that of the water close to the mouth of the river (Johannisfors). It is also evidenced by the similar or even identical classifications of the lake waters in Table 13.

Table 12. The ionic composition (equiv %, average values) and water colour (mg Pt/l) at two stations in the River Forsmarksån; Lake Vikasjön, in the upper part of the river system, and Johannisfors, 1.5 km from the outlet to the Baltic Sea. Average values from regular monitoring programmes (SLU 1999) compared to the standard composition according to Rodhe (1949).

Water colour	Ca	Mg	Na	K	HCO_3	SO_4	Cl	Water
L Vikasjön, 28 m a.s.l.	73	10	14	2	76	8	15	180
Johannisfors, 3 m a.s.l.	79	8	11	2	74	15	11	75
Standard composition (Rodhe 1949)	63.5	17.4	15.7	3.4	73.9	16.0	10.1	–

The ionic composition of the water in the River Forsmarksån (Table 12) indicates, despite the relatively strong water colour, a hardwater system with dominance of Ca^{2+} and HCO_3^- ions. This is due to the odd combination in the drainage area of calcareous soils covered by peatlands. This is typical for the brownwater lakes in lowland areas of Uppsala County in general (Brunberg & Blomqvist 1998).

Characteristic of these as well as of other brownwater lakes is the strong colour of the water. Tables 12 and 13 show a gradual decrease in water colour downstream the system, although there is still a significant colour of the water at Johannisfors, 1.5 km from the outlet to the Baltic Sea. Due to the large amounts of humic substances, brownwater lakes are typically high in total organic carbon (TOC); most of which is present as dissolved organic compounds (DOC). The brownwater lakes in the Forsmark area are no exception to this rule and concentrations of TOC at the two stations of the river monitored by SLU (1999) show very high concentrations of TOC, with a long-term average of 25 mg C/l in Lake Vikasjön and 20 mg C/l in the river at Johannisfors. These values are higher than those of most Northern Swedish rivers; for example a typical Swedish forest river like the River Öreälven has an average TOC concentration only about half as high as River Forsmarksån (SLU 1999). Much of the humic substances entering the lakes are in the form of DOC and the sedimentation of these substances is very low, less than 5% (Jonsson & Jansson 1997). Elements associated with the DOC also show low retention in the lakes basins. For example, Malmgren & Jansson (1995) calculated that the retention of ^{137}Cs from the Chernobyl accident, to a great extent associated with humic substances, in Lake Örträsket through sedimentation was less than 10% both initially (1986) and later. The phosphorus concentrations of the lakes in River Forsmarksån are usually moderately high (12.5–25 µg P/l). Considering the high amounts of humic substances, it is likely that a large part of the phosphorus is associated with dissolved organic compounds and thereby less available to the primary producers. Only two of the lakes have phosphorus concentrations which are classified as "high" (Table 13). Regarding Lake Skälsjön this may be explained by the use of this lake as a recipient for sewage water from Lövstabruk, while the classification of Lake Åkerbysjön is based on very few measurements and thus very precarious. The alkalinity is high for brownwater lakes in general (*cf* Lydersen 1998) and varies between about 0.5 meq/l in the upstream lakes and 1.5 meq/l in the lowland lakes closer to the coast. Thus, the values are well above 0.20 meq/l which is the limit for the highest classification used by the Swedish Environmental Protection Agency (Naturvårdsverket 1999). The oxygen situation during winter is normally good in the lakes, again due to the fast flow of water through the system. Only two of the lakes may meet substantial oxygen deficiency during long winters; Lake Älgsjön, which is very shallow and not situated in the main river, and Lake Bruksdammen. The latter is a man-made lake flooding former mires and to a large extent covered by vegetation. It is regulated for freshwater water supply to the nuclear power plant at Forsmark, and may thus experience minimum water volumes followed by oxygen depletion under the ice during wintertime.

Table 13. Water chemistry classification for brownwater flow-through lakes in the Forsmark area. Data from Brunberg & Blomqvist (1998), partly re-classified according to new recommendations from the Swedish Environmental Protection Agency (Naturvårdsverket 1999).

Lake	Total P µg/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=≤0.02	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
Fågelfjärden	2	1	4	
Bruksdammen	2	1	4	4
Södra Åsjön		1	4	2
Älgsjön	2	1	4	4
Norra Åsjön	2	1	4	2
Skälsjön	3	1	4	2
Ensjön	2	1	4	2
Åkerbysjön	3	1	4	1
Lissvass	2	1	4	1
Finnsjön	2	1	4	1
Fälaren	2	1	5	1
Vikasjön-Skälsjön	2	1	5	2
Stora Agnsjön	2	1	5	1
Lilla Agnsjön			5	2
Average	2.2	1.0	4.3	1.9
Median	2.0	1.0	4.0	2.0
Max	3	1	5	4
Min	2	1	4	1
N obs	12	13	14	13

3.5.6 Water biology

The ecosystem of brownwater lakes can, in accordance with those in most other lakes, be divided into three main habitats; the pelagial zone (the open water), the littoral zone (bottom areas with photosynthesising plants) and the profundal zone (bottom areas lacking photosynthesising plants). A further division of the littoral zone is then possible and has been presented in section 3.4.6. Of the resulting five key habitats, two can be identified as of minor importance in the brownwater lakes of River Forsmarksån. The lakes there are generally too small to develop a typical wind-exposed littoral zone. The light-exposed soft-bottom zone is also lacking, as the strong colour of the water prevents the light from penetrating down to the bottom at depths where emergent macrophytes do not grow. This presentation of the major biological constituents of the brownwater lakes and their ecological functioning will therefore be concentrated to the three important key habitats: the pelagic zone, the emergent macrophyte zone and the profundal zone. Fish, which are present within all parts of the lakes, are described separately at the end of this section.

The pelagic zone

Few studies of the plankton community have been performed in the lakes of River Forsmarksån. Four general limnological investigations of Lakes Skälsjön, Lissvass, Ensjön and Åkerbysjön, respectively, were performed by limnology students from Uppsala University during February-March 1976 (Appelberg *et al.* 1976, Conover *et al.* 1976, Danielsson *et al.* 1976, King *et al.* 1976). The results, which are very similar for all the four lakes regarding flora and fauna, give some general information about the structure of the lake ecosystems. The phytoplankton biomasses were found to be very low, also when taking into account that the investigations were performed during winter. The phytoplankton communities were dominated by chrysophytes and cryptophytes, but also green algae, cyanobacteria, and remnants of diatoms were found. Large, microscopically visible, bacteria constituted a substantial part of the plankton communities. The zooplankton communities were dominated by copepods, principally adults of the genus *Eudiaptomus*. Among Rotatoria cold-water forms dominated, while the abundance and biomass of Cladocera was very low. The studies reflect a typical winter situation in unpolluted lakes in the county in general, but tells very little about the differences between these and other types of natural systems.

Summer investigations of the planktonic community in the lakes are, as far as the authors have found, restricted to measurements of chlorophyll concentrations in Lake Vikasjön (SLU 1999). The maximum value recorded is 27 mg Chl a/m^3, with an average value for 1996–1998 of 12 mg/m^3 (n=11).

Despite the few studies of the plankton in the lakes of River Forsmarksån, the pelagic ecosystem of brownwater lakes in general have been subject to extensive research during the last decades, as new methods for characterisation of organic compounds (humic substances) as well as for determination of biomass and production of heterotrophic bacteria have been developed. In a recent publication edited by Hessen & Tranvik (1998) current knowledge about brownwater lakes in general is summarised. From the many chapters in this book, the following information about the ecosystem can be extracted: The production at the base of the food web of brownwater lakes relies to a great extent on bacterial utilisation of allochtonous organic compounds. Primary production is depressed, partly by competition with bacteria for available inorganic nutrients and partly by deterioration of the light climate due to the extinction of light caused by the humic substances. Furthermore, although concentrations may be relatively high, most of the phosphorus in the systems is associated to humic substances and difficult for the organisms to attain. However, the pelagic habitat may be as well developed as that in oligotrophic and mesotrophic lakes in terms of diversity and production of planktonic communities. The phytoplankton community is generally dominated by flagellates and the biomass is low. Many of the phytoflagellates obtain their nutrients from feeding on bacterioplankton (mixotrophy). The zooplankton community is dominated by fine-particle feeders such as cladocerans (*e.g. Diaphanosoma* and *Daphnia*), rotifers, and ciliates.

The pelagic ecosystem of the brownwater lakes in Uppsala County may differ somewhat from this general picture due to their relatively recent isolation from the Baltic Sea and thereby comparatively high ion- and nutrient contents. Data from other brownwater lakes in Uppsala County (*e.g.* Blomqvist *et al.* 1981, Lindström 1998) indicate that among phytoplankton, diatoms, cyanobacteria and the large phytoflagellate *Gonyostomum semen*, may constitute a relatively large share of the total biomass. This may be the case also in the lakes of River Forsmarksån, as indicated by the presence of these organisms in the winter samples. The relatively high concentrations of chlorophyll a, measured in Lake Vikasjön, indicate that phytoplankton biomasses can be higher than in brownwater lakes in general. However, it can not be excluded that the high values were due to dominance of *Gonyostomum semen* which, when it occurs, often forms swarms that may contribute to occasional extreme biomass values in single samples (*cf* Rosén 1981). The two brownwater lakes Siggeforasjön and Tvigölingen, both located in the drainage area of the nearby River Fyrisån, were studied with respect to biomass of different groups of biota by Lindström (1998). In Lake Siggeforasjön, where the phytoplankton community included both diatoms and cyanobacteria, she found bacterioplankton biomass to exceed phytoplankton biomass, while metazooplankton was the largest constituent of the total plankton community biomass. Contrarily, in Lake Tvigölingen, where the phytoplankton community included the flagellate *Gonyostomum semen*, total planktonic biomass was dominated by phytoplankton, followed by metazooplankton and bacterioplankton.

In conclusion, the pelagic zone of the brownwater lakes in the Forsmark area is characterised by high alkalinity in combination with a high water colour and moderate concentrations of total phosphorus. In the water chemistry, the only atypical values are those of the alkalinity, which are much higher than in brownwater lakes in general. Phytoplankton biomasses are relatively low but highly variable, maybe due to the presence of rare species like *Gonyostomum*. Biomasses of bacterioplankton and metazooplankton may be as high or even higher than those of phytoplankton which is another characteristic of brownwater lakes. Altogether, it may be suggested that the pelagic zone is the most important habitat to total production in these as well as in other brownwater lakes. However, there is a considerable lack of data to verify this hypothesis.

The emergent macrophyte zone

The emergent macrophyte zone of the brownwater lakes in the River Forsmarksån is similar to that of the oligotrophic hardwater lakes described above (3.4.6) in the sense that the innermost part often is made up by the surrounding mire. However, in the larger lakes of the system there is most likely, both in the natural state and in the previously regulated systems present today, an outer zone dominated by *Phragmites* growing on the bottom of the lake (*cf* 3.5.2). The limnological winter investigations of the former regulated Lakes Skälsjön, Ensjön and Åkerbysjön (Appelberg *et al.* 1976, Danielsson *et al.* 1976, King *et al.* 1976) revealed that between 30 and 50% of the lake areas were covered with emergent macrophytes. The dominating species of emergent macrophytes in these three lakes as well as in Lake Lissvass (Conover *et al.* 1976) was *Phragmites australis* (common reed), with some contribution from *Scoenocplectus lacustris* (bulrush) and in two of the lakes (Lissvass and Ensjön) also from *Typha angustifolia* (lesser reedmace). As in the case of the oligotrophic hardwater lakes, quantitative data on the biomass and production of these littoral zones are very sparse or totally lacking for the actual lakes. However, the following general statements regarding the functioning of the littoral zone may contribute to an integrated view of the ecosystem functioning: First of all, the *Sphagnum* mosses are known to function as cation exchangers (Clymo 1963, 1964), sieving off and altering the chemical composition of the surrounding water by taking up Ca^{2+} and Mg^{2+} ions while releasing hydrogen ions and dissolved organic compounds (organic acids). Hence, the development of a mire around the lakes most likely has a profound influence on the diffuse inflow of water from the nearby drainage area. This water most likely changes its character from high in dissolved salts, alkalinity, and pH, to low in dissolved salts, lower in pH and alkalinity, and rich in humic substances. Secondly, the light penetration into the outer emergent macrophyte zone is most likely restricted, both due to the shading by the plants themselves and to the strong colour of the lake water. This will reduce the growth of photosynthesising organisms in the water. However, heterotrophic organisms that are able to utilise the released organic substances would thrive in this environment, *i.e.* bacteria and fungi, and they may be important as a link to higher trophic levels in the food web at least in the *Phragmites* zone to which larger organisms as benthic fauna and fish have access.

In conclusion, several aspects of the structure and functioning of the *Sphagnum/ Phragmites* littoral are yet to be disentangled (*cf* 3.4.6). However, it seems possible to state that the relative contribution of the littoral zone to total lake turnover of carbon and nutrients is smaller than in the oligotrophic hardwater lakes which are completely surrounded by littoral. In the brownwater lakes of River Forsmarksån, the dominant flow of water and thereby input of carbon and nutrients takes place via the main river. The relative importance of the littoral zone for the ecosystem functioning is tightly coupled to the hydrology of the system, *i.e.* how much water that is filtered through the littoral zone compared to the inflow from the main river. Nevertheless, the functioning of the littoral zone as a sieve and sink for substances entering from local sources (*i.e.* via diffuse inflow of water) may be considerable.

The profundal zone

The profundal zone of a lake is by definition lacking photosynthesising organisms, due to restricted light availability. As a consequence of the strong water colour, and thereby shallow euphotic layer, profundal zones are dominating the bottom areas of brownwater lakes in general. The benthic organisms that are found in this environment includes benthic macro-, meio-, and microfauna, heterotrophic bacteria, and fungi. The larger benthic fauna is the most well-known group, including in lakes in general *e.g.* insect larvae, molluscs, crustaceans and other invertebrate animals. All the benthic organisms participate in a well-structured foodweb, decomposing and utilising organic carbon which is imported to this habitat by sedimentation, resuspension and re-sedimentation processes. Chemical processes occurring at different environmental conditions also interact with the biological and microbial processes. The benthic organisms are often classified according to their role in the processing of organic material. Some examples are shredders, filter feeders etc among the higher benthic fauna, and methanogens, nitrifiers etc among the bacteria. The sediments of brownwater lakes have a high content of organic matter, mainly originating from allochtonous sources (not produced within the lake). Calculations from a brownwater lake in Northern Sweden, showed that about 30% of the sedimented organic carbon was lost through respiration (Jonsson 1997). The organic material which reaches the profundal zone has often been depleted of important nutrients as well as of easily accessible and degradable organic compounds. Thus, the characteristic allochtonous "dy" sediments of the brownwater lakes are a relatively poor environment, supporting a restricted biomass of organisms. Investigations of the bottom fauna in Lakes Skälsjön, Lissvass, Ensjön and Åkerbysjön confirm the general picture of a poor environment by reporting low biomasses of the larger benthic fauna. Chironomid larvae (midge larvae) were strongly dominating the species composition in all the four lakes (Appelberg *et al.* 1976, Conover *et al.* 1976, Danielsson *et al.* 1976, King *et al.* 1976).

In conclusion, the profundal zones of the brownwater lakes in the River Forsmarksån are, in terms of production of organisms, probably the least productive of the three key habitats.

Fish

Twelve of the lakes in the River Forsmarksån have been subject to standardised gill net fishing (Nyberg 1999). Fish was caught in all these lakes (Table 14). The average catch (catch per unit effort, CPUE) was 1.9 kg in terms of biomass and 45 individuals in terms of abundance. On average 7.1 species were found per lake. Totally 9 species were encountered; pike (*Esox lucius*), roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), bream (*Abramis brama*), white bream (*Blicca bjoerkna*), rudd (*Scardinius erythrophthalmus*), tench (*Tinca tinca*) and Crucian carp (*Carassius carassius*). The highest species diversity was found in Lakes Bruksdammen and Skälsjön, where all 9 species were present. Roach, perch and rudd were caught in all lakes. Perch was the dominating species in seven of the lakes, both regarding biomass and number of individuals. Roach dominated in terms of both biomass and numbers in three of the lakes. In two of the lakes perch and roach were sharing the position as dominating species. In Lake Lissvass, finally, tench was dominating in terms of biomass but roach in terms of numbers.

The results from the gill net fishing show a relatively diverse fish community, including the species that would be expected to occur in lakes in this part of the country. The number of species caught, 7.1 per lake, was higher than the average (5.8 species) for the 81 lakes of Uppsala County included in the gill net survey (Nyberg 1999). On the other hand, the biomass and abundance of these fish species were much lover; in average 45 individuals and 1.92 kg per gill net, compared to 81 individuals and 3.6 kg for the whole county (Nyberg 1999). The highest catch per unit effort (CPUE), both in terms of individuals and biomass, was found in Lake Skälsjön. This may be explained by the fertilisation of this lake from municipal sewage water. The poor development of fish populations in brownwater lakes is well known (Brunberg & Blomqvist 1998, Nyberg 1999) but the reason is not fully understood. Hessen (1998) suggests that poor spawning opportunities may be the reason, but this does not seem to hold for the lakes in River Forsmarksån, where the fish can spawn along the entire river.

There is no clear co-variation between the fish community composition and the oxygen conditions in the lakes (Table 14). This can be explained by the fact that very few of the lakes have any problems with low oxygen concentrations during the winter period. Crucian carp, which was found to be correlated with bad oxygen conditions in the oligotrophic hardwater lakes (section 3.4.6), was caught in two of the lakes, but only one of these lakes is predicted to experience severe oxygen deficiency. The high flow of water through the entire river system prevents the depletion of oxygen, even under the ice cover during wintertime. In addition, the River Forsmarksån is to a large extent an open system for migratory organisms. Thus, fish populations have the possibility to avoid unfavourable conditions by migration to other parts of the river system. When the lakes recover from the oxygen deficiency, the fish may recolonise and thereby counteract the development of species populations that tolerate oxygen deficiency (*i.e.* Crucian carp).

In conclusion, the brownwater lakes of River Forsmarksån have a fish community which is somewhat richer in number of species compared to the average lake of the county, but poor in abundance and biomass. Threats to the fish populations due to bad oxygen conditions seldom occur in the brownwater flow-through lakes, and if they should occur the fish populations have the possibility to migrate and survive in better oxygenated parts of the river system.

Table 14. Data from standardised survey gillnet fishing in lakes of the River Forsmarksån. Pi=pike, Ro=roach, Pe=perch, Ru=ruffe, Br=bream, Wh=white bream, Rd=rudd, Te=tench, Cr=Crucian carp. Oxygen conditions: See Table 7 for explanations of the numbers.

Lake	Elevation m.a.s.l.	Lake area km^2	Lake depth average	max	Oxygen conditions	Fish species	No of species	CPUE no of ind.	kg
Fågelfjärden	4	0.12	–	–	–	–	–	–	–
Bruksdammen	12.4	2.06	–	–	4	Pi,Ro,Pe,Ru,Br,Wh,Rd,Te,Cr	9	24	2.0
Södra Åsjön	12.4	1.98	2.3	3.8	2	Pi,Ro,Pe,Ru,Br,Wh,Rd,Te	8	34	1.8
Älgsjön	22.7	1.17	0.6	1.2	4	Pi,Ro,Pe,Rd,Te	5	49	2.2
Norra Åsjön	12.4	1.77	2.1	4.0	2	Pi,Ro,Pe,Ru,Br,Wh,Rd	7	51	1.3
Skälsjön	13.3	1.83	0.8	1.5	2	Pi,Ro,Pe,Ru,Br,Wh,Rd,Te,Cr	9	88	4.1
Ensjön	28	0.34	0.5	1.4	2	Ro,Pe,Ru,Br,Wh,Rd	6	38	1.2
Åkerbysjön	28	1.11	0.9	2.2	1	Ro,Pe,Ru,Br,Wh,Rd,Te	7	42	1.8
Lissvass	28.6	0.35	0.7	1.2	1	Pi,Ro,Pe,Ru,Br,Wh,Rd,Te	8	64	3.7
Finnsjön	28.6	4.09	1.9	3.4	1	Pi,Ro,Pe,Ru,Br,Wh,Rd,Te	8	57	1.6
Fälaren	32	2.05	1.5	2.6	1	Ro,Pe,Ru,Br,Wh,Rd,Te	7	18	1.2
Vikasjön-Skälsjön	28.6	1.04	–	3.3	2	Ro,Pe,Ru,Br,Wh,Rd	6	44	0.42
Stora Agnsjön	30.1	0.24	2.8	3.7	1	Ro,Pe,Ru,Br,Rd	5	32	1.7
Lilla Agnsjön	32	0.09	2.1	2.7	2	–	–	–	–
Average	22.4	1.30	1.47	2.58	1.9		7.1	45	1.92
Median	28.0	1.14	1.50	2.65	2.0		7	43	1.75
N obs	14	14	11	12	13		12	12	12
Max	32	4.09	2.8	4.0	4		9	88	4.1
Min	4	0.09	0.5	1.2	1		5	18	0.42

3.5.7 Ontogeny of the brownwater lakes of the Forsmark area

From a historical and ontogenic point of view the catchment of River Forsmarksån, and thereby also its lakes, may be divided in to parts with different ontogeny; the area upstream and downstream, respectively, of the 13 m high falls at Lövstabruk.

Lake Vikasjön, which is situated in the upper part of River Forsmarksån, has been subject to extensive paleoecological studies led by Tord Ingmar and co-workers (referred in Brunberg & Blomqvist 1998). A detailed study of the composition of diatoms within the sediments has been performed, giving an excellent record of the conditions within the lakes in this area, dating back to the time before the isolation from the sea about 5 000 years ago (Ingmar unpubl, Jonsson 1973). All the lakes in this area, with the exception of Lake Fälaren, were originally different parts of a large ancient lake which was isolated from the sea about 4 000–5 000 years ago. The area of this ancient lake was approximately 50 km^2. Lake Fälaren was about three times larger than nowadays, having a separate outlet creek to the large lake. The surroundings within the catchment were dominated by till (Jonsson 1973).

The paleoecological studies show that Lake Vikasjön, or rather the ancient lake of which Lake Vikasjön was one part, passed through an oligotrophic hardwater stage after the isolation from the sea, during which "cyanophycée-gyttja" was settled. This corresponds to the present situation in the oligotrophic hardwater lakes along the coast (*cf* 3.4). This stage had a duration of about 1 000 years, and was followed by a period of 1 000–2 000 years when the lake basins successively were isolated from each other and partly were grown over by mires. The sediments in the remaining lake basins then switched to "dy" sediments due to the influence of humic compounds from the surroundings. Thus, most of the lakes in the upper parts of River Forsmarksån have the same or at least a similar historical record in the sediments.

The lakes which are situated below the 13 m fall at Lövstabruk have a different history. Due to the substantial difference in the topography they were isolated from the sea at least 2 000–2 500 years later than the upstream lakes. At this time period, the upstream lakes (*e.g.* Lake Vikasjön) had passed the oligotrophic hardwater stage, and were already more or less brownwater systems. The inflowing water from the upstream areas to the newly formed lakes thus was less alkaline, draining soils which already had been leached for thousands of years. This water from the main river constituted a major share of the inflowing water to the newly formed lake basins. The large flow of water dominated, and still dominates, the hydrology of the system, thus diluting and washing out the contributions from the land areas in the close vicinity of the newly formed lakes. Consequently, no oligotrophic hardwater stage has been present in the chain of lakes situated along the main river below Lövstabruk. Instead they developed to brownwater flow-through lakes more or less directly after the isolation.

3.5.8 The brownwater lakes in the Forsmark area downstream Lövstabruk –a synthesis of the ecosystem functioning

Summarising the sparse information about the brownwater lakes in River Forsmarksån, and using general information about the conditions in brownwater lakes, a tentative model of the ecosystem functioning of the brownwater lakes downstream Lövstabruk can be formulated (Figure 4). The dominating feature of these lakes is the rapid flow of water through the system, which continuously brings allochtonous substances from the upstream wetland and forest areas. The inflowing water is characterised by a strong colour caused by humic substances, mainly in the form of dissolved organic carbon compounds. A large part of the lake water phosphorus is associated with the dissolved organic compounds, and thereby less available to the primary producers.

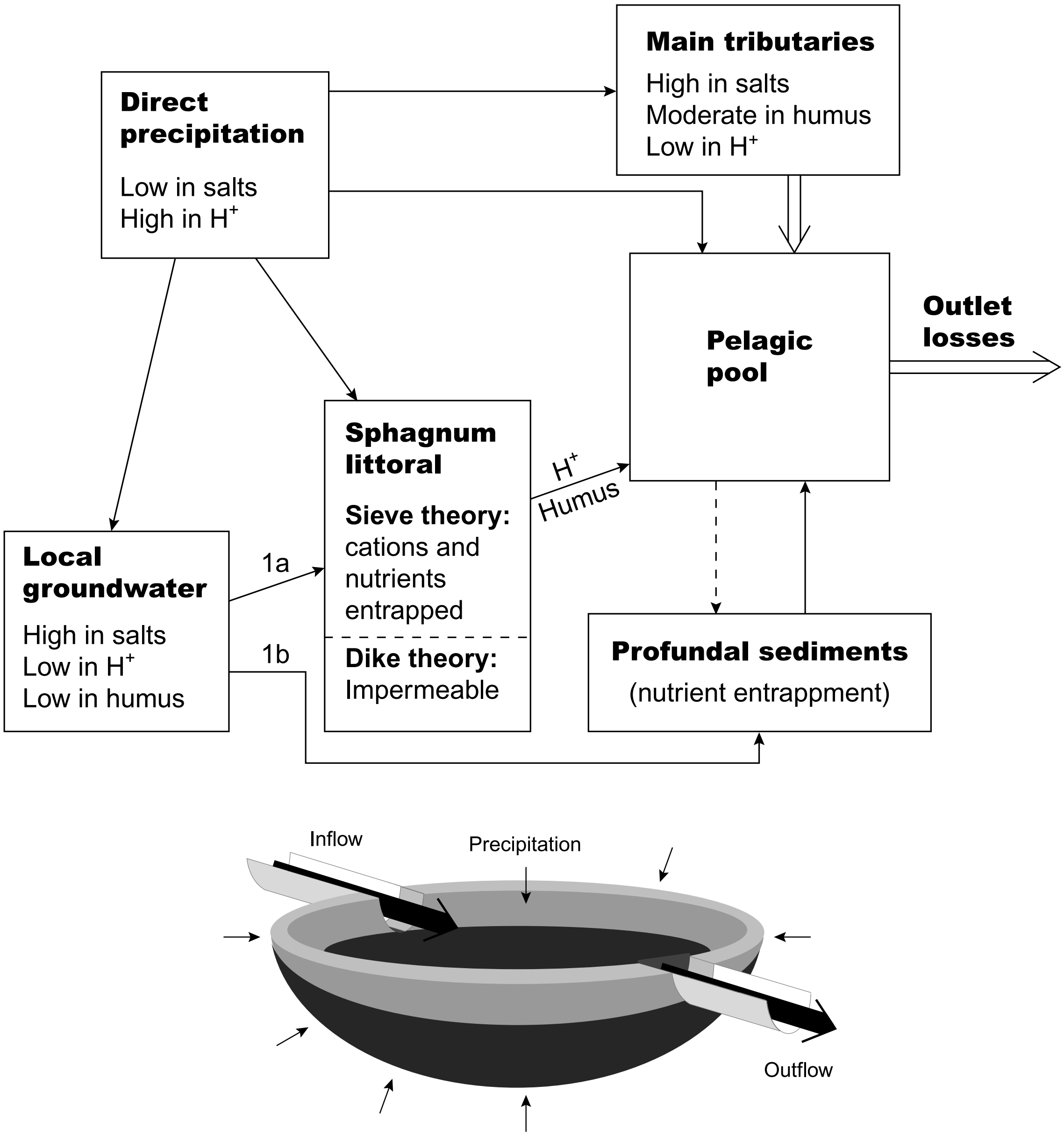

__Figure 4.__ A tentative model for the functioning of the brownwater lakes downstream Lövstabruk in River Forsmarksån.

The three main habitats of the lakes are the pelagic zone, the emergent macrophyte zone and the profundal zone. Despite both low availability of nutrients and a poor light climate, the pelagic community may be well developed, although of a more heterotrophic character than in less humic lakes. Heterotrophic bacteria, produced within the lake or transported from the upstream areas, mobilise energy to the system at the base of the food web by utilising the organic substances in the lake water. The primary production of the phytoplankton is restricted by the low light conditions as well as of the competition with bacterioplankton regarding nutrients. Nevertheless, in shallow lakes where the euphotic zone is a relatively larger part of the water, phytoplankton may contribute significantly to the basic production. In addition, the phytoplankton community is usually dominated by mixotrophic flagellates. These organisms are able to ingest bacteria and thereby survive during environmental conditions that restrict purely autotrophic organisms. Both bacterioplankton and phytoplankton are utilised as food for zooplankton, which may have a high production in the brownwater lake ecosystems.

The high flow of water rapidly transports both dissolved and particulate matter through the lakes. As a consequence, the accumulation of material by sedimentation in the lake basins is restricted to a rate of about one millimetre per year. The sediments are of allochtonous character, with low concentrations of nutrients. The poor food quality restricts the growth of benthic fauna organisms, the community of which is characterised by low diversity as well as low productivity. The fish community of the lakes in River Forsmarksån seems to keep a high diversity, although the production is low.

The emergent macrophyte zone is often well developed along the shores of the lakes. Usually a surrounding mire, dominated by *Sphagnum* mosses, functions as a filter for the water entering the lake, and affects the quality by exchanging cations and nutrients for H^+ ions and organic acids. The three-dimensional mire littoral is also a more or less closed system for larger organisms, *e.g.* benthic macrofauna and fish. Rooted emergent macrophytes, typically *Phragmites*, form a border zone between the mire and the open water. Neither this part of the littoral zone to any greater extent seems to provide food items for benthic fauna and fish. The primary production is restricted by low light availability due to shading from the *Phragmites* as well as due to the coloured lake water. However, heterotrophic organisms, *e.g.* bacteria and fungi, may provide some energy that can be linked to higher trophic levels in the lake ecosystem. The extent and efficiency of this food web is more or less unknown.

In conclusion, the lakes in the downstream parts of River Forsmarksån may be characterised as pronounced flow-through systems. They may have a relatively high production at the base of the food web, mainly in the form of pelagic production by hetrotrophic bacterioplankton, but a low energy transfer to higher trophic level such as benthic fauna and fish. A major share of the production is exported to downstream localities. Despite the high inflow of water and carbon, the accumulation of organic material in the system is low. This is also true for all the elements entering the lake associated to the humic substances.

3.6 Description and characterisation of the deep eutrophic lakes

In order to characterise the deep eutrophic lakes that may be formed in the Forsmark area in the future, we have used data from two lakes situated in the Norrtälje area 60 km south of Forsmark; Lake Erken and Lake Limmaren (Table 15). These two lakes are today situated at a level of 11.7 and 3.9 meters above the sea, respectively, thus at an altitude similar to that of many of the oligotrophic hardwater lakes and brownwater lakes in the Forsmark area and with a similar history of isolation from the Baltic Sea. In contrast to the oligotrophic hardwater lakes and the brownwater lakes of the Forsmark area described above (3.4, 3.5), a lot of data has been gathered about these two lakes. Lake Erken is well known from more than 50 years of limnological research, having a well-reputed limnological station (the Erken laboratory) situated on the shore. Weyhenmeyer (1999) has compiled limnological data from various sources regarding Lake Erken. All data from Lake Erken presented in this report originates from Weyhenmeyer (1999) or from references cited therein, unless other sources are referred. The other lake, Lake Limmaren, has been selected for several limnological studies during the last years, and has thereby been monitored for *e.g.* water chemistry parameters and plankton community composition. Lake Limmaren has also been subject to investigations by the local authorities of Norrtälje community, concerning the high nutrient concentrations and the regularly occurring cyanobacterial water blooms.

Table 15. Two representatives of deep eutrophic lakes along the Baltic coast ca 60 km South of the Forsmark area. Catchment numbers according to SMHI (1985), coordinates according to the Swedish National Grid System (RT 90, 2.5 gon W).

Catchment no	Lake name	Coordinates for outlet x, y	Elevation above sea level, m
58	Lake Erken	664060, 165948	11.7
59/60	Lake Limmaren	662767, 166446	3.9

Table 16. Characteristics of the catchments of Lake Erken and Lake Limmaren.

Catchment		Area km^2	Forest %	Wetland %	Farmland %	Lakes %	Other land use %
58	Erken	141	70	0	10	20	0
59/60	Limmaren	21.1	68	0	6	26	0

3.6.1 The drainage area

The catchments of Lakes Erken and Limmaren, respectively, differ substantially in size (Table 16), but so does also the size of the lakes. Hence, the relative composition of the catchment is very similar between the two lakes. Characteristic for both catchments is the large percentage of lake area; 20 and 26%, almost exclusively made up by Lake Erken and Lake Limmaren, respectively. Other lakes in the catchments are small and their contribution to the total lake area is minimal. Forest is dominating the drainage areas, while farmland has a minor contribution. Wetland is almost totally lacking, which is a striking difference to the two other lake types described in this report.

The geology is similar in both drainage areas and also similar to that of the Forsmark area. Thus, the bedrock is dominated by granites and gneisses and is covered by lime-rich till of glacial origin. Minor areas, both in the lake basins and on land (coinciding with agricultural areas), have glacial and post-glacial clay deposits.

3.6.2 The riparian zone

Both the shores of Lake Limmaren and Lake Erken are characterised by very narrow riparian zones, in most parts consisting of a thin zone of alder trees forming a border between mature coniferous forest and open water or a thin belt of *Phragmites*. Particularly in Lake Erken, which has the characteristic vegetation-free wind-exposed littoral zone in large parts of the main basin, there is a more or less direct transition from forest to open water. In Lake Limmaren, which is smaller and does not have so much of the wind-exposed habitat, the transition from mature forest to a *Phragmites*-belt of 10–30 m thickness is equally sharp. Due to the lowering of the water level, and particularly in Lake Erken, wetlands in the form of alder forest interspersed with *Phragmites* constitute a major share of the riparian zone in sheltered bays along the Western and Southern shores.

Table 17. Lake morphometry for Lake Erken and Lake Limmaren.

Lake	Area, km^2	Average depth, m	Maximum depth, m	Volume, Mm^3	Water renewal time, days	Lowering of water level, m
Erken	24.2	9.0	20.7	213.5	2 701	1.5
Limmaren	5.9	4.7	7.8	27.3	2 137	1.1

3.6.3 Lake morphometry

In comparison with other lakes in Sweden (SMHI 1983) both Lake Limmaren and Lake Erken can be classified as large, both belonging to the 10% largest of the more than 50 000 lakes in the country. Lake Erken, with an area of 24 km^2 (Table 17), in fact belongs to the 380 largest lakes in the country. Both lakes have a relatively modest maximum depth for Swedish lakes in general. However, compared with other lakes in the province of Uppland, and particularly with those in Uppsala County, they belong to the deepest lakes with average depths of 9 and 4.7 m, respectively. Because of their large volumes and limited drainage areas, the renewal time of the water in the lake basins, 7.4 years for Lake Erken and 5.8 years for Lake Limmaren, is long, especially compared to that of the lakes in the Forsmark area. Both lakes have been subject to drainage projects, the aim of which has been to gain farmland, and they have been lowered with more than one meter. These figures should be added to the present elevation above the sea level in order to calculate the approximate time for isolation from the Baltic Sea. With a shoreline displacement of ca 0.5 meter per century, the isolation of Lake Erken can be calculated to year 2500 BP and that of Lake Limmaren to year 1000 BP.

3.6.4 Sediment characteristics

The sediments of Lake Erken have been thoroughly investigated from different aspects, and many investigations of the chemical composition of the surface soft-bottom sediments have been published. Both Lake Erken and Lake Limmaren have characteristic gyttja sediments, with a dark greenish-grey colour. The organic material within the sediments originates mainly from autochthonous production (*i.e.* material produced within the lake), and the ratios between carbon and nitrogen concentrations are typically low; 7.5 and 7.0, respectively (Table 18). The sediment chemistry is generally similar between the two lakes (Table 18). In Lake Erken, a major part of the sediment phosphorus is found in the "residual" phosphorus fraction, which is considered to consist mainly of organically bound P. Lake Limmaren has a higher total concentration of phosphorus, most of which is associated to Fe compounds (NaOH-P) and to organic material (residual-P). In both lakes, phosphorus is released from the sediments during some periods of the year. The "internal" phosphorus release from Lake Limmaren is large enough to cause a net transportation of phosphorus out of the lake (Pettersson & Lindqvist 1993), but in Lake Erken there is a net accumulation of phosphorus in the lake when calculated on a yearly basis.

Due to the large size and wind exposure of the lakes, the accumulation of sediments at the bottom is very heterogeneously dispersed. Investigations of Lake Erken sediments show a difference between 1.5 and 10 m of sediment thickness (including both fresh-

Table 18. Sediment data from Lake Erken and Lake Limmaren compiled from Pettersson (1986) and Pettersson and Lindqvist (1993).

Lake	C/N	Ca mg/g dw	Fe mg/g dw	Total-P mg/g dw	Largest fraction* of sediment P
Erken	7.5	8	32	1.2	residual-P
Limmaren	7.0	5	33	1.5	NaOH-P, residual-P

* Sediment phosphorus fractions according to Hieltjes & Lijklema (1986).

water and marine sediments) in different parts of the lake (Fries 1969). True accumulation sediments are found only in the deepest parts of the lakes, while other soft-bottoms are subject to substantial resuspension by waves and internal seiches, followed by further transport to the deeper areas ("sediment focusing"). This causes difficulties when assessing the sedimentation rate and sediment growth. A yearly sedimentation of ca 6 mm has been calculated for Lake Erken. This is in contrast to sedimentation rates calculated from Fries (1969), which gives averages for the period after isolation ranging between 0.4 and 0.8 mm per year in the deepest parts of Lake Erken. Hence, although initial sedimentation rates may be high, processes like redistribution, mineralisation, and compaction of the sediment contributes to considerably lower rates over longer time periods.

3.6.5 Water chemistry

Lake Erken and Lake Limmaren show great similarities in water chemistry, but differ regarding mixing regime (Table 19); Lake Erken is dimictic while Lake Limmaren is unstratified during summer. Both lakes are covered by ice during three to four months, from December to April. Lake Erken normally stratifies in early June and stratification lasts till early September. Both lakes have water rich in salts, and pH values as well as alkalinity of the water are high. They are both typical hardwater systems with dominance of Ca^{2+} and HCO_3^-. In comparison with the standard composition of freshwater lakes (Rodhe 1949), Lake Erken has more SO_4^{2-} than the average lake while Lake Limmaren has more Na^+ and Cl^-. The reason behind the higher relative contribution of SO_4^{2-} in Lake Erken is unknown, but may be explained by influence of sulphur-rich marine sediments in the drainage area. The higher relative contribution of Na^+ and Cl^- in Lake Limmaren typically reflects that the lake is situated close to, and has recently been isolated from, the Baltic Sea.

Regarding concentrations of total phosphorus, both lakes can be considered as nutrient rich, and particularly Lake Limmaren has very high concentrations of total phosphorus for a lake where influence of human activities is minimal. Concentrations of total nitrogen are moderately high, resulting in very low N/P quotients (24 and 18, respectively) in the lake water. Water colour is very low while concentrations of total organic carbon (TOC) are high, together indicating that most of the organic carbon stems from the high autochtonous production typical of nutrient rich lakes.

Table 19. Typical physical and chemical data from Lake Erken (values from Weyhenmeyer 1999) and Lake Limmaren (SLU 1999, Blomqvist & Brunberg unpubl).

Parameter	Lake Erken	Lake Limmaren
Mixing regime	Dimictic	Monomictic
Duration of ice cover (days)	100–140	100–140
Duration of summer stratification (days)	100	–
Conductivity (mS/m)	25.4	24.7
pH value	8.0	8.0
Alkalinity (meq/l)	1.8	1.4
Calcium, Ca^{2+} (meq/l)	2.00 (64%)	1.53 (64%)
Magnesium, Mg^{2+} (meq/l)	0.70 (23%)	0.31 (13%)
Sodium, Na^{+} (meq/l)	0.35 (11%)	0.51 (21%)
Potassium, K^{+} (meq/l)	0.06 (2%)	0.06 (2%)
Bicarbonate, HCO_3^{-} (meq/l)	1.80 (60%)	1.40 (65%)
Sulphate, SO_4^{2-} (meq/l)	1.00 (33%)	0.30 (14%)
Chloride, Cl^{-} (meq/l)	0.21 (7%)	0.45 (21%)
Total N (µg/l)	660	985
Total P (µg/l)	27	54
Silica (µg Si/l)	1.10	1.76
TOC (mg/l)	8.5	9.2
Water colour (mg Pt/l)	20	20

3.6.6 Water biology

Characteristic of large lakes in general, both Lake Limmaren and particularly Lake Erken show high habitat diversity. A total of five key habitats (*cf* 3.4.6) can be identified in both lakes, including a pelagial zone, a littoral zone dominated by emergent macrophytes, a wind-exposed littoral zone, a light-exposed soft-bottom zone, and a profundal zone. In the following description, these habitats and their characteristics are presented. Fish, which can move freely between habitats, are discussed in a separate section.

The pelagic zone

Phytoplankton biomasses, measured as the concentration of chlorophyll a, are high both in Lake Erken (annual average 5.4 µg chl a/l) and in Lake Limmaren (annual average 21 µg chl a/l) and phytoplankton is the dominant constituent at the base of the pelagic food web. Vrede (1987) calculated bacterioplankton biomass to be approximately 27% of that of phytoplankton during summer (21 and 78 µg C/l, respectively). Phytoplankton primary production in Lake Erken is high during the open water season, and typically ranges between 600 and 900 mg C/m^2 day (Pierson 1990). Bell (1984) estimated bacterioplankton production during spring on an areal basis to be some 20% of the primary production. The long water renewal times in the lakes, and subsequent low influence of allochtonous organic material, in combination with the high production of phytoplankton compared to bacterioplankton, indicate that bacterioplankton are dependent on organic carbon produced by biota within the lake basin (*e.g.* phytoplankton). The relationship between these two groups of producers may be described as a "microbial loop" (Azam *et al.* 1983). Vrede (1987) analysed the relationship between the two groups and concluded that there was no direct dependence of bacterioplankton on phytoplankton-derived carbon during summer stratification, but that bacterioplankton at least indirectly were controlled by autochtonous production of carbon. Hence, the conclusion that the production of carbon by phytoplankton is the most important energy mobilising process in the pelagial seems to be justified.

Diatoms and nitrogen-fixing cyanobacteria are the dominant components of the phytoplankton community in both lakes, with maxima during spring and autumn circulation, and during the later part of the summer stratification, respectively. In Lake Erken, chrysophytes (in early summer) and dinoflagellates (in late summer certain years) are also important.

Because of the long water renewal time most of the autochtonously produced organic matter is retained and respired or stored within the lake basin. A considerable share of the primary production is utilised by bacterioplankton and higher trophic levels already in the lake water, but removal by sedimentation is also a significant loss of carbon from this habitat. Losses through the outlet, on the other hand, are minimal. Among the dominant groups of phytoplankton, particularly the diatoms settle out in their vegetative state and constitute the most important fuel for the production of profundal biota (see below). Other phytoplankton groups, and particularly nitrogen-fixing cyanobacteria and flagellates, form grazing-resistant resting stages before settling.

The primary consumers of the particulate organic matter produced in the water are omnivorous zooplankton, mainly crustaceans. Their biomass has not been calculated on a carbon basis, but can be estimated to be of the same order of magnitude as that of phytoplankton (*cf* McCauley & Kalff 1981). In Lake Limmaren, the biomasses of heterotrophic bacterioplankton as well as those of zooplankton are considerably lower than that of phytoplankton. Nauwerck (1963) estimated the production at different trophic levels in the pelagial of Lake Erken per square meter and year to be 32 mg dry weight for phytoplankton, 8.6 mg dry weight for omnivorous zooplankton, and 1.4 mg dry weight for carnivorous zooplankton. He also concluded that bacteria and detritus were needed to cover the evident lack of phytoplankton carbon to cover the demands of omnivorous zooplankton. Finally, Rodhe (1958) concluded that in terms of primary production of carbon per unit of surface area, the pelagial is by far the most important habitat in Lake Erken, a statement that most likely also holds true for Lake Limmaren.

In conclusion, the pelagial zone is most likely the most important habitat contributing to total production of carbon in large lakes with long residence time of the water, such as Lake Erken and Lake Limmaren. Among pelagic biota, phytoplankton are the most important in terms of production. Bacterioplankton production to a great extent relies on phytoplankton-derived organic carbon and is therefore considerably lower. In terms of standing stock, phytoplankton are most important followed by herbivorous zooplankton and bacterioplankton. Much of the carbon produced is utilised by other biota in the pelagial, but a considerable share is lost to the profundal habitat through sedimentation. Losses though the outlet are small.

The emergent macrophyte zone

This zone is characterised by pronounced dominance of macrophytes and particularly by one single species, *Phragmites*, which forms dense and up to 4–5 meter high reed belts in sheltered locations. The dense vegetation gives some shelter to the area, which promotes sedimentation of fine particles and further growth of macrophytes in the soft substrate.

Due to the restricted exchange of water that follows, a highly variable environment is formed, with diurnal changes in temperature and concentrations of dissolved oxygen, nutrients etc. The canopy of macrophyte leaves above the surface restricts the light penetration to the sediments. Photosynthesising microorganisms are instead colonising the stems and leaves of the macrophytes, which constitute a three-dimensional substrate with large surface area. This microflora is one part of a rich and highly diverse periphyton community, consisting of organisms such as microalgae, cyanobacteria, heterotrophic bacteria, fungi, protozoa and nematodes. The biofilm in combination with the varying conditions within the macrophyte belt gives a diverse and rich fauna of larger benthic organisms, *e.g.* snails, insect larvae and crustaceans. The emergent macrophyte habitat is also an important "nursery" for fish fry, as it provides shelter and protection from predators as well as a wide variety of food items.

Due to the three-dimensional structure the littoral, and especially the periphyton community, acts as a very efficient filter of the water passing through from groundwater or from smaller tributaries. After the passage through the littoral zone, most of the nutrients and easily available dissolved organic compounds have been lost, and the water entering the pelagic zone contains mostly refractory organic matter (Wetzel 1996). However, there are also processes that may act in the opposite direction. Migration of fish and other organisms occurs frequently, acting as a transport mechanism for material between the littoral and other parts of the lake. The dramatic event of ice-out is another mechanisms that may reorganise and transport organic material and other substances within the lake.

The production of the emergent macrophyte habitat is high. Primary production of emergent macrophytes, calculated on an areal basis, may exceed pelagic phytoplankton production with between 5–8 times (Rodhe 1958, Wetzel 1992).

Altogether the emergent macrophyte habitat of Lake Erken and Lake Limmaren is much smaller, but considerably more productive, than the open water. The structure of the habitat is fairly well known in terms of diversity of the different communities. Measurements of biomass and primary productivity are rare and even more so are measurements of productivity of the higher trophic levels in this habitat.

The wind-exposed littoral zone

Characteristic of the wind-exposed littoral habitat in both Lake Erken and Lake Limmaren is the stony substrate and the dominance of the macroalga *Cladophora glomerata* which forms a dense belt close to the shoreline. This and other macroalgae serve as substrate for a very productive and diverse flora of diatoms and other microalgae. Few measurements of primary productivity exist from this habitat. According to Wetzel (1992), primary production among epiphytic algae can exceed the pelagic primary production by up to 6 times, calculated on an areal basis. The high primary production by small organisms provides a high flow of carbon energy to higher trophic levels. Due to the extremely short turnover time of the water, most of the carbon produced in this habitat is lost to deeper parts of the lake, and the organic accumulation is minimal. Snails (*e.g.* Theodoxus fluviatilis) and other omnivorous organisms scraping the rich flora off the substrate dominate the benthic fauna. In the most wind-exposed locations the benthic fauna, dominated by caddis larvae such as *Tinodes waeneri*, is firmly attached to the substrate and feeds on microalgae growing on the gallery. The algae in turn benefits from nutrients recycled by the omnivore in a complex trophic interaction (Hasselrot 1993). Also the wind-exposed littoral is an important spawning habitat for many species of fish from other parts of the lake.

The zebra mussel (*Dreissena polymorpha*), is a non-native species which was accidentally introduced in Lake Erken in the mid 1960'ies. It is now a major constituent of the fauna on hard bottoms at a depth of about 1–10 meters. Hjellström & Saetre (1992) studied Dreissena along transects in the eastern part of the lake and found that the abundance varied between 200 and 2 000 individulas/m^2 and that the biomass varied between 0.3 and 2.9 kg/m^2 with the highest values on larger stones. They concluded that the most important factor regulating the distribution of the mussel was the quality of the bottom substrate; the harder the more densely colonised. Particularly in shallow areas, the mussel was restricted to large substrates. The population was found to be dominated by old individuals while recruitment probably was low, indicating that the population may have been close to the carrying capacity. The clearance rate of the mussels has been estimated to 50–300 ml/individual hour (Sprung & Rose 1988; Horgan & Mills 1997). Multiplying this value with the abundance figures given by Hjellström & Saetre (1992), it is evident that the mussel has a potential to affect many of the organisms in plankton as has been suggested also in other studies (Horgan & Mills 1997).

Altogether, the wind-exposed littoral can be characterised as a highly productive habitat, in which accumulation of organic matter is low. Most of the carbon produced is either respired or lost to deeper parts of the lake.

The light-exposed soft-bottom zone

A light-exposed zone without macrophytes but with photosynthesising organisms in the form of cyanobacteria, diatoms and in certain areas also the green alga *Cladophora aegagrophila* is characteristic of both Lake Erken and Lake Limmaren. The productivity of this zone, which extends down to depths of 6–8 m in Lake Erken and to 2–3 m in Lake Limmaren is not known, but it seems likely that it may contribute substantially to the total production of carbon (*cf* above). Also the composition and diversity of higher trophic levels are virtually lacking. However, Andersson (1969) studied areas at a depth of 4–6 m in Lake Erken, covered by *Cladophora aegagrophila*, and found a benthic fauna community very rich in individuals, dominated by the omnivorous *Asellus aquaticus*. Average biomass of this animal was 15.6 g ww/m^2 and its annual production was calculated to 31.6 g/m^2 year. In terms of production of carbon, this corresponds to 1.5 g C/m^2 year, while the corresponding primary production is approximately 180 g C/m^2 year in the pelagial. Assuming 90% losses in the transfer from plants to *Asellus*, production of this animal alone consumes almost 10% of the total areal production. Such a high production of organisms at higher trophic levels may be taken as an indication that the primary production in the habitat is substantial. However, an alternative hypothesis is that *Cladophora* provides *Asellus* with shelter from fish predation while carbon energy to sustain its growth is imported from the pelagic zone.

Altogether, very little is known about the structure and production of the food web in the light-exposed soft-bottom habitat. Primary production may be substantial, which merits further investigations.

The profundal zone

The structure and functioning of the profundal habitat was generally described in chapter 3.5.6. Characteristic for the deep eutrophic lakes is that their profundal zone is the end station of the rich pelagic production. This autochtonously produced material to a great extent settles to the bottom and is utilised by various organisms living in the sediment.

Due to the depth of these lakes, transformation and decomposition processes occurring already in the lake water may alter the composition and nutrient status of the organic material that reaches the profundal. However, compared to the brownwater lakes where most input of organic substances have allochtonous origin, the organic matter reaching the profundal zones of the eutrophic lakes is more available to and easily degradable by the benthic organisms. This is reflected in a comparatively higher biomass and diversity of the benthic fauna. The profundal habitat is also highly dynamic, immediately responding to seasonal variation in the input of organic matter. Goedkoop (1995) studied the pelagic-benthic coupling in Lake Erken and found highly taxon-specific responses closely correlated to feeding behaviour of the different groups. A rapid response to the spring diatom sedimentation was recorded for nematodes and ostracodes and considerable time-lags were found for population development of copepods and chydorids, whereas the predominant macroinvertebrates, chironomides, did not immediately benefit from the input of fresh organic carbon. Carbon budget calculations showed that during spring between 8 and 57% of deposited organic carbon was utilised by the meiobenthos, while the chironomides utilised less than 2%. Total bacterial production in the surface sediments was more correlated to temperature, although a significant correlation to the availability of newly settled organic material was also noted. However, on average bacteria mineralised only 4% of the deposited organic matter. An experimental study of benthic microbial response to an autumn sedimentation dominated by diatoms in Lake Erken (Törnblom & Rydin 1998) also showed a quick response of bacterial activity, in this case resulting in a microbially mediated utilisation of about 10% of the added carbon. Thus, a substantial portion of the settling material seems to remain undegraded.

Investigations of the effects of autumn sedimentation events in eutrophic lakes where cyanobacteria are dominating have shown that the cyanobacteria are more resistant to decomposition (Brunberg 1993). It is also important to note that the settling of organic matter is not solely a one-way process. Cyanobacteria and many other phytoplankton form resting stages, which settle to the bottom and later may be recruited to the water column as inocula for phytoplankton growth. These resting stages, and in some cases also the vegetative form of the cyanobacteria, are able to survive for long time periods within the sediments. Attempts to quantify the size of the benthic inocula to cyanobacterial water blooms are currently performed both in Lake Erken and Lake Limmaren (Karlsson & Brunberg in prep). Calculations based on the growth of phytoplankton in lake water have shown that between 5 and 17% of the pelagic biomass must be recruited from sediments. Other processes that may recycle organic carbon to the lake water or even further to terrestrial ecosystems, is migration of fish between the different lake habitats and hatching of insect larvae.

Attempts to quantify the total amount of the utilisation of carbon in sediments have shown that roughly half of the yearly sedimentation of carbon in eutrophic lakes is mineralised (Hamilton-Taylor *et al.* 1984, Cappenberg *et al.* 1982), while the rest may be more or less permanently buried in the sediments.

In conclusion, the profundal habitat of deep eutrophic lakes is fuelled mainly by settling autochtonous matter, which shows pronounced seasonal variations in amounts and quality. The fate of the added carbon is loss by respiration processes, transfer to higher trophic levels of the profundal zone and recycling to the lake water by recruitment (plankton) or migration (fish, insects) processes. A significant proportion of the carbon is permanently buried in the sediment.

Fish

Both Lake Erken and Lake Limmaren have been subject to standardised gill net fishing, performed 1996 and 1991, respectively (Table 20). In Lake Erken a total of 9 different species were found, and the CPUE (catch per unit effort) was 66 individuals and 2.0 kg. Data from various studies performed over several of the past decades (Weyhenmayer 1999) show that the fish community of lake Erken altogether includes at least 16 different species, with dominance of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), smelt (*Osmerus eperlanus*), ruffe (*Acerina cernua*), pike (*Esox lucius*), burbot (*Lota lota*) white bream (*Blicca bjoerkna*), and bleak (*Alburnus alburnus*).

The standardised gill net fishing in Lake Limmaren gave a CPUE of 165 individuals and 4.6 kg. In addition to the 7 different species caught in this investigation, earlier studies (referred in Pettersson & Lindqvist 1993) have found the additional species rudd (*Scardinius erythrophthalmus*) and pike (*Esox lucius*).

In comparison with the average number of species and CPUE of individuals and biomass in lakes in Uppsala County (5.8 species, 81 individuals, and 3.6 kg) both lakes have a more diverse fish community. This is partly due to that both lakes are large enough to harbour pelagic planktivoruos school-forming species in the form of smelt (*Osmerus eperlanus*) and accompanying predators, *e.g.* pikeperch (*Lucioperca lucioperca*). Lake Limmaren has a higher standing stock and higher number of individuals than the average lake in Uppsala County, while the situation in Lake Erken is the opposite. Both lakes are richer in terms of number of species and number of individuals than both the brownwater and the oligotrophic hardwater lakes in the Forsmark area (*cf* Chapter 3.4.6 and 3.5.6). By biomass both lakes are richer than the brownwater lakes while compared to the oligotrophic hardwater lakes, Lake Limmaren is richer but Lake Erken is poorer. Finally, in comparison with lakes in Sweden in general, the values are higher in both cases, presumably a result of the nutrient-rich conditions of the freshwaters of the province of Uppland.

Altogether, both lakes can be characterised as having a diverse and productive fish community including all species typical of lowland lakes and, in addition, pelagic planktivores and their predators.

Table 20. Data from standardised survey gillnet fishing in Lake Erken and Lake Limmaren. From Odelström *et al.* (1998) and Pettersson & Lindqvist (1993). Pi=pike, Ro=roach, Pe=perch, P-P=pike-pearch, Ru=ruffe, Br=bream, Wh=white bream, Bl=bleak, Sm=smelt

Lake	Elevation m.a.s.l.	Lake area km^2	Lake depth average	max	Fish species	No of species	CPUE no of ind.	kg
Erken	11.7	24.2	9.0	20.7	Pi,Ro,Pe,P-P,Ru, Br,Wh,Bl,Sm	9	66	2.0
Limmaren	3.9	5.9	4.7	7.8	Ro,Pe,P-P,Ru, Br,Wh,Sm	7	165	4.6
Average	7.8	15.0	6.8	14.2		8.0	115.5	3.3

3.6.7 Ontogeny of the deep eutrophic lake type

Based on the studies of Fries (1969) the ontogeny of Lake Erken over the 10 000 coming years can be estimated. The accumulation of lake sediments in the deepest parts of the basin is maximally 1 m over the 2 500 years that have passed since the lake was isolated from the Baltic Sea. Assuming the same rate of sediment deposition, the accumulation of sediments during the coming 10 000 years would be 4 meters. The accumulation of sediments in other parts of the lake would be considerably lower. Thus, even after 10 000 years from now, Lake Erken will be a large and, for the region, relatively deep lake (maximum depth ca 16 m).

The situation in Lake Limmaren is different. First, the sedimentation rate over the past 1 000 years has been considerably higher than that in Lake Erken, with an accumulation of some 1.4 m of sediment in the deepest part of the lake (Brunberg & Blomqvist unpublished). Secondly, Lake Limmaren is much more shallow than Lake Erken, with a maximum depth of 7.8 m and a mean depth of 4.7 m. Calculated for the coming 10 000 years, the accumulation of sediments in Lake Limmaren will be about 14 m. This sedimentation rate is valid only for the deepest part of the lake, but in view of the fact that Limmaren has a large part of the bottom area at a depth larger than 6 m, it seems reasonable to conclude that the basin will be completely filled with sediments somewhere between 5 000 and 10 000 years from now. The ontogeny of this kind of lake is difficult to judge since, as far as we know, there are no good examples in the area to compare with. A first transition to a reed-marsh seems very likely but whether the end station is a mire or a wetland forest (dominated by alders) is highly uncertain and merits investigation by a physical geographer.

3.6.8 The deep eutrophic lake –a synthesis of the ecosystem functioning

Summarising the rich information about the ecosystems of the eutrophic Lakes Erken and Limmaren, a hypothetical model for the ecosystem functioning in this kind of lakes can be formulated (Figure 5). Due to the large volume of water and the limited drainage area, the water renewal time is low and, as a result internal processes dominate the metabolism of carbon in the systems. Habitat diversity is high and includes all the five key habitats that can be distinguished in lakes (*cf* 3.4.6). Traditionally, the most important habitat in terms of production of organisms at the base of the food web is considered to be the pelagic zone (*cf* Rodhe 1958). That pelagic production really is important is evidenced by the fact that primary production alone contributes up to one gram of carbon per m^2 and year (Pierson 1990). However, also the littoral zones may contribute significantly, especially in Lake Erken, which has a relatively high transparency. Assuming the euphotic zone extend down to four meters, which is a conservative estimate, the area covered by littoral producers would be 4.7 km^2 or some 20% of the lake area. Wetzel (1992) argues that productivity in the emergent macrophyte and submersed littoral zones may be up to 7–8 times higher per unit of area than that of the pelagial. Hence, primary production in the littoral zone of Lake Erken may well match that of the production in the pelagial. Although Lake Limmaren has a much shallower euphotic zone, ca 2 meters, the corresponding calculation yields that also in this lake production in the littoral zone may match that of the pelagial.

Because of the long water renewal time and the resulting small losses of material through the outlet, most of the pelagic production will sooner or later end up in the profundal sediments (Figure 5). The same is valid also for most of the production in

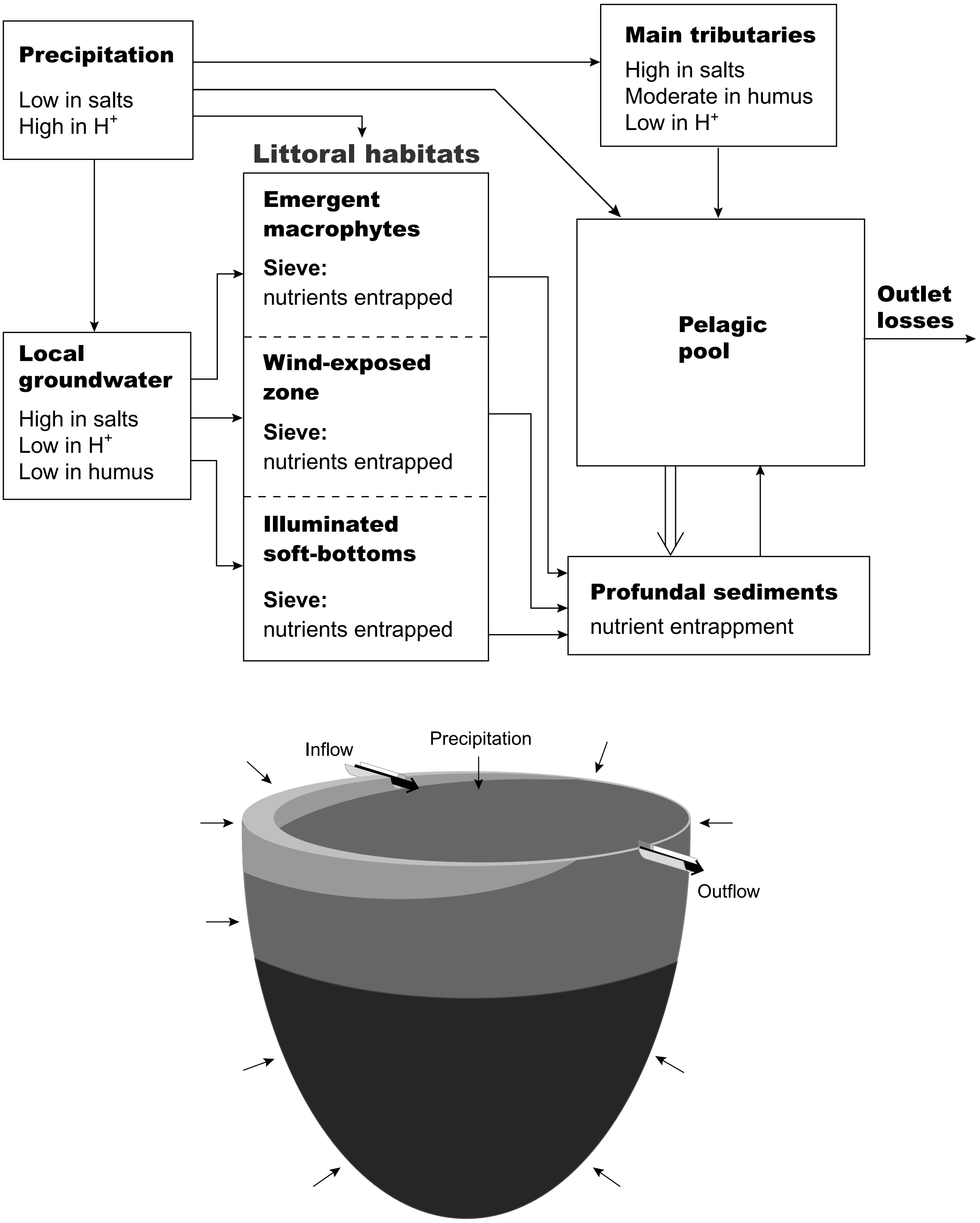

Figure 5. A tentative model for the functioning of the deep eutrophic Lakes Erken and Limmaren.

the wind-exposed and illuminated soft-bottom areas, respectively. Until recently, the emergent macrophyte zone was considered to be a zone where produced organic carbon may accumulate. However, results from an ongoing project, the aim of which is to determine the velocity and direction of water currents in different parts of Lake Erken, indicates a surprisingly high turnover of water also inside the reed belts (Weyhenmeyer 1999, pers. com.). Thus, also the organic production in the wind-sheltered littoral, from organisms other than rooted plants, may well end up in profundal sediments.

Far from all of the settled organic material is finally deposited in the profundal sediment. Of the sedimenting organic carbon roughly 50% is recycled by resuspension, respiration and various biological transport processes (migration, hatching of insects etc). Regarding other elements, final deposition may be both higher and lower than that of carbon. For example, it seems like the sediments of Lake Limmaren at present serve as a source of phosphorus to the water column (Pettersson & Lindqvist 1993) while in Lake Erken the phosphorus retention calculated on an annual basis is 30% (Pettersson 1985). In contrast, Broberg & Andersson (1991) calculated the retention of Cs-137 to vary between 80 and 100% in lakes with long turnover time of the water.

Altogether, the information about the structure and functioning of the deep eutrophic lake ecosystems such as those of Lakes Erken and Limmaren is, with few exceptions, good enough for mathematical modelling of the flow of energy and material through the systems. Regarding relationships between different habitats within the lake basin, there is still need for studies on the production and trophic relationships among biota in the littoral zone and its sub-compartments. Particularly, the role of the light-exposed softbottom zones has been poorly studied. Regarding the fate of contaminants entering the basin via diffuse inflow of water, studies of the hydrology of the lake basin are also needed.

4 The formation of new lake basins in the Forsmark area during the coming 10 000 years

The formation of new lakes due to the shoreline displacement in the Forsmark area has been analysed by Brydsten (1999). Altogether, 14 larger lake basins that will be formed in the area between Forsmark and Gräsö have been identified (Figure 6). These lakes, which will appear between 2 600 and 7 700 years from now, vary in size from 0.3 to 8.1 km^2 (Table 21). Most of the lakes will be relatively shallow, with mean and maximum depths below 3 and 6 meters, respectively. However, a chain of large and relatively deep lakes will be isolated late (more than 5 000 years from now) along the W side of the island of Gräsö. These lakes will have average and maximum depths of more than 4 and 19 meters, respectively. From the point of view of effects of a possible leakage of radioactive material from the low level repository SFR, lake number 4 (in the following termed "Lake 4") has been identified as the most important since the SFR will be located in the drainage area of this lake (Figure 6). This lake, which will emerge about 2 900 years from now, will have a surface area of 1 km^2, a mean depth of 1.7 m and a maximum depth of 4.1 m, thus belonging to the majority of small and relatively shallow lakes. The size of its drainage area has been estimated to 29.4 km^2 and the water renewal time to 102 days. One of the lakes present in the Forsmark area today, Lake Eckarfjärden, will drain to Lake 4 and the catchment of this lake will represent the uppermost part of the catchment of Lake 4. The differences in elevation within the catchment of Lake 4 will be relatively small, at most ca 30 meters (calculated from the maximum altitude of the catchment of L Eckarfjärden and to the depth of the threshold of Lake 4 at –15 m). At present, a major share of the catchment area is submerged, *i.e.* located at the bottom of the Baltic Sea. The geology of the catchment in its entirety has been assumed to be similar to that of Lake Eckarfjärden, with bedrock consisting of granites and gneisses covered by glacial till. As an area weighted mean value from a depth of 0.5–1 m, this glacial till will contain more than 20% of calcareous matter in the fine grain fraction. In the following chapter, these data have been used to predict the initial lake type to be formed and, together with information about existing lakes, its ontogeny during the first millennia after formation.

After leaving Lake 4, the water will pass through a short river north of the basin and enter a chain of tightly coupled small lakes (Lakes 5–8) before the river turns east towards Gräsö. The water from this river will then enter the large and relatively deep lakes 13 and 14 which will be isolated from the Baltic Sea some 6 800 and 7 700 years from now. These lakes will also drain both the two existing rivers Forsmarksån and Olandsån which will join into one river less than a millennium from now. As a result of the drainage of the combined river Forsmarksån-Olandsån, lakes 13 and 14 will be characterised by having a very large drainage area. The river draining the area including Lakes 4–8 will in comparison be relatively small.

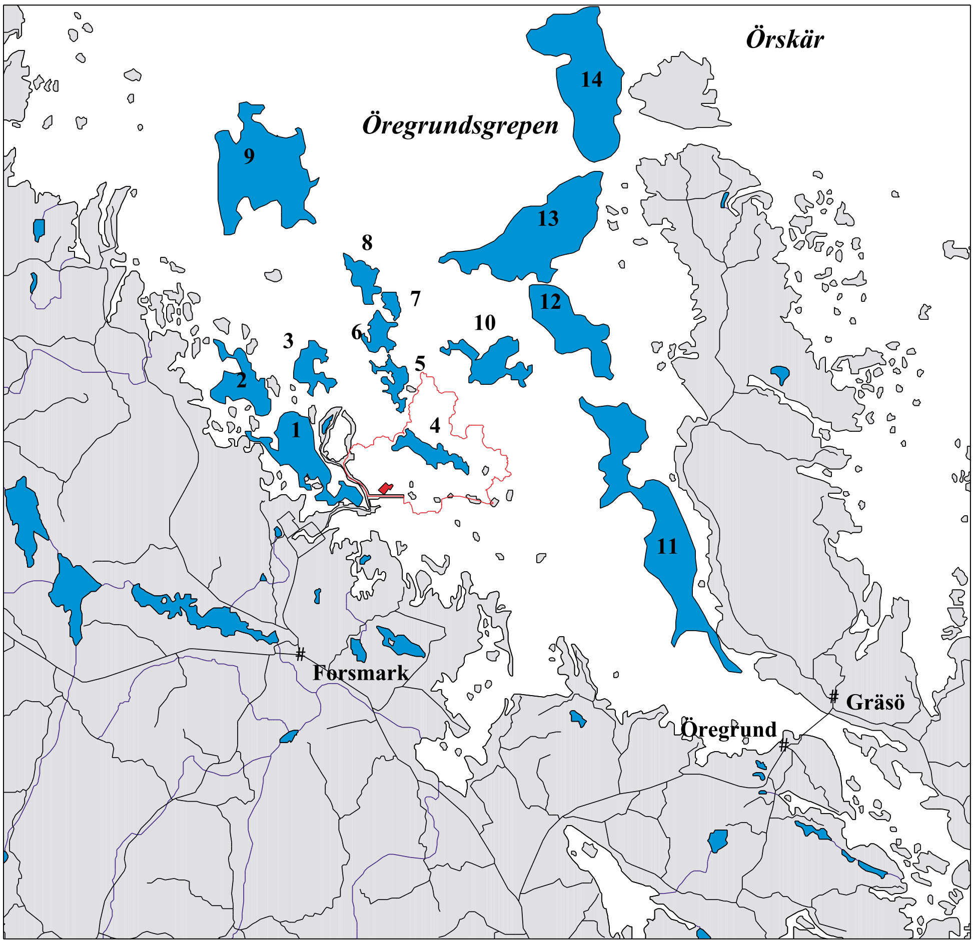

Figure 6. Formation of larger lake basins in the area between Forsmark and Gräsö during the coming 10 000 years. Numbers refer to Table 21. From Brydsten (1999).

Table 21. Current elevation (negative values), lake morphometry, and date of birth of future lakes in Öregrundsgrepen. The location of the lakes is presented in Figure 6.

Code	Elevation (m)	Area (km^2)	Volume ($m^3 \cdot 10^6$)	Average depth (m)	Max depth (m)	Born (AD)
1	–3.60	3.08	8.3	2.7	6.0	2600
2	–6.00	1.82	0.9	0.5	2.4	3000
3	–9.30	1.04	1.7	1.6	4.2	3600
4	–15.20	1.06	1.8	1.7	4.1	4900
5	–15.20	0.74	1.0	1.3	4.2	4900
6	–15.20	0.73	1.7	2.3	5.2	4900
7	–15.20	0.31	0.3	0.9	2.0	4900
8	–15.20	0.79	0.9	1.1	3.1	4900
9	–15.70	7.11	25.0	3.5	7.2	4900
10	–16.20	1.83	3.3	1.8	6.6	5000
11	–21.40	8.14	33.3	4.1	19.3	5400
12	–22.90	3.33	23.7	7.1	34.6	6800
13	–22.90	7.12	36.4	5.1	22.3	6800
14	–26.40	7.61	31.5	4.2	19.9	7700

5 Discussion

5.1 What kind of ecosystem will develop in Lake number 4 shortly after its isolation from the Baltic Sea?

In the search for different lake types that potentially may emerge in the Forsmark area due to land-rise during the coming 10 000 years a total of three, functionally highly different, lake types have been identified. Existing information about these lakes; the oligotrophic hardwater type, the brownwater flow-through type, and the deep eutrophic type, has been presented in Chapters 3.4, 3.5 and 3.6, respectively, and will only be briefly summarised here.

The oligotrophic hardwater lake type can be regarded as an ephemeral stage with duration of 1–2 millennia and which most of the isolated lakes initially undergo. This lake type is often relatively small, but most importantly always shallow, and has an intermediate water renewal time. The inflow of water to the lake basin is characteristically "diffuse"; *i.e.* most of the water enters through the bottom of the lake basin while visible inlets are missing. Initially, the ecosystem is characterised by two major habitats, the illuminated soft-bottom sediments and the pelagial zone. Later in the ontogeny a third important habitat, the *Sphagnum*-littoral, develops and a mature oligotrophic hardwater lake can thus be characterised as having three key habitats. By production of organisms, the soft-bottom area is most likely strongly dominant as it functions as a sieve for nutrients and organic carbon in the inflowing water before it enters the pelagic zone. A similar function may also be characteristic of the *Sphagnum*-littoral in its initial developmental stages. However, as this habitat matures, it is successively uncoupled from the main inflow of groundwater to the lake basin, forming an isolated, rainwater-fed hydrological system. The less developed of the three habitats is the pelagic zone, the bioproduction in which most likely relies on biologically mediated nutrient transport processes from the soft-bottom area (*e.g.* excretion by fish). A characteristic fish community of mature oligotrophic hardwater lakes has a high biomass but a low diversity and is dominated by Crucian carp (*Carassius carassius*). The pronounced dominance of this species reflects the poorly oxygenated conditions that typically occur in this shallow lake type during winter.

The oligotrophic hardwater lake type successively, as the *Sphagnum*-littoral expands, evolves into a brownwater lake type, although brownwater lakes that have not passed the hardwater stage are also found in the area. The latter brownwater lake type is typically found within the main part of the River Forsmarksån and is characterised by a high flow-through of water from the upper parts of the drainage area, which are dominated by mires. Already at isolation from the sea, this lake type receives highly stained water rich in humic substances. The humic matter reduces the depth of the euphotic zone and this results in that on most of the bottom area light is not enough to sustain photosynthesis. Also in this lake type a *Sphagnum*-littoral successively develops, and in a mature lake three key habitats can be identified. The dominant habitat in terms of production of organisms is most likely the pelagic zone, in which bacterioplankton dominate the mobilisation of energy at the base of the food web. Most of their energy originates from allochtonous organic carbon imported from the catchment area. Due to the characteristically short water renewal time, sedimentation processes are of relatively small importance and most of the carbon produced is lost through the outlet. Production of organisms in the *Sphagnum*-littoral and profundal zones is low, due to the lack of light and due to the poor quality of the humic matter as a substrate for bacterial growth. However, regarding diffuse inflow of groundwater, both these habitats may at least partly function as sieves for nutrients and organic carbon. Production at higher trophic levels (*e.g.* benthic fauna and fish) within the brownwater lake type is very limited and the fish community is typically characterised by low biomasses and abundances, while the diversity may be as high as in other lowland lake types.

The deep eutrophic lake type is not represented among the existing lakes in the Forsmark area today. However, this lake type is found in an adjacent area some 60 km from Forsmark. It is characterised by a limited drainage area, a large lake volume and a slow turnover time of the water. All the five key habitats that maximally are found in lakes are represented in this lake type: the pelagial, the emergent macrophyte dominated littoral zone, the wind-exposed littoral zone, the light-exposed soft-bottom zone, and the profundal zone. Traditionally, the pelagial has been regarded as the dominant habitat in terms of mobilisation of carbon energy in the system. However, calculations using recent data about the productivity in the littoral habitats indicate that altogether, these three units may be equally important to the pelagial. As a result of the long turnover time of the water, most of the production of carbon is retained within the lake basin and sedimentation to the profundal zone is the main retention process. The fact that very little sediment accumulation takes place in the three littoral habitats is an indication that most of the production there most likely also ends up in the profundal zone. The retention of different elements in the profundal sediments is highly variable – from between 0–30% regarding certain nutrients (*e.g.* P and N) to almost all of the deposited material regarding for example Cs-137. Regarding carbon, estimates of the final burial vary between about 30 and 70% for different types of lakes. A reasonable estimation for the average of eutrophic deepwater lakes seems to be 50%. The other 50% are either respired or are transported back to the lake water via resuspension or various biological recycling mechanisms.

Using information about the three main lake types described above, the characteristics and ontogeny of new lake basins isolated from the Baltic Sea due to the land rise, and particularly those of Lake 4, can be prognostisised. Existing data about Lake 4, and corresponding values for the three different lake types are presented in Table 22. Comparing the values, it is evident that Lake 4 in many respects will be most similar to the brownwater lakes of River Forsmarksån. Regarding lake area, average depth, and maximum depth the similarity is striking. However, by volume of water, Lake 4 will be almost twice as large as the brownwater lakes and, consequently, the water renewal time

Table 22. Lake morphometry and drainage area characteristics of Lake 4 compared to those of the three main lake types present today along the coast of the province of Uppland. For hardwater and brownwater lakes the figures represent median values from Tables 4, 5, 10 and 11.

Lake	Area, km^2	Average depth, m	Maximum depth, m	Volume, Mm^3	Water renewal time, days	Catchment area, km^2	Ca in soils %
Lake 4	1.06	1.7	4.1	1.8	89	29	>20
Hardwater	0.07	0.9	2.0	0.07	240	1.9	>20
Brownwater	1.14	1.5	2.7	1.0	31	106	<6
Erken	24.2	9.0	20.7	213	2 700	141	?
Limmaren	5.9	4.7	7.8	27	2 140	21	?

will also be substantially longer. The drainage area of Lake 4 is considerably smaller than that of the brownwater lakes, and in this respect it is more similar to the hardwater lakes. Another important aspect by which Lake 4 is most similar to the hardwater lakes is by the average calcium content of the surface soils in the drainage area (Ca in soils, Table 22) which is very high, exceeding 20%. Altogether, from this comparison, Lake 4 takes an intermediate position between the brownwater and hardwater lake types.

Knowing the morphological coherence of Lake 4, next question to be analysed is: which characteristics of the lake ecosystem are coupled to morphology? The key features of the three different main lake types with respect to morphometry and drainage area characteristics are presented in Figure 7. The hardwater lakes are small, shallow, and have an intermediate turnover time of the water, and their drainage areas are characterised by very high calcium content of the surface soils. As a result of these characteristics, the water, which is rich in dissolved salts, is relatively clear and large parts of the sediments have light enough to develop a soft-bottom habitat dominated by photosynthesising organisms. This is the key habitat in the lake, functioning as a filter for inflowing groundwater entrapping nutrients and base cations via biological uptake and/or precipitation followed by storage in the sediments. Based on the fact that Lake 4 meets the demands of this lake type to be shallow and to have a high calcium content of soils in the drainage area, it seems likely that this new lake will undergo an oligotrophic hardwater stage just after formation. However, looking at another key factor for the development of the hardwater stage, the water renewal time, which in turn is coupled to the colour of the water, the prediction becomes less certain.

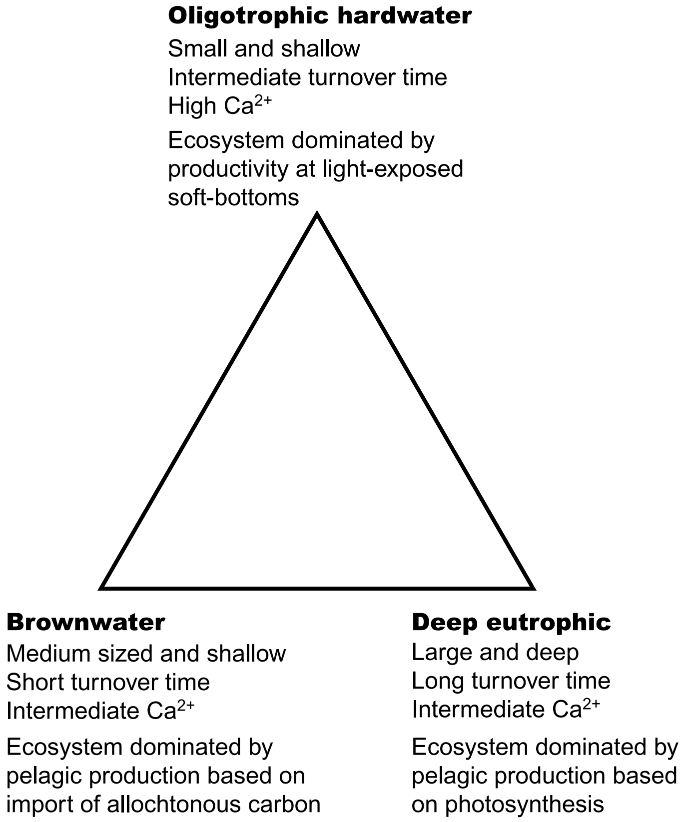

***Figure** 7. Characteristics of the three different lake types in the Forsmark area.*

By turnover time, Lake 4 is more similar to the brownwater lakes, which then indicates that the water colour already at formation will be considerable. Notably, the lakes that were formed in River Forsmarksån below the 13 m high falls at Lövstabruk do not seem to have passed through an oligotrophic hardwater stage, despite their relative shallowness. The most likely reason is that the water colour initially was high enough to prevent light from penetrating to the soft-bottom sediments. If this is true, there must be some coupling between the oligotrophic hardwater stage and the presence of a thick microbial mat at the surface sediment dominated by photosynthesising organisms. However, the importance of photosynthesising biota to the development of the hardwater stage is unknown and merits further investigation. A factor that must be coupled to the inflow of humic matter to the lake ecosystem is the time of isolation of major parts of the drainage area, since the presence of humic matter is a function of the percentage of mires in the area. The altitude difference between the lakes downstream Lövstabruk in river Forsmarksån is 42–43 meters, with a large part of the area (> 60% in the case of N Åsjön) located above the 13 m high falls at Lövstabruk. The average elevation of the drainage area of N Åsjön is 28.6 meters and the lake is situated at 12.4 meters. Using a shore-line displacement rate of about 0.5 m per century (Brydsten 1999), these areas were isolated from the sea more than 2 600 years before the lake, a time which evidently allows for mires to develop. The corresponding altitude difference for the catchment of Lake 4 is some 30 meters, and the areas already isolated from the Baltic Sea, at heights in the future between 15 (present shoreline) and 30 meters, are relatively smaller. The average elevation of the drainage area is –5.8 meters and the lake is located at –15 meters. Thus, large parts of the drainage area of Lake 4 will be isolated from the sea relatively shortly from the isolation of the lake itself. Therefore it seems unlikely that mires would have developed to such an extent that the water colour at formation of the lake would be high enough to prevent light exposure of shallow sediments. Summarising this knowledge it seems likely that Lake 4 will undergo an oligotrophic hardwater stage shortly after formation, although the duration of this stage may be shorter than that of the existing hardwater lakes.

Both regarding the existing brownwater and hardwater lakes in the Forsmark area, it is evident that there is a successive growth of mire around the lake basin, which results in the formation of a *Sphagnum*-littoral habitat at the border between the mire and the lake. There is no reason to believe that Lake 4 would deviate from this pattern. The functioning of this habitat, as a sieve for nutrients and cations in the inflowing water or as a dike, which groundwater from the soils of the drainage area has to pass under to reach the lake, is highly uncertain and is another key to the entrapment of nutrients (as well as eventual contaminants) from the inflowing water. Most likely, there is a successive change in the function of the *Sphagnum*-littoral, from being a sieve to being a dike (*cf* 5.2 below).

Another important difference between the hardwater and the brownwater lakes, related to the function of lake ecosystems as traps for nutrients and contaminants of the inflowing water, is the presence or absence of open watercourses through the system. The brownwater lakes are characterised by a dominant flow of material through the system from a main tributary passing through the lake. Furthermore, due to the presence of very high amounts of organic matter, most of the nutrients are tied to organic compounds and their bioavailability is low. Combined with the lack of filtering of this water through a littoral system, most of the substances entering the lake most likely are transported further to downstream localities. Contrastingly, in the mature hardwater lakes which are completely surrounded by a *Sphagnum*-littoral, the water is filtered twice; first at the inflow to the basin (which either is through the *Sphagnum*-littoral or through the microbial mat at the soft bottoms or both) and then again as it leaves the lake through the mire. A highly reasonable conclusion about the consequence of this double filtration is that most of the ions in the water will be trapped in the lake basin and that transport to downstream localities is minimal. Thus, depending on the character of the system, nutrients (and contaminants) can either be trapped or exported to downstream localities. Lake 4 most likely will take an intermediate position is this respect.

Assuming that Lake 4 does not function as a trap for contaminants, these substances will flow via a chain of smaller lakes (Lakes 5–8, Figure 6) and end up in the larger and deeper basins 13 and 14. These large lakes have morphometrical characteristics similar to those of Lakes Limmaren and Erken. They will be somewhat larger and deeper and have a slightly larger volume than Lake Limmaren but will be smaller than Lake Erken in all respects but maximum depth. A considerable difference between Lakes 13 and 14 and Lakes Erken or Limmaren will be that the drainage area of these new lakes, which will include both the large Rivers Olandsån and Forsmarksån, will be very large. As a consequence, the turnover time of the water will be much shorter than that of Lakes Erken and Limmaren and the water colour will be much higher. Using the combined drainage area of Rivers Forsmarksån and Olandsån today (1 261 km^2), and a volume of lake 13 and 14 of 36.4 and 31.5 Mm^3, respectively, the turnover time of the water in these lakes would be 42 days for lake 13 and 36 days for Lake 14. Since the real drainage area will be larger than that used in the calculation, the turnover time of the water will be even shorter. Hence, in this respect Lakes 13 and 14 will very much resemble the brownwater lakes, with highly stained water and a thin productive layer. Based on this conclusion and on the fact that nutrients as well as contaminants to a large extent will be tied to the dissolved organic matter and not to any greater extent be taken up by biota or subject to direct sedimentation, it seems unlikely that these two lakes will concentrate contaminants in the sediments. Instead, most of the material entering these lake basins will be transported further downstream, *i.e.* to the Baltic Sea.

Altogether, during the first millennium after formation, it seems likely that nutrients and contaminants entering the drainage area of Lake 4 will be trapped in the *Sphagnum*-littoral or in the microbial mat on the illuminated soft bottoms, especially if entering the lake basin directly via the groundwater. If entering the lake basin with the relatively small river, a considerable share will most likely be transported further downstream to the Baltic Sea. In later developmental stages the functioning of the lake ecosystem of Lake 4 will most likely change due to the growth of mire around the basin.

5.2 How will the ecosystem of Lake 4 develop during the first millennia after isolation?

Assuming that Lake 4 directly after isolation develops into an oligotrophic hardwater lake, the ontogeny of its basin will principally follow that of the oligotrophic hardwater lakes described in Figure 2. During the first millennium (judged from the conditions in Lake Vikasjön (*cf* brownwater lakes, 3.5), the system will be characterised by one key habitat of major importance to the turnover of nutrients and other ions in the system, *i.e.* the light-exposed softbottom zone. Successively another important habitat will develop; the mire-littoral zone dominated by *Sphagnum*. As long as the formation of peat between the bottom of the lake and the *Sphagnum*-littoral is not complete, this habitat will most likely function as a sieve for inflowing groundwater and thus accumulate eventual contaminants. Later, when the habitat is well developed, it may act as a dike and force inflowing groundwater to enter the lake basin after passage underneath the peat layer. Also in that case, the microbial mat on the illuminated soft-bottoms will act as a sieve and nutrients and other material will still be trapped in the basin. During later developmental stages, when the mire completely covers the basin and is in the process of developing into a bog, the former lake basin will most likely function as a flow-through system, in which water, nutrients, and contaminants are passing through along the open water in the lagg which creates the border between the wetland and the dry terrestrial ecosystems. The duration of the different developmental stages of Lake 4 is difficult to assess, as no data on growth of mires in this area are available. However, the duration of the oligotrophic hardwater stage in Lake Vikasjön in the upper part of the River Forsmarksån has been calculated to about 1 000 years, based on paleo-ecological studies of the sediments (Ingmar unpubl). From the same investigation, sedimentation rates have been calculated to 1–1.5 mm per year during the oligotrophic hardwater stage and 1 mm per year during the following brownwater stage. Applying these values on Lake 4, and assuming a similar duration of the oligotrophic hardwater stage, the life span of Lake 4 may be predicted to at least 3 600 years. This calculation does not include the effects of mire growing into the lake. The effects of the growth of mire may be that the life span of the lake is shortened, but it may as well counteract the process of filling out by enhancing the lake threshold if the mire grows also within the outlet. However, the latter process may be of less importance in this case, as Lake 4 will have a substantial flow-through of water (estimated water renewal time 89 days, Table 22).

Finally, it must be stressed that although the theoretical models about the functioning of the brownwater lakes and the hardwater lakes presented in this paper may seem clear, the facts behind the models to a great extent remains to be verified. The discussions and conclusions regarding the fate of contaminants that eventually may enter the lake systems are thus highly speculative. In the following chapter, we have outlined the most urgent research needs with respect to the potential functioning of the ecosystem as a trap for contaminants.

6 Need for further research

In this report, we have formulated tentative models of the functioning and ontogeny of three different lake types that are found today or that may develop in the future within the Forsmark area. We have identified some key pieces of a 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 ecosystems are functioning or will develop during different stages of their ontogeny. Some areas where more research is urgently needed include:

- Studies on the hydrology of the lake systems. This is essential for the basic understanding of the functioning of the lake as a biological system, and it is strongly needed to evaluate the tentative ecosystem models for the oligotrophic hardwater and brownwater lakes, respectively.
- Studies on the mire-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 strongly 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 areas of oligotrophic hardwater lakes, 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.
- Studies of the light-exposed soft bottom areas of deep eutrophic lakes is also needed, in order to assess the relative importance of this habitat vs pelagic lake metabolism.
- The pelagic ecosystem requires less attention, but for the oligotrophic hardwater lakes the relationship between primary production and bacterioplankton production needs to be examined and quantitative relationships between phyto- and zooplankton need to be determined.

Altogether, the conclusion from this report is that the emphasis in further research should be put on the understanding of the oligotrophic hardwater lake ecosystems. This ecosystem is the less well-known of the three lake types, and it will certainly develop in several of the new lakes in the Forsmark area; in Lake 4 as well in the many other, smaller lakes that will be formed (not included in Figure 6/Table 21). To evaluate their functioning as a trap for contaminants the studies need to focus on the hydrology of the lake basin and the basal production in the key habitats, *i.e.* the light-exposed soft bottoms and the mire-littoral system. The mire-littoral system of the brownwater lakes is also important to study, in order to assess the relative influence from the nearest parts of the drainage area compared to the flow of water from upstream areas of the river system. The deep eutrophic lakes are the most thoroughly studied and well-known systems of the three lake types. However, research directed towards a quantification of the production in the different littoral habitats, especially the light-exposed soft bottom zone, is needed to evaluate the relative contribution of these habitats to the total lake metabolism and their function as sinks/sieves for substances entering the lake.

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Appendix 1

Glossary

aerenchyma	luftfyllda rötter/rottrådar
allelopathic	påverkan från en levande växt på andra organismer i närmiljön
allochtonous organic carbon	organiskt kol som ej producerats i, utan tillförts sjön
Asellus aquaticus	vattengråsugga
autochtonous organic carbon	organiskt kol som producerats i sjön
autotroph	primärproducent, har förmåga till fotosyntes
bog	mosse
bream (*Abramis brama*)	braxen
burbot (*Lota lota*)	lake
Carex (sedge)	starr
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
Chironomid larvae (midge larvae)	fjädermygg-larver
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)
dioecious	skildkönad
Epipactis palustris	kärrknipprot
Equisetum (horsetail)	fräken
Eriophorum vaginatum	tuvull
Fen	kärr
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
pikeperch (*Leniusculus leniusculus*)	gös
Potamogeton pectinatus	borstnate
Primula farinosa	majviva
riparian zone	strandzon
Rhyncospora alba	vitag
roach (*Rutilus rutilus*)	mört
Rubus chamemorus	hjortron
rudd (*Scardinius erythrophthalmus*)	sarv
ruffe (*Gymnocephalus cernua*)	gärs
Scheuchzeria palustris	kallgräs
Scoenocplectus lacustris (bulrush)	säv, kolvass
Seepage lakes	grundvattenmatade sjöar, utan synligt tillopp
smelt (*Osmerus eperlanus*)	nors
Sphagnum	vitmossa
stoneworths	kransalger
tench (*Tinca tinca*)	sutare
trophogenic zone	det övre vattenskikt i en sjö där fotosyntes försiggår
Typha angustifolia (lesser reedmace)	smal-kaveldun
white bream (*Blicca bjoerkna*)	björkna

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