

Five Faroese Lakes

Physico-Chemical and Biological Aspects

Ritstjórar (Editors):

Kirsten Christoffersen

Erik Jeppesen

Pehr Henrik Enckell

Dorete Bloch



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Preface

Inngangur

Dorete Bloch

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The Faroe Islands are a relatively young archipelago, 50-60 million years old, located far from nearest large landmasses (290 km from Scotland, 430 km from Iceland and 550 km from Norway) in the temperate zone of the North Atlantic Ocean. Due to their geographical location, the islands are gifted with a unique animal and plant life in the context of dispersal, ecology, diversity and evolution.

During the past century, several investigations have been made of Faroese marine and terrestrial biotopes. Results from the major Danish-Faroese investigations that took place during 1924-1927 were presented as six volumes in the series "The Zoology of the Faroes" (1928-1972). Later, in 1978-1982, a Norwegian-Swedish research team undertook large-scale studies on terrestrial biotopes all over the archipelago and the results were published in *Fauna Norvegica*, Series B.

However, one biotope, namely lakes and other freshwater localities, has not been the subject of intensive studies. Therefore, the initiation of the NORLAKE project gave a

valuable opportunity to extend our knowledge of the freshwater biology of the Faroe Islands. NORLAKE is an inter-Nordic project that aims to provide data from various areas in the Nordic region to elucidate the biological diversity of aquatic ecosystems and the ways in which anthropogenic activities affect their structure and function. The project focuses on the western Nordic countries, Greenland, Iceland and the Faroes and is funded by the Nordic Arctic Research Programme (NARP 1999-2003).

The combined efforts by Faroese, Swedish, Norwegian, Icelandic and Danish limnologists allowed the undertaking of thorough investigations on the chemistry and biology of five major Faroese lakes during July and August 2000.

Lakes and streams in the Faroese Islands are used as recreational sites, both by anglers and tourists, who all enjoy the spectacular Faroese scenery and the special climate. This book will add significantly to our understanding of the Faroese aquatic environment and the highly varied vege-

tation and animal life found beneath the water surface.

We are grateful to the NARP foundation and the Danish Natural Science Research Council (North Atlantic Research Program) for supporting our studies and to also make it possible to include highly informative colour photographs of plants and animals as well as detailed lake maps. We thank the inhabitants for their goodwill to give access to localities, for a keen interest in our research and their help with our fieldwork.

The highly qualified assistance by A.M. Poulsen, T. Christensen, K. Møgelvang, A.

Kjeldgaard and J. Jacobsen during preparation of the manuscripts for publication in the present supplemental to Fróðskaparrit as well as by J. Dalsgaard and E. Olsen from Gramar during the printing phase is highly appreciated.

Finally, we wish to thank our Nordic partners for a very enthusiastic and fruitful teamwork during the driest summer experienced in the Faroese Islands for the past fifty years.

Previous Studies of Freshwater Biota in Faroese Lakes

Eldri kanningar av djóra- og plantulívi í føroyskum vøtnum

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Úrtak

Hóast elstu lýsingarnar av plantu- og djóralívnum í Føroyum stava úr 17. øld, og fleiri kanningar vóru gjørdar í 19. øld, hava sera fáar vístfrøðiligar kanningar verið gjørdar av vøtnunum í Føroyum. Eldri kanningar hava annaðhvørt verið avmarkaðar til einstøk vøtn ella avmarkaðar til serstøk øki av vistskipanini. Kanningar av botndýrum í Leynavatni í ymiskum árstíðum og samansetingin av plantuætistovnum í ellivu føroyskum vøtnum eru dømi um slíkar kanningar. Kanningar eru eisini gjørdar í fleiri vøtnum av, hvørja ávirkan alingin av sjósli og bleikju hevur á vatngóðskuna, og aðrar kanningar eru gjørdar av pelagiskum djórum og botndjórum. Hesar kanningar hava givið økta heildarvitan um vøtnini. Tá havt verður í huga, hvussu smá vøtnini í Føroyum eru, og hvussu long frástøðan er til vøtn á evropeiska meginlandinum, má sigast, at lívið í føroysku vøtnunum í høgðsheitum er av sama slag sum aðrastaðni í Skandinavia.

Nógva seyðahaldið, sum byrjaði í Føroyum fyri meir enn 1000 árum síðani, broytti plantugróðurin frá órørdum haga og bøi við runnum til haga, har seyður gekk á biti allastaðni. Hetta hevur uttan iva havt við sær, at djóra- og plantulívið í vøtnunum eisini broyttist, tá tilgongdin av serligum lívfrøðiligum tilfari minkaði, samstundis sum mongdin av føðsluevni øktist. Hesar broytingar mugu hava havt stóra ávirkan á botndýrini. Í dag er størsta menniskjaskapa ávirkanin frásetuvatn. Tær fáu kanningar, sum higartil eru gjørdar av evnafrøðini í vøtnunum og vatngóðskuni, vísa, at enn er taðingin av frárensluvatninum ikki komin á eitt hættisligt stig, men tað er av stórum týðningi at kanna og lýsa lívfrøðiliga samansetingina og vístfrøðina í føroyskum tjarnum og vøtnum, áðrenn skiligar og umfatandi broytingar henda.

Abstract

Only few ecological studies have been conducted of inland waters in the Faroe Islands despite the fact that the oldest descriptions of Faroese flora and fauna are from the 17th century and that several surveys were performed in the 19th century. The previous studies were either concentrated on one lake or on a restricted part of the ecosystem, such as a seasonal study of benthic community in Leynavatn and analyses of phytoplankton community composition in eleven lakes. Investigations focusing on the effects of trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) hatcheries on water quality, pelagic and benthic communities have been carried out in several lakes and the results obtained provide useful information on general conditions. Taking the small size and the remoteness from mainland Europe into consideration, it seems that Faroese lakes are inhabited by the same groups of freshwater organisms found elsewhere in Scandinavia.

The widespread sheep-farming starting in the Faroe Islands more than a millennium ago changed the vegetation from heath, meadows and shrubs into pastures. Intuitively, also the indigenous aquatic biota must have changed as the input of particulate organic material to the lakes has decreased, whereas that of nutrients increased. Such changes must have had a profound effect on the benthic communities. Today, the most important anthropogenic effect is that of wastewater. The few studies hitherto undertaken of lake chemistry and water quality indicate that eutrophication caused by waste waters has not yet reached alarming levels, but it is essential to investigate and describe in detail the biodiversity and ecology of Faroese ponds and lakes before any marked and widespread changes occur.

Introduction

Surprisingly, only few studies of the ecology of Faroese lakes and ponds have been carried out, despite the accessibility and mild climate of the islands. The small, steep-cliffed islands may have led researchers to believe that only streams and rivers occur, but there are in fact numerous ponds and lakes of which some are quite deep, examples being Leynavatn and Sörvágsvatn with recorded maximum depths of 33 and 59 m, respectively (Dali, 1975; 1977).

The oldest descriptions of the Faroese flora and fauna stem from the 17th and 18th centuries (Clausson, 1632; Svabo, 1782). A number of scientifically more intensive surveys were made during the following two centuries and many of the results are presented in "Flora of the Faroes" by Rostrup (1870), the series "Botany of The Faroes" edited by Warming during 1901-08, and the series "The Zoology of the Faroes" edited by Jensen *et al.* during 1928-71. These publications include descriptions of several organisms, ranging from eukaryotic unicellular algae to bryophytes, higher plants as well as invertebrate and vertebrate groups including nematodes, annelids, molluscs, crustaceans, insects and fish.

Aquatic organisms

Terrestrial ecology has been the subject of several investigations, whereas little attention has been paid to aquatic organisms - apart from fish. However, several general and popular overviews of Faroese freshwater flora and fauna based on the older

literature mentioned above have been published (Rasmussen, 1958; Spärck, 1958; Bengtson, 1982). A short summary of the original literature on the distribution of most freshwater organisms recorded as well as descriptions is given below.

Descriptions of water plants are scanty and comprehensive surveys including all the Faroese islands have not been made. Some information can, however, be found in Rostrup (1870), Warming (1908) and Ostenfeld and Grøntved (1934), as well as in Ostenfeld's earlier publications (cited in Warming 1908). The species richness is not overwhelming owing to the considerable distance to mainland Europe and the facts that the freshwaters are generally nutrient poor and that the substrate often consists of stones and pebbles. Several genera of submersed plants of e.g. *Isöetes* and *Potamogeton* are however represented. Macro- and microalgae such as *Chara*, diatoms and desmids typical of oligotrophic water also occur. Microalgae (phytoplankton) have been studied by several authors in the past (Börgesen, 1901; Östrup, 1901a, b; Börgesen and Ostenfeld, 1903) involving mid-summer sampling in eight Faroese lakes. More recent studies include a survey to detect changes due to eutrophication on the phytoplankton communities in eleven lakes (Danielsen, 1999) and the carbon uptake of submerged water plants from 10 lakes was recently (Madsen and Bagger, 1999).

In contrast to what is known about water plants, the information on freshwater invertebrates and fish fauna is much more detailed because of the intensive surveys made by numerous zoologists.

Oligochaetes are common in the Faroe Islands. Thirty-two species are found, of which several live in aquatic habitats (Ditlevsen, 1936). Peculiarly enough, only one species of Tubificidae has been recorded. Leeches (Hirudinea) are represented by only three species, possibly due to the scarcity of prey as indicated by Bruun (1928), or simply because these animals have poor dispersal potentials.

Freshwater Mollusca are represented by nine *Pisidium* species and at least two species of snails (Fog, 1971). The number of snail species is low compared to other North Atlantic areas such as the islands of Orkney and Shetland as well as Iceland - the latter having eleven species of *Pisidium*, three *Lymnaea* and one *Gyraulus* species (G. Gislason, pers. comm.). There is no obvious explanation for this.

Crustaceans are represented by a total of 41 species, including amphipods, cladocerans, copepods and ostracods. All species have been identified from material collected during 1924-27 (Poulsen, 1928), and especially the group of cladocerans is relatively diverse and has a species composition resembling that of northern Scandinavia and Iceland. However, Notostraca (e.g. *Branchinecta* and *Lepidurus*) have not been found in the Faroe Islands. It should be noted also that copepods are scarce in the lakes, which Poulsen (1928) attributes to the low temperatures and the remoteness of the islands. Interestingly, a harpacticoid crustacean, known as an ice age relict was recently found by Enckell (1995).

Fifteen species of Hydracarina were recorded and described by Lundblad (1930)

based on his examinations of the collections from the early 1900s.

Lake and stream benthic fauna is briefly described in several contributions found in Jensen *et al.* 1928-71. Information about Diptera is found in Pedersen (1971). The biology and distribution of Hemiptera and Trichoptera are described by Henriksen (1929a,b). The source material for these investigations derives from the main survey undertaken in 1924-27 initiated by S.-L. Tuxen, but also later contributions have added information on the ecology of benthos (Shire *et al.*, 1964; Jensen, 1987).

Early fish records

There are several reasons why fish have received more attention from researchers than other aquatic organisms - the more obvious being that fish are visible, eatable and thus well known by laymen.

The circumpolar Arctic charr (*Salvelinus alpinus*), believed to be a relict of the Ice Age when the islands were uplifted, was first recorded in Leynavatn by Svabo (1782). Its presence has been confirmed many times through the following 200 years (reviewed by Joensen and Tåning, 1970), and it may also have been found by Willemoes-Suhm (1873) in Kirkjuvatn (named "Kjirkin-Vatn" in the article) at Suðuroy. Specimens from Leynavatn were transferred successfully to hydropower reservoirs on the island of Vestmanna in the 1960s (and possibly before) and a well-established population was observed a few years later (Joensen and Tåning, 1970).

Sea trout (*Salmo trutta trutta*) and brown trout (*Salmo trutta fario*) were recorded

even earlier, in the 17th century (Clausson, 1632), and seem to have been common in many Faroese fresh and marine waters at that time although proper identification of the species apparently was troublesome (reviewed by Joensen and Tåning, 1970). Both species are still common in many of the inland waters and are popular among anglers, but are of no commercial importance. Exceptions are, however, the many land-based and coastal trout hatcheries and nurseries.

From the old literature it is known that Atlantic salmon (*Salmo salar*) has occurred in several Faroese rivers (Svabo, 1782), but recent information indicates that it is now only occasionally found to migrate into Leynavatn (Gydemo, 1983). The widespread damming practice may be the main reason for the exclusion of salmon from other freshwaters.

Three-spined stickleback (*Gasterosteus aculeatus*), which is widespread in coastal areas, brackish water, rivers and lakes, and eel (*Anguilla anguilla*) were recorded by Svabo (1782), mentioned by Willemoes-Suhm (1873) and later described in more detail by several other researchers (Joensen and Tåning, 1970).

Scarcity of ecological studies

Despite the numerous descriptions of aquatic biota, only few ecological investigations have been undertaken, primarily aimed to assess the impact of aquaculture or the establishment of power plants or reservoirs for other purposes.

A seasonal study (June to October 1976) of the water chemistry, primary production

and the zoobenthos communities of the littoral-profundal zone of Leynavatn was made by Lützen (1978). He found low levels of primary production as well as low biomass and production of benthic organisms and concluded that food scarcity was limiting secondary production. Lützen (1978) was probably the first to measure primary production in a Faroese lake and an annual net production of less than $10\text{ g C m}^{-2}\text{ yr}^{-1}$ can be estimated based on his measurements (obtained by the ^{14}C technique). A study conducted a few years later by Jensen *et al.* (1983) in four hydropower reservoirs at Vestmanna (Streymoy) and Eiðisvatn (Eysturoy) included measurements of primary production, water chemistry, macrophytes, zoobenthos and fish. They obtained somewhat higher primary production rates that remained, however, within the ranges found in nutrient-poor lakes and concluded, that the water quality was very good in all five lakes. A more recent study of the water quality was made by Danielsen (1999), who analysed basic water chemistry and the phytoplankton communities in eleven lakes during 1995-96. He concluded that several lakes were slightly eutrophicated, the reason most likely being input of untreated wastewater.

Ecological studies of trout and Arctic charr as well as water quality and the benthic community were conducted in Leynavatn, Eiðisvatn and Ryskinvatn by Gydemo (1983), Jensen *et al.* (1983) and Brattaberg (1995), respectively. The results show that trout and charr populations can co-exist (in some cases also with sticklebacks) and achieve fairly good conditions

as long as the population size is small. The preferred food items of trout and charr are benthos, zooplankton and to some extent young fish. Most fish populations have been manipulated (hatchery release, damming and/or angling) rendering it difficult to obtain data on genuine population sizes. The effects of a trout hatchery on the water chemistry and phytoplankton community structure of Vatnsnesvatn (Suðuroy) were surveyed once in August 1998 (Johnsen, 1998). Based on the relatively high nutrient levels recorded, it was concluded that a slight eutrophication had occurred having affected the composition of the phytoplankton community (dominance of cryptophytes). The zooplankton was not quantified, but Brattaberg (1995) concluded that only copepods were capable of withstanding strong predation by fish.

Final remarks

The Faroe Islands are inhabited by the same groups of freshwater organisms as found elsewhere in Scandinavia, which may seem logic because of the similar (though not identical) pre-glacial history. However, overall diversity seems to be lower than in neighbouring areas, such as Shetland and Iceland, most likely due to the presence of dispersal barriers.

When the first settlers introduced sheep (and goats) during the 7th and 8th centuries (Arge, 1991; Hannon and Bradshaw, 2000) the nature of the landscape changed from moor and meadows with shrubs into pastures due to grazing. Indirectly also the indigenous aquatic biota must have changed as the input of particulate organic material

from senescent vegetation to the lakes decreased, whereas the nutrient input derived from animal faeces and urine increased. These changes can be traced via paleoenvironmental reconstructions from lake and moor sediment cores (Hannon *et al.*, 2001) although simultaneous changes in climate as well as in eutrophication in the past cannot always be separated.

However, today's most important anthropogenic effects are those of untreated wastewater and the agricultural practice of fertilization of hay fields. The few studies so far conducted on lake chemistry indicate that eutrophication does occur, but has not yet reached the visual levels observed elsewhere (e.g. in Scandinavia).

During the 20th century the water level of a number of lakes was raised by damming of outlets to produce hydroelectric power and to ensure a sufficient drinking water supply. The effects of such regulations include flooding of wetlands and changes in the aquatic food webs due to the immediate disturbances as well as to changes in catchment size and the retention time of the lake water (Jensen *et al.*, 1983).

The present-day and early historic biodiversity and ecology of Faroese streams, ponds and lakes ought therefore to be investigated and described in detail before more marked and widespread changes occur, and the results obtained will be a useful tool in the hands of water management authorities when implementing water protective measures.

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The Geology and Physical Geography of some Lakes in the Faroe Islands

Jarðfrøðin og landalæran við fimm føroysk vøtn

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Úrtak

Vøtnini í Føroyum eru býtt ójávnt millum oyggjarnar. Fá vøtn finnast á teimum minstu og brattastu oyggjunum, meðan nógv eru á teimum stóru oyggjunum. Í greinini verður framlagt uppskot til eina flokkingarskipan av vøtnum í Føroyum, sum er grundað á lendiseginleikar í avfallsøkinum uttanum vøtnini. Sørvágsvatn og Toftavatn hoyra til 'low relief lake basins', har lendi uttanum fyri tað mesta er undir 300 m omanfyri sjóvarmálan. Saksunarvatn, Leynavatn og Mjáuvøtn verða flokkaði sum 'high relief lake basins', sum eru eyðkend við, at meir enn 50% av lendinum røkkur upp um 300 m omanfyri sjóvarmálan. Hetta fjallalendi hevur arktiskt veðurlag við øktum avfalli og óstöðugum, skriðukendum hallandi lendi.

Abstract

The Faroese lakes are unevenly distributed between the islands; few lakes are found on the smallest and steepest islands and many on the larger islands. This paper presents a classification system dividing lake basins into seven categories according to the physical landscape characteristics of lakes and watersheds. Our lake study included the five lakes: Eystara Mjáavatn, Leynavatn, Saksunarvatn, Sørvágsvatn and Toftavatn, of which Sørvágsvatn and Toftavatn were found to belong to the category 'low relief lake basins' characterized by a relatively low relief watershed mainly situated below 300 m a.s.l., while Saksunarvatn, Leynavatn and Eystara Mjáavatn were found to belong to the category 'high relief lake basins' with more than 50% of the land area reaching into the climatic arctic zone of the mountain regions that are characterized by higher precipitation and a high risk of slope instability influencing the lake environment.

Introduction

The total land area of the Faroe Islands of 1399 km² is distributed over 18 elongated islands divided by narrow fiords and sounds. In many regions the mountainous islands have a steep topography with seaward facing cliffs reaching a free fall of up to 700 m. The highest mountain, Slættara-tindur, is 882 m.

More than 800 lakes and ponds are estimated to occur in the Faroe Islands (Rudolphi, 1914) and the number may even be as high as 2500 if ponds smaller than approx. 300 m² are included (S. í. Dali, personal communication). As it appears from the topographic map series, scale 1:20.000, over the Faroe Islands published in the 1990s (Kort- og Matrikelstyrelsen, 1996) far from all lakes have been officially named. The map series refer to only approximately 266 named large lakes and ponds, whereas most medium to small lakes and ponds in mountain regions remain unnamed. Using this list with the precaution in mind that unnamed lakes have not been included, it becomes clear that the distribution of lakes in the Faroe Islands generally reflects the limited space

for lake basins due to the high relief topography (Fig. 1). No lakes occur on the smallest islands: Mykines, Koltur, Lítla Dímun and Stóra Dímun, and only few and small lakes are found on the steep northern islands of Fugloy, Svínø, Viðø, Borðø, Kunoy and Kalsoy. The number of lakes and large ponds is higher on Vágar, Streymoy and Eysturoy, while the highest number of lakes are found on the islands of Suðuroy and Sandoy, probably due to their relatively low relief topography.

In the following a classification system is proposed based on the landscape settings of the 266 named lakes, focusing on geology, landscape settings and selected meteorological characteristics which may influence properties of relevance for lake environments. The five lakes of the NOR-LAKE study, Eystara Mjáavatn, Leynavatn, Sørvágsvatn, Toftavatn and Saksunarvatn are classified and their landscape settings are described.

Outline of the basic geology of the large-scale landscape

The Faroe Islands are the remnants of a large low relief plateau of Tertiary flood basalts deriving from volcanic eruptions

almost 60 Myr ago prior to the opening of the North Atlantic Ocean basin. The Faroe basalt plateau is built up by layers of near horizontal basalt flows from mainly rift volcanism (Rasmussen and Noe-Nygaard, 1969).

Throughout the Tertiary period the plateau rifted away from its East Greenland counterpart. The Tertiary landscape evolution includes a history of tectonic movements, uplift and subduction within a subtropical type of climate resulting in a type of erosion working actively on the whole regional land surface. The result of the Tertiary landscape development was a general breakdown of the size of the land area where the low relief plateau character was preserved.

A pattern of almost evenly spaced slightly curved parallel weakness lines was superimposed on the basalt plateau at an early stage as a result of the volcanic or later tectonic activity. These weakness zones became lines of depressions that were exploited by the drainage system and with time developed into a large-scale system of valleys, fiords and sounds with a distinct directional trend from northwest to southeast.

Table 1. Meteorological and climatic parameters in Tórshavn (57 m a.s.l.) and Sornfelli (726 m a.s.l.). Data from Cappelen and Laursen (1998) and Christiansen and Mortensen (2002).

Meteorological parameters	Tórshavn 57 m a.s.l. (1961-2000)	Sornfelli 726 m a.s.l. (2000)
Mean annual temperature (°C)	6.5	1.7
Mean warmest month (°C)	10.6 (August)	6.5 (August)
Mean coldest month	3.6 (February)	-2.2 (April)
Absolute maximum temperature (°C)	22 (August 1976)	14.6 (July)
Absolute minimum temperature (°C)	-11 (February 1969)	-10.6 (March)
Number of days with frost	48.5	150
Precipitation (mm)	1284	

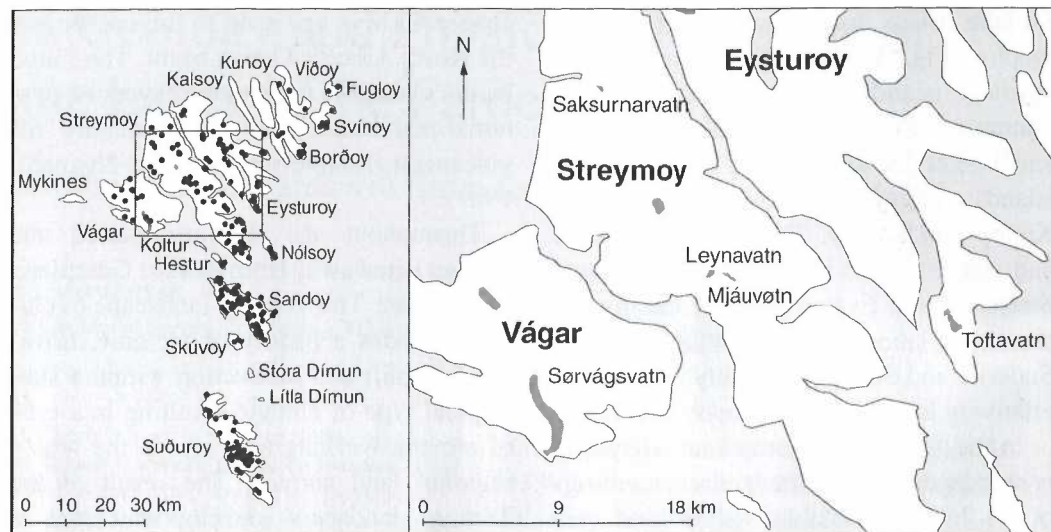


Figure 1. Distribution of lakes in the Faroe Islands. Left: The 266 named lakes in the Faroe Islands are unevenly distributed over the islands, with few or no lakes on the small islands and many lakes on the large islands. Right: The location of the five lakes presented in this paper, Sørvágsvatn, Saksunarvatn, Leynavatn, Eystara Mjáavatn and Toftavatn.

Quaternary shaping of the large-scale landscape

The Tertiary landscapes with aligned low relief depressions trending northwest-southeast set the physical topographic environment for the glaciations of the Quaternary period. Glaciers accumulated in existing depressions in the early drainage system, causing extensive local erosion and deepening of the major valley systems, particularly in main channel zones where glacier ice moved towards the sea. During glaciation glaciers accumulated in the upper inner valleys, reaching in places a thickness of up to 350-400 m (Christiansen, 1998; Humlum and Christiansen, 1998a; 1998b; 1999). The maximum height of glaciation reached about 700 m a.s.l. at Reyða-

fellstindur in the central region of Eysturoy (Jørgensen and Rasmussen, 1986).

The Faroe Islands constituted an independent glacial area, with valley glaciers radiating outwards in all directions from a few main centres (Waagstein and Rasmussen, 1975; Humlum *et al.*, 1996).

In some regions the glacial processes reshaped the former plateau to a high relief landscape, deep valleys with steep sides and flat bottoms evolved deepening the general northwestern-southeastern system of depressions of the previous landscape.

Modern climate

Surrounded by the North Atlantic Current the Faroe Islands have a cool temperate climate close to sea level, grading into an arctic climate with altitude. (Table 1). The

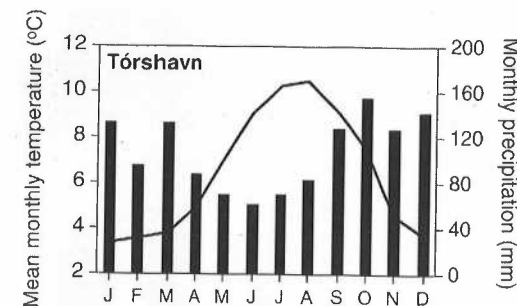


Figure 2. Monthly precipitation and temperature in Tórshavn 1961-1990. Temperature is presented with a line corresponding to the left x-axis, and precipitation is presented as a histogram corresponding to the right x-axis.

mean annual temperature close to sea level in Tórshavn is 6.5 °C, while the annual mean temperature was 1.7 °C at Sornfelli 726 m a.s.l. in 2000 (Christiansen and Mortensen, 2002). The warmest month is August and the coldest month January with, respectively, 10.5 °C and 3.4 °C in Tórshavn (Fig. 2).

There is a significant spatial variation in annual precipitation depending on region and altitude. The annual precipitation in the coastal regions of the Faroe Islands varies from 800 mm at Mykines and Akraberg, to 1300 in the central regions, increasing to 3300 mm in the northern regions (Cappelen and Laursen, 1998). The months of May and June are statistically dry, while the autumn months of October and November exhibit the highest precipitation. Very little information exists about river runoff and increased precipitation with altitude in the mountainous regions. However, model calculations from the Danish Meteorological Institute show an annual precipitation

exceeding 4000 mm in the mountainous regions (Danmarks Meteorologiske Institut, 1997). Monitoring of precipitation and river runoff up to an altitude of 400 m a.s.l. during the period 1952 to 1957 (Winther, 1958) in Vestmanna showed a precipitation increase of 0.125 % m⁻¹ a.s.l. up to 400 m, the level expectedly declining above this altitude. All the five study lakes are situated below 100 m a.s.l. within coastal regions with an annual precipitation of approx. 1200 to 1400 mm. Short-term winter monitoring shows that if the precipitation increases with altitude by 0.125 % m⁻¹, annual precipitation will expectedly exceed 2000 mm at 400 m altitude. Above this altitude annual precipitation will expectedly increase even further, exceeding 4000 mm.

Preliminary classification system of lake basins

Seen within the context of the physical environment, the majority of the present-day Faroese lakes are the result of glacial erosion and sedimentation. In many main valleys and fiords overdeepening has occurred upstream glacier fronts, leaving a rock basin with a solid rock barrier after deglaciation. In other places glacial sediments have created hollows that are today occupied by lakes. Although some of these valley and mountain lakes are located in geological fraction zones or mires, both types owe their basin creation to glacial erosion.

Different groupings of lake types in the Faroe Islands have been suggested by several authors. Rudolphi (1914) surveyed 67

lakes and placed them into two categories: glacial lakes and coastal lakes. Rasmussen (1982a,b) added another category by dividing the lake basins into three types: glaciated lake basins, tectonic lake basins and coastal lake basins. In the following a system involving categorization of lake basins into 7 types based on landscape settings is suggested (Table 2). Manmade dams and ponds have not been included.

Low relief lake basins

Especially on the southern part of Vágar, Streymoy and Sandoy relatively low relief areas can be found with valleys and fiords cutting across the land area exhibiting a clear directional trend from northwest to southeast. These areas were glaciated during the glaciations, but because of a relatively low topography the glacial erosion did not transform the areas into alpine high relief landscapes.

The depth of the large-scale depressions cutting through the islands from northwest to southeast varies. The deeper depressions are below water level and have become sounds and fiords, while the more shallow depressions have become valleys cutting across islands.

Some of these often long and relatively low relief valleys are occupied by elongated lakes whose basins are quite deep as a result of glacial overdeepening. They are among the largest and deepest Faroese lakes. A common characteristic of low relief valley lake basins is a large watershed within the low relief NW-SE trending topography. Commonly, only approx. 10 % of the area reaches above 300 m a.s.l.,

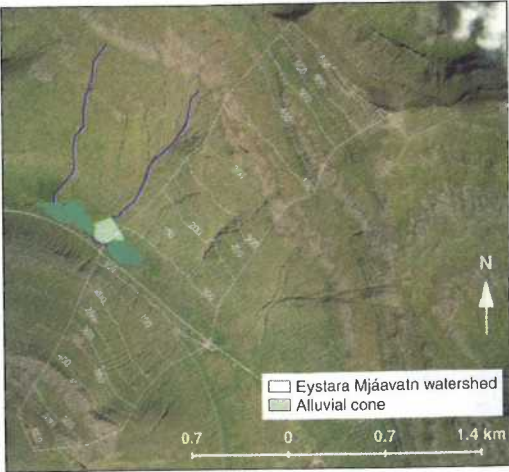


Figure 3. The Eystara Mjáavain watershed is located east of Leynavain.

which implies that the watersheds may have a relatively strong vegetation cover and are only negligibly affected by slope instability and high sediment load in the rivers. Since most of the area does not reach into the mountain zone characterized by arctic climate with increased precipitation and snow, the frequency of high runoff events is expected to be low.

Examples of low relief lake basins are Sørvágsvain and Toftavain.

High relief lake basins

Especially in the northern parts of the islands where the topography is relatively high, extensive glacial erosion has transformed the early basalt plateau into a high relief alpine landscape. Since the lakes occupy basins of deeply eroded main valleys, the shape of the lakes reflects the main NW to SE directional trend. The lake basins may be deep in places due to glacial

Category of basin	Description of lake and watershed	Approx. occurrence of lakes, (%)	Common lake basin characteristics	Directional trend	Size of watershed	Area above 300 m a.s.l. (%)	Frequency of high runoff	Examples of lakes
Low relief lake basins	Lakes within low relief valleys. Predominant northwestern to southeastern direction. Lake shape is elongated, often large and deep	6	Large	NW to SE	Low	~10	Low	Sørvágsvain, Toftavain
High relief lake basins	Lakes within high relief valleys with steep valley slopes and wide valley beds. May show the same directional trends as the low relief lake basins. Lakes vary in shape, size and depth. Often characterized by high sediment load and well-developed delta prograding into the lakes.	3	Large	NW to SE	High	~50	High	Leynavain, Eystara Mjáavain, Saksunarvain
Fault zone lake basins	Lakes in V-shaped valleys with a relatively high relief. The centre line of the valley hosting the lake basin is a fault zone. Lake shape is strongly elongated and narrow, relatively deep. Low sediment load of water entering the lake.	3	Small	Varies	High	~20-50	Low	Heðavain on Streymoy
Mountain plateau lake basins	Lakes in highland plateau areas including highland mountain passes. These lakes are usually small and shallow. Lakes shape shows no directional trends.	26	Small	None	Low	~20-70	Low	Lakes on Hestur high land plateau
Mire lake basins	Lakes in low relief valleys and mountain areas formed when a lake closes up by plant growth and mire formation.	6	Small	None	Low	~10 - 50		Mýramir in Vestmanna and Eiðisvain.
Cirque lake basins	Lakes within cirque valleys characterized by high relief topography upslope the lakes. Lake shape is often round with a shallow depth. River inlets may have a high sediment load.	48	Small to large	None	High	~70	Low to high	Hvannavain on Suðuroy
Coastal lake basins	A number of freshwater lakes having a water level close to the present sea level, and which are separated from the sea by a solid rock barrier often covered by rocks or sand.	8	Small to large	Varies	Low	~10	Low to high	Sandvain, Gróthúsavain, Vainið á Møluni Eiði

Table 2. Preliminary classification system of lakes in the Faroe Islands based on landscape settings.

overdeepening and are often further affected by strong postglacial erosion of local rifts and fault zones. This type of watersheds may be large and more than half of the area may be located above 300 m a.s.l. Areas above 300 m have a significantly extended winter season with more precipitation, snow and days with frost. The watersheds are therefore characterized by profound slope instability, reflected by events of high precipitation rates, high sediment load in inlet rivers, especially during the spring thawing, and high precipitation rates in the autumn. An evidence of the high sediment load events is the deltas that build up into the inflow areas to the lakes.

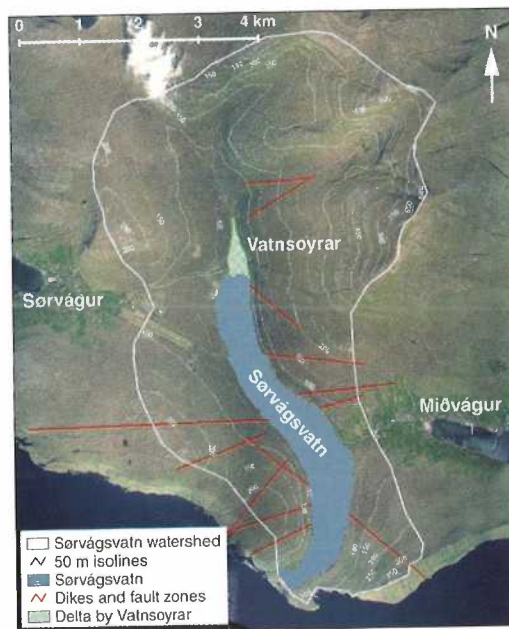


Figure 5. The Sørvágsvatn watershed. The largest and deepest Faroese lake located in the southern part of a low relief valley penetrating the island of Vágar.



Figure 4. The Leynavatn watershed has a high relief glaciated topography. More than 50 % of the land area is above 300 m a.s.l., indicating that the watershed and thus the lake environment are affected by increased precipitation and slope instability in the upper part of the landscape.

Examples of high relief lake basins are Leynavatn, Eystara Mjáavatn and Saksunarvatn.

Fault zone lake basins

These lakes are often deep and narrow and are located in rock basins in narrow valleys. The lake basin has been formed by glacial erosion in a weak tectonic fault zone in depressions situated in the periphery of the main large-scale valley system. The watersheds of these lake basins are usually high relief, but small. The lake basins are strongly elongated, but the directions vary and show no directional trend. The proportion of the area reaching above 300 m

a.s.l. varies, but is often 50 % or more, since the basins are located above the lower regions of the mountains. Although the watersheds reach into the zone above 300 m a.s.l., the small size may limit the event frequency of slope instability and high river runoff.

Examples of fault zone lake basins are Heiðavatn in northern Streymoy.

Mountain plateau lake basins

This category of lakes includes shallow and small lakes located in relatively low relief terrain of rolling hills that are the remnants of the old Tertiary landscape in high-mountain areas. These lakes may be as small as 300 m² and usually occupy an area of rock basins that is not clearly delineated by early drainage systems, rifts and faults. The shapes of the lakes do therefore not reflect any directional trend. The watersheds of these lake basins are often small and have a relatively low relief. The proportion of the areas reaching into the zone above 300 m a.s.l. is generally high and many of the lakes are partly or fully frozen during winter. Although most of these watersheds lie in high-mountain areas the low proportion of steep slopes means that the risk of slope instability is low as is the frequency of sediment rich high runoff events.

According to the maps of named lakes 26 % fall within this category. However, the number of lakes belonging to this category is probably much higher, as many small lakes remain unnamed.

Examples of mountain plateau lake basins are the ones situated in the island of Hestur,

at the Skálafjall mountain on Eysturoy and Barmur on Borðoy.

Mire lake basins

Mire lake basins are found in low relief regions in the mountains, they are often formed as a rock basin being slowly closed up by plant growth and mire formation. Lakes and ponds of this type are most common on the larger islands.

The watersheds of these basins are usually small with a low relief topography. The proportion of the watershed above 300 m a.s.l. may vary significantly as the mire lake basins may be found adjacent to and downslope high relief landscapes. The frequency of high runoff events is usually low, which is reflected by the low degree of sediment input and water erosion in the mires.

The best known examples of this type of lake basin are the former mires of Eiðisvatn and Mýrarnar at Vestmanna, which are today both under water being parts of hydro-power dams.

Cirque lake basins

These lake basins are mostly shallow, inner parts of cirque valleys and may occupy a rock basin or be dammed by a till barrier. The watersheds vary in size from small to medium, with a high relief topography upslope and often also downslope the lake basins. Many of these lakes are situated within mountain regions reaching into the zone above 300 m a.s.l., and some of these lakes thus freeze to the bottom during winter. With the high relief topography follows slope instability and the landscape

may be characterized by recurrent debris slides on the steep slopes. The frequency of sediment rich river runoff events is therefore expectedly high during autumn and late spring.

Examples of this type of lake basins are Hvannavatn on Suðuroy and the lakes of Vatnsdalur in Oyndarfjørður.

Coastal lake basins

These lakes are located close to sea level but separated from the sea by small barriers of sand or water abraded boulders. The shape and settings of these lakes and their watersheds share common characteristics with the low relief lake basins. The size of the watersheds may be medium to large, often with a low relief topography. The lake shapes reflect the directional trends of the large-scale landscape. Usually a small proportion of the watershed reaches above 300 m a.s.l., implying that the event frequency of high river runoff may be low to moderate.

Examples of such lakes are Gróthúsvatn and Sandsvatn on Sandoy, and Vatnið á Mølini on Eiði. These lakes have been categorized as former inland lagoons by Rudolphi (1914) and Rasmussen (1982b), but recent research carried out by Grauert (1999) and Grauert *et al.* (2001) indicates that they have always been freshwater lakes and do not have a marine history.

Description of selected lakes within their landscape context

Eystara Mjáavatn

The two lakes Eystara Mjáavatn and Vestara Mjáavatn are located east of Leynavatn

in a glaciated valley penetrating the island of Streymoy approximately to the west of Leynar to Kollafjørður. The two lakes drain westwards into Leynavatn (Fig. 3).

The watershed of Eystara Mjáavatn includes the valley upstream the river Breiðadalsá. Where Breiðadalsá meets the lakes an alluvial cone has developed. The two lakes have approximately the same depth, around 6 to 7 m adjacent to the alluvial cone (Dali, 1977). This indicates that the two Mjáuvøtn lakes may have been one lake at the end of the last ice age and perhaps during the major part of the Holocene as well. From observations during a visit in 1879, Geikie (1880) refers to one lake Mjáavatn being divided by a detritus cone, which may indicate that the present shallow area between the lakes may have been under water at the time of his visit. If this was the case, it was most likely a temporary event, as the German visitor Graba (1987) from a visit in 1828 describes the lakes of Mjáuvøtn as two separate lakes.

The watershed of Eystara Mjáavatn is a high relief landscape beginning at the lake water level of 76 m a.s.l. reaching up to Árnafjallstindur 718 m a.s.l. More than half of the area is above 300 m a.s.l., which affects the runoff regime of the area with periodically high precipitation rates and a relatively high frequency of slope failures and high runoff.

Leynavatn

The lake basin of Leynavatn is located at the crossing of two large valley systems,

one running from the north and one from the east, both draining to the west (Fig. 4). These two valleys form part of a main drainage system of Tertiary origin.

The glaciated high relief alpine topography of the watershed begins at the lake water level of 63 m a.s.l. reaching up to Sneis 747 m a.s.l. Almost 60 % of the area is above 300 m a.s.l., implying that the watershed is affected by high precipitation rates and cold temperatures and has a long winter season. The event frequency of slope instability and sediment rich high runoff is relatively high.

The high relief topography of the watershed features a number of weakness zones of rifts and fault zones of which some cross Leynavatn and are likely to weaken the lake bed. The overdeepening of the lake may be caused by the collision of two glaciers during the Quaternary glaciations. The main glacier came from the north and collided into the mountain of Sátan and an ice body from the east. This may have released energy to overdeepen the lake basin of Leynavatn in a location already weakened by fault zones (Rudolphi, 1914; Dali, 1975).

The grass plain north of Leynavatn indicates that the lake at some stage has been larger than today and has extended further north. Less than a kilometre north of the lake a deep canyon has developed. The canyon is narrow, long and deep with sharp edges meeting the above landscape. The outlet from the canyon has developed an undisturbed alluvial cone of sediments. The abundant sediments have created a delta, silting up the former northern part of

the lake (Geikie, 1880; Hansen, 1990; Mortensen, 1996).

Sørvágsvatn

Sørvágsvatn is located in a main valley of Tertiary origin penetrating the whole island of Vágar in a curved northwestern-southeastern line (Fig. 5).

Sørvágsvatn is by far the largest and deepest lake in the Faroe Islands. Its rock basin is adjacent to the sea, with a water level 32 m a.s.l., and the water from the lake drains into the sea via a high waterfall, Bøsdalafossur. Most of the lake bed is situated lower than the present sea level and the deepest part of the lake is 59 m, reaching 27 m below sea level. The lake basin of Sørvágsvatn demonstrates the ability of glacial erosion to overdeepen basins upstream a glacier front.

The watershed of Sørvágsvatn is a large relatively low relief area barely reaching into the mountain zone above 300 m a.s.l. The lake environment receives inflowing water from a relatively large area, but is only insignificantly affected by slope failure and snow melting in upstream areas. Reflecting the relatively rare periods of high sediment load from the wide watershed, a small delta accumulates in the inflow region at Vatnsøyrar in the northern end of the lake.

Toftavatn

Toftavatn is located in the southeastern part of Eysturoy in a wide valley north of Runavík. The depression is part of the Skálafjørður main valley system that originates in the north by Elduvík and Funning and

bends through the valley of Millum Fjarða on its way southeast crossing the whole island. At Runavík the main valley system is divided into two arms, a deep western arm hosting the bed of the Skálafjørður fiord, and an eastern arm located above sea level including the Toftavatn depression (Fig. 6).

The Toftavatn lake basin is asymmetrical, with a shallow and narrow northern section and a wider 22 m deep southern section reaching 7 m below the present sea level. The remarkable depth of the lake is the result of glacial erosion, when the glacier of Skálafjørður in times of maximal glaciation spilled over across the Toftavatn area towards its way southeast.

The watershed of Toftavatn is small with a low relief surrounded by hills up to a maximal height of 165 m at Vatnfelli. The watershed is characterized by dense vegetation cover as the whole area is below the arctic climate zone of slope instability. Consequently, the water entering the lake contains a low load of sediments. Toftavatn is therefore the basin with the most tranquil inflow regime influenced only insignificantly by upland precipitation increase and snow.

Saksunarvatn

Saksunarvatn is located in the northern part of a high relief glaciated valley penetrating the northern part of Streymoy from Saksun to Hvalvík. The lake is 17 m deep with a water level 25 m a.s.l. This part of the valley is characterized by zones of rifts and dikes, some of which cross the lake (Fig. 7). The deepest part of the lake coincides

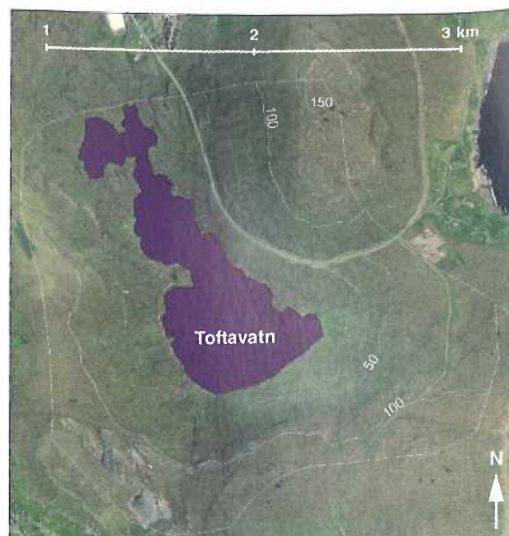


Figure 6. The Toftavatn watershed is a low relief landscape rising to a maximum height of only 165 m a.s.l.

with the weakness zone caused by a dike crossing the lake.

The high relief watershed of Saksunarvatn is moderately large reaching up to the altitude of 701 m at Gívrufelli. High mountains above 500 m border the watershed, and about 50 % of the watershed is above 300 m a.s.l. The Saksunarvatn watershed is therefore characterized by frequent slope failures and events of sediment rich high water inflows, both in periods of high precipitation and in periods of snow melting.

Concluding remarks

The five Faroese lakes selected in the NORLAKE study are all located below 100 m a.s.l. and are situated on the islands of Vágar, Streymoy and Eysturoy. The lakes are typical representatives of Faroese lowland lakes (Fig. 8 and Table. 3)

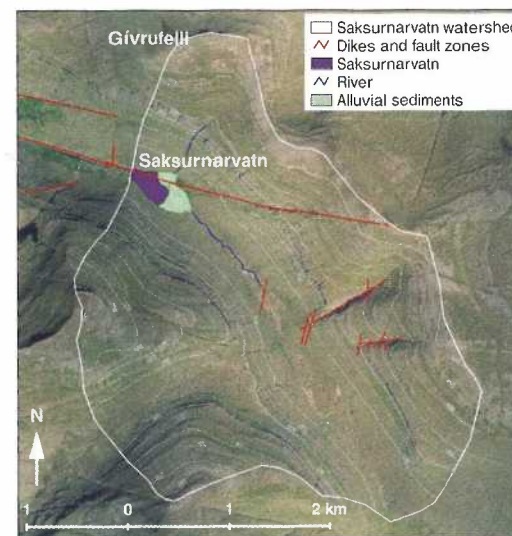


Figure 7. The Saksunarvatn watershed is located in the alpine northern part of a valley penetrating the northern part of Streymoy from Saksun to Hvalvík. The watershed included characteristic alpine landscapes, implying that the lake may experience extreme runoff situations.

The largest lake is Sörvágsvatn, and the second largest Toftavatn, which have, respectively, the very largest and one of the smallest watersheds in the study. Both lakes fall within the category of low relief lake basins characterized by a relatively low frequency of high energy inflow events. Especially Toftavatn has a characteristic low energy environment. Another interesting feature of Toftavatn and Sörvágsvatn is that their lake beds reach below present sea level as a result of glacial over-deepening.

Four of the five lakes are located in northwest/southeastwards oriented valleys cutting through entire islands, with a water divider in the highest part of these valleys

from where water runs in separate directions. Only the northern valley of Leynavatn closes up into a cirque. The southern part of the Leynavatn watershed comes into contact with the valley running from Leynar to Kollafjørður cutting through Streymoy in an east-westerly direction.

Calculations of watershed topography (Fig. 8) elucidate some main differences between lakes located in low relief lake basins and high relief lake basins. Both lake types are located within depressions of the landscape inherited from the early large-scale Tertiary drainage system. Only small areas of low relief lake basins are found above an altitude of 300 m, while in the case of the high relief alpine landscapes of Leynavatn, Eystara Mjáavatn and Saksunarvatn, 49 % to 59 % of the area is above 300 m a.s.l. The highest altitudes of these three watersheds reach above 700 m a.s.l., implying that a large proportion of the area of the high relief watersheds is characteri-

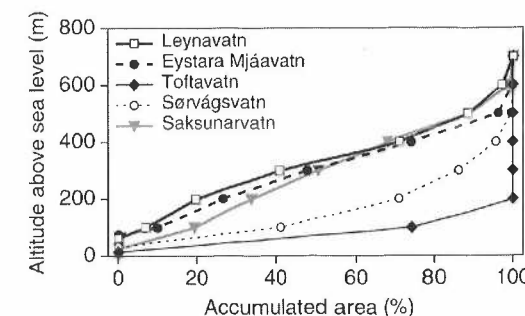


Figure 8. Hypsograph of the watersheds of the five selected lakes. Sörvágsvatn and Toftavatn belong to the 'low relief lake basin type', while Saksunarvatn, Leynavatn and Eystara Mjáavatn belong to the 'high relief lake basin' type with more than 50% of the area lying above 300 m a.s.l.

Table 3. Parameters of the five selected lakes and topography of their watersheds.

	Lake water level (m a.s.l.)	Lake area (ha)	Max water depth (m)	Watershed area (km ²)	Max altitude within watershed (m a.s.l.)	Area above 300 m a.s.l. (%)
Eystara Mjáavatn	76	8.2	7	3.6	718	52
Leynavatn	63	18.1	33	16.6	747	59
Sørvágsvatn	32	355.7	59	35.2	675	14
Saksunarvatn	25	8.2	17	12.3	701	49
Toftavatn	15	51.9	22	3.6	165	0

zed by an arctic climate with a mean temperature below 10 °C during the warmest month (Christiansen and Mortensen, 2002).

The mountain areas above 200-300 m a.s.l. usually show slope instability increasing with altitude. In parts of these regions vegetation is sparse and disturbed by soil erosion and slope failure. This implicates that the lake environments of the category ‘high relief lake basins’ may be characterized by high precipitation, snow, slope failure and high load of sediments of the rivers into the lakes.

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General Description of Five Faroese Lakes

Lýsing av fimm føroyskum vøtnum

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Úrtak

Summarið 2000 gjørdi ein kanningarbólkur við gransk- arum úr Føroyum, Danmark, Íslandi, Noregi og Svøríki lívfrøðiligar kanningar á fimm føroyskum vøtnum. Endamálið við kanningin var at fáa meira at vita um lív- frøðina og vistfrøðina á vøtnunum.

Tey fimm vøtnini vóru Eystara Mjáavatn, Leynavatn og Saksunarvatn í Streymoynni, Sørvágsvatn/Leitisvatn í Vágoynni og Toftavatn í Eysturoynni (Mynd 1). Vøtn- ini eru ymisk í formi, skapi og lívfrøðiligari saman- seting. Støddin á vøtnunum er millum 0,03 til 3,56 fer- kilometrar, størsta dýpið er millum 7 og 59 metrar, og upplendið er millum 1,8 og 35,2 ferkilometrar.

Abstract

In summer 2000, a research team from the Faroe Is- lands, Denmark, Iceland, Norway and Sweden under- took a biological investigation of five Faroese lakes. The purpose of the investigation was to gain more knowledge of the biology and ecology of the lakes.

The five study lakes were Eystara Mjáavatn, Leyna- vatn and Saksunarvatn on the island of Streymoy, Sørvágsvatn/Leitisvatn on the island of Vágur and Tofta- vatn on the island of Eysturoy (Fig. 1). The lakes differ in morphometry, physical nature and biological com- munity structure and vary in size from 0.03 to 3.56 km², maximum depth ranging from 7 to 59 m and catchment area from 1.8 to 35.2 km².

Introduction

There are many small and medium sized lakes in the Faroe Islands, located both in the low-lying valleys and in the hills and mountains (Rasmussen, 1982). The largest lakes are found on the island of Vágur, but most lakes are found on Suðuroy, Sandoy, Streymoy and Eysturoy. Some of the lakes are of glacial origin, the results of erosion by ice in valleys or in the highland basalt. Others are of tectonic origin, and yet others are inland lagoons (Rasmussen, 1982; Mortensen, 2002).

Eystara Mjáavatn

Eystara Mjáavatn (Fig. 2) is located on the island of Streymoy between the two villa- ges of Kollafjørður and Leynar at an alti- tude of 76 m (Table 1). The lake is the smal- lest and most shallow of the lakes studied, with an area of 0.03 km² and a maximum length and width of 250 and 160 m, respec- tively. The maximum depth recorded is 7.0 m and the mean depth is 3.0 m. The shore is flat and mostly composed of gravelly sand.



Figure 1. Map of the Faroe Islands showing the five investigated lakes.

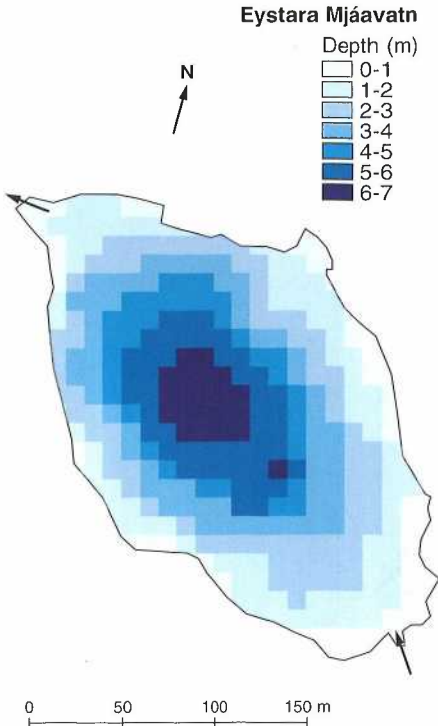


Figure 2. Contour plot of Eystara Mjáavatn with arrows marking the largest in- and outlets.

Eystara Mjáavatn has a small catchment area, only 1.8 km², consisting of extensive grass fields on stony hills (Table 2). The input of nutrients and other materials to the lake derives mainly from natural erosion of the surroundings and from precipitation. The main inlet is located at the southeastern side of the lake, but several small brooks enter the lake from the northeast and southwest. The outlet runs into the nearby Vestara Mjáavatn, which is further connected with Leynavatn at 63 m a.s.l.

Leynavatn

The area of Leynavatn (Fig. 3) is 0.18 km², and the maximum length and width are 680 and 350 m, respectively. Maximum depth measured by Dali (1975) is 33 m, while the average depth of the lake is 13.7 m. There is a big sandy beach at the northern and eastern sides of the lake, while the southern and western sides are more hilly and stony. The catchment area is 16.6 km², of which just 1 % is cultivated fields and 99 % are extensive grass fields in a hilly area. The input of nutrients to Leynavatn mainly originates from 10 households situated in

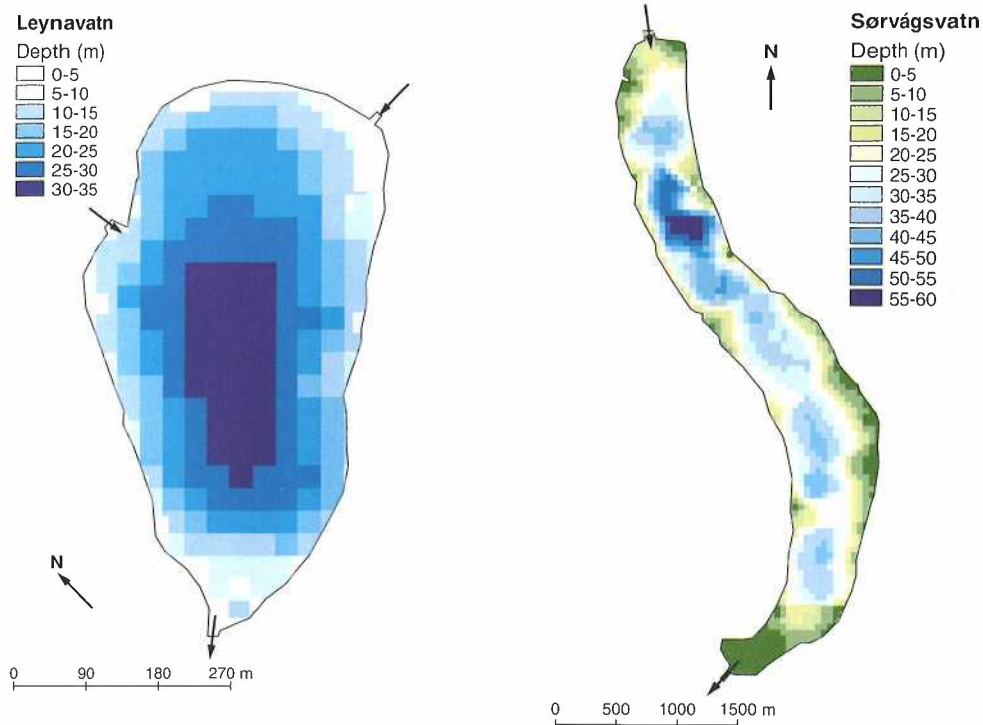


Figure 3. Contour plot of Leynavatn with arrows marking the largest in- and outlets.

the infield area and from natural erosion of the surroundings. The main inlets derive from the north via the Dalá, and the outlet from Vestara Mjáavatn. The Leynará runs from the southeast end of the lake and into the sea.

Sørvágsvatn

Sørvágsvatn, also named Leitisvatn (Fig. 4), is the largest and deepest lake in the Faroe Islands. It is located at an altitude of 32 m between the two towns of Sørvágur and Miðvágur at the southern end of the island of Vágar. The lake is situated at the

Figure 4. Contour plot of Sørvágsvatn with arrows marking the largest in- and outlets.

south end of a valley crossing the island from the north to the south (Mortensen, 2002). The lake is long and relatively narrow with a maximum length and width of 6000 and 800 m, respectively. The lake covers an area of 3.56 km². The maximum depth measured by Dali (1975) was 59 m and the mean depth of the lake is 27.5 m. A small sandy beach is found near the village of Vatnsøyrar, otherwise the shore is stony. The catchment area is 35.2 km², which is the largest for the five lakes. It comprises of 6 % cultivated fields (including the airport runway) and 94 % of extensive grassland

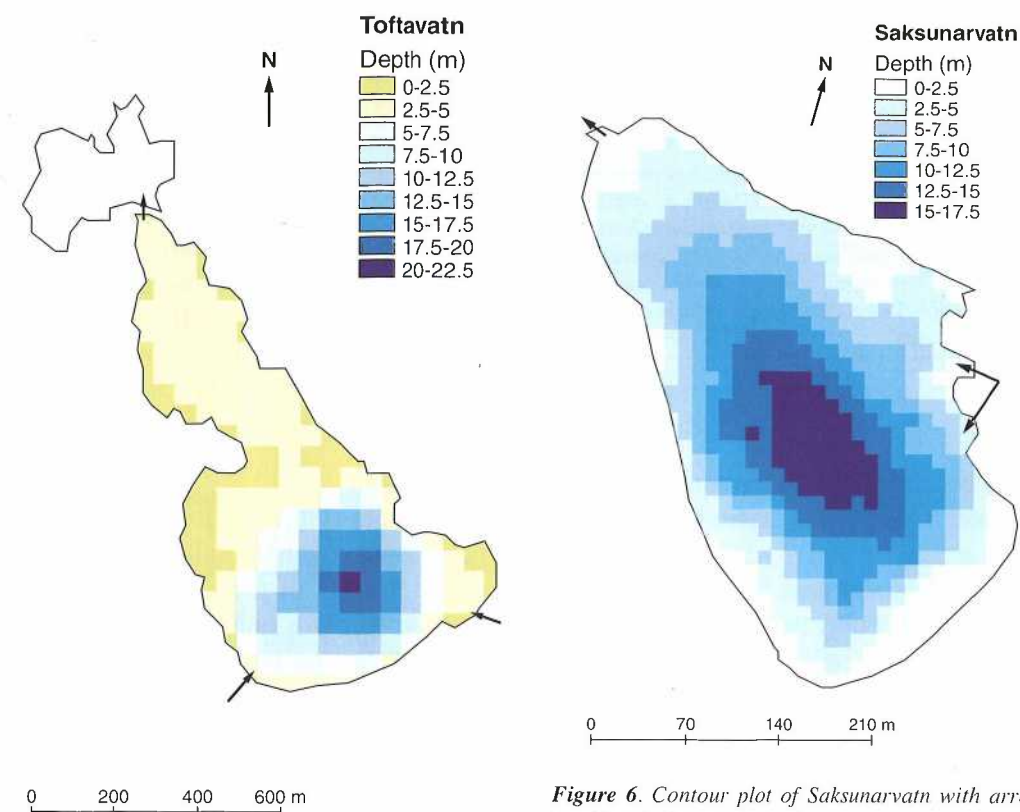


Figure 5. Contour plot of Toftavatn with arrows marking the largest in- and outlets.
No data from the northern basin.

and stony fields. The cultivated percentage is the highest for the five lakes. The main input of nutrients to Sørvágsvatn can be attributed to wastewater from households in the village of Vatnsøyrar and to runoff from the airport runway due to the ammonia-containing defroster system used during the winter months.

The main inflow is the Skjatlá at the north, but many small brooks enter the lake along the entire shore. The lake outlet runs via the Bøsdalafossur to the sea.

Figure 6. Contour plot of Saksunarvatn with arrows marking the largest in- and outlets.

Toftavatn

Toftavatn (Fig. 5) is located at an altitude of 15 m between the towns of Toftir and Runavík on the island of Eysturoy. The lake is 1500 m long and 770 m wide and covers an area of 0.52 km². The lake is divided into a shallow northern basin and a deep southern basin, with a maximum depth of 3.5 and 22 m, respectively (Dali, 1975). In the northern basin a multitude of rocks and stones break the water surface. Moderate depth and a small, deep central part characterize the southern basin. The mean depth of the whole lake is 5.8 m. A small

Table 1. Morphometric characteristics of the five lakes. Areas are measured in the software program Arcview on 1:100,000 maps. Other data derived from Dali (1975; 1977).

	Area (km ²)	Altitude (m a.s.l.)	Max. depth (m)	Mean depth (m)
Eystara Mjáavatn	0.03	76	7	3.0
Leynavatn	0.18	63	33	13.7
Sørvágsvatn	3.56	32	59	27.5
Toftavatn	0.52	15	22	5.8
Saksunarvatn	0.08	25	17	6.5

sandy beach is found at the southern end of the lake; otherwise the shore is broken and stony.

The catchment area is 3.6 km², consisting of 2 % cultivated fields and 98 % extensive grass fields in a flat area. The cultivated grass fields to the south and southeast of the lake are used as summer pasture for sheep, and the extensive fields are dominated by heath. Many small brooks enter the lake and the outlet of the lake runs from the north through the town of Runavík. The nutrient input derives mainly from 3-4 households and the summer pastures.

Saksunarvatn

Saksunarvatn (Fig. 6) is located on the island of Streymoy in the valley of Saksunardalur to the east of the village of Saksun. Saksunardalur is a rather long valley running southeast to northwest. The lake is surrounded by very steep hills on all sides, except the flat and sandy south and southeast part of the shore. The lake is situated at 25 m a.s.l. and is 450 m long and 160 m wide at the widest part. The lake covers an area of 0.08 km². The lake bottom of Saksunarvatn has a maximum depth of 17 m and a mean depth of 6.5 m.

The catchment area is 12.3 km², consist-

Table 2. Catchment areas including the lake areas and catchment type. Catchment areas and types are measured in the software program Arcview on 1:100,000 maps and on topographic 1:20,000 maps, respectively. The cultivated fields and the extensive fields correspond to the terms infields and outfields, respectively.

	Catchment area (km ²)	Cultivated fields (%)	Extensive fields (%)	Catchment area divided by lake area
Eystara Mjáavatn	1.8	0	100	60
Leynavatn	16.6	1	99	92
Sørvágsvatn	35.2	6	94	10
Toftavatn	3.6	2	98	7
Saksunarvatn	12.3	1	99	154

ting of 1 % cultivated grassland and 99 % extensive fields. The most important inlet is the Dalá, which enters the lake at the east end. The smaller Tvørá enters the lake from the eastern end of the valley too, while a few small brooks enter the lake from the north and southwest sides. The nutrient load to Saksunarvatn derives from four households, the small infield area, and natural erosion of the environment and precipitation. The lake has the highest catchment to lake surface area ratio.

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Water Chemistry of Five Faroese Lakes

Evnafrøðin í fimm føroyskum vøtnum

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Úrtak

Evnafrøðin í fimm føroyskum vøtnum (Eystara Mjáavatni, Leynavatni, Saksunarvatni, Sørvágsvatni og Toftavatni) varð máld í august 2000. Øll fimm vøtnini kunnu flokkast sum vøtn við lítlum taðfalli (oligotrof) við einum savnaðum fosforinnihaldi á millum 3 og 16 µg P l⁻¹ og við einum blaðgrøni-innihaldi millum 0.8 og 1.7 µg l⁻¹. Hægstu savnaðu fosfor- og blaðgrønis-nøgdirnar vóru funnar á Eystara Mjáavatni, sum eisini hevði minsta klára vatni (Secchi-dýpið). Størstu mongdirnar av køvievni vóru at finna í Sørvágsvatni. Hetta kemst helst av, at frostveska rennur av flogvøllinum oman í vatnið.

Abstract

Physico-chemical variables were measured in August 2000 in five Faroese lakes (Eystara Mjáavatn, Leynavatn, Saksunarvatn, Sørvágsvatn and Toftavatn). All lakes can be classified as oligotrophic with total phosphorus concentrations between 3 and 16 µg P l⁻¹ and chlorophyll *a* between 0.8 and 1.7 µg l⁻¹. The highest total phosphorus and chlorophyll concentrations and the lowest Secchi depth were recorded in Eystara Mjáavatn. The highest nitrogen level was found in Sørvágsvatn, most probably derived from runoff from the defrosting chemicals at the nearby Vágur airport.

Introduction

So far only few investigations have been undertaken of the limnology of Faroese lakes. Most former studies have focussed on lake biology including only few physical and chemical variables (Christoffersen, 2002). A few specific studies have encompassed selected physico-chemical variables (Lützen, 1978; Johnsen, 1998; Madsen and Bagger, 1999) and the effects of rearing of salmon fry on the environmental state of specific lakes (Brattaberg, 1995; Johnsen, 1998), but no investigations have included land use and other anthropogenic factors, and no scientifically based evaluation of human impact on lake water quality exists.

Materials and methods

Investigations were undertaken in five Faroese lakes, three lakes on Streymoy (Eystara Mjáavatn, Leynavatn and Saksunarvatn), one on Vágur (Sørvágsvatn) and one on Eysturoy (Toftavatn). Each lake was visited once and sampling took place from a boat positioned approx. at the deepest part.

The transparency was measured using a Secchi disc (25 cm in diameter). Water temperature (± 0.1 °C), oxygen (± 0.2 mg l⁻¹), conductivity (± 1 % µS cm⁻¹) and pH (± 0.2 unit) were measured in situ using a Mini-Sonde multiprobe (Hydrolab, USA) where each probe was calibrated according to the manual prior to the survey. Samples for chemical analyses (total and dissolved reactive phosphorus, total nitrogen, nitrate and total alkalinity) were taken as depth-integrated, mixed samples from the entire water column or from the epilimnion and the hypolimnion in the stratified lakes using a Schindler sampler. Total alkalinity was measured by titration with HCl within a few hours. Chlorophyll *a* samples were filtered onto GF/C filters and the concentrations measured spectrophotometrically after ethanol extraction (Jespersen and Christoffersen 1987). The remaining samples were kept frozen for subsequent analysis. Dissolved reactive phosphorus (DRP) was determined on GF/C-filtered samples as molybdate-reactive phosphorus, and total P as DRP after oxidation. After oxidation, nitrate and total nitrogen (TN) concentrations were measured as nitrite in a flow-injection analyser fitted with a copper-cadmium reductor column.

Results and discussion

Of the five lakes only Leynavatn and Saksunarvatn were stratified. Especially Leynavatn had a clear stratification with a low temperature (9.2 °C) in the hypolimnion. All lakes had relatively high alkalinity levels (0.1–0.2 meq l⁻¹) and a pH close to neutral (6.7–7.1, Table 1). In the two strati-

fied lakes, temperature and oxygen concentrations were slightly lower in the hypolimnion compared to the epilimnion. Conductivity was relatively low (94–174 µS cm⁻¹) in all five lakes and unaffected by stratification. The conductivity level of the three Streymoy lakes was lower than in the other two lakes, most likely due to a lower geologically based input of ions.

A comparison of the present results (median TP: 6 µg P l⁻¹ and median TN: 220 µg N l⁻¹) with data from lakes in Iceland, Svalbard and Bear Island (Skjelkvåle, 2001) showed relatively similar concentration levels of both phosphorus (median TP: 8 µg P l⁻¹ (Iceland), 22 µg P l⁻¹ (Svalbard and Bear Island) and total nitrogen (median TN: 125 µg N l⁻¹ (Iceland), 100 µg N l⁻¹ (Svalbard and Bear Island)). Even though all five lakes can be classified as oligotrophic according to international standards (e.g. OECD, 1982), nutrient status, chlorophyll *a* as well as Secchi depth differ, and each lake will therefore be treated separately.

Eystara Mjáavatn

Eystara Mjáavatn is the smallest and most shallow (mean depth = 3.0 m) of the five lakes. Its total phosphorus concentration was the highest recorded (16 µg P l⁻¹), whereas the inorganic nitrogen concentration was low (Table 1). However, based on a characterization of the catchment (Landkildehus *et al.*, 2002), there is no evidence of higher nutrient loading to this lake compared to the other four lakes included. This most likely reflects the low mean depth of the lake, implying stronger effects of nutri-

Table 1. Physico-chemical variables of the 5 study lakes. Samplings were undertaken in August 2000. "<" indicates that the value is below the detection limit. DRP: Dissolved reactive phosphorus.

	Eystara Mjáavatn	Leynavatn	Sørvágsvatn	Toftavatn	Saksunarvatn
Lake area (km ²)	0.03	0.18	3.56	0.52	0.08
Mean depth (m)	3	13.7	59	5.8	6.5
Cultivated area as % of catchment	0	1	6	2	1
Water temperature (°C)	15.0	12.2	12.0	14.6	13.0
-“- in epilimnion	-	13.6	-	-	14.1
-“- in hypolimnion	-	9.2	-	-	11.0
Oxygen (mg O ₂ l ⁻¹)	10.8	11.5	11.4	11.1	10.3
-“- in epilimnion	-	11.8	-	-	12.0
-“- in hypolimnion	-	10.6	-	-	7.1
pH	7.1	6.7	6.7	6.7	6.7
Conductivity (µS cm ⁻¹)	112	94	174	166	107
Total alkalinity (meq l ⁻¹)	0.21	0.16	0.11	0.16	0.23
Total phosphorus (µg P l ⁻¹)	16	3	5	11	6
DRP (µg P l ⁻¹)	3	<1	<1	2	2
Total nitrogen (µg N l ⁻¹)	252	168	318	220	114
Nitrate (µg N l ⁻¹)	<5	14	158	<5	<5
TN:TP ratio (by weight)	16	56	64	20	19
Chlorophyll <i>a</i> (µg l ⁻¹)	1.7	1.3	0.8	1.1	1.3
Secchi depth (m)	4.3	10.0	12.5	5.8	8.8

ent release on the sediment. Wind-induced resuspension from the most shallow parts of the lake may also contribute to the higher total phosphorus concentration compared to deeper lakes. The high nutrient concentrations result in a relatively higher phytoplankton biomass (Brettum, 2002), and the Secchi depth was consequently low.

Leynavatn

In Leynavatn, the concentrations of total and inorganic phosphorus and nitrogen were low (Table 1), probably reflecting the low agricultural activity in the catchment

(only 1% is cultivated). In consequence, the chlorophyll concentration was relatively low and Secchi depth quite high compared to most of the other lakes. However, the chlorophyll concentration was higher and the Secchi depth lower than indicated by the low nutrient concentrations. This may reflect a particularly high predation pressure on the zooplankton in this lake, which hosts large populations of both Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) (Jeppesen *et al.*, 2002; Malmquist *et al.*, 2002). Therefore, the grazing pressure on phytoplankton is probably low.

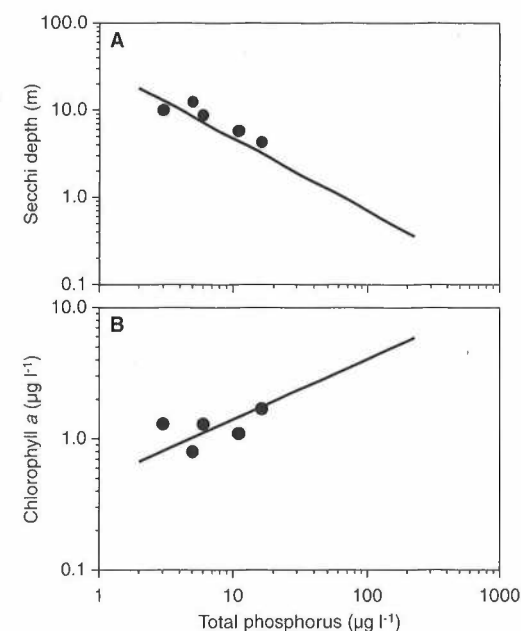


Figure 1. Relationships between total phosphorus and Secchi depth (A) and chlorophyll *a* (B) in the five lakes. The lines show general relationships derived from a data set including 31 Faroese lakes sampled in July-August 2000 (Jeppesen *et al.*, unpubl. data): Secchi depth = $32PTOT^{-0.83}$, $P < 0.001$ ($r^2 = 0.76$), chlorophyll = $0.49PTOT^{0.46}$, $P < 0.002$ ($r^2 = 0.82$).

Sørvágsvatn

In Sørvágsvatn, the largest lake both in terms of depth and surface area, total and dissolved reactive phosphorus concentrations were low (Table 1), whereas both total nitrogen and nitrate were high. The high nitrogen concentration probably reflects wastewater input from the nearby village of Vatnsoyar and not least an input of ammonia from the defrosting facilities at Vágur airport. Cultivation of the catchment is considered less important, although the cultivation percentage was the highest

among the five lakes (6 %) (Landkildehus *et al.*, 2002). The relatively higher nitrogen input was reflected in the TN:TP ratio, which was 64 in Sørvágsvatn compared to 16-56 in the other lakes.

The chlorophyll content of Sørvágsvatn was the lowest among the 5 lakes, and Secchi depth the highest (12.5 m). The higher concentrations of nitrogen did therefore not lead to increased phytoplankton abundance, which indicates that phosphorus limited phytoplankton growth.

Toftavatn

The catchment of Toftavatn is characterized by extensive grass fields dominated by heath plants (91 % of the catchment). Nevertheless, the second highest total phosphorus concentration was recorded here (Table 1). Toftavatn has two basins, of which only one is deep, implying that large parts of the sediment surface are in contact with the epilimnion, which again leads to higher phosphorus concentrations. Also sewage input from a few houses situated near the lakes may have been a contributing factor. The nitrogen concentration was moderate and the nitrate concentration below the detection limit. Secchi depth was relatively low compared to the other lakes, it being lower only in Eystara Mjáavatn. Accordingly, the chlorophyll concentration was higher than in the other lakes.

Saksunarvatn

Saksunarvatn exhibited the lowest nitrate and total nitrogen concentrations of the lakes (Table 1), probably resulting from the low agricultural use of the catchment. Also,

both total and dissolved reactive phosphorus concentrations were low. Despite the high catchment to lake area ratio (Landkildehus *et al.*, 2002), and thus a potentially high hydrological loading, the nutrient concentrations were low, indicating low nutrient loading. However, the chlorophyll concentration was not as low as could be expected from the recorded nutrient concentrations, and also Secchi depth (8.8 m) was smaller than in both Leynavatn and Sørvágsvatn.

Conclusion

All five lakes investigated can be categorised as oligotrophic. Different impacts of natural and anthropogenic catchment factors result, however, in somewhat different physico-chemical conditions. Total phosphorus seems to be the most important limiting factor for phytoplankton growth and the relationships between total phosphorus and chlorophyll concentrations and between total phosphorus and Secchi depth in the five lakes follow the general relationships established for Faroese lakes (Fig. 1). The five lakes range within the low end of the phosphorus scale observed in other Faroese lakes.

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Phytoplankton Species Composition and Biovolume in Five Faroese Lakes

Plantuæti og mongdin av lívrúnum evni í fimm føroyskum vøtnum

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Úrtak

Í samband við NORLAKE kanninginina í Føroyum fyrst í august 2000, varð nágreinaliga nøgdin av plantuæti kannað í fimm føroyskum vøtnum. Kanningarnar vórðu gjørdar við einari speglvendari sjóneyku, og roknað varð fram til savnaðu nøgdinar av einstøku sløgnum, av høvuðsbólkunum og av samlaðu platuætinøgðini. Samlaða mongdin av plantuæti var millum 84 (Sørvágsvatn) og 211 (Saksunarvatn) mm³ m⁻³. Lægsta talið av ymiskum sløgum, 16, varð funnið í royndunum frá Saksunarvatni, meðan hægsta talið, 35, varð funnið í Sørvágsvatni. Hesi tøl eru smá, um tey verða samanborin við líknandi kanningar av norskum vøtnum. Í Saksunarvatni og Eystara Mjáavatni var bólkurin Cryptomonads ráðandi, meðan mongdin av hinum høvuðsbólkunum av plantuæti var nøkulunda javnt býtt í hinum trimum vøtnunum. Úrslitið bendir á, at øll vøtnini eru vøtn við lítlum taðfalli (oligotrofar).

Abstract

In connection with the NORLAKE study in the Faroe Islands in early August 2000, quantitative samples for phytoplankton analyses were collected in five Faroese lakes. The samples were examined using an inverted microscope and the volume of each species, main groups and total volume of phytoplankton calculated. The total biovolume of phytoplankton varied between 84 (Sørvágsvatn) and 211 (Saksunarvatn) mm³ m⁻³. The lowest number of taxa, 16, was recorded in the Saksunarvatn sample, while the highest number, 35, was found in the sample from Sørvágsvatn, a relatively low species number compared to Norwegian lakes. In Saksunarvatn and Eystara Mjáavatn, the phytoplankton community was quantitatively dominated by crypto-

monads, while the phytoplankton biovolume of the other three lakes was more equally distributed among several main groups of phytoplankton. The results suggest that all lakes are oligotrophic.

Introduction

Only few lake studies conducted in areas surrounding the Norwegian Sea have included quantitative and qualitative analyses of phytoplankton communities, some of the limited examples being Willén's (1970; 1980) studies in Bear Island and Spitsbergen, Jónasson *et al.*'s (1992) investigations in Thingvallavatn, Iceland, and different reports from the Norwegian Institute for Water Research (NIVA) (e.g. Faafeng *et al.*, 1990; 1999). The phytoplankton communities of Faroese freshwater lake have been studied in some cases. Faroese lakes are mainly oligotrophic due to their geological origin and low input of wastewater. The phytoplankton biomass is consequently low but contains a wide range of species belonging to nutrient poor and alpine lakes (Brettum, 1989). Börgesen and Ostfeld (1903) investigated the phytoplankton in net samples from Faroese

lakes, including Sørvágsvatn. Recently, a more detailed view of the composition of the phytoplankton communities in Faroese lakes has been obtained from the studies conducted by Johnsen (1998) in Vatnsnesvatn on Suðuroy in August 1998, also including quantitative estimates of small forms such as flagellates and monads, and by Danielsen (1999), who analysed phytoplankton net samples from several Faroese lakes including those presented here.

The purpose of the present study was to describe quantitatively and qualitatively the phytoplankton communities to increase our insight into phytoplankton species richness and biovolume in five lakes in the Faroe Islands.

Materials and methods

The studied lakes are small, excepting Sørvágsvatn with a surface area of 3.56 km² and a maximum depth of 59 m (Landkildehus *et al.*, 2002). Only Eystara Mjáavatn is slightly alkaline, while the other lakes are slightly acid. Judged from the content of total phosphorus and nitrogen, the lakes are oligotrophic and calcium-poor, even though Eystara Mjáavatn had a somewhat higher content of total phosphorus than the rest of the lakes (Jensen *et al.*, 2002).

Only one quantitative phytoplankton sample was taken from each of the five lakes in the beginning of August 2000, which unpublished data on Norwegian oligotrophic lakes has shown to be the period of the growth season when the lakes exhibit the most diverse phytoplankton communities. The samples were mixed

from the epilimnion. All the samples were preserved with Lugol's solution to which acetic acid was added.

The samples were analysed according to Utermöhl (1958) and the phytoplankton volumes calculated using the recommendations given by Rott (1981). Sedimentation chambers of 10 and 50 ml were used for the sedimentation procedure, and 2 to 4 transects of the chamber bottom were examined.

A Leitz Fluovert FS inverted microscope with phase contrast was used to examine the sedimentation chambers. The total number of individuals per species or taxa were counted in transects, and 10 individuals per species (taxa) measured. From these measurements the mean specific volume per species (taxon) was calculated, comparing the form of the species with simple geometric figures (Rott, 1981; Olrik *et al.*, 1998). For large species with a low number of individuals, the whole bottom area of the sedimentation chamber was examined. Phytoplankton biovolumes were then calculated for each species (taxon), the main groups (chlorophytes, dinoflagellates, etc.) and the total volume of phytoplankton. All the biovolumes are given as mm³ m⁻³, which, with a fair degree of accuracy, is equal to mg m⁻³ wet weight (Brettum, 1984).

Results

Saksunarvatn

The largest total volume of phytoplankton among the lakes investigated, 211 mm³ m⁻³, was recorded in this lake. On the other hand, the lowest number of species (taxa),

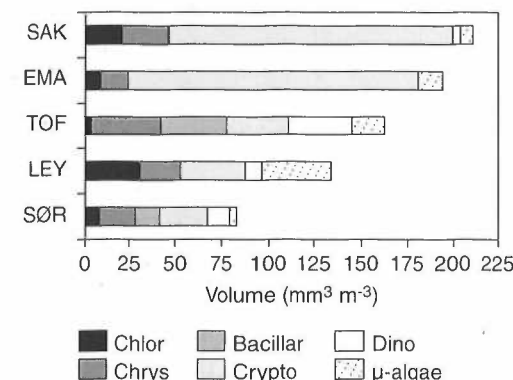


Figure 1. Volume of the main groups and total phytoplankton volume in five Faroese lakes sampled in August 2000.

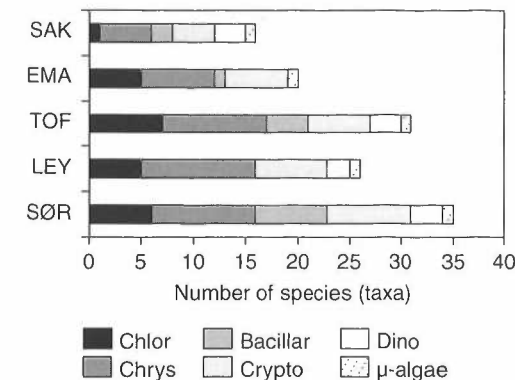


Figure 2. Species (taxon) number of main phytoplankton groups in five Faroese lakes sampled in August 2000.

16, was recorded here as well. Cryptomonads dominated the phytoplankton community at the time of sampling, constituting approx. 73 % of total volume, while chrysomonads constituted 12 % and chlorophytes 10 % of total volume, the latter being represented by only one species identified with some uncertainty as *Oocystis marssonii*. The cryptomonads were dominated by a species of the genus *Chroomonas*. Among the low number of species (taxa) found, five were chrysomonads and four cryptomonads.

Eystara Mjáavatn

At the time of sampling in early August, the phytoplankton biovolume was 195 mm³ m⁻³ and the community was completely dominated by cryptomonads, constituting approx. 80 % of the total phytoplankton volume (Fig. 1). The most abundant species in this group was probably belonging to the genus *Chroomonas*. This group is

often difficult to identify to a species level from preserved material. In addition, different species of the genus *Cryptomonas* were found, among others *Cryptomonas erosa* var. *reflexa*. Other groups were of minor importance, including chrysomonads that normally dominate in oligotrophic lakes. The total number of species (taxa) recorded was 20 (Table 1), most of them belonging to Chrysophyceae (five), Cryptophyceae (six) and Chlorophyceae (four).

Toftavatn

This lake had a total phytoplankton volume of 164 mm³ m⁻³ and a relatively high number of species (taxa) compared to the other four lakes. No specific group dominated the phytoplankton community at the time of sampling and four of the main groups contributed almost evenly to the total volume; chrysomonads (24 %), diatoms (Bacillariophyceae) (22 %), crypto-

Table 1. Phytoplankton analyses of quantitative samples from five lakes in the Faroe Islands 2000. (l=length, d=diameter). Values given in mm³ m⁻³ (=mg m⁻³ wet weight).

	Eystara Mjáavatn	Leynavatn	Saksunarvatn	Sørvágsvatn	Toftavatn
Cyanophyceae (cyanobacteria)					
<i>Snowella lacustris</i>					1.0
Total					1.0
Chlorophyceae (green algae)					
<i>Ankistrodesmus falcatus</i>		0.2			
<i>Botryococcus braunii</i>				4.0	
<i>Chlamydomonas</i> sp. (l=8µm)	6.2	0.1			0.1
<i>Cosmarium abbreviatum</i>		0.4			
<i>Cosmarium cf.ornatum</i>				2.7	
<i>Cosmarium margaritiferum</i>	0.7				
<i>Crucigenia quadrata</i>				0.2	
<i>Euastrum elegans</i>	0.4				
<i>Monoraphidium dybowskii</i>					0.9
<i>Mougeotia</i> sp.	0.8				
<i>Oocystis cf.marssonii</i>			20.8		
<i>Oocystis submarina</i> var. <i>variabilis</i>		0.3		0.1	
<i>Scourfieldia complanata</i>					0.3
<i>Sphaerocystis Schroeteri</i>					1.2
<i>Staurodesmus indentatus</i>				0.5	0.7
<i>Tetraedron caudatum</i>					0.2
Undet. coccoid green algae (d=5µm)		29.5			
Undet. coccoid green algae (d=6µm)	0.5				
Undet.elliptic green algae				0.2	
Total	8.6	30.5	20.8	7.7	3.4
Chrysophyceae (golden algae)					
<i>Chromulina</i> sp. (<i>Chr.pseudonebulosa</i> ?)	0.1	1.6			0.2
<i>Craspedomonads</i>				0.1	0.1
<i>Dinobryon borgei</i>				0.3	2.6
<i>Dinobryon crenulatum</i>		0.2		0.8	0.4
<i>Kephyrion litorale</i>	0.4				
<i>Kephyrion</i> sp.			0.8	0.1	0.5
<i>Mallomonas akrokomos</i> (var. <i>parvula</i>)	3.2	0.2	7.2		
<i>Mallomonas</i> spp.	2.0	5.1		0.2	17.8
<i>Ochromonas</i> sp.		0.9			
<i>Ochromonas</i> sp. (d=3.5-4µm)	3.1	2.4	2.7	2.4	2.9
Small chrysomonads (d<7µm)	6.1	9.1	14.0	11.9	9.0
<i>Spiniferomonas</i> sp.		0.2		0.4	0.5
Large chrysomonads (d>7µm)	0.9	1.7	0.9	3.9	4.7
Undet.chrysomonade (<i>Ochromonas</i> sp.?)		0.7		0.7	
Undet.chrysophyceae		0.1			
Total	15.7	22.3	25.5	20.6	38.8

	Eystara Mjáavatn	Leynavatn	Saksunarvatn	Sørvágsvatn	Toftavatn
Bacillariophyceae (diatoms)					
<i>Aulacoseira alpigena</i>				0.2	
<i>Cyclotella comensis</i>				2.9	
<i>Cyclotella comta</i> var. <i>oligactis</i>				7.4	28.6
<i>Cyclotella glomerata</i>					1.5
<i>Cyclotella radiosa</i>				2.8	5.1
<i>Eunotia</i> sp.			0.2		
<i>Fragilaria</i> sp. (l=40-70µm)			0.2	0.5	0.6
<i>Nitzschia</i> sp.	0.1				
<i>Rhizosolenia eriensis</i>				0.1	
Total	0.1		0.4	13.8	35.9
Cryptophyceae (cryptomonads)					
<i>Chroomonas</i> sp.			149.9		14.4
<i>Cryptomonas erosa</i> v. <i>reflexa</i> (<i>Cr.reflexa</i> ?)	28.6			0.4	
<i>Cryptomonas marssonii</i>	1.3	5.3		1.4	3.6
<i>Cryptomonas</i> sp. (l=15-18µm)	0.7				
<i>Cryptomonas</i> sp. (l=20-22µm)		3.4		5.0	
<i>Cryptomonas</i> spp. (l=24-30µm)	51.2	4.1		8.5	4.0
<i>Katablepharis ovalis</i>	0.3	1.1	2.0	1.0	2.0
<i>Rhodomonas lacustris</i> (+var. <i>nannoplantica</i>)		2.6		7.6	8.1
Undet.cryptomonade (<i>Chroomonas</i> sp.?)	75.1	18.3	0.8	0.8	
Undet.cryptomonade (l=6-8µm) <i>Chro.acuta</i> ?		0.6	0.2	0.1	0.2
Total	157.2	35.3	153.0	24.9	32.4
Dinophyceae (dinoflagellates)					
<i>Amphidinium</i> sp.		0.4			
<i>Gymnodinium cf.lacustre</i>			1.1	2.9	1.1
<i>Gymnodinium</i> sp.				9.6	33.0
<i>Gymnodinium</i> sp. (l=14-16µm)			2.4		
<i>Peridinium umbonatum</i> (<i>P.inconspicuum</i>)					0.4
<i>Peridinium willei</i>		8.0			
Undet.dinoflagellate			0.5	0.3	
Total		8.4	4.0	12.8	34.5
„µ-algae“	13.3	38.2	6.8	4.1	17.2
Total	13.3	38.2	6.8	4.1	17.2
Total volume	194.8	134.7	210.4	83.9	163.1
Number of taxa	20	26	16	35	3

monads (20 %) and dinoflagellates (21 %). The diatom *Cyclotella comta* var. *oligactis* was relatively abundant. Among the chrysophytes, species of the genus *Mallomonas* appeared abundantly, while one species of the genus *Chroomonas* dominated the cryptomonads and one species of the genus *Gymnodinium* prevailed among the dinoflagellates. As mentioned above, the number of species (taxa) recorded was high, 31 in total.

Leynavatn

The total volume of phytoplankton was 135 mm³ m⁻³, and as shown in Figure 1 no specific group dominated the phytoplankton community at the time of sampling. Cryptomonads constituted approx. 26 % of total volume, chlorophytes 23 % and chrysomonads 16 %. Microalgae („µ-algae“), containing small unidentified species with a diameter of 2-4 µm, are often numerous in oligotrophic lakes, as was the case in Leynavatn, where they constituted 28 % of the total phytoplankton volume (Table 1). Also in Leynavatn a cryptomonad species occurred, probably belonging to the genus *Chroomonas*, together with different species of the genus *Cryptomonas*, as for instance *C. marssonii*. Dinophyceae was represented by the rather large and easily identifiable species, *Peridinium willeyi*. The total number of species (taxa) recorded was 26 (Table 1), most chrysomonads (11). Cryptomonads contributed with seven species (taxa) and chlorophytes with five species.

Sørvágsvatn

Sørvágsvatn had the lowest total biovolume among the five lakes at the time of sampling, only 84 mm³ m⁻³, but on the other hand, the highest number of species (taxa). In all, 35 species were recorded, which is twice the number found in Saksunarvatn. No specific group dominated the phytoplankton community, and the relatively high number of species (taxa) was fairly equally distributed among the main groups: chrysomonads (10), cryptomonads (eight), diatoms (seven) and chlorophytes (six). The occurrence of diatoms (Bacillariophyceae) was relatively high. Six species were identified, the most frequent being *Cyclotella comta* var. *oligactis*. In some taxonomic revisions (Krammer and Lange-Bertalot, 1991), this species is grouped with *C. radiosa*. Some of the species recorded by Börgesen and Ostensfeld (1903) were also found in the present sample, but a comparison of the phytoplankton communities cannot be made, since their analyses were based on net samples and ours on a quantitative sample.

Discussion

Based on the present data on species composition and total biovolume of the phytoplankton in five Faroese lakes, it is obvious that the oligotrophic status is the most striking feature. The frequently found desmids (Chlorophyceae) and chrysophytes as well as diatoms (Bacillariophyceae) are species with low nutrient requirements and low temperature optima (Reynolds, 1984; Brettum, 1989). Several species among the recorded dinoflagellates and

chrysophytes are known to be mixotrophic which seems to be more common when inorganic nutrients are depleted or scarce (Porter, 1988). Also, the high contribution of small algae to the total biovolume is typically found in oligotrophic lakes (Søndergaard, 1990). Cyanobacteria were of no quantitative importance in the studied phytoplankton communities, although an earlier study by Danielsen (1999) based on net samples revealed a number of cyanobacteria species.

The above findings are in accordance with other studies in nutrient-poor waters (Heinonen, 1980; Brettum, 1989; Lepistö, 1999; Willén, 1999).

Leynavatn and Sørvágsvatn had the lowest levels of phytoplankton biomass but the most diverse communities. A similar pattern has been recorded in oligotrophic Norwegian lakes (Brettum, unpubl. data). In many temperate oligotrophic lakes, August is the period exhibiting the most diverse phytoplankton communities. Maximum total biovolume of phytoplankton is often recorded at that time, although variations occur depending on factors such as latitude, climatic conditions, morphometric characteristics of the lake and trophic level.

The number of species recorded in the samples varied widely between the lakes. In Sørvágsvatn, 35 species were recorded, which is twice the number found in Saksunarvatn. Norwegian studies undertaken in oligotrophic lakes in late July or early August, i.e. when the phytoplankton community is usually most diverse, revealed a species number ranging between 30

and 50 (Brettum, unpubl. data), which is only 50-70% of the total number recorded when samples are collected and analysed several times throughout the season. Compared with oligotrophic lakes in Norway and elsewhere (Heinonen, 1980; Brettum, 1989; Lepistö, 1999; Willén, 1999), the number of species recorded in the Faroese samples was low.

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Aquatic Macrophytes in Six Faroese Lakes

Størri vatnplantur í seks føroyskum vøtnum

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Úrtak

NORLAKE verkætlanin kannaði útbreiðsluni av plantuvækstrinum undir vatni, bæði eftir dýpd, og hvussu plantuvæksturinn spenti yvir botnin, í seks føroyskum vøtnum (Toftavatni, Sørvágsvatni, Sandavatni, Leynavatni, Eystara Mjáavatni og Saksunarvatni). Harumframt vóru tey evnafrøðiligu viðurskiftini av týðningi fyri vatnvækstur kannaði. Greiningarnar av vatnplantunum vístu, at 24 ymisk sløg vóru at finna, og av teimum vóru fýra sløg ongantíð funnin áður í føroyskum vøtnum. Sum heild vóru leggstreingjaplanturnar, sum liva fram við vatnsbakkanum, ráðandi niður á 5 metra dýpi, meðan bólkurin Charophytes vera ráðandi á dýpi millum 5 og 10 metrar.

Abstract

During the NORLAKE project six Faroese lakes (Toftavatn, Sørvágsvatn, Sandavatn, Leynavatn, Eystara Mjáavatn and Saksunarvatn) were investigated for the distribution, zonation, and coverage of submerged vegetation. Furthermore, some physical/chemical characteristics important for vegetation were analysed. The identification of water plants revealed 24 species of which four have never been recorded in Faroese lakes before. In general, the vascular plants of the littoral zone covered water depths from 0 to 5 m, whereas charophytes dominated the 5 to 10 m depth zone.



Figure 1. The SCUBA divers with the photo-equipment.

Introduction

The Faroese flora as such is well-described and well-known from previous botanical records and observations (Ostenfeld, 1908; Warming, 1908; Ostenfeld and Grøntved, 1934; Hansen, 1964; 1966; Jóhansen, 2000). However, little attention has been paid to the aquatic vegetation of Faroese lakes, although the number of lakes identified from a 1:100,000 map exceeds 150. Further, coverage, zonation and depth distribution of aquatic macrophyte species have not been quantified.

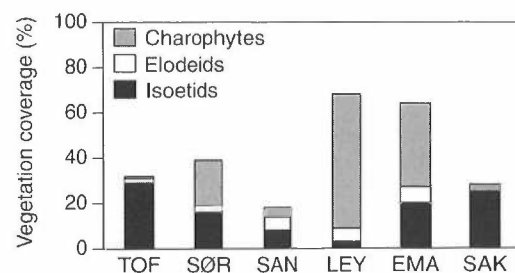


Figure 2. Average vegetation coverage based on 10 transects (Toftavatn, TOF), 22 transects (Sørvágsvatn, SØR), 9 transects (Sandsvatn, SAN), 15 transects (Leynavatn, LEY), 4 transects (Eystara Mjáavatn, EMA) and 9 transects (Saksunarvatn, SAK).

This paper presents the results obtained on species diversity, density and depth distribution of submerged and floating leaved plants from the investigations undertaken in six large, natural and unmanaged lakes situated on four of the major islands. The aim of the investigations was to describe the species distribution of the aquatic macrophytes, to quantify their abundance and to compare species diversity to that of the other Nordic countries.

Materials and methods

Study area and lake description.

The lakes investigated in 2000 represent Faroese lakes in general as to depth classes and size. Table 1 shows lake areas from 0 to 5 m lake depth indicating the depth range for the distribution of vascular plants as well as lake areas from 5 to 10 m lake depth indicating the range where charophytes dominate. Charophytes are, however, found in-between the vascular plants in the shallow parts of the lakes as well. The lakes are generally characterized by lack of reed swamps because of grazing sheep and wave erosion due to exposure to strong winds.

All study lakes are oligotrophic and calcium-poor (Table 2, see also Jensen *et al.*, 2002).

The description of aquatic macrophyte depth distribution and coverage is based on three different methods: identification of species, transect analysis and underwater photography.

Terminology of life forms used.

Our investigation focused on submerged and floating leaved plants; including vascu-

lar plants and stoneworts (charophytes). The vascular plants are grouped into growth forms: isoetids (small submerged, rosette-plants with well developed roots), elodeids (elongated and submerged plants, poorly rooted, some of them also with floating leaves), nymphaeids (plants mainly with floating leaves) and lemids (free floating plants).

Registration of species.

We used a standard method for recording the macrophyte diversity in lakes involving recording of plants at different localities in the lake (with different erosion conditions, outlet, inlet, shallow and deep area etc.) using an aquascope, and plant collection by dredging from a boat. Species abundance was ranked according to a semi-quantitative scale, where 1 = rare, 2 = scattered, 3 = common, 4 = locally dominant and 5 = dominant.

Transect analyses.

The number of transects in each lake depended on lake size. Transects were defined at regular intervals and rowed from shore to shore in shallow lakes or from shore to a depth devoid of plants or were

not found using a rake sampler in deeper lakes. Degree of total plant coverage (%) was judged by the Hult-Sernander method (5 = 100-50 %, 4 = 49-25 %, 3 = 24-13 %, 2 = 12-5 %, 1 = <5 %, 0 indicates no vegetation). Furthermore, the degree of coverage (%) for each species within the vegetation was recorded.

Underwater photography.

The photographic sampling (modified from Rørslett *et al.*, 1979) was carried out by SCUBA divers (Fig. 1). The camera (Nikonos V) and flash were attached to a square frame with a size of 0.25 m². The pictures were taken randomly from approx. 0.5 m depth to below the deepest observed vegetation (maximum 10-11 m depth). Presence and coverage (%) of different plant species were determined from the pictures. The photo sampling was performed at two localities in each lake, except in Eystara Mjáavatn where we had only one locality. A total of 740 pictures were obtained from the lakes. All depths given relate to the current water level during the investigation period. Information about water level fluctuations in the lakes is unavailable, but due to the very dry summer in 2000 the water

Table 1. Lake physical characteristics (also see Landkildhus *et al.*, 2002). Lake areas based on Dali 1975; 1977; 1982). Shoreline developments are calculated according to Wetzel (2001).

Lake	Lake area (km ²)	Area of Z = 0-5m ¹ (%)	Area of Z = 5-10m ² (%)	Total area of vegetation zone (%)	Shoreline develop- ment, D _L	Max. depth, Z _{max} (m)	Elevation above sea level (m)
<i>E. Mjáavatn</i>	0.03	82.5	18	100	1.19	7	76
<i>Leynavatn</i>	0.18	15	9	24	2.13	33	63
<i>Saksunarvatn</i>	0.08	41.6	22	64	1.27	17	25
<i>Sandsvatn</i>	0.8	100	0	100	1.75	2	2
<i>Sørvágsvatn</i>	3.56	~16	9	25	2.17	59	32
<i>Toftavatn</i>	0.52	80.8	8	89	1.76	22	15

1: (Sandsvatn 0-2m), 2: (Eystara Mjáavatn 5-7 m)

Table 2. Lake physical/chemical characteristics recorded in August 2000 (Jensen *et al.*, 2002).

Lake	Temperature (°C)	Cond (µS cm ⁻¹)	pH	Alk (meq l ⁻¹)	Total P (µg l ⁻¹)	Total N (µg l ⁻¹)	Ca mg l ⁻¹	Secchi Depth (m)
<i>E. Mjáavatn</i>	15	112	7.1	0.21	16	252	2.93	4.3
<i>Leynavatn</i>	12.2	94	6.7	0.16	3	168	2.45	10.0
<i>Saksunarvatn</i>	13	107	6.7	0.23	6	114	3.27	8.8
<i>Sandsvatn</i>	16	954	8.5	0.46	43	-	-	2
<i>Sørvágsvatn</i>	12	174	6.7	0.11	5	318	3.05	12.5
<i>Toftavatn</i>	14.6	166	6.7	0.16	11	220	3.06	5.8

level was observed to be lower than normal.

Charophytes were identified according to Blindow and Krause (1990) and vascular plants according to Hansen (1981), Lid and Lid (1994) and Jóhansen (2000).

Plant volume infested (PVI) (Canfield *et al.*, 1984) was estimated from percentage coverage, plant height and water depth.

Results and discussion

The physical characteristics of the lakes are presented in Table 1. Although the lakes are among the large, natural lakes within the Faroes, most of the them are fairly small when compared worldwide, except Sørvágsvatn with a lake area of 3.56 km². However, the variations between lakes were significant, as reflected in the approximately 100-fold and 30-fold differences in lake area and maximum depth, respectively. Despite a large shoreline development in Sørvágsvatn and Leynavatn, the area of the vegetation zone relative to the whole lake area was low.

All the lakes were oligotrophic, neutral to slightly alkaline with low alkalinity and with a relatively high transparency (Table 2, Jensen *et al.*, 2002). Consequently, a low species diversity but luxuriant growth of species confined to soft water lakes was to be expected.

As an exception, Sandsvatn was influenced by the sea and had slightly brackish water as reflected in the high conductivity. Moreover, the water quality of Sandsvatn may be influenced by airborne carbonates brought into the lake from the beach and nearby dunes.

Species richness

The lakes were characterized by absence of reed swamps, probably because of sheep grazing and wave erosion. We found a total number of 24 submerged species in the six lakes: six isoetids, 14 elodeids, one nymphaeid and four charophytes (Table 4). Toftavatn, Sandsvatn and Saksunarvatn had the highest species richness with 14 species each (Table 3).

There is usually a high correlation between lake area and species richness of aquatic macrophytes, with large lakes tending to have higher species richness than small lakes due to higher habitat diversity (Rørslett, 1991). However, there seems to be little correlation between species richness and lake area when the area is less than approximately 3 km² (Mjelde, 1997). Consequently, the rather low variation in species number found in this study was to be expected.

The most abundant species in the lakes was the charophyte *Nitella opaca* (Table 3), growing in dense stands from 0.5 m down to a depth of 10–11 m. The isoetids, especially *Isoetes lacustris* and *Littorella uniflora*, were common and dominated the shallow water area. *Myriophyllum alterniflorum* was the most frequently appearing elodeid, but total distribution of this functional group was scattered. Toftavatn differed from the other lakes with *Isoetes lacustris* being the dominant species, but it also had abundant stands of *Potamogeton* species, especially in the western part of the lake. Because of the highly indented morphology of Toftavatn's littoral zone, it may contain a higher number of niches

Table 3. The aquatic macrophytes in the six Faroese lakes surveyed during 2000. Species abundance is ranked according to a semi-quantitative scale, where 1 = rare, 2 = scattered, 3 = common, 4 = locally dominant, 5 = dominant and x = no data.

Growth habit forms/Latin names	Eystara Mjáavatn	Leyna- vatn	Saksunar- vatn	Sands- vatn	Sørvágs- vatn	Toftavatn
ISOETIDS						
<i>Isoetes echinospora</i> Durieu	2	2	1-2	2		1
<i>I. lacustris</i> L.	2	2	2	3	5	5
<i>Juncus bulbosus</i> L.	2	1	5		2	3
<i>Littorella uniflora</i> (L.) Ascherson	3-4	3	3	4	4	3-4
<i>Ranunculus reptans</i> L.			2	2		2
<i>Subularia aquatica</i> L.	x	1			x	2
ELODEIDS						
<i>Callitriche brutia</i> Petagna	2	2		2		
<i>C. hamulata</i> Kütz. ex Koch	2	1	3		1	
<i>C. palustris</i> L.			2			
<i>C. sp.</i>		x	x			
<i>Myriophyllum alterniflorum</i> DC.	2	3	3	2-3	3	3
<i>Potamogeton alpinus</i> Balbis			4			2
<i>P. berchtoldii</i> Fieber						2-3
<i>P. filiformis</i> Pers.				3-4		
<i>P. gramineus</i> L.				3		3-4
<i>P. obtusifolius</i> Mert. and Koch						x
<i>P. perfoliatus</i> L.				3		3-4
<i>P. praelongus</i> Wulfen			x	x		
<i>P. x sparganifolius</i> Laest. ex Fr.					2	
NYMPHAEIDS						
<i>Potamogeton natans</i> L.			4	x	x	
CHARACEAE						
<i>Chara globularis</i> Thuill.					3	4
<i>Nitella translucens</i> (Pers.) Ag.	x		x	x		x
<i>N. opaca</i> Ag.	5	5	5	4	4	
<i>Tolypella nidifica</i> (Müller) A. Br.				x		
Number of species	10	10	14	14	10	14

suitable for growth of broadleaved macrophytes. Further, the sediment quality may differ from that found in the other lakes investigated but this was not investigated in the present study.

Compared to earlier lists of macrophytes (Hansen, 1966), we observed four new species in the Faroe Island lakes; *Callitriche palustris*, *Potamogeton perfoliatus*, *Tolypella nidifica* and the hybrid *Potamogeton x sparganifolius* (*P. gramineus* x *natans*).

Callitriche brutia (earlier named *C. pedunculata* DC.) is a small plant found on the shore around the water level in Eystara Mjáavatn, Leynavatn and Sandsvatn. This species was recorded from the Faroe Islands by Hultén (1971), but is not mentioned elsewhere, neither by Hansen (1966) nor in other Scandinavian flora investigations. In Norway it is included among the coastal plants and has a westerly distribution with a few localities north of Bergen, in river mouths and on clayey alluvium in slightly brackish water, and has probably been brought to these localities by bird dispersal (Fægri *et al.*, 1960). Also in Denmark, *C. brutia* is rare and only found scattered in Jutland and on the island of Bornholm (Moeslund *et al.*, 1990). In Iceland it has been observed at a few localities around Reykjavík and at one locality in the north-western part of the island (Kristinsson, 1998). However, in the Faroe Islands *C. brutia* seems to be fairly common.

The charophyte *Tolypella nidifica* was for the first time in the Faroe Islands observed in Sandsvatn. *T. nidifica* is a rare charophyte, which in 1996 had been found at only 15 localities on the northern hemisphere, in Norway, Sweden, Denmark, Great Britain and at one locality in Greenland (Langangen *et al.*, 1996). It is only found in brackish water, which emphasizes the marine influence of the sea on Sandsvatn.

From a floristic point of view, the lakes investigated represent a group of oligotrophic soft water lakes except for mesotrophic Sandsvatn. This is in accordance with the

low alkalinity and low concentrations of total phosphorus (Table 2). The elodeids *Potamogeton filiformis* and *P. perfoliatus* are indicative of calcium-rich freshwater or brackish water. The occurrence of these species together with *Tolypella nidifica* in Sandsvatn is further evidence of the marine influence on the lake. The occurrence of the charophyte *Chara globularis* in Sörvágsvatn and Toftavatn was unexpected based on the concentration of calcium in the bulk water, which seemingly was below the limit for this species. In Norway, the distribution of *C. globularis* is restricted to waters with a calcium concentration above 4-5 mg Ca l⁻¹ (Langangen, 1974; Mjelde, unpubl.).

In addition to our observations, Hansen (1966); Langangen (1996) and Madsen and Bagger (1999) found 10 vascular plant species and two charophytes in Faroe Island lakes: *Eleocharis acicularis*, *Lobelia dortmanna*, *Callitriche hermaphroditica*, *C. platycarpa*, *C. stagnalis*, *Hippuris vulgaris*, *Utricularia vulgaris*, *Persicaria amphibia*, *Sparganium angustifolium*, *Nymphaea alba*, *Chara deliculata* and *Nitella flexilis*. Most of these species were rare (1-4 localities), except for *C. stagnalis* and *S. angustifolium*, which have both been reported previously from more than 20 localities. In addition, *Potamogeton polygonifolius* is a species commonly occurring in Faroese streams (Hansen and Jóhansen, 1982).

Potamogeton alpinus had previously only been recorded in Lake Eiðisvatn (Hansen, 1966; Schierup, unpubl.), but since this lake has been left devoid of submerged

vegetation due to a recent damming, it was pleasant to observe that the species was found in both Toftavatn and Saksunarvatn.

Species richness in the Faroe Island compared with other Nordic countries.

A comparison between species number in the Faroe Islands and other Nordic countries may not seem fair, since results from only six Faroese lakes were included in this investigation, but data from floras and other literature mentioned above including Schierup (unpubl.) have also been taken into consideration.

The low species number in Faroese lakes relative to lakes in the other Nordic countries (Table 4) may be ascribed to the low alkalinity of Faroese lakes as compared to the much broader amplitude of alkalinity in the other countries. High alkalinity favours elodeids, because many elodeids take up both carbon dioxide and bicarbonate, and the availability of bicarbonate increases with increasing alkalinity (Maberly and Spence, 1983), whereas isoetids take up only carbon dioxide. Also, high nutrient levels, favouring elodeids, lemids and

nymphaeids, are only rarely found in the Faroese lakes. In addition, not all species that might be able to find a settlement niche in Faroese lakes have yet spread from the surrounding countries. So, in general the flora of the lakes can be characterized as typical for softwater lakes although a number of elodeide species due to their high carbon extraction capacities are able to survive despite low concentrations of inorganic carbon (Madsen and Bagger, 1999).

Two threats to the flora of Faroese lakes are, however, becoming increasingly important: 1) hydropower production. The fluctuations in water level are often much more dramatic in reservoirs than in natural lakes (Rørslett, 1988), causing changes in the light climate in the water and in the erosion conditions on the lake sediment as well as within the aquatic vegetation whose abundance and species richness in both shallow and deeper water decline (Rørslett, 1989). The raised water level in reservoirs in general inundates peat areas that are an unsatisfactory substrate for water plants compared with the sandy sediment usually found. Also leaching of humic matter from

Table 4. Number of water plant species in the Faroese study lakes compared with species numbers in other Scandinavian countries. For vascular plants the numbers are based on: 1) this investigation, 2) Mjelde *et al.*, 2000, 3) Euroala and Kukku-Oja, 1986, 4) Moeslund *et al.*, 1990 and 5) Kristinsson, 1998. 6), our investigations including Hansen (1966), Langangen (1996) and Schierup (1987, unpubl.).

	Faroe Islands ¹	Faroe Islands ⁶	Norway ²	Sweden ³	Finland ³	Denmark ⁴	Iceland ⁵
Isoetids	6	6	19	20	9	12	10
Elodeids	13	19	58	73	47	53	21
Nymphaeids	1	3	15	21	9	4	6
Lemnids	0	0	5	6	5	8	0
Total vascular plants	20	28	97	120	70	77	37
Charophytes	3	5	18	34	Lack of inf.	23	Lack of inf.

Table 5. Degree of water plant coverage (%) in the Faroese study lakes and Plant Volume Infested (PVI) in the littoral zone at 0-5 m depth (macrophytes) and at 5-10 m depth (charophytes).

	Toftavatn	Sørvágsvatn	Sandsvatn	Leynavatn	E. Mjáavatn	Saksunarvatn
<i>Coverage %</i>						
Isoetids	29	16	8	3	20	25
Elodeids	2	3	6	6	7	0
Charophytes	1	20	4	59	37	3
<i>Plant volume infested</i>						
PVI 0-5m	3	1	3	1	2	2
PVI 5-10m	1	1	1	1	1	<1

the peat in the grassland surrounding the former lake shore decreases the light intensity for the invasion of vegetation in the freshly inundated areas.; 2) fish breeding. In general, water plants are absent from these lakes, according to local information probably because they have been treated with a pesticide prior to the present use for fish breeding.

The number of lakes used for fish breeding has increased considerably during the last 10-15 years, as has the number of lakes dammed for hydropower production.

Vegetation cover and plant volume infested in the lakes.

The submerged vegetation in Faroese lakes is typically found in a sandy or gravelly littoral zone or between boulders. Leynavatn and Eystara Mjáavatn have the largest coverage of macrophytes. These lakes are fairly small and are perhaps less wind-swept than most of the others.

From an ecological point of view, an important role of the submerged vegetation is to stabilize the sediment against erosion even though the vegetation is sparse. The plant volume infested (Table 5) is very low, and the role of vegetation as a shelter for

Table 6. Recorded maximum depths for different species in the lakes. The most important species are shown in bold, while species with an average coverage <1% are marked with small italic figures.

<i>Species</i>	<i>Eystara</i>					
	<i>Mjáavatn</i>	<i>Leynavatn</i>	<i>Saksunarvatn</i>	<i>Sandsvatn</i>	<i>Sørvágsvatn</i>	<i>Toftavatn</i>
<i>Isoëtes lacustris</i>		2.6	1.3	1.0	4.8	4.1
<i>Littorella uniflora</i>			1.0		1.3	
<i>Juncus bulbosus</i>			3.3			
<i>Myriophyllum alterniflorum</i>	0.8	3.8	5.0	1.0	2.6	3.9
<i>Potamogeton alpinus</i>			5.0			
<i>P. berchtoldii</i>						4.3
<i>P. gramineus</i>						2.3
<i>P. perfoliatus</i>				1.4		
<i>Chara globularis</i>						4.2
<i>Nitella opaca</i>	4.7	10.1	10.5	1.8	6.1	



Figure 4. The charophyte *Nitella opaca* at 4.3 m depth in Sørvágsvatn.

zooplankton and fish fry is probably of minor importance.

Depth distribution.

The macrophytes, which were generally dominated by isoetids and elodeids, reach the limit of distribution at a water depth of 5 m (Fig. 3). Charophytes are, however, scattered in-between the vascular plants and reach their limit of distribution at a water depth of approx. 10 m; *Nitella opaca* being the dominant species at 7-10 m.

The lakes represent different vegetation types and depth distributions, as shown by the depth distributions of the aquatic macrophytes in Leynavatn, Saksunarvatn and Toftavatn (Fig. 3).

In Leynavatn, the charophyte *Nitella opaca* had high coverage throughout most of the vegetated area, from shallow water down to 7-8 m depth with isolated speci-

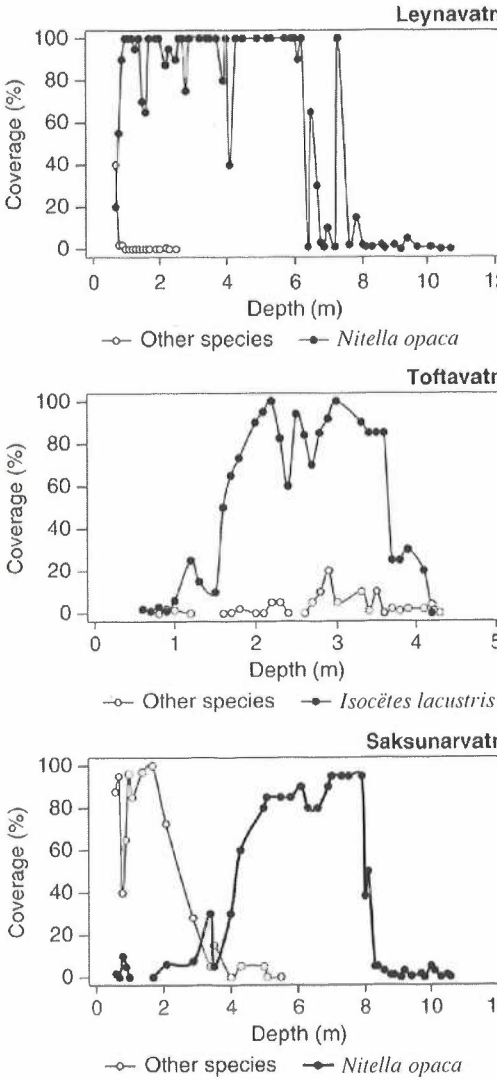


Figure 3. Depth distribution of the dominant species in Toftavatn, Saksunarvatn and Leynavatn. The figure shows one locality from each lake. Note the difference in depth scales.

mens at 10 m depth. Other species, primarily *Isöetes lacustris* and *Myriophyllum alterniflorum*, were most common in very shallow water, < 1m, but had a very



Figure 5. *Potamogeton alpinus* at 2.7 m depth in Saksunarvatn.

scattered distribution and low coverage compared with *N. opaca*. We found the same vegetation type in Eystara Mjáavatn and Sørvágsvatn (Fig. 4) and therefore suggest that this is the most common vegetation type in Faroese lakes (Table 3). Even though *I. lacustris* had a comparable low coverage in Sørvágsvatn, it made stands down to 4-5 m depth.

In Saksunarvatn, other species, primarily *Juncus bulbosus*, *Myriophyllum alterniflorum*, *Potamogeton alpinus* (Fig. 5) and *P. natans*, dominated and had high coverage from the shore down to 3-4 m depth. However, Saksunarvatn as most of the lakes in our survey, also hosted large *Nitella* stands in deeper water.

Toftavatn exhibited a completely different vegetation type, *I. lacustris* being the dominant species making stands from 1 m to approx. 4 m depth, and absence of

charophyte vegetation on deeper water. The dense stands of several *Potamogeton* species in the western part of the lake were not included in the photo transects, but at 3-4 m depth the coverage of *Potamogeton* species, especially *P. berchtoldii*, reached 40-60 %.

Conclusion

The Faroese lakes investigated are oligotrophic as reflected by the water chemical analysis and by the vegetation. The sparse submerged vegetation is dominated by charophytes and isoetids, but includes also elodeids in all the lakes. But even though the vegetation is sparse as indicated by low figures of PVI it plays a role in stabilizing the littoral sediment. In total 20 species of macrophytes were identified including 14 species of elodeids and six isoetids. Four species of charophytes were identified of which *Nitella opaca* was quantitatively important in all the lakes investigated. Lake vegetation exhibits zonation, vascular plants dominating in the littoral from 0-5 m water depth and charophytes in the 5-10 m zone. The occurrence of submerged vegetation in the Faroese lakes is threatened by hydropower production and by fish breeding and since the submerged vegetation is highly sensitive to changes in the hydrology and the water quality these factors should be taken into account from a limnological point of view.

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Abundance and Biomass of Microbial Communities in Relation to Phyto- and Bacterioplankton Production in Five Faroese Lakes

Nøgðin av smáverubólkum og lívrunna vekt teirra í mun til framleiðsluna av plantu- og bakteriuæti í fimm føroyskum vøtnum

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Úrtak

Mongdin av bakterium, pikoalgum, heterotropiskum nanoflagellatum (HNF) og siliatum ella samansetingin av smáverum í vistskipanini í fimm føroyskum vøtnum var lík mongdini í vøtnum við lítlum taðfalli í artiskum og sub-arktiskum økjum, men sum heild lægri enn mongdin í vøtnum við størri taðfalli í tempreraðum økjum. Mongdirnar vóru fyri bakteriar (< 1 µm í tvørmati) millum 0,4 og 1,5 x 10⁶ ml⁻¹, fyri pikoalgur (0,8 til 2 µm í tvørmati) millum 1,5 og 4,3 x 10⁴ ml⁻¹, fyri HNF (miðal tvørmat 1,18 µm) millum 0,1 og 0,4 x 10³ ml⁻¹ og fyri siliatur (<20 til 100 µm í tvørmati) millum 2,1 og 6,8 kyknur ml⁻¹. Bara siliaturnar kundu greinast í sløg, og sløgin *Strombidium/Strombilidium* spp. og *Didinium* spp. vóru vanlig. Lýst í eindum av lívfrøðiliga kolevnatilfeingi (carbon biomass) var heilt greitt, at teir einkynaðu bólkarnir (HNF og siliatur) høvdu minni at týða fyri smáverustovnarnar, enn bæði bakteriar og pikoalgur høvdu. Eitt høgt ræningartrýst frá krabbadýrum í vøtnunum, har lítil fiskur var (sum t.d. Eystara Mjáavatn og Toftavatn), eins og lítil lívfrøðilig framleiðsla sum heild í øllum vøtnunum forðaði fyri, at teir ymisku partarnir av smáverum og serliga HNF kundu koma fyri í stórum mongdum.

Lívfrøðiliga mongdin av bakterium hevði eina positiva korrelatión (r² = 0,41), meðan lívfrøðiliga mongdin av pikoalgum hevði eina negativa korrelatión (r² = 0,40). Frumframleiðslan var lág (17 og 35 mg C m⁻² d⁻¹), við eini livitíð hjá plantuætistovnunum uppá millum 6 og 24 dagar. Árliga frumframleiðslan kundi koma upp á

3 til 7 g C m⁻² ár⁻¹, um málignarnar av frumframleiðsluni eru umboðandi fyri alla vakstrartíðina (vakstrartíðin er 200 dagar). Miðal bakteriuframleiðslan var 0,9 µg C l⁻¹ d⁻¹ (undantikið í einum vatni, har framleiðslan var triggjar ferðir so høg), og hetta gevur eina árliga bakteriuframleiðslu uppá 1 til 5 g C m⁻² ár⁻¹ (her verður roknað við 200 framleiðsludøgum og somu framleiðslu í øllum vatnstøðum). Tá framleiðslan av platuæti er lág, rokna vit við, at piko- og nanoætiverurnar eru týðningarmiklar fyri stóru siliatu bólkarnar eins og djóraæti, og hetta hevur við sær høg tropisk stig.

Abstract

The abundances of bacteria, picoalgae, heterotrophic nanoflagellates (HNF) and ciliates, i.e. the microbial component of the aquatic food web, in five oligotrophic Faroese lakes were similar to the levels found in oligotrophic arctic or sub-arctic lakes, but lower than the concentrations generally found in mesotrophic-eutrophic, temperate lakes. The abundances was 0.4 to 1.5 x 10⁶ ml⁻¹ for bacteria (< 1 µm in diameter), 1.5 to 4.3 x 10⁴ ml⁻¹ for picoalgae (0.8 to 2 µm in diameter), 0.1 to 0.4 x 10³ ml⁻¹ for HNF (average diameter 1.18 µm) and 2.1 to 6.8 cells ml⁻¹ for ciliates (< 20 to 100 µm in diameter). Identification of species was only possible for ciliates and revealed that *Strombidium/Strombilidium* spp. and *Didinium* spp. were common. Expressed in units of carbon biomass it was obvious that the protozoan populations (HNF and ciliates) contributed less to the microbial community than did both bacteria

and picoalgae. A high predation pressure from crustaceans in lakes with low fish density (such as Eystara Mjáavatn and Toftavatn) as well as the general low productivity in all lakes prevented the microbial components and especially HNF from obtaining high abundances.

Bacterial biomass was positively correlated ($r^2 = 0.41$) whereas picoalgal biomass was negatively correlated with total phosphorus concentrations ($r^2 = 0.40$), both relationships being significant. The depth-integrated daily primary production rates were low (17 and 35 mg C m⁻² d⁻¹), with phytoplankton population turnover times of 6 to 24 days. Annual primary production rates would reach 3 to 7 g C m⁻² yr⁻¹ based on the assumption that the measured production rates were representative for the whole growing season (lasting 200 days). The average bacterial production rate was 0.9 µg C l⁻¹ d⁻¹ (except in one lake with 3 times higher levels), yielding an annual bacterial net production of 1 to 5 g C m⁻² yr⁻¹ (assuming 200 production days and uniform production rates throughout the water column). Since the phytoplankton primary production is low, we expect pico- and nanoplanktonic organisms to be important food particles for large-sized ciliate populations as well as zooplankton, thus supporting higher trophic levels.

Introduction

Faroese lakes are mainly oligotrophic due to their geological origin and low anthropogenic impact (Bengtson, 1982; Mortensen, 2002). The abundance and biomass of planktonic organisms in such low-productive lake ecosystems are generally lower than in more nutrient-rich lakes, although the species richness may be higher than in high-productive systems (Kalff, 2002). Also the moderate average air temperatures in summer of around 10 °C in July-August in the Faroe Islands (Cappelen and Laursen, 1998) act as a regulatory mechanism for diversity and abundance, because low water temperatures generally restrict growth rates and exclude thermophile organisms.

Previous studies of the species distribu-

tion, biomass and production of phytoplankton and zooplankton in a number of Faroese lakes have clearly shown low productivity (Börgesen and Ostensfeld, 1903; Poulsen, 1929; Lützen, 1978; Jensen *et al.*, 1983). None of the studies have included the microbial communities, i.e. bacteria, picoalgae, and protozoans (non-pigmented flagellates and ciliates). However, in studies undertaken in nutrient-poor lakes in Arctic and Antarctic regions as well as in alpine lakes, low species numbers and absolute abundances of micro-organisms have been observed (Hobbie *et al.*, 1999; Laybourn-Parry, 1994; Straškrabová *et al.*, 1999), which does not *per se* imply that the microbial components of the food webs are negligible also in Faroese lakes. Since the photosynthetic rates by phytoplankton are considered low, it is likely that bacterial production contributes significantly to the overall carbon flow. Furthermore, the smallest heterotrophic consumers (e.g. protozoans) may constitute an important link between phyto- and bacterioplankton and the zooplankton, as has been shown in temperate oligotrophic lakes (Riemann and Christoffersen, 1993).

In the present study we measured the abundance and biomass of picoalgae, bacteria, and protozoans (heterotrophic nanoflagellates and ciliates) as well as phyto- and bacterioplankton production rates to evaluate the absolute and relative importance of these components in the pelagic food webs of five Faroese lakes. To obtain as reliable data as possible on primary and bacterial production rates as well as bacterial abundance, we applied two indepen-

dent methods (phytoplankton biomass in terms of chlorophyll *a* was likewise measured using two different methods, see Jensen *et al.*, 2002).

Materials and methods

Water samples were taken at intervals of 1 to 5 m through the water column from the surface to the bottom at the maximum depth of the lake. Samples from all depths were pooled in a container and subsamples were collected for enumeration of bacteria, picoalgae, heterotrophic nanoflagellates and ciliates. Additionally, the subsamples were used for *in situ* measurements of bacterial and phytoplankton production. Samples were collected in clean bottles and preserved by glutaraldehyde to a final concentration of 2 %. The samples were kept in darkness until counting was performed. Abundance of bacterial cells was analysed by: a) flow cytometry using the nucleic acid stain Syto 13 (del Giorgio *et al.*, 1996) and b) epifluorescent microscopy using 4',6-diamidino-2-phenylindole (DAPI) as a fluorochrome (Porter and Feig, 1980). A minimum of 5000 cells were counted on a FACSort flow cytometer (Becton Dickinson) calibrated with a solution of fluorescent beads (Fluoresbrite Carboxy YG. 1.64 µm diameter). Cells were separated from noise and fluorescent beads added in a double logarithmic plot of side scatter and green fluorescence. Samples were stored 2-3 months at +4 °C before counting was performed. For epifluorescent microscopy. The staining procedure was as follows: DAPI to a final concentration of 0.5 µg ml⁻¹ was added to each

sample, and the samples were then incubated for 10 min before being filtered onto 0.2 µm black polycarbonate filters (Poretics, CA, USA). The filters were rinsed with 0.2 µm filtered distilled water mounted on glass slides with non-fluorescent immersion oil before counting. The slides were kept frozen at -20°C until microscopic analyses were performed. A minimum of 200 cells stained with DAPI were counted in an Olympus BH2 microscope at 1250 times magnification. The microscope was equipped with a ultra-violet and blue filter set with excitation and emission wavelengths of 365 and 390 nm.

Abundances of heterotrophic nanoflagellates (HNF) were also obtained by counting DAPI-stained cells in the epifluorescence microscope. The staining and filtration procedures as described for bacteria, except that HNF were filtered onto 0.8 µm filters.

Picoalgae were filtered directly onto 0.2 µm polycarbonate filters, mounted on glass slides with non-fluorescent immersion oil and identified by their red autofluorescence when excited with green light in the epifluorescent microscope. Ciliates were counted from the sedimented material in settling chambers (usually 50 ml) using an inverted microscope (Leitz) at 100-250 times magnification.

The average cell biovolumes of bacteria, HNF, picoalgae and ciliates were obtained from measurements directly in the microscope of linear dimensions of 10 to 25 individuals per sample using a scaled micrometer, or from enlarged microphotographs (bacteria) using a ruler. Bacterial net pro-

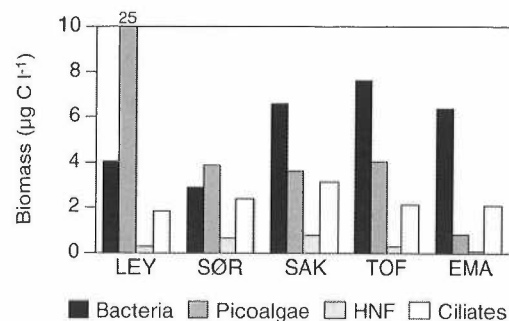


Figure 1. Biomasses of bacteria, picoalgae, heterotrophic nanoflagellates (HNF) and ciliates in five Faroese lakes, July/August 2000, based on enumeration and measurements of biovolume. The lakes are ranked according to increasing total phosphorus levels. See Jensen *et al.* (2002) for further information). LEY = Leynavatn, SØR = Sørvgvatn, SAK = Saksunavatn, TOF = Toftavatn and EMA = Eystara Mjáavatn.

duction was measured using the leucine and thymidine incorporation methods. The leucine incorporation method followed Smith and Azam (1992). Water samples were incubated *in situ* with ^3H -leucine (Amersham, UK) to a final concentration of 100 nM in triplicate Eppendorf tubes plus one trichloroacetic-killed control (final concentration of 4.5 %) at each depth. The incubations lasted for 60 to 90 min and were terminated by addition of trichloroacetic acid (4.5 % final concentration). After centrifugation, the bacterial pellet was rinsed with 4.5 % trichloroacetic acid and 80 % ethanol. The radioactivity was assessed in a Beckman LU 6500 scintillation counter after addition of a scintillation cocktail (Ecoscint A, Kimberly Research). Bacterial carbon production was calculated according to Smith and Azam (1992). Bacterial net production was measured by incorporation of ^3H -thymidine (Amers-

ham, UK) into DNA for 20 min according to Fuhrman and Azam (1980). Analyses were performed with three live and three trichloroacetic-killed samples. The final concentration of ^3H -thymidine was 50 nM and the incubation time 30 min. An average conversion factor of 2×10^{18} cells mol^{-1} of incorporated thymidine was applied (Smits and Riemann, 1988).

Primary production was measured from incorporation of inorganic radiolabelled bicarbonate ($\text{H}^{14}\text{CO}_3^-$) (sensu Steemann-Nielsen, 1952) in four lakes. Two independent incubation and calculation methods were used. Method 1 involved incubation of water samples from 0.05, 0.1, 0.2, 0.4, 0.75 and 2 times the Secchi depth in triplicate 60 ml glass bottles that received $\text{H}^{14}\text{CO}_3^-$ for 3.75 to 4.5 h at the respective sampling depths. One of each set of triplicate bottles was wrapped in aluminium foil for measurement of dark fixation. The incubated water samples were filtered onto 0.45 μm membrane filters that were fumed with formaldehyde and HCl for 10 min. Subsequently, a scintillation cocktail was added to the filters (Ecoscint A, Kimberly Research) and they were left for one day before being assayed in a scintillation counter. The hourly volumetric primary production at each depth was calculated according to conventional rules. The integrated aerial production was estimated according to Vollenweider (1965). Method 2 included incubation of a mixed water sample (from 0 m to 2 x Secchi depth) into duplicate 25 ml glass bottles (Jena) with $\text{H}^{14}\text{CO}_3^-$ for 24 h at 4–8 depths within the 2 x Secchi depth. A duplicate set of bottles

Table 1. Basic information on the five Faroese lakes, August 2000. Average chlorophyll *a* (Chl. *a*) and total phosphorus concentrations as well as temperatures (Temp.) are from Jensen *et al.* (2002). ND = no data.

Lake	Chl. <i>a</i> ($\mu\text{g l}^{-1}$)	Total P ($\mu\text{g l}^{-1}$)	Temp. ($^{\circ}\text{C}$)	DIC (mg C l^{-1})	POC (mg C l^{-1})	DOC (mg C l^{-1})
<i>E. Mjáavatn</i>	1.7	16	15.0	0.60	1.55	2.67
<i>Leynavatn</i>	1.3	3	12.2	0.68	0.60	0.84
<i>Sørvgvatn</i>	0.8	5	12.0	0.67	0.82	2.40
<i>Toftavatn</i>	1.1	11	14.6	0.69	1.00	2.68
<i>Saksunavatn</i>	1.3	6	13.0	ND	1.06	2.05

wrapped in aluminium foil was included as dark controls. The water samples were filtered onto 0.45 μm membrane filters that were transferred to plastic vials and left overnight with HCl. A scintillation cocktail was added (Ultima Gold, Packard) and the filters were left on a rotating wheel for 12 h before being assayed in a scintillation counter. The daily (24 h) volumetric primary production at each depth was calculated according to conventional rules and the aerial production calculated by trapeze integration with depth.

Concentrations of dissolved organic carbon (DOC) and particulate organic carbon (POC) were measured from 5 ml subsamples filtered through pre-combusted 13 mm GF/F filters. The particulate material retained on the filters (POC) was dried for 3 h at 60 $^{\circ}\text{C}$ and combusted at 600 $^{\circ}\text{C}$ in a quartz tube-furnace and the CO_2 was measured in an infrared gas analyser (ADC 22 MK). The dissolved material passing through the filters (DOC) was collected in pre-combusted glass vials, acidified with one drop of 2 N HCl and then purged with nitrogen gas to remove inorganic carbon.

DOC concentrations were measured by the dry combustion method using a Shimadzu TOC-5000 (Japan). Dissolved inorganic carbon (DIC) was measured from unfiltered water samples kept frozen in acid washed plastic vials and analysed using a Shimadzu TOC-5000 total carbon analyser.

Results

The dissolved inorganic carbon content as well as the particulate organic and dissolved carbon pools of the lakes were similar, with levels of 0.6 to 0.7 mg C l^{-1} , 0.6 to 1.6 mg C l^{-1} and 0.8 to 2.7 mg C l^{-1} , respectively (Table 1). Water temperatures were 12–15 $^{\circ}\text{C}$ during the sampling period (Table 1).

Abundances of bacteria, picoalgae, heterotrophic nanoflagellates (HNF) and ciliates varied among the lakes (Table 2). The abundance of bacteria ranged from 0.4 to $1.5 \times 10^6 \text{ ml}^{-1}$, the highest values being found in Toftavatn and Eystara Mjáavatn. The values derived from the two counting techniques were not statistically different (Student's *t*-test; data not shown). Most bacteria were coccoid with a diameter of

Table 2. Abundances and average individual biovolume of bacteria, picoalgae, heterotrophic nanoflagellates (HNF) and ciliates in five Faroese lakes, August 2000.

Lake	Bacteria (10 ⁶ ml ⁻¹)	Picoalgae (10 ⁴ ml ⁻¹)	HNF (10 ³ ml ⁻¹)	Ciliates (ml ⁻¹)
E. Mjáavatn	1.42	1.71	0.11	2.63
Leynavatn	0.61	2.29	0.42	4.43
Sørvágsvatn	0.38	3.75	0.25	2.05
Toftavatn	1.49	3.57	0.42	6.82
Saksunarvatn	0.76	1.50	0.32	4.89

less than 1 µm. Abundances of picoalgae, defined as unicellular autotrophs of 0.5 to 2 µm in diameter, were 1.5 to 4.3 x 10⁴ ml⁻¹, with the highest level occurring in Leynavatn and the lowest in Saksunarvatn (Table 2). The average diameter was 1.18 µm. HNF were found in densities of 0.1 to 0.4 x 10³ ml⁻¹, while ciliate abundance ranged from 2.1 to 6.8 cells ml⁻¹. The average individual biovolume of HNF (per lake) ranged between 6 and 23 µm³ (mean 9.2 µm³, data not shown). The ciliate abundance ranged between 2 and 7 ml⁻¹, with

highly fluctuating individual biovolumes (1-36 x 10³ µm³). Nano-ciliates of 1-2 x 10³ µm³ (i.e. less than 20 µm in diameter, data not shown) were, however, always present.

The corresponding carbon biomasses of the microbial communities based on the above average size measurements and abundances revealed substantial differences between the lakes (Fig. 1). The bacterial biomass was around 3 to 8 µg C l⁻¹ with a significant positive relation to total phosphorus ($y = 0.24x + 3.55$; $r^2 = 0.406$), the highest values being recorded in Toftavatn and Eystara Mjáavatn. The differences in picoalgal biomass were much larger, being 25 µg C l⁻¹ in Leynavatn and 0.9 µg C l⁻¹ in Eystara Mjáavatn (Table 3).

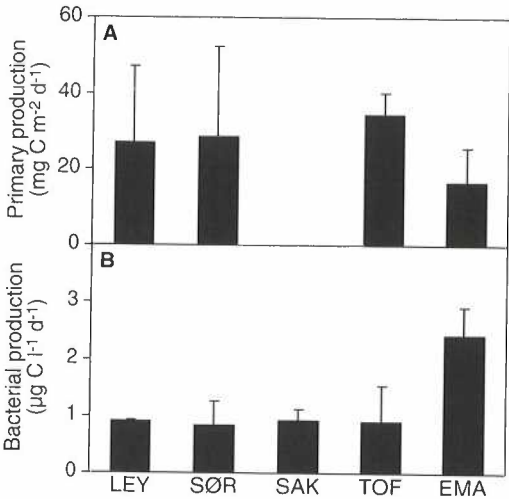


Figure 2. A) Areal phytoplankton net primary production in five Faroese lakes, July/August 2000, based on enumeration and measurements of biovolume. B) Volumetric bacterial net production. The bars are averages of two independent incubation methods; the error bars show the total variation between the results. The lakes are ranked according to increasing total phosphorus levels (see Jensen et al. (2002) for further information. LEY = Leynavatn, SØR = Sørvágsvatn, SAK = Saksunarvatn, TOF = Toftavatn and EMA = Eystara Mjáavatn.

Table 3. Calculated bacterial and phytoplankton population turnover time (B/P) as well as a crude estimate of annual aerial net phytoplankton (NPP) and net bacterial production (NBP), assuming a growth season of 200 days, in the five Faroese lakes, August 2000. ND = no data.

Lake	Bacteria (days)	Phytoplankton (days)	Annual NPP (g C m ⁻² y ⁻¹)	Annual NBP (g C m ⁻² y ⁻¹)
E. Mjáavatn	2.6	9	3.3	1.5
Leynavatn	4.5	20	5.4	2.5
Sørvágsvatn	3.4	24	5.7	4.6
Toftavatn	8.5	6	6.9	1.0
Saksunarvatn	7.1	ND	ND	1.2

The picoalgal biomass was significantly negatively correlated with total phosphorus ($y = -1.12x + 17.32$; $r^2 = 0.403$). Neither the biomass of HNF (0.07-0.81 µg C l⁻¹) nor that of ciliates (1.8-3.2 µg C l⁻¹) showed such relationships. The ciliate biomass was dominated by unidentified species in Leynavatn and Saksunarvatn, while *Strombidium/Strombilidium* spp. (35-40 µm in diameter) dominated in the other lakes. The species *Didinium* spp. (25-30 µm in diameter) accounted for 10% of total biomass in Saksunarvatn, but was otherwise found only in low densities (data not shown).

The depth-integrated primary production rates from the four lakes ranged between 17 and 35 mg C m⁻² d⁻¹ and did not vary significantly according to incubation method (Fig. 2A). Production was not measured in Saksunarvatn due to heavy winds. The calculated phytoplankton population turnover times were 6 to 24 days (Table 3) based on areal primary production rates and volumetric chlorophyll *a* concentrations converted to carbon by a carbon:chloro-

phyll ratio of 30:1 and multiplied by mean lake depth. The calculated annual primary production rates were 3.3 to 6.9 g C m⁻² yr⁻¹ based on the assumption that the measured productions rates were representative for the growth season lasting 200 days per year.

Bacterial production rates were almost identical, approx. 0.9 µg C l⁻¹ d⁻¹, except in Eystara Mjáavatn where production was 2.4 µg C l⁻¹ d⁻¹ (Fig. 2B). There were no significant differences between the two methods applied. A positive significant correlation between the bacterial production rate and total phosphorus was observed ($y = 0.064x + 0.41$; $r^2 = 0.688$). The bacterial population turnover times were 3-9 days and the annual bacterial net production (assuming 200 productive days and uniform production rates throughout the water column) ranged between 1.2 and 4.6 g C m⁻² yr⁻¹ (Table 3).

Table 4. Ranges of conductivity, chlorophyll and abundances of various members of the microbial community in recently studied lakes in West Greenland, Europe, New Zealand and the lakes of the present study. The number of lakes included in each survey is given in parentheses. Data are given as min-max values. ND = no data.

Parameter	West Greenland lakes (15) ¹	European alpine lakes (13) ²	New Zealand lakes (5) ³	Faroe Islands lakes (5)
Conductivity ($\mu\text{S cm}^{-1}$)	17-38	6-148	ND ⁴	94-174
Temperature regime	Subarctic-arctic	Cold-temperate	Temperate	Cold-temperate
Chlorophyll ($\mu\text{g l}^{-1}$)	0.4-2.0	0.2-83 ⁵	1.6-5.8	0.7-1.8
Picoalgae (10^4 ml^{-1})	2.7-7.2	0.06-2.3	0.6-5.0	1.5-4.3
Bacteria (10^6 ml^{-1})	0.6-2.2	0.06-9.79	ND	0.6-1.5
HNF (10^3 ml^{-1})	0.2-2.8	0.06-0.4	0.3-1.0	0.1-0.4
Ciliates (ml^{-1})	0.8-7.7	1-20	3.8-26.1	2.6-6.8

¹) Unpubl. data from lakes at 66°N (K. Christoffersen and E. Jeppesen), ²) Straškrabová *et al.* 1999, ³) Jeppesen *et al.* 2000, ⁴) total phosphorus < 10 $\mu\text{g l}^{-1}$, ⁵) converted from carbon biomass assuming a carbon:chlorophyll ratio of 30:1.

Discussion

The five lakes are all oligotrophic with a dilute ion concentration (Table 4) and total phosphorus levels below 15 $\mu\text{g l}^{-1}$ (Table 1, but see Jensen *et al.*, 2002). The lakes are furthermore situated in a relatively cold region with average summer temperatures not exceeding 10.5 °C and with generally strong winds (Cappelen and Laursen, 1998). The biomass and production rates of the planktonic organisms are thus supposedly lower than in more nutrient-rich and warmer regions (Kalff, 2002).

The abundances of the microbial components of the food webs - i.e. bacteria, picoalgae, HNF and ciliates - did indeed range within the levels found in oligotrophic and mesotrophic lakes (Table 4), in temperate lakes (Jeppesen *et al.*, 2000), arctic lakes (Jeppesen *et al.*, unpubl., Christoffersen, unpubl.) and in alpine lakes

(Straškrabová *et al.*, 1999), but differed from mesotrophic-eutrophic, temperate lakes (e.g. Riemann and Christoffersen 1993).

In terms of carbon biomass it was obvious that the protozoan populations (HNF and ciliates) were generally the least prominent contributors to the microbial community, while both bacteria and picoalgae contributed more (Fig. 1). It should be noted, however, that the total contribution of the microbial communities only made up between 1 and 5 % of the total organic particulate pools. The observed trend in bacterial biomass versus total phosphorus may be related to increased biological activity and thus increased availability of dissolved organic substrates. Bacterial production rates were generally two orders of magnitude lower than primary production rates on a volumetric basis (data not shown), which is

in accordance with the fact that healthy phytoplankton populations lose a small proportion of fixed carbon as dissolved organic substrates that is taken up by bacteria (Søndergaard, 1997). The pool of dissolved organic carbon (Table 1) was, however, much higher than the bacterial carbon demand that can be estimated from the daily bacterial production rates, assuming a growth efficiency of 50 %. This does, however, not exclude the possibility of substrate limitation, since the standing dissolved carbon pool is most likely dominated by refractory compounds (Søndergaard, 1997).

The observed negative relationship between picoalgal biomass and total phosphorus seems to follow the pattern described for a number of Danish lakes (Søndergaard, 1991). At increasing nutrient concentrations, increasing levels of particulate matter and lower transparency are to be expected. Thus, the low nutrient level and high Secchi depth in Leynavatn (Jensen *et al.*, 2002) most likely favour picoalgae (Fig. 1). The relatively high biomass of picoalgae (compared to net-phytoplankton) in this lake may, however, also be an effect of the low zooplankton abundance created by fish predation (Jeppesen *et al.*, 2002). In contrast, picoalgal biomass was found to be low in Eystara Mjáavatn, a possible explanation being the generally lower light intensity (Secchi depth 4.3 m) and grazing by the abundant crustaceans (*Daphnia* and *Bosmina*), ciliates and rotifers.

Compared to bacteria and ciliates the abundances and biomasses of HNF were low (Fig. 1). Since the amount of pico-

sized food particles seems sufficient to support both the HNF and the ciliate populations, except in Sørvágsvatn, (calculated assuming a growth efficiency of 30 %), it seems likely that a high predation pressure by crustaceans (especially in Eystara Mjáavatn) prevents the HNF from obtaining a larger biomass. A strong regulatory impact from cladocerans is typical of meso- and eutrophic lakes (Christoffersen, 1998).

The measured primary production rates in four Faroese lakes lie within the range found for similar oligotrophic lakes in the Northern hemisphere (Kalff, 2002). An average production rate of 5.4 $\text{g C m}^{-2} \text{ yr}^{-1}$ (3.3-6.9 $\text{g C m}^{-2} \text{ yr}^{-1}$) was obtained assuming a 200-day growth season. This is comparable to the level reported by Lützen (1978) who measured the primary production rate in Leynavatn (also included in the present study) five times (July-September 1976 and 1977) from ¹⁴C-incorporation. The daily production rates in Lützen's study averaged 42 $\text{mg C m}^{-2} \text{ d}^{-1}$ or approx. 8.5 $\text{g C m}^{-2} \text{ yr}^{-1}$ (200 days). However, Jensen *et al.* (1983) found annual production rates of 30-60 $\text{g C m}^{-2} \text{ yr}^{-1}$ in five oligotrophic lakes studied in 1983 (other lakes than presented here). Their results were obtained from measurements conducted twice during May and August using ¹⁴C-incorporation (2 hour incubations). The lakes had total phosphorus and chlorophyll levels comparable to those of the present and other studies (e.g. Danielsen, 1999). Therefore, the rather high annual production may be related to methodological differences.

The turnover times for phytoplankton populations in the five lakes in the present study (Table 2) are an indication of nutrient limitation, as the phytoplankton communities were primarily composed of small forms belonging to chloro- and chrysophytes (Brettum, 2002) with known high growth rates. The longest turnover times (20 and 24 days) were found in the two deepest lakes, which probably have the largest mixing depth and thus low average light intensity. The overall conclusion from this study is that the abundances and biomasses of the microbial components of the pelagic food webs in these lakes were low but within similar ranges as arctic aquatic systems and in temperate systems of comparable trophic status. Relationships in bacterial and picoalgal biomasses versus total phosphorus seem to exist, but the present data set is too limited to allow any general conclusions to be drawn. Since the phytoplankton primary production is low, we assume both pico- and nanoplankton to be important food particles to both large-sized ciliate populations and zooplankton, thus supporting higher trophic levels.

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The zooplankton community of five Faroese lakes

Djóraæti í fimm føroyskum vøtnum

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Úrtak

Djóraæti varð kannað í fimm føroyskum vøtnum tíðliga í august 2000. Í vøtnunum vóru fá sløg av djóraæti at finna. Tey vóru: seks Cladocerar, trýggir Copepodar og átta Rotiferar. Cladocerarnir vóru fleiri í talið enn Copepodarnir í fyra av teimum fimm kannaðu vøtnunum, og lutfallið teirra millum var millum 1,2 og 16,8. Hetta lutfall samsvarar við tøl frá vøtnum á evropeiska meginlandinum og er eitt sindur hægri enn í vøtnum í arktiska økinum. Tættleikin av Cladocerum vaks, tá fosformongdirnar vuku. *Bosmina longispina* og *Daphnia hyalina/longispina* vóru vanligastu sløgini og vóru millum 89 og 100 % av samlaðu nøgdini av Cladocerum. Í teimum báðum djúpastu vøtnunum var *Holopedium gibberum* at finna. Niðurstøðan er, at ymisku sløgini av djóraæti eru á leið líka nógv í tali ella eitt sindur færri enn í íslenskum vøtnum og vøtnum í subarktiska økinum á meginlandinum. Harafturat vístu kanningarar, at hóast fiskur var í øllum fimm vøtnunum, so legði fiskurin einans lítið ræningartrýst á djóraætið. Hetta trýst samsvaraði við støðuna í íslenskum vøtnum, men var lægri enn trýstið í grønlenskum vøtnum.

Abstract

The zooplankton communities of five Faroese freshwater lakes were studied during early August 2000. Only six cladocerans, three copepods and eight rotifers species/genera were observed in the lakes. Cladocerans dominated numerically over Copepoda in four of the five lakes and the Cladocera/Copepoda ratio ranged from 1.2 to 16.8, which is within the range of European continental lakes and somewhat higher than in Arctic lakes. Cladocera density increased with the total phos-

phorus concentration, *Bosmina longispina* and *Daphnia hyalina/longispina* being the dominant species with 89 to 100 % of total Cladocera abundance. *Holopedium gibberum* was found in the two deepest lakes. It is concluded that the zooplankton of Faroese lakes have a similar or lower species richness than Icelandic and continental subarctic lakes. Furthermore, fish predation on zooplankton is only moderately high as in Icelandic lakes and lower than in arctic Greenland lakes.

Introduction

Very few studies exist on the zooplankton composition of Faroese freshwater lakes. As far as we are aware, only two other studies have surveyed Faroese lakes. In 1898, lakes around Tórshavn were sampled by a French expedition (Poulsen, 1928) and in 1924-1927 zooplankton were collected at 250 locations by the Zoological Museum of the University of Copenhagen (Poulsen, 1928). The French expedition registered 11 species/genera, while a total of 41 crustacean species were recorded in the 1924-1927 investigations (Poulsen, 1928), Cladocera contributing with 24 species, Copepoda with 12 species and Amphipoda and Ostracoda with two and three species, respectively. In a more recent study, zooplankton were sampled but not quantified

in Vatnsnesvatnet on Suðuroy by Johnsen (1998).

The Faroe Islands are an archipelago situated just south of the subarctic region. The climate is cold and humid and the annual average temperature as 6 °C (Cappelen, 2002), with a high summer average of 11 °C and a low winter average of 3 °C (Cappelen and Laursen, 1998). The low temperatures have probably influenced the species richness of zooplankton, which is relatively low. However, species richness in this region depends not only on temperature, but also on geographical features such as latitude, altitude, isolation and dispersal potential (Haberbosch, 1916; Poulsen, 1928; Hebert and Hann, 1986; Antonsson, 1992; Rautio, 2001; Swadling *et al.*, 2001).

Here, we present zooplankton data from five Faroese lakes and describe the differences between the lakes, comparing the findings with those of previous studies as well as with other sub-arctic and arctic regions. Additionally, we discuss zooplankton composition in relation to nutrient level and fish occurrence.

Study areas

The studied lakes are Sørvágsvatn located on the island of Vágar, Leynavatn, Eystara Mjáavatn and Saksunarvatn situated on Streymoy, and Toftavatn on Eysteroy. The lakes range in size between 0.03 and 3.41 km² (Landkildhus *et al.*, 2002). Mean and maximum depths vary from 3 to 27 m and 7 to 59 m, respectively. The temperature varied from 13.5 to 15.3 °C at the sampling time and nutrient status from 3 to 16 µg total phosphorus (TP) per litre (Table 1).

For more details on lake morphometry and catchments, see Landkildhus *et al.* (2002), for physical and chemical data see Jensen *et al.* (2002).

Materials and methods

Zooplankton were collected in the central open water areas of the lakes with a 3.3 l modified Patalas sampler (Patalas, 1954). At each station, a depth-integrated sample was taken by pooling samples from 6-8 depths to represent the entire water column. Of this pooled sample, a 10-litre subsample was filtered onto a 20 µm mesh net. Samples were preserved in 4 % Lugol's solution. In the laboratory, the zooplankton were identified and counted using a stereomicroscope. Cladocerans were identified to species or genus level and copepods and rotifers to genus level (*Keratella* to species level). Density is presented as mean number of individuals per litre. For biomass estimations of cladocerans and copepods, 50 individuals (if possible) per genus/species from each lake were measured and biomass was calculated according to Bottrell *et al.* (1976). As for rotifers, biomass standard values for each individual taxon were used.

Results

Bosmina longispina and *Daphnia hyalina/longispina* were the dominant Cladocera in all five lakes, with densities ranging from 2 to 123 ind l⁻¹ and from 1 to 43 ind l⁻¹, respectively. For both species, the highest densities were found in Eystara Mjáavatn and the lowest in Sørvágsvatn (Table 2). The density of the two species was 10 to 60

Table 1. Morphometric data, chlorophyll *a* and total phosphorus concentrations in five Faroese lakes. LEY = Leynavatn, SØR = Sørvágsvatn, SAK = Saksunarvatn, TOF = Toftavatn and EMA = Eystara Mjáavatn. Lakes are sorted according to increasing total phosphorus concentrations. Chlorophyll *a* and total phosphorus data are from Landkildehus *et al.* (2002).

	LEY	SØR	SAK	TOF	EMA
Area (km ²)	0.18	3.56	0.08	0.52	0.03
Max. depth (m)	33.0	59.0	17.0	22.0	7.0
Mean depth (m)	13.7	27.5	6.5	5.8	3.0
Total P (µg l ⁻¹)	3	5	6	11	16
Chlorophyll <i>a</i> (µg l ⁻¹)	1.3	0.8	1.3	1.1	1.7

times higher in Eystara Mjáavatn than in the other four lakes. *B. longispina* and *D. hyalina/longispina* constituted from 89 to 99.9 % of total cladoceran abundance in the five lakes.

Three species/genera were found in low densities (less than 0.1 ind l⁻¹) in one lake only, namely *Chydorus* spp. in Leynavatn, *Acroperus* sp. in Eystara Mjáavatn and *Polyphemus pediculus* in Toftavatn. *Holopedium gibberum* occurred in low densities (1.3 and 0.1 ind l⁻¹, respectively) in Leynavatn and Sørvágsvatn (Table 2).

In all the lakes, Copepoda were dominated by cyclopoid copepodites, with densities ranging from 1.3 to 8.4 ind l⁻¹ (Table 2) in Sørvágsvatn and Eystara Mjáavatn, respectively. Adult *Cyclops* sp. and *Eucyclops macruioides* were found in low densities in Toftavatn and Eystara Mjáavatn (Table 2). Copepodites constituted from 50 to 85 % of the total number of copepods in the five lakes and nauplii were found in all lakes, ranging in abundance from 1.1 to 3.7 ind l⁻¹.

The ratio of Cladocera/Copepoda was 16 in Eystara Mjáavatn and only one in

Sørvágsvatn. In Sørvágsvatn and Leynavatn, the ratio ranged between 1 and 2 (Fig. 1), Copepoda thus being almost as common as Cladocera. On average the Cladocera/Copepoda ratio in the Faroese lakes was 5.8, which is higher than in the Arctic

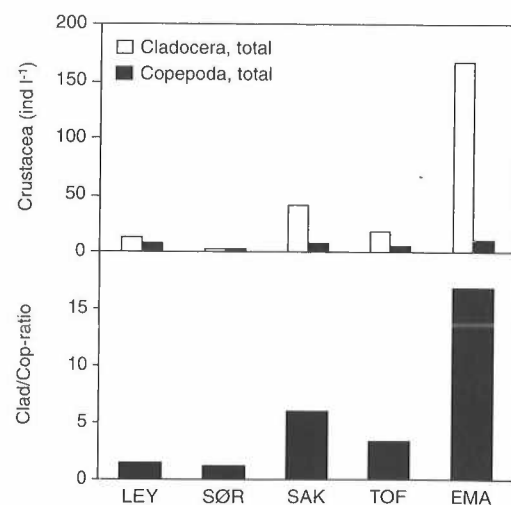


Figure 1. Total density of Cladocera and Copepoda and the Cladocera/Copepoda-ratio (Clad/Cop-ratio) in the five Faroese lakes sampled in July/August 2000. LEY = Leynavatn, SØR = Sørvágsvatn, SAK = Saksunarvatn, TOF = Toftavatn and EMA = Eystara Mjáavatn.

Table 2. Densities (No. l⁻¹ ± standard deviation, SD) of zooplankton species/genera in five Faroese lakes sampled in August 2000. Lakes are sorted according to increasing total phosphorus concentrations. LEY = Leynavatn, SØR = Sørvágsvatn, SAK = Saksunarvatn, TOF = Toftavatn and EMA = Eystara Mjáavatn.

	LEY	SØR	SAK	TOF	EMA
Cladocera					
<i>Acroperus</i> sp.					0.1
<i>Bosmina longispina</i>	10±3	2±0.2	21±2	14±3	123±34
<i>Chydorus</i> spp.	0.1±0.1				
<i>Daphnia hyalina/longispina</i>	1±0.5	0.7±0.4	24±6	5±2	43±14
<i>Holopedium gibberum</i>	1±0.7	0.1±0.1			
<i>Polyphemus pediculus</i>				0.1±0.1	
Copepoda					
Cyclopoid copepodites	5±1	1±0.4	6±3	4±0.3	8±6
<i>Cyclops</i> sp.				0.6±0.2	
<i>Eucyclops macruioides</i>					0.3±0.5
Nauplii	4±0.7	1±0.9	1±0.6	2±0.9	1±2
Rotifera					
<i>Asplanchna</i> spp.		2±0.6		0.8±0.4	
<i>Cephalodella</i> spp.	0.1±0.3	0.1±0.2			
<i>Conochilus</i> spp.	35±12	5±5	0.1±0.1	36±21	
<i>Kellicottia</i> spp.		0.3±0.4	0.9±1	19±4	
<i>Keratella cochlearis</i>		22±6		14±6	0.4±0.8
<i>K. quadrata</i>				0.2±0.4	
<i>Polyarthra</i> spp.	187±52	19±6	204±17	245±63	627±70
<i>Trichocerca</i> spp.			0.1±0.1	0.2±0.4	5±8

(Hansson, L.-A., Tranvik, L. and Granéli, W., unpubl.), but in the lower end of continental European lakes (Gyllström *et al.*, unpubl.) (Table 3). Due to the enormous range in Cladocera/Copepoda ratios among the continental European lakes, the differences are, however, insignificant (ANOVA; $p > 0.10$). For Cladocera/Rotifera ratios a similar trend as for Cladocera/Copepoda is found (Table 3).

Eight species/genera of Rotifera were recorded in the lakes (Table 2). *Polyarthra* spp. was the most common genus found in

all the lakes, densities ranging from 19 ind l⁻¹ in Sørvágsvatn to 627 ind l⁻¹ in Eystara Mjáavatn, followed by *Conochilus* spp. (Table 2), *Keratella* spp., *Kellicottia* spp. and *Trichocerca* spp. The highest taxa richness was found in Toftavatn with seven species/genera, whereas Eystara Mjáavatn and Leynavatn exhibited the lowest richness.

Ranging the lakes along a productivity gradient according to the TP (total phosphorus) level reveals an increasing density and biomass of all zooplankton groups.

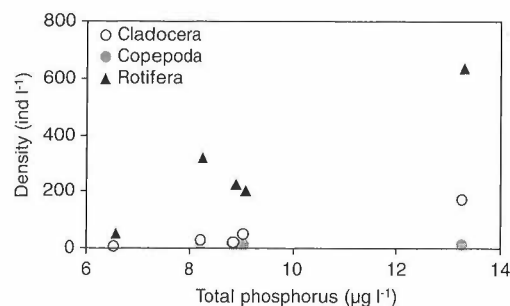


Figure 2. Cladocera, Copepoda and Rotifera densities (ind l⁻¹) versus total phosphorus concentrations (µg l⁻¹) in the five Faroese lakes sampled in August 2000.

Based on densities, rotifers showed the strongest response to increased phosphorus levels, whereas the response of cladocerans was intermediate and that of copepods weak (Fig. 2).

On a biomass basis total zooplankton increased with increasing TP, from 25 µg l⁻¹ in Sørvágsvatn to more than 1100 µg l⁻¹ in Eystara Mjáavatn (Fig. 3). The biomass of all zooplankton groups increased with TP. However, the contribution of the different groups varied between the lakes, the share of Rotifera being low at high TP and higher at low TP (Fig. 3), despite an increase in density.

Discussion

The zooplankton population was dominated by cladocerans in four of the five study lakes. Copepoda constituted only a minor fraction of the total zooplankton density, which corresponds well with former results and is characteristic of Faroese lakes. In Poulsen's investigation from 1928, three species of *Daphnia* were registered, *D.*

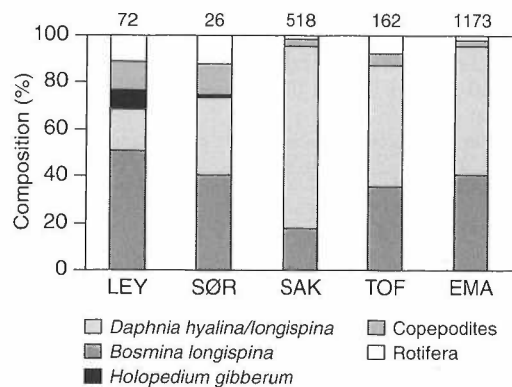


Figure 3. Frequency distribution of zooplankton in the five Faroese lakes sampled in August 2000. Total zooplankton biomass (µg l⁻¹) is given on top of the figure. LEY = Leynavatn, SØR = Sørvágsvatn, SAK = Saksunarvatn, TOF = Toftavatn and EMA = Eystara Mjáavatn.

hyalina/longispina being most common. The other two species were *D. pulex* and *D. cucullata*, which only occurred in one of the 250 lakes sampled. We recorded *D. hyalina/longispina* in all five study lakes, which confirms its position as the most common *Daphnia* species.

Holopedium gibberum had hitherto only been found in the deep Sørvágsvatn (Poulsen, 1928), but was in our study recorded in both Sørvágsvatn and Leynavatn. Both Sørvágsvatn and Leynavatn are deep lakes (Table 1) and a possible explanation of why *H. gibberum* has not been recorded elsewhere before may be its restricted occurrence in the infrequently sampled pelagic part.

Chydorus spp. occurred only in Leynavatn. This contrasts with the observations of Poulsen (1928) who considered it to be the most common cladoceran in the Faroes.

However, the 1928 sampling technique differed from ours, since Poulsen used horizontal hauls by throwing a net from the shore, a method that favours the littoral and macrophyte related species. Thus, the different sampling techniques may explain the different results. Poulsen (1928) also claimed that the sampling method partly explained the recorded dominance of Cladocera over Copepoda. However, our sampling methods did not change the fact that cladocerans dominated the zooplankton community in four of the five investigated lakes.

Copepods were found in all the lakes studied, cyclopoid copepodites being completely dominant. In Eystara Mjáavatn, a single individual of *Eucyclops macroroides* was observed, a species that has never been recorded before in the Faroe Islands. In accordance with previous results, calanoid copepods were not observed in the lakes, indicating that apart from the brackish species *Eurytemora velox* (Poulsen, 1928) calanoids do not occur in the Faroe Islands.

Rotifers may suffer considerably from predation by cyclopoid copepods (Hansson *et al.*, 1998). Hence, the more than 10-fold increase in rotifer densities along the productivity gradient may not owe solely to increased nutrient concentrations, but also to the relatively minor increase in cyclopoid copepod density observed at increasing nutrient concentrations (Fig. 2). Hence, it may be argued that as the resource basis for rotifers increases with increasing nutrient availability, the increase in copepod predation is relatively lower, leading to a net increase in rotifer densities as shown

in Fig. 1. Moreover, when fish predation is low, large cladocerans tend to be stronger competitors for food than copepods. Since cladocerans were generally dominant over copepods, this may indicate that the threat by fish to cladocerans is low in Faroese lakes compared to lower latitude lakes.

Despite more than a doubling of phosphorus concentrations along the productivity gradient, no response in algal biomass (chlorophyll) was recorded (Table 1). This is most likely due to the fact that the abundance of all zooplankton groups increased with increasing phosphorus concentrations (Fig. 2), thereby enhancing the grazing pressure on algae. The increase in cladoceran biomass along the productivity gradient is another argument supporting the suggestion that secondary production is significantly limited by nutrients and less so by fish predation. In correspondence with this, relatively high numbers of fish were caught in Eystara Mjáavatn (Malmquist *et al.*, 2002), the lake with the highest nutrient concentrations as well as highest densities and biomasses of both large and small zooplankton.

Even though the zooplankton populations appear to depend strongly on nutrients, fish undoubtedly impact the zooplankton community as well by exerting a higher predation pressure on cladocerans than on copepods (Brooks and Dodson, 1965). The ratio of Cladocera/Copepoda varied between the five lakes, being low in Leynavatn and Sørvágsvatn and high in Saksunarvatn and Eystara Mjáavatn. This corresponds well with Malmquist *et al.*'s (2002) finding of high numbers of *Daphnia*

Table 3. Means ($\pm$ SD), ranges and coefficients of variation (CV) in ratios of Cladocera/Copepoda and Cladocera/Rotifera in European continental lakes ($n = 126$; Denmark, Germany, The Netherlands, Poland, United Kingdom, Ireland. Latitude range: 48–57°N); Faroese lakes ($n = 5$; latitude: 62°N), and arctic lakes ($n = 20$; Nunavut, Canada. Latitude range: 62°–78°N).

	Cladocera/Copepoda			Cladocera/Rotifera		
	Mean (SD)	Range	CV	Mean (SD)	Range	CV
Arctic*	1.0 (1.5)	0.04-6.9	2.9	0.08 (0.24)	0-1.0	2.9
Faroe	5.8 (6.5)	1.2-16.8	1.1	0.1 (0.1)	0.06-0.26	0.8
Europe**	6.8 (16.9)	0-110	2.5	0.5 (1.4)	0-9.20	2.7

* After Hansson, L.-A., Tranvik, L. and Granéli, W. (unpubl.)

** After Gyllström *et al.* (unpubl.)

and *Bosmina* in the guts of Arctic charr (*Salvelinus alpinus*) in Leynavatn, yielding a low Cladocera/Copepoda ratio compared to that of Saksunarvatn and Eystara Mjáavatn where *Daphnia* and *Bosmina* contributed with a minor part. In addition, the findings were supported by isotope analyses showing that Arctic charr fed mostly on pelagic food items in Leynavatn, while brown trout (*Salmo trutta*), the only fish present in Eystara Mjáavatn, fed opportunistically in the pelagic and the littoral zone (Jeppesen *et al.*, 2002). In Sörvágsvatn, the Cladocera/Copepoda ratio was similar to that of Leynavatn, i.e. indicative of predation on Cladocera; however, fish guts were not investigated in this lake. Nevertheless, data from Jeppesen *et al.* (2002) showed that brown trout generally fed outside the littoral zone. In Toftavatn, the lake with the fewest fish (Malmquist *et al.*, 2002), the Cladocera/Copepoda ratio ranged between the ratios found in Leynavatn/Sörvágsvatn and Saksunarvatn/Eystara Mjáavatn. In Toftavatn,

brown trout fed among other items on *Daphnia* but not on *Bosmina* (Malmquist *et al.*, 2002). Depending on lake morphology and fish populations, trout tended to be planktivorous (Jeppesen *et al.*, 2002).

The fact that *Daphnia* are present in Faroese fish-containing lakes stands in contrast to Greenland lakes where daphnids do not co-exist with fish (Lauridsen *et al.*, 2001). However, in other sub-arctic regions (e.g. Iceland and northern Scandinavia) with a longer growth season than in North Greenland, *Daphnia* is found to co-exist with fish (Antonsson, 1992; Malmquist, 1992). As to *Daphnia* presence, it seems that Faroese lakes have more in common with sub-arctic than with arctic lakes. This is supported by the fact that *D. hyalina/longispina* is not found in the Arctic, but is commonly found in northern Scandinavia (Rautio, 2001), Shetland (Poulsen, 1928) and Iceland (Haberbosch, 1916; Antonsson, 1992).

Our study confirmed the absence of both arctic and temperate species of *Bran-*

chianecta and *Lepidurus* in Faroese lakes. This is most likely due to the presence of fish combined with dispersal problems. Another species that was not found during our survey was *Daphnia pulex*, which is a species commonly occurring in Greenland, Iceland as well as elsewhere in Europe and North America. It has only rarely been found in Faroese lakes (Poulsen, 1928), which seems paradoxical seen in the light of the common occurrence of *D. hyalina/longispina* that is found in all the other regions except Greenland. From Poulsen (1928) we know that *D. pulex* has been found in the Faroe Islands, where it seemingly has not had the potential of colonizing a large number of lakes, including our five lakes. This cannot, however, be explained as a problem of dispersal, as *D. hyalina/longispina* has not been affected. Rather the explanation is size selectivity of fish in their choice of prey (Eggers, 1982), implying that the predation pressure on the large-sized *D. pulex* will always be higher than on smaller species. The same is true for 15 Alaskan lakes (O'Brien, 1975), where the large *Daphnia middendorffiana* and the smaller *D. longiremis* never occurred together. O'Brien explained this by size selective predation by fish since the large species was never found in lakes with fish.

Differences in ratios between Cladocera/Copepoda and Cladocera/Rotifera reflect differences in conditions for large (Cladocera), medium-sized (Copepoda) and small (Rotifera) zooplankton groups. Such conditions may be predation pressure or food quality and availability (compe-

tion) and the effects on the algal community may be profound. A comparison of the Cladocera/Copepoda ratios from the Faroese lakes with continental European lakes (Spain to Denmark; $n = 126$; Gyllström *et al.*, unpubl.) reveals that the Faroese lakes lie within the lower part of the continental European range (Table 3). A similar comparison with arctic lakes (latitude: 62–78 °N) (Hansson, L.-A., Tranvik, L. and Granéli, W., unpubl.) reveals higher ratios in Faroese than in Arctic lakes. When comparing Cladocera/Rotifera ratios a similar trend as for Cladocera/Copepoda is found. Obviously, there is a tendency to lower mean ratios with increasing latitude (Table 3), and the Faroese lakes occupy an intermediate position between continental European and Arctic lakes, which was only to be expected from a biogeographical viewpoint.

Based on this and previous studies, it is concluded that the zooplankton communities of Faroese lakes have a similar or somewhat lower species richness than those of continental sub-arctic lakes. Density and biomass of all groups of zooplankton are positively affected by the TP level, while the effect of fish predation on the zooplankton community is similar to that in Icelandic and other sub-arctic lakes, but lower than in Greenland lakes.

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Zoobenthos in the Littoral and Profundal Zones of Four Faroese Lakes

Botndjór í strandaðkinum og profundala økinum í fyra føroyskum vøtnum

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Úrtak

Tættleikin og sløgini av størri ryggleysum djórum í vatnbakkanum og profundal økinum í fyra føroyskum vøtnum, Leynavatni, Eystara Mjáavatni, Saksunarvatni og Toftavatni, vórðu kannaði tíðliga í august 2000. Miðal tættleikin av størri ryggleysum djórum í grýtutum vatnbakkaðkjum var millum 11,272 og 37,239 djór m⁻², meðan tættleikin í profundala økinum var millum 30,199 og 175,387 djór m⁻². Fyri bæði økini var lægsta talið at finna í Leynavatni, sum hevði minst taðfall (mest oligotrof) og var tað størsta og tað djúpasta av teimum fyra vøtnunum. Býtið millum ymsu bólkarnar av ryggleysum djórum í vatnbakkanum var so at siga líka í øllum vøtnunum. Cladocerarnir vóru vanligast, síðani komu mýggjabitaormverur og Copepodar og at enda liðmaðkar. Í profundala økinum var stórir munur á tættleikanum millum djórabólkarnar í teimum ymisku vøtnunum. Í Leynavatni og Eystara Mjáavatni vóru Ostracodar fleiri í tali enn onnur sløg, í Saksunarvatni vóru liðmaðkar flest í tali, og í Toftavatni vóru mýggjabitaormverurnar størst í tali. Bæði í vatnbakkanum og í profundala økinum var stórir munur á tættleikanum av Cladocera sløgnum í teimum ymisku vøtnunum. Samlaði tættleikin á báðum økjum í øllum fyra vøtnunum lá millum lægsta og hægsta talið, sum er skrásett í íslenskum vøtnum, men stórir munur var á, hvussu ymisku bólkarnir vóru samansettir. T.d. vóru mýggjabitar av undirbólknum Diamesinae og sporlappadurækjan *Lepidurus arcticus* og calanoidi ættarbólkurin *Diaptomus* ikki at finna í føroyskum vøtnum. Harumframt vóru fyra sløg av várflugum (Trichoptera) funnin í Føroyum, sum ikki eru í Íslandi. Munurin á,

hvørji sløg koma fyrri í føroyskum og íslenskum vøtnum, kann koma av, at munur er á hitanum í vøtnunum í báðum londunum. Um summarið og á vetri er hitin munandi hægri í føroysku vøtnunum.

Abstract

Density and species composition of macroinvertebrates in the littoral and profundal zones of the four Faroese lakes Leynavatn, Eystara Mjáavatn, Saksunarvatn and Toftavatn were studied in early August 2000. Mean density of macroinvertebrates on rocky substrate in the littoral zone ranged between 11,272 and 37,239 ind m⁻², and mean density in the profundal ranged between 30,199 and 175,387 ind m⁻². For both habitats, the lowest densities were recorded in Leynavatn, the most oligotrophic, largest and deepest of the four lakes. Relative density contribution of invertebrate groups in the littoral zone was similar among the lakes, cladocerans being the most abundant group, followed by chironomid larvae, copepods and finally oligochaetes. In the profundal, density contribution of invertebrate groups differed considerably among the lakes, with ostracods outnumbering other taxa in Leynavatn and Eystara Mjáavatn, oligochaetes dominating in Saksunarvatn and chironomid larvae in Toftavatn. For both the littoral zone and the profundal, there was a considerable difference among the lakes in density proportions of cladoceran species. Total densities in both habitats of all the lakes were within the range recorded in Icelandic lakes, but there were some distinct

differences in taxon composition. Thus, chironomids of the Diamesinae sub-family, along with the tadpole shrimp *Lepidurus arcticus* and the calanoid genus *Diaptomus* were absent in the Faroese lakes. Furthermore, none of the four trichopteran species identified from the Faroese samples occur in Iceland. The taxonomic difference, at least for Diamesinae and *L. arcticus*, may be related to a difference in lake temperature between the two countries, late summer and winter temperatures being considerably higher in Faroese lakes than in Iceland.

Introduction

For a number of reasons, the Faroe Islands provide an interesting opportunity for biological studies, not least because of their geographical isolation, their relatively small size and a short colonization period since the glacial retreat about 11,000 years ago. These features raise the questions of biogeography and evolutionary processes of species, community structures and ecosystem functions (e.g. MacArthur and Wilson, 1967; Buckland, 1992; Vitousek *et al.*, 1995; Sadler, 1999). Also, because of the isolated location in the North Atlantic Ocean, the biology of the Faroe Islands is an important reference point along extensive latitudinal and longitudinal gradients in studies of climatic effects on species and their systems (Jeppesen *et al.*, 2002a).

Apart from the present study, only two quantitative studies have been carried out on zoobenthos in Faroese lakes. In 1976-1977, Lützen (1978) examined the profundal macrofauna of Leynavatn, and in 1994 Brattaberg (1995) studied the soft bottom macrofauna in the shallow reservoir of Ryskivatn on the Suðuroy island in connection with her study of the brown trout (*Salmo trutta*). Additionally, several

qualitative and semi-quantitative studies have been made on Faroese freshwater zoobenthos. For more information on previous limnological studies in the Faroe Islands, see Christoffersen (2002).

In the present study, we examined the density and species composition of macro-invertebrates on rocky substrate in the littoral zone and in sediment in the profundal of four Faroese lakes. The study, along with several other studies of Faroese lakes (Christoffersen *et al.*, 2002), is a part of the NORLAKE project, a cross-system analysis of freshwater biological data from lakes in Greenland, Iceland, the Faroe Islands and northern Norway (Jeppesen *et al.*, 2002a).

The present study is the first to consider quantitatively the macrofauna in the littoral zone of Faroese lakes. The main aim of the study is to enhance our knowledge of the macrozoobenthic element in the ecology of Faroese freshwater ecosystems. The results will be mainly discussed in relation to zoobenthos characteristics of Icelandic lakes.

Materials and methods

General lake description

Benthic macroinvertebrates were collected in the littoral zone and the profundal bottom sediment in Eystara Mjáavatn, Leynavatn, Saksunarvatn and Toftavatn during the period 31 July to 4 August 2000 (Table 1). All lakes are located on the island of Streymoy, except Toftavatn, which is situated on the Eysturoy island. The lakes are relatively small, as are most lakes in the Faroe Islands, but their mean and maxi-

mum depths vary considerably. For most lakes, the littoral zone is relatively narrow and steep and their basins thus concave, as is typical of glacier excavations.

The Faroe Islands are a part of the Wyville-Thomson ridge, traversing from Great Britain, through Iceland to Greenland (Mortensen, 2002). The thick bedrock, up to 3 km, is primarily a Basalt formation from the Upper Tertiary (50-60 Myr ago). In general, the Faroe Islands have thin soil and vegetation cover and dense bedrock with low permeability. The groundwater level is thus rather shallow and precipitation is washed rapidly off the land and runs directly into the sea and the lakes.

In the littoral zones of Leynavatn, Saksunarvatn and Toftavatn, the size composition of rocky substrate is very similar, but in Eystara Mjáavatn, medium sized and large stones are scarce, but small stones abundant. Also, in Leynavatn an extensive part of the littoral zone consists of sand. For all lakes the rocky substrate is dominated by smooth to medium eroded stones, whereas rough and little eroded stones are rare. For more information on catchment characteristics of the lakes, see Landkildehus *et al.* (2002), and for information on chemical characteristics, see Jensen *et al.* (2002).

Sampling the littoral zone

In each lake, samples were taken in the littoral surf zone at four stations dispersed evenly around the lake according to the cardinal directions (N, E, W and S). At each station, five stones, 10-15 cm in diameter, were picked up from depths of

20-50 cm. Because of lack of sufficiently large stones at stations 1, 2 and 4 in Eystara Mjáavatn, 20-25 smaller stones (4-8 cm in diameter) were taken. A bottom racket with a frame of 25 x 25 cm and a net bag of 250 µm mesh size was held under the stones as they were picked up. The stones were brushed clean in a bucket of water and the contents sieved through a 250 µm sieve and preserved in 3-4 % formalin buffered with calcium carbonate. Overhead projections of the stones were drawn on paper for measurement of area coverage. Mean area of the sampled stones in Leynavatn, Eystara Mjáavatn, Saksunarvatn and Toftavatn was, respectively, 156.8, 51.2, 119.7 and 136.0 cm².

Sampling the profundal

In each lake, samples were taken with a Kajak corer (diameter 52 mm, 21.24 cm²) at two stations off the littoral zone at different depths. In Leynavatn, the Kajak samples were taken at 17.0 and 30.0 m depth, in Eystara Mjáavatn at 3.3 and 5.5 m depth, in Saksunarvatn at 7.0 and 15.0 m depth, and in Toftavatn at 3.0 and 16.5 m depth. At each station, five samples were collected and they sieved through a 250 µm sieve and preserved in 3-4 % formalin buffered with calcium carbonate.

Fauna and data treatment

For both samples from the littoral zone and the profundal, identification and counting of animals were made under a stereomicroscope with up to 90 times magnification. Taxonomic resolution (given in parenthesis) depended on taxa and ranged from: Coelenterata (genera); Nematoda

Table 1. Morphometrics and physico-chemical variables of the Faroese lakes studied during the period 31 July – 4 August 2000. Temperature, conductivity and pH are averages of four measurements at littoral stations. At one pelagic station, alkalinity, turbidity and total organic carbon (Tot-C) are based on one sample, while Secchi depth is based on four measurements. Other data are derived from Landkildehus et al. (2002) and Lützen (1978).

	Leynavatn	Eystara Mjáavatn	Saksunarvatn	Toftavatn
Altitude	63	76	25	15
Lake area (km ²)	0.18	0.03	0.08	0.52
Mean depht (m)	13.7	3.0	6.5	5.8
Max depht (m)	33	7	17	22
Volume (Gl)	3.06	0.12	1.20	1.17
Catchment area (km ²)	16.6	1.8	12.3	3.6
Temp (°C)	15.4	16.5	14.0	15.6
Conductivity (µS cm ⁻¹)	95	107	112	166
pH	7.1	7.3	6.9	7.2
Alkalinity (meq l ⁻¹)	0.175	0.238	0.246	0.175
Secchi depht (m)	10.5	4.3	9.5	6.0
Turbidity (FNU)	0.32	1.90	0.53	0.42
Tot-C (mg l ⁻¹)	0.82	1.70	0.83	2.30

(single unit); Oligochaeta (families); Hirudinea (species); Mollusca (species); Cladocera (species); Copepoda (genera); Ostracoda (single unit); Amphipoda (species); Trichoptera (species); Hemiptera (families); Chironomidae (sub-families; species or genera in Leynavatn); other Diptera (single unit, including Limoniidae, Empididae, Muscidae, Ceratopogonidae and Dolichopodidae); Acarina (single unit); Collembola (single unit) and; Tardigrada (single unit).

Densities (abundances) are presented as geometric mean number (including zero values if not otherwise stated) of individuals per m². The variables were log transformed (log₁₀ (n+1)) prior to statistical treatment according to Sokal and Rohlf (1981).

Results

Littoral zone

Zoobenthos density and group composition

Total mean densities of macroinvertebrates in the rocky littoral zone of the four lakes varied considerably (Table 2). In Eystara Mjáavatn, Saksunarvatn and Toftavatn, densities did not differ significantly among the lakes (Tukey $P = 0.907$), but mean density in Leynavatn was only about one third of that observed in the other three lakes and was significantly lower in all cases ($F_{3,75} = 6.289$, $P \leq 0.001$, $R^2 = 0.463$; Tukey $P \leq 0.006$).

The overall low density of macroinvertebrates in Leynavatn compared to the other lakes was reflected in low mean density of chironomids ($F_{3,75} = 26.614$, $P < 0.001$, $R^2 = 0.718$; Tukey $P < 0.001$),

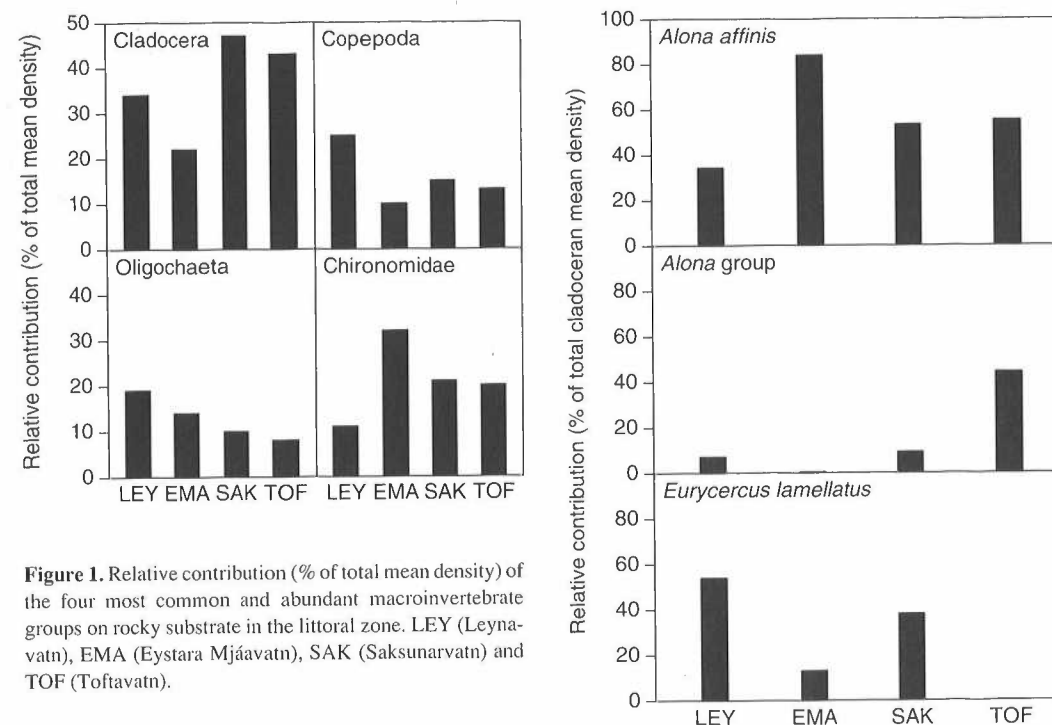


Figure 1. Relative contribution (% of total mean density) of the four most common and abundant macroinvertebrate groups on rocky substrate in the littoral zone. LEY (Leynavatn), EMA (Eystara Mjáavatn), SAK (Saksunarvatn) and TOF (Toftavatn).

ostracods ($F_{3,75} = 22.231$, $P < 0.001$, $R^2 = 0.686$; Tukey $P < 0.001$), cladocerans ($F_{3,75} = 16.062$, $P < 0.001$, $R^2 = 0.625$, Tukey $P \leq 0.018$) and trichopterans ($F_{3,75} = 12.941$, $P \leq 0.001$, $R^2 = 0.584$, Tukey $P \leq 0.001$). There was, however, no significant difference among the four lakes in mean density of molluscs ($F_{3,75} = 0.630$, $P = 0.598$), oligochaetes ($F_{3,75} = 1.112$, $P = 0.350$), or copepods ($F_{3,75} = 1.771$, $P = 0.159$).

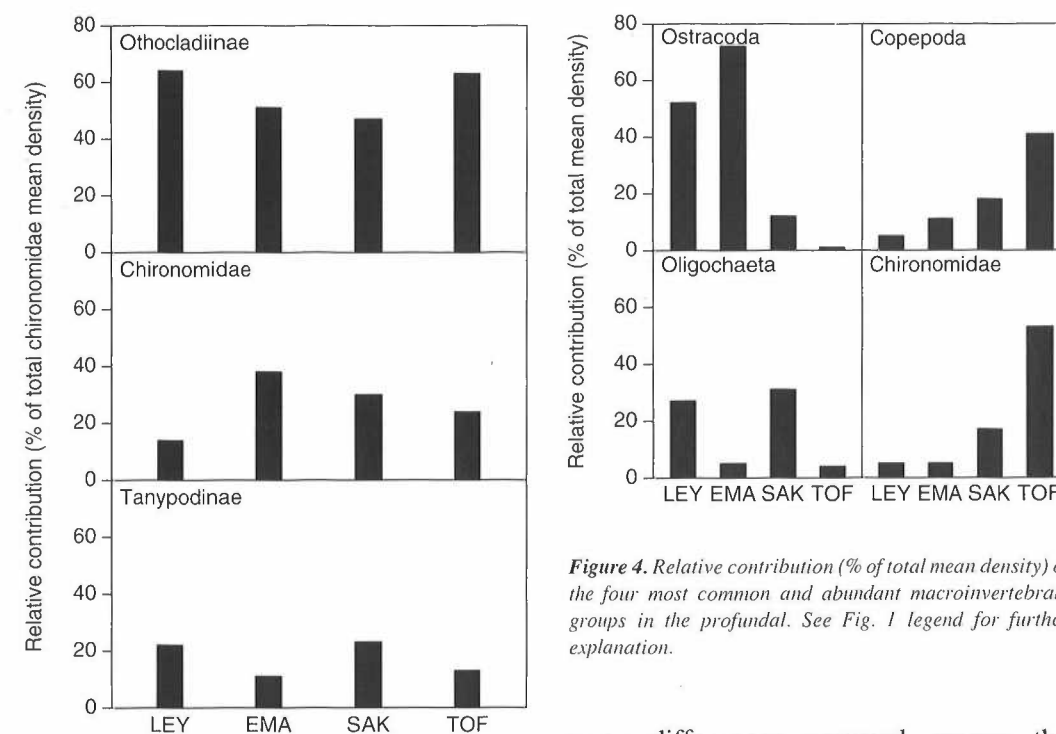
The relative contribution of the four most common and abundant macroinvertebrate groups to total mean density was similar in the lakes (Fig. 1). In Leynavatn, Saksunarvatn and Toftavatn, cladocerans were the most abundant group, accounting for 34–47 % of total mean density. In both Saksunarvatn and Toftavatn, mean density

Figure 2. Relative contribution (% of total cladoceran mean density) of the three most common and abundant cladoceran taxa on rocky substrate in the littoral zone. The *Alona* group includes *A. quadrangularis*, *A. costata*, *A. guttata* and *A. intermedia*. See Fig. 1 legend for further explanation.

of cladocerans was significantly higher (Tukey $P \leq 0.049$) than in Leynavatn and Eystara Mjáavatn. In Eystara Mjáavatn, cladocerans were second in relative abundance with a 22 % contribution. In Saksunarvatn and Toftavatn, chironomids were the second most abundant group with a 22 % and 20 % contribution respectively. In Eystara Mjáavatn, chironomids were the most abundant group (32 %), whereas chironomids contributed only about 11 % to total

Table 2. Frequency of occurrence (F, percentage of stones with taxon) and mean density (MD, geometric mean no. ind m⁻²) of macroinvertebrates on rocky substrate in the littoral zone.

	Leynavatn		Eystara Mjáavatn		Saksunarvatn		Toftavatn	
	%F	MD	%F	MD	%F	MD	%F	MD
Hydrozoa <i>Hydra</i> spp.	75	130	32	62	30	3	100	1.523
Nematoda	70	81	63	30	50	17	80	101
Oligochaeta	90	1.434	100	3.622	100	2.599	100	2.684
Naididae	90	1.354	100	3.395	100	2.437	100	2.233
Tubificidae	5	1	53	12	20	2	45	9
Enchytraeidae	45	10	53	12	50	13	50	20
Lumbriculidae	5	1			10	1	5	1
Hirudinea <i>Helobdella stagnalis</i>	5	1	21	2	5	1		
Mollusca	70	232	95	286	85	157	80	96
<i>Lymnaea pereger</i>	70	231	95	285	85	151	70	48
<i>Pisidium</i> spp.			5	1	15	1	50	13
Hydracarina	95	183	100	566	90	133	95	267
Cladocera	100	2.494	100	5.942	100	12.705	100	14.321
<i>Daphnia</i>			42	10	10	1		
<i>Bosmina coregoni</i>	10	1	68	66			50	18
<i>Chydorus sphaericus</i>	20	2	11	1	15	1	25	2
<i>Alona affinis</i>	65	113	100	3.580	100	4.841	100	6.456
<i>Alona</i> ssp.	55	22	53	17	95	825	100	5.116
<i>Alonella</i> sp.	5	1						
<i>Holopedium gibberum</i>	40	5						
<i>Acroperus harpae</i>	40	6	63	37	40	10	70	57
<i>Eurycercus lamellatus</i>	85	180	100	539	100	3.419	65	22
<i>Iliocryptus sordidus</i>							5	1
<i>Polyphemus pediculus</i>							20	2
<i>Graptoleberis testudinaria</i>	20	2	5	1	10	1	30	3
<i>Simocephalus vetulus</i>					5	1		
Ostracoda	75	46	100	3.680	100	536	100	654
Copepoda	95	1.870	100	2.811	100	3.998	100	4.497
Cyclopoidae	95	618	100	2.465	100	2.666	100	3.057
Canthocamptidae	80	609	47	15	90	381	100	678
Amphipoda <i>Gammarus lacustris</i>	10	1	16	1				
Trichoptera	75	95	100	1.220	100	974	100	2.672
Polycentropodidae	70	29	95	397	100	528	95	1.130
Psychomyidae	50	19	84	120	90	171	95	514
Other	20	1	84	122	10	1	45	215
Chironomidae	100	806	100	8.550	100	5.780	100	6.545
Chironominae	70	57	100	2.863	100	1.523	100	1.431
Orthocladiinae	85	261	100	3.845	100	2.420	100	3.810
Tanypodinae	70	91	100	816	100	1.193	100	833
Empedidae			21	1	5	1		
Other	15	1	32	3	10	1	30	3
Total mean		11.272		31.550		30.549		37.239
95% Lower Cl.		5.470		24.603		21.232		20.760
95% Upper Cl.		23.226		40.457		44.055		45.185
n		20		19		20		20

**Figure 4.** Relative contribution (% of total mean density) of the four most common and abundant macroinvertebrate groups in the profundal. See Fig. 1 legend for further explanation.**Figure 3.** Relative contribution (% of total chironomidae mean density) of the three most common and abundant chironomid subfamilies on rocky substrate in the littoral zone. See Fig. 1 legend for further explanation.

mean density in Leynavatn. In Saksunarvatn and Toftavatn, copepods were the third most abundant group with 15 % and 13 % contribution respectively, whereas copepods were the second most abundant group (25 %). In Eystara Mjáavatn, copepods made up only 10 % of total density, which was 4 % lower than the contribution of oligochaetes. For Leynavatn, Saksunarvatn and Toftavatn, the share of oligochaetes was, 19 %, 10 % and 9 % respectively.

Despite general similarity in the relative composition of most invertebrate groups,

some differences occurred among the lakes. In Toftavatn, the mean density of trichopterans and hydrozoans was far greater than in the other three lakes. The relative density contribution of hydrozoans and trichopterans in Toftavatn was 5 % and 8 % respectively. Also, in Eystara Mjáavatn, contrary to the other three lakes, the contribution of ostracods to total density was 14 %. In the other three lakes the share of ostracods ranged between 1 and 2 %.

Zoobenthos composition within groups

For cladocerans, the most common and abundant macroinvertebrate group in the four lakes, the number of species was very similar for all four lakes (Table 2). Furthermore, in all lakes, the same three taxa, the benthic detritus feeders *Alona affinis*,

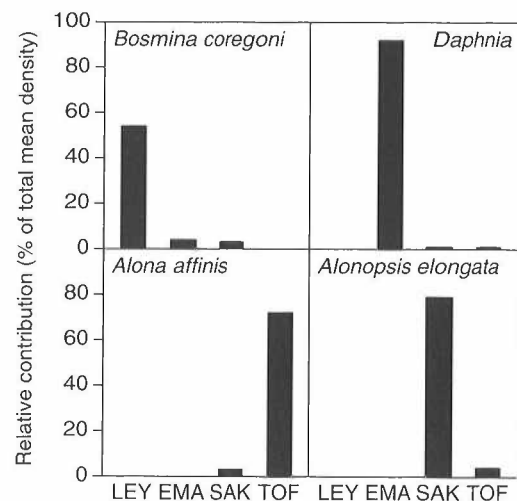


Figure 5. Relative contribution (% of total cladoceran mean density) of the four most common cladoceran species in the profundal. See Fig. 1 legend for further explanation.

Eurycercus lamellatus and *Alona* spp., were most important in terms of relative density contribution (Fig. 2). The *Alona* group consisted of 3-4 species, tentatively identified as *A. quadrangularis*, *A. costata*, *A. guttata* and *A. intermedia*. In Saksunarvatn, Eystara Mjáavatn and Toftavatn, *Alona affinis* together with *Alona* spp. constituted 62-99 % of mean cladoceran density and 41 % in Leynavatn. In Leynavatn, *E. lamellatus* was the most frequent and abundant species (54 % share), whereas in Eystara Mjáavatn and Saksunarvatn, *E. lamellatus* was the second most abundant cladoceran (13 % and 38 % respectively). Interestingly, *E. lamellatus* was very scarce in Toftavatn, with less than a 1 % share of total mean density of cladocerans.

Cyclopoidae were identified to genera. Only *Cyclops* occurred in all four lakes

(Table 2). Among the Canthocamptidae, the genus *Canthocamptus* was observed in all the lakes. On the other hand, notostracans and Diaptomidae species were absent from all four lakes. The only amphipod species identified in the present study was *Gammarus lacustris* in Eystara Mjáavatn and Leynavatn.

For chironomids, the second most abundant macroinvertebrate group, the relative composition of the three subfamilies identified was rather similar among all the four lakes (Fig. 3), with Orthoclaadiinae being most abundant (47-64 % of chironomids), followed by Chironominae (11-38 %) and the predatory Tanytopodinae (11-23 %). The subfamily Diamesinae was absent in all lakes. A total of 22 chironomid taxa were identified from Leynavatn. Diversity was much higher within the littoral zone (10-18 species/group) than in the profundal (6-7 species/group). The dominant chironomid taxa in the littoral zone were the genera *Synorthocladus*, *Orthocladus*, *Arctopelopia* and *Micropsectra*. The dominant chironomids in the profundal were *Procladius*, *Tanytarsus* and *Chironomus salinarius* group.

One species was identified within each of the two common Trichopteran families Polycentropodidae and Psychomyidae, i.e. *Polycentropus flavomaculatus* (Polycentropodidae) and *Tinodes waeneri* (Psychomyidae). *Agrypnia obsoleta* (Phryganeidae) and *Mesophylax impunctatus* (Limnephilidae) occurred more sporadically and in lower numbers. For all species, larval stages outnumbered pupal stages.

Table 3. Frequency of occurrence (F, percentage of samples with taxon) and mean density (MD, geometric mean no. ind m⁻²) of macroinvertebrates in the profundal.

	Leynavatn		Eystara Mjáavatn		Saksunarvatn		Toftavatn	
	%F	MD	%F	MD	%F	MD	%F	MD
Nematoda			50	41	17	2	50	83
Oligochaeta	100	5.847	100	2.811	100	17.295	83	649
Naididae	40	13	17	2	33	9	50	44
Tubificidae	100	5.151	100	2.691	100	15.724	50	32
Enchytraeidae	40	12			33	17	33	9
Lumbriculidae	10	1	17	1	67	152	33	8
Hirudinea			33	7	17	2		
Mollusca								
Pisidium spp.	60	126	50	25	50	73	67	94
Hydracarina	20	3	17	2	50	23	17	2
Cladocera	100	2.460	83	3.555	100	9.704	67	854
Daphnia			50	287	17	2	17	1
Bosmina coregoni	70	118	33	13	50	36		
Chydorus sphaericus	20	3						
Alona affinis					33	36	67	615
Alona spp.	20	2	17	2	50	114	50	67
Alonopsis elongata					67	877	50	34
Holopedium gibberum	10	1						
Acroperus harpae			17	2	17	3		
Eurycercus lamellatus	10	1	33	9	50	28	17	2
Iliocryptus sordidus	60	93			33	12	67	122
Graptoleberis testudinaria							33	9
Ostracoda	100	11.454	100	39.536	83	6.760	33	8
Copepoda	90	1.152	100	6.338	100	10.208	100	6.713
Cyclopoidae	90	1.152	100	6.151	100	10.208	100	6.713
Chironomidae	90	981	100	2.660	100	11.640	100	8.608
Chironominae	80	386	100	2.505	100	9.622	100	1.380
Orthoclaadiinae	30	5	17	2	50	30	100	6.765
Tanytopodinae	30	67	33	7	100	1.344	50	34
Other	30	4	17	2	17	619		
Total mean		30.199		91.200		175.387		32.508
95% Lower Cl.		22.645		11.560		123.309		97.723
95% Upper Cl.		40.270		207.940		249.458		107.894
n		10		6		6		6

Within oligochaetes, the family Naididae outnumbered other families (Table 2). Several species were tentatively identified, but the genus *Chaetogaster* dominated, constituting 40-50 % of total naidid density, followed by *Stylaria lacustris* and *Nais* spp.

Profundal zoobenthos density and group composition

Total mean density of macroinvertebrates in the bottom sediment of the profundal varied considerably between the four lakes (Table 3) and was significantly lower in Leynavatn and Toftavatn compared with

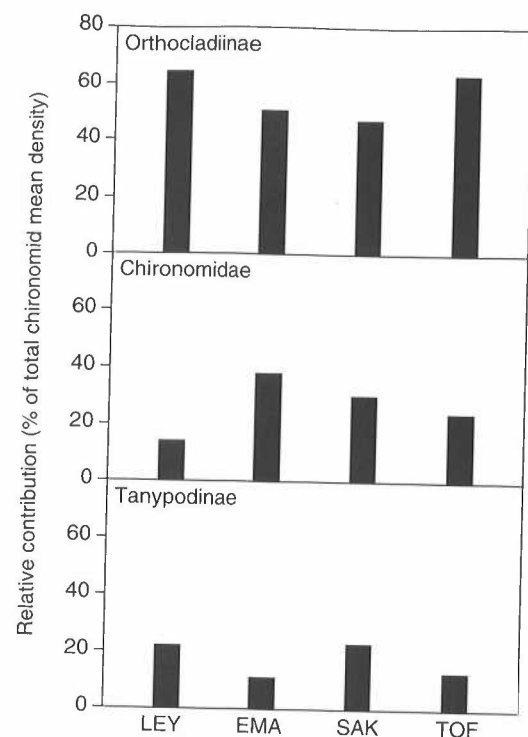


Figure 6. Relative contribution (% of total chironomid mean density) of the three chironomid sub-families identified in the profundal. See Fig. 1 legend for further explanation.

Eystara Mjáavatn and Saksunarvatn ($F_{3,24} = 10.217$, $P < 0.001$, $R^2 = 0.749$; Tukey $P \leq 0.044$).

The contribution of the four most common and abundant macroinvertebrate groups differed markedly among the four lakes (Fig. 4). In Leynavatn and especially Eystara Mjáavatn, ostracods outnumbered the other groups, whereas oligochaetes outnumbered other groups in Saksunarvatn, and chironomids and copepods in Toftavatn. Furthermore, the density of

cladocerans was quite high in Saksunarvatn (17 %) compared to the other three lakes (5-11 %).

Zoobenthos composition within groups

For all lakes, the contribution of individual taxa among oligochaetes and copepods, respectively, was more or less the same (Table 3). All copepods identified belonged to the genus *Cyclops*. As for tubificids, a tentative identification revealed *Tubifex tubifex*, *Limnodrilus hoffmeisteri* and *Pelosclex* spp. Of these, *T. tubifex* was far the most common species. Two species of lumbriculids, *Lumbriculus variegatus* and *Stylo-drilus heringianus*, were identified.

The relative density of cladoceran species in the profundal differed among the lakes, with one species outnumbering other species in all lakes (Fig. 5). *Alonopsis elongata* was only observed in Saksunarvatn and Toftavatn.

The relative density of Orthoclaadiinae was quite high in Leynavatn and Toftavatn, and significantly higher than the densities of Chironominae and Tanypodinae (Fig. 6). In Leynavatn, the proportion of Chironominae was particularly low compared to the other three lakes. For Eystara Mjáavatn and Saksunarvatn, the relative densities of Chironominae and Orthoclaadiinae were fairly similar.

Discussion

The taxonomic composition of macroinvertebrates in the littoral zone and in the profundal, respectively, was similar in the four lakes studied. However, the total density and relative density composition of

macroinvertebrate taxa differed among the lakes.

Total density in the profundal, and especially in the littoral zone of Leynavatn, was much lower compared with the other lakes. Of the four lakes, the lowest densities of zooplankton were also observed in Leynavatn (Lauridsen and Hansson, 2002). The low zoobenthos density in Leynavatn is in agreement with its oligotrophic nature in terms of physico-chemical parameters. Of the four lakes, conductivity, total organic carbon and turbidity were lowest in Leynavatn and Secchi depth was greatest (Table 1). Also, the concentrations of nutrients (Jensen *et al.* (2002)) indicate low phytoplankton activity relative to the other lakes (Brettum, 2002). Macrophytes were also least abundant in Leynavatn (Schierup *et al.*, 2002) and an extensive part of the littoral zone consists of sand (Landkildehus *et al.*, 2002). Both these physical features may help explain the relatively low abundance of zoobenthos in the littoral zone of Leynavatn. Furthermore, Leynavatn is the deepest and largest of the four lakes, and although the water mass is probably mixed in the entire water column in most years, a thermocline may develop, as observed by Lützen (1978) at 15-20 m depth in August 1977. The thermocline may contribute to decreased recycling and mixing of nutrients and organic material between the profundal bottom and the euphotic zone. Other factors may also contribute to low zoobenthos density in Leynavatn. Regarding the littoral zone, it is interesting to note that the water level of the lake may fluctuate considerably, or close to 0.5 m

within 24 h, as was observed in a heavy rain some days in the summer of 1976 (Lützen, 1978). Due to such water level fluctuations, the littoral surf zone in Leynavatn may be unstable as a habitat for benthic invertebrates. Unfortunately, detailed information on the frequency and amount of water level fluctuations in Leynavatn, as well as on the other three lakes, is unavailable.

Predation pressure from fish may also be a factor contributing to the comparatively low zoobenthos density in Leynavatn (Jeppesen *et al.*, 2002b). However, catch statistics, indicating density of fish and consequently the potential predation pressure, do not support this. Catch per unit effort of fish in Leynavatn was slightly lower than that in Saksunarvatn and only a little higher than in Eystara Mjáavatn (Malmquist *et al.*, 2002), but the zoobenthos densities in the latter two lakes were about three times higher than in Leynavatn. Furthermore, the contribution of planktonic food in the four lakes studied was most prominent in the diet of fish in Leynavatn (Malmquist *et al.*, 2002), indicating that the predation pressure on zoobenthos might be lesser in Leynavatn than in the other three lakes.

Lützen (1978) studied the profundal in Leynavatn in June-September 1976 and August 1977. He only presented the results on density for the five most abundant species (*T. tubifex*, *L. variegatus*, *Pisidium* sp., *Procladius* sp. and *Chironomus anthracinus*) and excluded crustaceans. Nevertheless, the results from Lützen (1978) regarding these species agree with the present results. In addition to the species already

mentioned, Lützen (1978) identified the following species from Kajak samples: *Uncinaiis uncinata* (Naidae); *Stylodrilus heringianus* (Lumbriculidae); *Erpobdella octoculata* (Hirudinea); *Lymnaea pereger* (Mollusca) and several chironomid genera (*Chironomus* sp., *Macropelopia* sp., *Arctopelopia* sp., *Tanytarsini* sp.) and a few species of Orthocladinae.

Comparison with Iceland

The densities of macroinvertebrates, excluding crustaceans, in the littoral zone of the Faroese lakes are comparable with those observed in the littoral zone of Icelandic lakes (data on crustaceans not available, Jónsdóttir *et al.*, 1998; Malmquist *et al.*, 2000). For the Faroese lakes, mean macroinvertebrate density excluding crustaceans was 5,198 ind m⁻² for Leynavatn, 16,443 ind m⁻² for Eystara Mjáavatn, 10,913 ind m⁻² for Saksunarvatn and 15,666 ind m⁻² for Toftavatn. In the littoral zone of 35 Icelandic lakes, sampled with the same method as the Faroese lakes, the range in mean density was 97–32,727 ind m⁻², with average means about 12,000 ind m⁻² (Malmquist *et al.*, 2000). About 20 % of the Icelandic lakes had densities greater than 15,000 ind m⁻², and about 35 % of the lakes had densities lower than 5,000 ind m⁻² (Malmquist *et al.*, 2000).

The densities of macroinvertebrates in the profundal zone of the Faroese lakes lie within the range observed for Icelandic lakes (Jónsdóttir *et al.*, 1998; Malmquist *et al.*, 2000). In 23 Icelandic lakes, sampled with the same method as in the Faroese lakes, mean total density of macroinverte-

brates ranged between 5,000 and 135,000 ind m⁻² and the average mean density centred around 35,000 ind m⁻² (Jónsdóttir *et al.*, 1998), or similar to that observed for Leynavatn and Toftavatn. About 20 % of the Icelandic lakes had densities higher than 100,000 ind m⁻². In shallow (max depth < 2 m) Icelandic mountain lakes, situated above 600 m a.s.l., mean total density in the profundal was very variable, ranging between 5,000 and 50,000 ind m⁻² (Jónsdóttir *et al.*, 1998; Malmquist *et al.*, 2000).

The taxa composition in the littoral zone and the profundal seems to be rather similar in the Faroese and Icelandic lakes. As for some taxa, however, there are some distinct and interesting differences. For example, the large benthic detritivore cladoceran *Macrothrix hirsuticornis*, which is quite common in the soft sediment of Icelandic lakes (Malmquist *et al.*, 2001; ESIL-database, unpubl. data), was not observed in any of the Faroese zoobenthos samples in the present study, nor in pelagic samples (Lauridsen and Hansson, 2002). Curiously enough, this cosmopolitan species has not been recorded in the Faroe Islands (Poulsen, 1928; Danielsen, 1999). The same applies to *Diaptomus* calanoids, which is also absent in the Faroese lakes (see also Lauridsen and Hansson, 2002). In Icelandic lakes, this genus is quite common and represented by two species, *D. minutus* and *D. glacialis* (Malmquist *et al.*, 2001).

Another crustacean absent from Faroese lakes, but abundant in lakes and ponds in the highlands of Iceland, was the large notostracan tadpole shrimp *Lepidurus arc-*

ticus. Conversely, no freshwater gamma-rids have been recorded in Iceland, but *Gammarus lacustris*, identified in Leynavatn and Eystara Mjáavatn in the present study, has previously been identified in another Faroese lake, Djupidalurvatn on the island of Eysturoy (Brabrand, 1989). Poulsen (1928) described two other species found in Faroese lakes, *G. duebeni* and *G. pulex*, but did not mention *G. lacustris*. According to Poulsen (1928), these species were rather common in lakes, ponds and rivulets, occurring in the lowland and the mountains. Lützen (1978) also found *G. pulex* in the littoral zone of Leynavatn.

The Faroese lakes do not seem to be inhabited by Diamesinae, a subfamily very common in Icelandic lakes and streams (Lindegaard and Jónasson, 1979; Lindegaard, 1992; Malmquist *et al.*, 2001; 2000; Ólafsson *et al.*, 2001). Diamesinae appeared to be primarily associated with low temperatures and oligotrophic freshwater ecosystems (e.g., Ólafsson *et al.*, 2001; Lods-Crozet *et al.*, 2001; Malmquist *et al.*, 2001). In the littoral zone of 35 Icelandic lakes, the average lake temperature in August is 10.4 °C (s.d. = 2.10, range 6.6–15.2 °C) (Malmquist *et al.*, 2000). For the four Faroese lakes studied, lake temperature is about 5 °C warmer (Table 1) than in the Icelandic lakes. Moreover, the winter climate in the Faroe Islands is much milder than in Iceland and, contrary to Iceland, most Faroese lakes rarely freeze in winter. The lack of Diamesinae and *L. arcticus* in the Faroese lakes may thus be due to unfavourable lake temperatures. Other factors, such as sporadic colonization events

by species on small, remote islands, as accounted for by the theory of island biogeography (MacArthur and Wilson, 1967), may also explain the faunal difference between the Faroe Islands and Iceland.

Henriksen (1928) identified 17 trichopteran species in six families at various localities in the Faroe Islands and in 1962 Shire *et al.* (1964) identified 15 species in five families. None of the four Trichoptera species identified from Leynavatn and Toftavatn occurs in Iceland (Gíslason, 1981; Malmquist *et al.*, 2000; 2001). The identification of Trichoptera from Eystara Mjáavatn and Saksunarvatn is not completed, but total densities have been estimated. The Trichoptera species in Faroe Islands bear a close resemblance to the fauna of Scandinavia (Svensson and Tjeder, 1975; Solem and Andersen, 1996) and Scotland and northern England (Edington and Hildrew, 1981; Wallace *et al.*, 1990). Two out of the 17 Trichoptera species recorded from the Faroe Islands have not been recorded in Scandinavia, but are found in the British Isles. In the shallow Ryskivatn on Suðuroy, three species were identified, *A. obsolete*, *P. flavomaculatus* and *Limnethius incius* (Brattaberg, 1995).

Besides the difference in species composition, there also appears to be a profound difference in trichopteran density between Faroese and Icelandic lakes. Thus, in the littoral zone of 35 Icelandic lakes, average mean density of Trichoptera, primarily *Apatania zonella*, was about 250 ind m⁻² (range of means 0–937 ind m⁻²) (Malmquist *et al.*, 2000), whereas the average mean density for the four Faroese lakes

was 1,240 ind m⁻² (range of means 95-2,672 ind m⁻²).

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Biology of Brown Trout (*Salmo trutta*) and Arctic Charr (*Salvelinus alpinus*) in Four Faroese Lakes

Sjósíl (*Salmo trutta*) og bleikja (*Salvelinus alpinus*)
í fyra føroyskum vøtnum

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Úrtak

Seint í juli og tíðliga í august 2000 vóru kanningar gjørðar av sjósíli (*Salmo trutta*) og bleikju (*Salvelinus alpinus*) í fyra føroyskum vøtnum. Lutfalsligi tættleikin og konditiónin av sjósíli var lægst í Leynavatni og hægst í Saksunarvatni. Bleikja var bara at finna í Leynavatni, har hon kom 2,7 ferðir oftari fyri enn sjósíl. Fyri øll vøtnini var galdandi, at fiskurin vaks seint og var lítil, og hægsti aldurin á fiskinum var eisini lágur. Elsti fiskurin í Toftavatni av 5+ ára gamal, meðan elsti fiskurin í allari kanninginini var 9+ ára gamal. Hann var funnin í Saksunarvatni. Endalongdin á bleikju í Leynavatni var uml. 21 cm., meðan endalongdin á sjósíli var uml. 25 cm. bæði í Leynavatni og Toftavatni. Á sjósílinum í Eystara Mjáavatni og Saksunarvatni varð ongin endalongd funnin. Smáir, men týðandi munir vóru funnir á skapinum á sjósílinum í teimum ymisku vøtnunum samsvarandi við munin, sum var funnið á føðini hjá fiskinum. Sjósílini í Toftavatni høvdu ein meiri klovnan stert, og har var føðin meir pelagisk/djór á botninum (epibenthic) enn í hinum vøtnunum. Í Leynavatni ótu sjósílini serliga botndjór, og tey høvdu eina rundari gron enn sjósílini í hinum vøtnunum. Hetta kann vera orsakað av, at sjósílini í Leynavatni mugu kappast við bleikju. Onki sást til nakað frávik í skapinum ella vistfrøðiliga sundurbýtinum (polymorphismuni) á bleikjuni í Leynavatni,

og hon át bæði botndjór og æti. Ílegukanningar av bleikjuni á Leynavatni vístu smærri munir á flestu ílegustøðunum og stór „homozygosity“ og „genotypic“ ójavnvág var millum trý ílegustøð. Hetta bendir á nógva innannøring og eina tilvildarlaga býtisbroyting av ílegunum í smáum, avbyrgdum stovnum. Orsøkin til, at bleikja bert er í einum føroyskum vatni, er helst, at hitin í vøtnunum ikki er til vildar. Kanningarúrslitini vísa, at seini vøksturin, líttla støddin og stutta livitíðin á bleikju og sjósíli í Leynavatni kann koma av kappingin millum bæði sløgini og av vánaligum føðiviðurskiftum í vatninum.

Abstract

The biology of Brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) was studied in four Faroese lakes in late July – early August 2000. Relative density and condition of Brown trout were lowest in Leynavatn and highest in Saksunarvatn. Arctic charr only occurred in Leynavatn, where it outnumbered Brown trout by a factor of 2.7. For all fish populations, growth rates were slow, fish were small and maximum age of fish was low. The oldest fish in Toftavatn was 5+ yr and the oldest fish in the study, in Saksunarvatn, was 9+ yr. Asymptotic length was ca. 21 cm for arctic charr in Leynavatn and ca. 25 cm for Brown trout in both Leynavatn and

Table 1. Morphometrics and physico-chemical variables of the Faroese lakes studied during the period 31 July – 4 August 2000. Temperature, conductivity and pH are averages of four measurements at littoral stations. At one pelagic station, alkalinity, turbidity and total organic carbon (Tot-C) are based on one sample, while Secchi depth is based on four measurements. Other data are derived from Landkildehus et al. (2002) and Lützen (1978).

	Leynavatn	Eystara Mjáavatn	Saksunarvatn	Toftavatn
Altitude	63	76	25	15
Lake area (km ²)	0.18	0.03	0.08	0.52
Mean depht (m)	13.7	3.0	6.5	5.8
Max depht (m)	33	7	17	22
Volume (Gl)	3.06	0.12	1.20	1.17
Catchment area (km ²)	16.6	1.8	12.3	3.6
Temp (°C)	15.4	16.5	14.0	15.6
Conductivity (µS cm ⁻¹)	95	107	112	166
pH	7.1	7.3	6.9	7.2
Alkalinity (meq l ⁻¹)	0.175	0.238	0.246	0.175
Secchi depht (m)	10.5	4.3	9.5	6.0
Turbidity (FNU)	0.32	1.90	0.53	0.42
Tot-C (mg l ⁻¹)	0.82	1.70	0.83	2.30

Toftavatn, but for Brown trout in Eystara Mjáavatn and Saksunarvatn, no asymptote was observed. Small but significant differences in morphology were observed among Brown trout populations with corresponding differences in diet. Brown trout in Toftavatn had a more forked caudal fin and the diet was more pelagic/epibenthic than in the other lakes. In Leynavatn, Brown trout fed more on benthic diet and had a more curved snout than Brown trout in the other lakes, which may be signs of character displacement resulting from interspecific competition with Arctic charr. The Arctic charr in Leynavatn did not show signs of morphological or ecological polymorphism and their diet was both of benthic and planktonic origin. Genetic analyses of Arctic charr showed minor variation at most loci, high homozygosity and genotypic disequilibrium between three loci, indicating extensive inbreeding and random genetic drift in a small, isolated population. It is suggested that the restriction of Arctic charr to one natural lake in the Faroe Islands is primarily due to unfavourable water temperatures. Evidence suggests that the slow growth, small size and short lifespan of Arctic charr and Brown trout in Leynavatn may be due to interspecific competition between the two species along with relatively poor food conditions in the lake.

Introduction

Only two native species of salmonid fishes (family Salmonidae) are found in Faroese freshwaters. These are Brown trout (*Salmo trutta* L.), which is widespread in lakes and rivers, and Arctic charr (*Salvelinus alpinus* (L.)), with a native population in only one lake, Leynavatn on the island of Streymoy (Larsen et al., unpubl.; Reinert, 1982). In 1956 and again in 1961, Arctic charr from Leynavatn were released in the reservoir Frammi á Vatni and the dammed lake Á Mýrum. From these waters, the charr spread further downstream in the reservoir-complex of Lomundaroyri and Heygardalsvatn above the town of Vestmanna (Larsen et al., unpubl.; Jensen, 1983). In recent years, Brown trout have also been released in several lakes and rivers, including Leynavatn and Saksunarvatn (Brattaberg,

Table 2. Microsatellite primers used for genetic analysis of Arctic charr from Leynavatn. Shown are primer sequences and the type of fluorescent label used. * indicates labelled primer.

Microsatellite primers	Fluorescent label	Forward	Reverse
<i>Ssa85DU</i>	FAM	*AGGTGGGTCTCCAAGCTAC	ACCCGCTCCTCACTTAATC
<i>Ssa456NCVM</i>	HEX	CTTCCCAGGAGTCATCATAAATCT	*TAAACCCCACTGCTTGTGAGTGT
<i>µ85INRA</i>	NED	ACTTAAGACTGGGAACCTT	*CTACACGGCCTTCGGGTGAGA
<i>Ssa20.19UCG</i>	FAM	TCAACCTGGTCTGGCTTCGAC	*CTAGTTTCCCAGCACAGCC
<i>One11ASC</i>	NED	*GTTTGGATGACTCAGATGGGACT	TCTATCTTTCCTGTCAACTTCCA

1995; Dorete Bloch, pers. comm.). Atlantic salmon (*S. salar* L.) is found in a few streams and lakes, but these populations are recently stocked and there exists no evidence for the past few centuries of an original, naturally spawning salmon stock in the islands (Reinert, 1982). Also occurring in the Faroe Islands are three-spined stickleback (*Gasterosteus aculeatus* L.) (Jeppesen *et al.*, 2002a; b; own unpublished results), nine-spined stickleback (*Pungitius pungitius*) (Jeppesen *et al.*, 2002a) and American eel (*Anguilla anguilla* L.) (Brabrand, 1989; Brattaberg, 1995; Jeppesen *et al.*, 2002a).

Anadromous and lake resident Arctic charr are widely distributed in arctic and sub-arctic areas and the species is renowned for extensive phenotypic variability, both among and within lakes, reflecting adaptations to different ecological environments (Balon, 1980; Skúlason *et al.*, 1992, 1999; Jonsson and Jonsson, 2001). In some lakes, Arctic charr features distinct sympatric trophic morphs exploiting different habitats and food resources, resulting in differences in life history, morphology and genetics. A clear example of this are the

four Arctic charr morphs in Thingvallavatn, Iceland (Sandlund *et al.*, 1987; Jonsson *et al.*, 1988; Malmquist *et al.*, 1992; Snorrason *et al.*, 1994b). As opposed to the quite intensive research on Arctic charr, morphological studies on Brown trout are few (Hanken and Hall, 1993).

In the present study we analyse life history traits, morphology and food of four Brown trout populations and one Arctic charr population from four Faroese lakes. As for Arctic charr, genetic analyses were also included. The present study, along with several other studies of Faroese lakes (Christoffersen *et al.*, 2002a), is a part of the NORLAKE project, a cross-system analysis of freshwater biological data from lakes in Greenland, Iceland, the Faroe Islands and northern Norway. The general aim of the present study is to enhance ecological knowledge of fish in Faroese freshwater ecosystems. Also, and more specifically, we are interested in the following questions: 1) do Brown trout living in sympatry with Arctic charr in Leynavatn show signs of character displacement in morphology, life history and diet?; 2) do trout populations differ in morphology, life

history and diet among lakes? and; 3) do Arctic charr in Leynavatn show signs of trophic polymorphism?

Materials and methods

General lake description

Fish studies were conducted in Leynavatn, Eystara Mjáavatn, Saksunarvatn and Toftavatn during the period 31 July – 4 August 2000 (Table 1). The lakes are located on the island of Streymoy, except Toftavatn, which is situated on Eysturoy. The lakes are relatively small, as are most lakes in the Faroe Islands, but mean and maximum depth vary considerably. Except for Toftavatn, the littoral zone is narrow and steep and the lake basin thus concave, as is typical of glacially formed lakes. For more information on physico-chemical characteristics of the lakes studied, see Landkildehus *et al.* (2002) and Jensen *et al.* (2002). For biological information on the lakes, see Schierup *et al.* (2002), Brettum (2002), Christoffersen *et al.* (2002b), Lauridsen and Hansson (2002), Malmquist *et al.* (2002) and Jeppesen *et al.* (2002a, b).

Fish sampling

In each lake, nine single mesh, single strand nylon gillnets (Lundgren series) were set perpendicular to the lake shore, from ca. 2 m depth close to the shore and onwards, down to a maximum depth of ca. 25 m (in Leynavatn). The nets were left overnight for about 12 h (10.5–14 h). The gillnets were 25 m long, 1.5 m high, and the following mesh sizes were used: 10, 12.5, 15, 19.5, 24, 29, 35, 43 and 55 mm (knot to knot). Total net area used was 338 m² in all

lakes, except 169 m² in the small Eystara Mjáavatn.

In addition to gillnetting, four metal traps (Canadian, type MT 18) with a mesh size of 3.2 mm were used in each lake for sampling fry and three-spined sticklebacks. The traps were set for about 12 h overnight in the littoral zone at depths between 2–4 m. Only in Toftavatn were four three-spined sticklebacks caught in one trap, but the results are not treated further here.

Fish processing and data treatment

Life history and food. Fork length (nearest 0.1 cm) and wet weight (nearest 0.5 g) were measured for all fish and the stomach was removed for food analysis. Sex was identified and sexual maturity recorded according to Dahl (1917). For age determination, scales were used for Brown trout and otoliths for Arctic charr. Fulton's condition factor (K) was calculated for each fish as $K = 100 \times W \times L^{-3}$ (Bagenal and Tesch, 1978) where W is wet weight in g and L fork-length in cm. Stomach fullness was visually estimated and assigned to four categories: empty (0), trace (1, < 1/3), half (2, 1/3–2/3) and full (3, > 2/3). Food items were identified to family, subfamily or species level and counted under stereomicroscope. The percentage by number and ash-free dry weight of food items/classes were calculated for each fish. Conversion from number of food items to ash-free dry weight (mg) of food items was performed according to Malmquist *et al.* (1992) and unpublished data from the ESIL-project (Ecological Survey of Icelandic Lakes) (Malmquist *et al.*, 2000).



Figure 1. For morphological analysis of fish, morphological traits were measured on 33 lengths between 24 landmarks on each fish (white lines). Brown trout from Saksunarvatn, a 7+ yr old male, 30.2 cm long and 294 g in wet weight.

Statistical treatment of the data followed Sokal and Rohlf (1981). Discrete variables (Catch Per Unit Effort (CPUE, no. of fish m^{-2} of gillnet), sex ratios, frequencies of stomach fullness classes) were analysed by nonparametric methods, *G*-test or Mann-Whitney *U*-test, whereas continuous variables (fork length and condition factor) were analysed by parametric methods, including *t*-test, analysis of variance (ANOVA) and Pearson's coefficient of correlation.

Morphology. For morphological measurements, Arctic charr and Brown trout were placed on the right side on a wooden, grooved plate, with the fins pinned down in a straightened position, and the fish photographed (35 mm, 100 ASA Kodak negative film). The films were digitized (600x800 pixels) and the photos analysed using image analysis software from NIH distributed on the World Wide Web. In all, 24 landmarks were defined and the lengths of 33 variables measured (Fig. 1).

Principal Component Analysis (PCA)

was used to analyse the variance of log-transformed lengths. The first three components were analysed. As expected, the first component was highly correlated with fish size, whereas variation in the second and subsequent components described shape in relation to size (Bookstein *et al.*, 1985). Scatterplots of scores for shape components (PCn) versus size (PC1) were used to evaluate shape and size variations within and among designated groups or populations. Factor loadings for each length measurement and component were calculated. Lengths having high loadings on particular components indicate that these lengths are highly correlated with the component in question. If segregation was detected in PCn/PC1 scatterplots, the lengths loading above 0.1 were investigated further. For high loading lengths, pooled regressions on size were made using the log-transformed raw data and the residuals plotted against fork length. Variation of the residuals among groups or populations was analysed by ANOVA (Reist, 1985).

Genetics. For Arctic charr, liver DNA was isolated and variations at five microsatellite loci (*Ssa85DU*, *Ssa456NCVM*, *μ85INRA*, *Ssa20.19UCG*, *One11ASC*) were assayed (Table 2). Protocols for amplification of the multiplex marker set and electrophoresis were as follows: multiplex PCR was performed in a volume of 11 μ l, containing 30–100 ng of genomic DNA, 280 μ M of each dNTP (Boehringer Mannheim), 30 mM Tris-HCl (pH 8.3), 150 mM KCl, and 1.5 mM $MgCl_2$ and 1.0 U Taq polymerase (Boehringer Mannheim). Fluorescently-

Table 3. Factor loadings and variance of the first two components in a PCA on 33 log-transformed morphometric measurements of populations of Brown trout from four Faroese lakes. Absolute values below 0.1 of factor loadings on PC2 are not shown. Explanations of abbreviations are given in the text.

	Factor 1	Factor 2
DPEP	0.93003	-0.132761
VPEP	0.93097	-0.133093
EPFCF	0.87882	0.117235
MENC	0.83504	0.500438
NCMEL	0.79922	0.557589
SNC	0.88921	-0.248896
Expl.Var.	28.56290	0.778855
Prp.Totl.	0.89259	0.024339

labelled and unlabelled primer (Perkin-Elmer and Gibco BRL) concentrations were 0.1 μ M for all primes, except *Ssa-20.19UCG* where the concentration was 0.3 μ M. Samples were amplified in 0.2 ml, 96-well, polypropylene microplates with PTC-100HB-96VTM thermocycler (MJ Research) using touchdown PCR. This allows loci of varying optimal annealing temperatures to be amplified simultaneously.

The touchdown PCR temperature profile for the multiplex was as follows: one cycle of 96 °C for 3 min; 19 cycles of 95 °C for 30 s, 55 °C for 1 min (-0.5 °C per cycle), and 72 °C for 4 min; 10 cycles of 95 °C for 1 min, 45 °C for 1 min and 72 °C for 4 min; followed by one cycle of 72 °C for 40 min. For gel analysis, 5.0 μ l of the PCR product were diluted in 35.0 μ l of ddH₂O and 0.6 μ l of the diluted PCR product was combined with 0.47 μ l of 100 % de-ionized formamide (Amresco), 0.105 μ l of internal line standard (350-Rox, Perkin-Elmer/Applied Biosystems) and 0.125 μ l blue dex-

tran loading dye. Samples were denatured for 2 min at 90 °C and 1.2 μ l was loaded onto a 4.5 % denaturing polyacrylamide gel (19:1 acrylamide/bis-acrylamide). Electrophoresis was performed on a PE/ABI PrismTM 377 DNA sequencer. PCR products were analysed by the GENESCANTM 3.1 (PE/ABI) software and genotypic data was generated using GENOTYPERTM 2.1 (PE/ABI) software.

Genetic polymorphism at each locus was estimated with GENETIX (Belkhir Bio-soft, 2000). Tests for Hardy-Weinberg equilibrium (HWE) on each locus for all charr and over all loci as well as tests for genotypic disequilibrium were done in GENEPop ver. 3.2a (Raymond and Rousset, 1995).

Results

Relative density of fish

For total CPUE, both fish species in Leynavatn combined, the rank of lakes, from low to high was: Toftavatn, Eystara

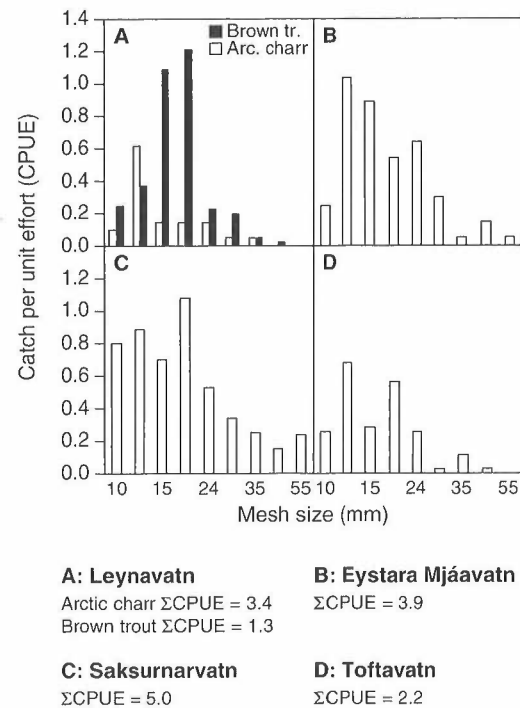


Figure 2. Catch per unit effort (CPUE, no. fish 100 m⁻² net h⁻¹) of Arctic charr (black columns) and Brown trout (white columns) for different mesh sizes (mm knot to knot) in the four Faroese lakes studied.

Mjáavatn, Leynavatn and Saksunarvatn (Fig. 2). Considering Brown trout only, CPUE in Leynavatn was significantly lower than in Saksunarvatn (Mann-Whitney test, $U = 6.5$, $df. = 1$, $P = 0.003$) and Eystara Mjáavatn ($U = 17.5$, $df. = 1$, $P = 0.040$), but not compared with Toftavatn ($U = 30.0$, $df. = 1$, $P = 0.351$). In Leynavatn, CPUE of Arctic charr was higher than for Brown trout in most mesh sizes (Fig. 2), especially in the 15.0 and 19.5 mm gillnets. The ratio of Arctic charr to Brown trout in Leynavatn was 2.7 (138:51) for all mesh sizes combined.

Life history traits

For all populations studied, growth rates were rather slow, fish were small, and maximum age of fish was low (Fig. 3). For Arctic charr in Leynavatn, the oldest fish was only 8⁺ yr and the growth rate, judged from length/age plots, decreased already from age 3⁺ and onwards, with a trend towards an asymptotic length of ca. 21 cm. The sex ratio was close to unity, 44 % males and 56 % females (G -test, $G = 0.440$, $df. = 1$, $P > 0.05$), where 32 % of males and 29 % of females were sexually mature (maturity stage 4, gonads fully developed in body cavity, egg diameter > 4 mm). For males, first age of sexual maturity was 4⁺ yr and this age class accounted for 57 % of all sexually mature males. For females, first age of sexual maturity was 5⁺ yr and this age class accounted for 38 % of sexually mature females.

As regards Brown trout in Leynavatn, length/age plots indicate an asymptotic length trend towards only ca. 25 cm, a little larger than for Arctic charr. Clearly, some individuals have a different growth pattern and the largest as well as the oldest fish, an 8⁺ yr old female, was 45.5 cm (1,080 g). The second largest fish, also an 8⁺ yr old female, was 29.9 cm (263 g). There were more males than females, but the sex ratio did not deviate significantly from unity, 59 % males and 41 % females ($G = 0.634$, $df. = 1$, $P > 0.05$). However, only 4 % of males (one fish, age 7⁺ yr) and 6 % of females (one female, age 8⁺ yr) were sexually mature.

In Eystara Mjáavatn, there is no apparent asymptote in length of Brown trout, but the

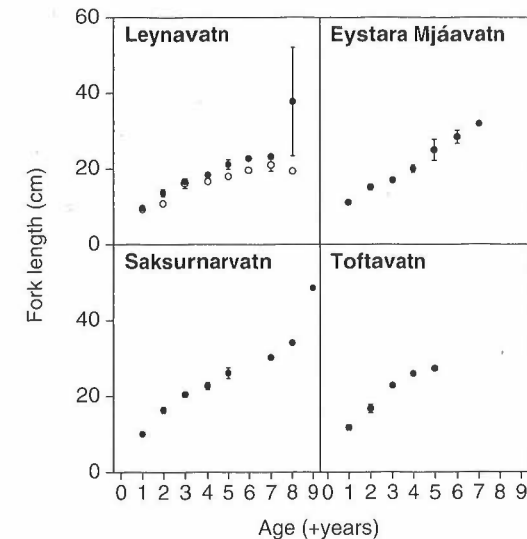


Figure 3. Age-specific length of Arctic charr (open circles) and Brown trout (black dots) in the four Faroese lakes studied. Values are means with standard error (bars).

oldest fish was only 7⁺ yr (female) and 34.7 cm (361 g). As in Leynavatn, males were more numerous than females, but the sex ratio, 60 % males and 40 % females, was not significantly different from unity ($G = 0.810$, $df. = 1$, $P > 0.05$). Contrary to Leynavatn, a large proportion of fish were sexually mature, i.e. 42 % of males and 25 % of females. For males, the first age of sexual maturity was 3⁺ yr and this age class accounted for 40 % of all sexually mature males. For females, the first age of sexual maturity was 5⁺ yr and this age class accounted for 25 % of sexually mature females.

For Brown trout in Toftavatn and Saksunarvatn, fork lengths of the age classes 3⁺ and 4⁺ were significantly longer than in

either Leynavatn or Eystara Mjáavatn (ANOVA, Tukey $P \leq 0.050$). In Toftavatn, the oldest fish was only 5⁺ yr (female, 27.3 cm, 202 g) and the largest fish (4⁺ yr female) was only 29.6 cm (283 g). The oldest fish in the study was caught in Saksunarvatn, a 9⁺ yr male (48.5 cm, 1,114 g). In Toftavatn, the sex ratio was near unity, 48 % males and 52 % females, whereas in Saksunarvatn, the sex ratio was skewed towards males, with 62 % males and 38 % females, but not significantly different from unity ($G = 1.784$, $df. 01$, $P > 0.05$). In Toftavatn, 16 % of males and 5 % of females were sexually mature, and in Saksunarvatn 37 % of males and 5 % of females were sexually mature. For males in Toftavatn, first age of sexual maturity was 3⁺ yr and this age class accounted for 33 % of all sexually mature males. For females in Toftavatn, only one female, 4⁺ yr old, was sexually mature. For males in Saksunarvatn, first age of sexual maturity was 3⁺ yr and this age class accounted for 38 % of all sexually mature males. As in Toftavatn, only one female, 5⁺ yr old, was sexually mature in Saksunarvatn.

The condition factor of Brown trout varied considerably among the four lakes, and the rank of lakes, from low to high was: Leynavatn, Toftavatn, Eystara Mjáavatn, and Saksunarvatn (Fig. 4). For Leynavatn, the condition of Brown trout was significantly lower than in Saksunarvatn ($t = -8.940$, $df. = 272$, $P < 0.001$) and Eystara Mjáavatn ($t = -3.315$, $df. = 127$, $P = 0.001$), but very similar to that in Toftavatn ($t = -1.060$, $df. = 88$, $P = 0.292$). As for Toftavatn, the condition factor was signi-

Table 4. Comparisons of residuals from a regression of log(MENC) on log(fork- length) among four Brown trout populations. Matrix of pairwise mean differences. $F = 13.2$, $P < 0.001$, using model MSE of 0.004 with 141 df. Bold values denote a significant difference ($P < 0.05$).

	L	M	S	T
Leynavatn (L)	0.000			
E. Mjáavatn (M)	-0.080	0.000		
Saksunarv. (S)	-0.070	0.010	0.000	
Toftavatn (T)	-0.060	0.020	0.010	0.000

ificantly lower than in Eystara Mjáavatn ($t = -2.594$, $df. = 117$, $P = 0.011$) and Saksunarvatn ($t = -8.388$, $df. = 262$, $P < 0.001$), the latter in turn being significantly higher than in Mjáavatn ($t = 3.710$, $df. = 301$, $P < 0.001$). For Arctic charr and Brown trout in Leynavatn, the condition factor did not differ significantly between the fish species (t-test, $t = -0.413$, $df. = 186$, $P = 0.680$), but within both species, condition decreased with age, the association being, however, significant only for Brown trout (Pearson's $R = -0.537$, $df. = 38$, $P < 0.01$). As in Leynavatn, the condition of Brown trout decreased with age in Saksunarvatn ($P = -0.429$, $df. = 50$, $P < 0.01$), Eystara

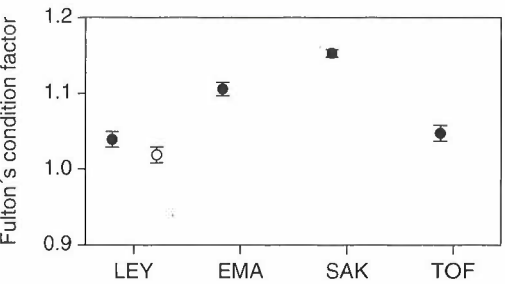


Figure 4. Fulton's condition factor of Arctic charr (open circle) and Brown trout (solid dots) in the four Faroese lakes studied. Values are means and standard errors (bars).

Mjáavatn ($R = -0.431$, $df. = 35$, $P < 0.01$) and Toftavatn ($R = -0.559$, $df. = 38$, $P < 0.01$).

Morphology

For Brown trout, PC1 accounted for 89 % of the total variation in morphological parameters (Table 3), as was expected because of the extensive variation in size. PC2 accounted for 2.43 % of the total variation. The PC2 of Brown trout in Leynavatn differed significantly from that of Brown trout in the other three lakes, indicating significant shape differences (Fig. 5). Character loadings on PC2 show, on the one hand, contrasts between MENC (mid-eye to nose curve), NCMEL (nose curve to mid-eye line) and EPFCF (end of peduncle to fork of caudal fin), and between SNC (snout to nose curve) and VPEP (ventral peduncle to end of peduncle) on the other. Pooled regression analysis of PC2 scores on PC1 showed that MENC and NCMEL were longer in trout from Leynavatn than in trout from the other lakes (Table 4 and 5). Thus the trout in Leynavatn had a more curved snout than trout in the other lakes. EPFCF was shorter in trout from Toftavatn than in the other lakes (Table 6), indicating a more forked caudal fin.

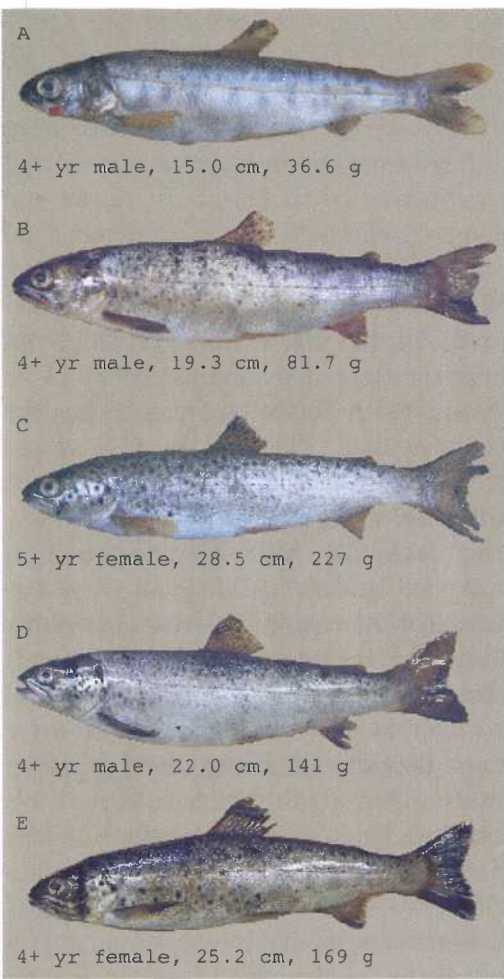


Figure 5. Arctic charr from Leynavatn (A) and Brown trout from Leynavatn (B), Eystara Mjáavatn (C), Saksunarvatn (D) and Toftavatn (E).

Morphological analysis of Arctic charr in Leynavatn indicated a monomorphic population.

Genetics

For Arctic charr in Leynavatn, the mean observed and expected heterozygosity over

all loci was 0.1832 and 0.2442, and the mean number of alleles over all loci was 4.4. Microsatellite loci had few numbers of alleles, ranging from 2 to 6, and the observed heterozygosity was generally low (Table 7). All loci, except *OneIIASC*, had one allele in high frequency and close to fixation. A significant genotypic disequilibrium ($P \leq 0.007$) was observed between three loci, *Ssa85DU* and *Ssa456NCVM*, *Ssa85DU* and *OneIIASC*, and *Ssa456NCVM* and *OneIIASC*. Tests for HWE for each locus showed that only two loci were in HWE while the other three showed significant heterozygote deficiency. Also, all loci considered together were not in HWE (Table 7).

Food

Stomach fullness was similar among the Brown trout populations in Leynavatn and Eystara Mjáavatn, but in Saksunarvatn significantly more fish (G-test, $G = 95.066$, $df. = 3$, $P < 0.001$) had full stomachs than in the other three lakes. In Toftavatn, significantly more Brown trout ($G = 23.328$, $df. = 3$, $P < 0.001$) had stomachs with traces of food compared with Brown trout in the other three lakes. In Leynavatn, significantly more Arctic charr than Brown trout ($G = 9.772$, $df. = 1$, $P < 0.005$) contained traces of food in their stomachs.

In all lakes except Toftavatn, chironomids (larvae and pupae) were the most important food items for Brown trout, with a contribution of 50-60 % in terms of both number and ash-free dry weight (Fig. 6). Also, for Arctic charr, chironomids were very important food items, especially in

terms of weight, with a contribution of 62 %. For both Arctic charr and Brown trout, the Chironominae and Tanypodinae (primarily larvae) subfamilies were much more prominent in the diet than Orthocladiinae, both in terms of number and weight. In Leynavatn and Saksunarvatn, the numeric ratio of Chironominae to Tanypodinae was ca. 1:4, 10:1 in Eystara Mjáavatn and 1:1 in Toftavatn.

In the diet of both fish species, cladocerans were second to chironomids both in terms of numerical and weight contribution, with a share ranging between 17 % and 53 % by number and 10 % and 24 % by weight (Fig. 6). There was a considerable difference in cladoceran composition, both between the two fish species in Leynavatn, and between Brown trout among lakes. Thus, in Leynavatn, Arctic charr fed primarily on the planktonic *Daphnia* sp., whereas Brown trout fed mostly on the benthic *Eurycercus lamellatus*. In Toftavatn, Brown trout fed almost exclusively on *Daphnia* sp., but in Eystara Mjáavatn and Saksunarvatn, *E. lamellatus* was the principal cladoceran in the diet. Other cladocerans eaten by both fish species, but in relatively low numbers, were *Bosmina coregoni* (Leynavatn, Eystara Mjáavatn

and Toftavatn), and in Leynavatn Arctic charr also preyed upon *Holopedium gibberum* and the cyclopoid *Cyclops* spp.

In Toftavatn, the diet of Brown trout differed from that in other lakes by a large contribution of trichopterans (pupae and imagos), with 16 % in terms of number and 52 % in terms of weight (Fig 6). Also, Hydracarina exceeded 5 % by number only in the diet of Brown trout in Toftavatn. Further, three-spined sticklebacks were eaten only in Toftavatn, yet consumed by only one trout.

Discussion

The fact that native Arctic charr is restricted to only one lake in the Faroe Islands is interesting. It is also noteworthy that native Brown trout, and in some cases also Atlantic salmon, but not Arctic charr, are present in several streams accessible from the sea, the outlet river of Saksunarvatn being an example (Larsen *et al.*, unpubl). This raises the question of why Arctic charr, whether resident or anadromous, is so rare in the Faroe Islands?

Water temperature is probably an important factor, as has been suggested also for the absence of several groups of macroinvertebrates in Faroese lakes (Malmquist *et*

Table 5. Comparisons of residuals from a regression of log(NCMEL) on log(fork- length) among four Brown trout populations. Matrix of pairwise mean differences. F = 13.2, P < 0.001, using model MSE of 0.005 with 141 df. Bold values denote a significant difference (P < 0.05).

	L	M	S	T
Leynavatn (L)	0.000			
E. Mjáavatn (M)	-0.087	0.000		
Saksunarv. (S)	-0.083	0.004	0.000	
Toftavatn (T)	-0.081	0.006	0.002	0.000

Table 6. Comparisons of residuals from a regression of log(EPFCF) on log(fork- length) among four Brown trout populations. Matrix of pairwise mean differences. F = 8.5, P < 0.001 R² = 0.153, using model MSE of 0.004 with 141 df. Bold values denote a significant difference (P < 0.05).

	L	M	S	T
Leynavatn (L)		0.000		
E. Mjáavatn (M)		0.001	0.000	
Saksunarv. (S)	- 0.019	- 0.019	0.000	
Toftavatn (T)	- 0.057	- 0.057	- 0.038	0.000

al., 2002). For Arctic charr, a temperature of 10-12 °C has often been reported to be the upper thermal limit for the growth optimum of adult fish (e.g., Jobling, 1983). Above 14 °C, the allocation of energy to growth becomes less efficient. Further, at high temperatures, fish may suffer from induced susceptibility to diseases (e.g., Mitchum *et al.*, 1979; Alanärrä, 1990). Additionally, the optimum temperature regime for egg incubation and rearing of Arctic charr alevins is generally lower than for adult fish (Jobling, 1983). For Brown trout, the upper thermal limit for growth optimum of adult fish and egg incubation is considerably higher than for Arctic charr (Elliott, 1994). In the present study, the early August mean surface temperature in both the pelagic and littoral zone of the four Faroese lakes ranged between 14.0-16.5 °C (Table 1), matching and overriding the upper limit for the growth optimum of adult Arctic charr. Further, the temperature in the Faroese lakes is ca. 5 °C warmer than the August temperatures in the littoral zone of Icelandic lakes (Malmquist *et al.*, 2000), where Arctic charr is widespread and more common than Brown trout in both lakes and rivers. Also, contrary to Icelandic lakes, most Faroese lakes rarely freeze in

winter (Lützen, 1978; Dorete Bloch, pers. comm.), as is to be expected because of the high winter air temperature in the Faroe Islands (Cappelen and Laursen, 1998), with a mean of 4.2 °C in the coldest month, January, which is ca. 10 °C warmer than for the coldest month in Iceland. Further, because of the prevailing, relatively strong winds in the Faroe Islands, the lakes probably rarely stratify (see also Lützen, 1978; Jensen *et al.*, 2002), implying that the temperature is uniform throughout the water mass of the lakes. Leynavatn, the coldest and deepest of the four lakes studied, is apparently cold enough to sustain Arctic charr.

Until 1972, the outlet river of Leynavatn was impassable to fish due to the existence of several waterfalls (Larsen *et al.*, unpubl). Arctic charr, along with Brown trout, probably immigrated into Leynavatn in the early Holocene, or soon after the retreat of the ice-cap, and later became isolated because of isostatic uplift of the land mass. In 1972, the building of fish ladders in the outlet and inlet river was completed, thereby connecting Leynavatn with Eystara and Vestara Mjáavatn and enabling salmonids to ascend from the sea to the lakes (Larsen *et al.*, unpubl). So far, Atlantic salmon and

Table 7. Allele frequencies, observed (H_{obs}) and expected heterozygosity (H_{exp}) and Hardy-Weinberg equilibrium test (HWE) for five loci in Arctic charr from Leynavatn. HWE indicates Hardy-Weinberg equilibrium, + indicates significant ($P < 0.02$) heterozygote deficiency. N is the number of individuals genotyped.

Loci										
Ssa85DU		Ssa456NCVM		µ85INRA		Ssa20.19UCG		One11ASC		Multi-loci
Allele	Freq	Allele	Freq	Allele	Freq	Allele	Freq	Allele	Freq	
180	0.0208	224	0.0106	174	0.8488	104	0.0256	136	0.0729	
184	0.9167	226	0.0213	178	0.1512	108	0.8718	138	0.0521	
186	0.0417	228	0.0106			112	0.0897	140	0.7813	
188	0.0208	230	0.8936			114	0.0128	142	0.0625	
		232	0.0213					144	0.0313	
		234	0.0213							
		236	0.0213							
Hobs	0.0417		0.0851		0.2093		0.2051		0.3750	
Hexp	0.1517		0.1994		0.2566		0.2311		0.3767	
HWE	+	+		HWE		+		HWE		+
N	48	47		N	43	39		N	48	

Brown trout, but not Arctic charr, have been caught in the outlet river and reported to migrate from the sea into Leynavatn (Larsen *et al.*, unpubl). Consequently, the Arctic charr population in Leynavatn is considered resident (Larsen *et al.*, unpubl). That the Arctic charr in the lake is not anadromous is supported in the present study by the lack of bimodality in age-specific length distribution. The observation of three loci in genotypic disequilibrium and the heterozygote deficiency at three of five loci indicate that the Arctic charr population of Leynavatn is isolated, extensively inbred and, most likely, founded by very few individuals (e.g., Hill and Robertson, 1968; See also Gydemo, 1983). Besides a unimodal length frequency distribution, the Arctic charr in Leynavatn is characterized by slow growth, short asymptotic length (ca. 21. cm) and a short lifespan (oldest fish 8+ yr). These results agree with results of previous studies on

Arctic charr conducted in the lake (Larsen *et al.*, unpubl; Gydemo, 1983;). The present study also shows that the Arctic charr in the lake is monomorphic and exploits food resources in both the pelagic and the littoral benthic habitat. Further, there is no indication of dietary differences between age classes. The observed patterns in foraging behaviour of Arctic charr based on stomach analyses are supported by analyses of stable isotopes in the food web of the lake (Jeppesen *et al.*, 2002b).

Morphologically, and in terms of growth rate and diet, the Arctic charr in Leynavatn bears close resemblance to the situation in lakes where resident Arctic charr lives in sympatry with other fish species, usually Brown trout, which to a large degree, as observed in the present study, exploits the littoral habitat and feeds on surface insects and zoobenthos (e.g., Nilsson, 1963 Rombough *et al.*, 1978; Hindar and Jonsson, 1982; Walker *et al.*, 1988; Hesthagen *et al.*,

1997; Cavalli *et al.*, 1998). By contrast, where Arctic charr is the sole salmonid species, it feeds on a variety of food items from both the littoral and the pelagial. Also, a large proportion of the population may become older than 10-15+ yr and larger than 30-40 cm (e.g., Fraser and Power, 1980; Sparholt, 1985; Jonsson *et al.*, 1988; Venne and Magnan, 1989; Riget *et al.*, 2000). In this context it is important to emphasize that Arctic charr from Leynavatn transplanted to Heygardalsvatn and reared there in captivity on unrestricted food rations exhibits a fast growth rate and reaches a very large size, i.e., 50 cm in mean length and 3.2 kg in mean wet weight (Larsen *et al.*, unpubl.). This suggests that somatic growth of Arctic charr in Leynavatn is suppressed, possibly due to interspecific competition with Brown trout. Since the Brown trout is probably more territorial and aggressive (Nilsson, 1963; Noakes, 1980), it may push Arctic charr into the pelagic zone where the small size of food items can severely limit sustainable body size of the fish (see e.g., Malmquist *et al.*, 1992; Snorrason *et al.*, 1994a). However, as indicated by the diet of Arctic charr in the present study and by Jeppesen *et al.* (2002b), as well as by other studies of the two species in sympatry, the habitat and diet segregation may be interactive (Nilsson, 1963; Langeland *et al.*, 1991), i.e. diverge in lean times and converge in lax times.

A short lifespan and a slow and suppressed growth of Arctic charr, as well as Brown trout, in Leynavatn, may also result from other factors, alone or along with

interspecific competition. For example, the fish may be short of food because of poor condition of food resources in the lake. This may indeed be the case, as judged from the fact that the abundance of benthic macroinvertebrates was about 60% lower in Leynavatn than in the other three lakes studied (Malmquist *et al.*, 2002). Also, it is worth noticing that the life history and ecology of Brown trout may just as well, yet probably to a lesser degree, be negatively affected by competition from Arctic charr. Such an interaction is, along with possible shortage of fish food, indicated by the fact that for all lakes studied, the density of Brown trout was by far lowest in Leynavatn, and, indeed, much lower than that of Arctic charr. Furthermore, the growth rate and condition of Brown trout in Leynavatn were among the poorest observed among the four lakes, particularly compared to Saksunarvatn and Eystara Mjáavatn. Other studies have shown that Brown trout living in sympatry with Arctic charr may exhibit slow growth and small size compared to allopatric situations (e.g., Nilsson, 1963; Hesthagen *et al.*, 1997).

In general, the life history traits of Brown trout in the four lakes studied agree with results from previous studies of Faroese lakes (Brabrand, 1989, Brattaberg, 1995) and elsewhere, for instance Norway (Jonsson, 1989; Hesthagen *et al.*, 1997), Great Britain (e.g., Elliott, 1994) and Iceland (Jónsdóttir *et al.*, 1998 Björnsson, 2001; Steingrímsson and Gíslason, 2002;). According to these sources, life span and asymptotic size of lake resident Brown trout rarely exceed 10+ years and 45 cm,

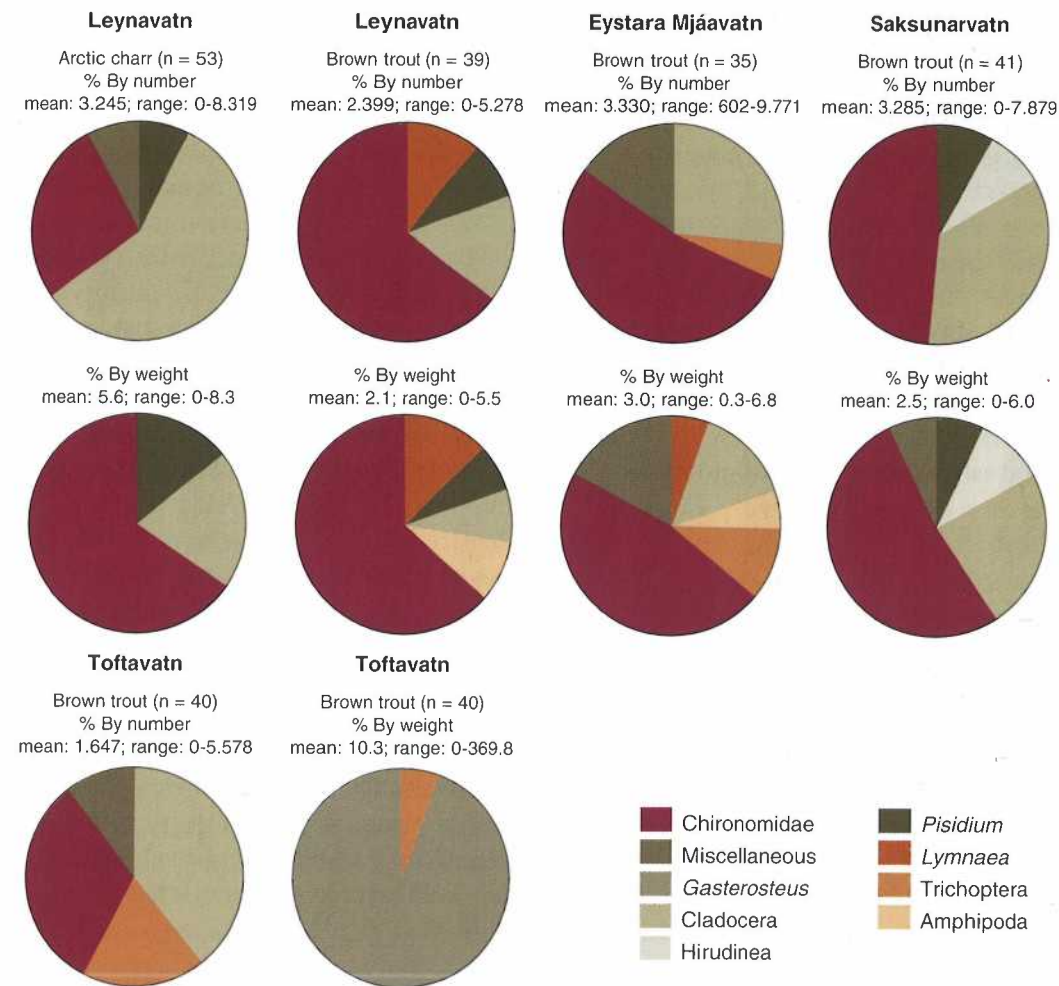


Figure 6. Stomach content of Arctic charr and Brown trout in the four Faroese lakes studied. The pies show percentage contribution of food items in terms of mean number and mean ash-free dry weight (AFDW, mg), respectively. Chironomidae and Trichoptera include larvae, pupae and adults. Miscellaneous denotes various food items with less than 5 % share.

respectively. For some lakes it is known that Brown trout change their food habits from benthivory to piscivory, whereupon they exhibit a markedly increased growth rate, attain a large size and even live longer

(e.g., Jonsson *et al.*, 1999), as has also been observed for Arctic charr (e.g., Malmquist *et al.*, 1992). Arctic charr in the present material did not consume fish and the same applied to Brown trout, except for one fish

in Toftavatn that had eaten three-spined sticklebacks. Also, Toftavatn was the only lake in the present study where sticklebacks were caught (four sticklebacks in one trap out of four). Thus, the general notion for the salmonid populations studied is that piscivory is rare, which is supported by results of stable isotope analyses in the lakes (Jeppesen *et al.*, 2002b). Furthermore, three-spined sticklebacks are apparently rare in Toftavatn and probably absent from the other three lakes. The rarity of three-spined sticklebacks in the lakes (see also Brabrand, 1989; Brattaberg, 1995) may possibly be due to predation pressure exerted by the salmonid fish.

Compared to 24 populations of Arctic charr from Europe, heterozygosity of the Arctic charr in Leynavatn is low for all loci examined, except locus *OneIIASC* (Gíslason, unpubl. data). In Leynavatn, locus *Ssa85DU* has less than 10% of mean heterozygosity observed in the European populations and the observed heterozygosity of only 0.0851 for locus *Ssa456NCVM* in Leynavatn is also very low compared to 0.589 in the European populations. For the loci *85INRA* and *Ssa20.19UCG*, the observed heterozygosity in Leynavatn is higher, yet only ca. 41 % and 31 %, respectively, of mean observed heterozygosity in the European Arctic charr.

Only locus *OneIIASC* has a higher observed heterozygosity in Leynavatn than in the European populations. Partly, this stems from the fact that Arctic charr in Leynavatn has five alleles at this locus, two (142, 144) of which are not found elsewhere (private alleles), compared with only

four alleles in the European charr populations, of which many have one allele fixed at this locus (Gíslason, unpubl. data). A comparable situation is found in Loch Mealt on the Isle of Skye, a lake with an impassable waterfall in the outlet river. In this lake, the charr generally had low variation and heterozygosity at all loci, except for *OneIIASC*, where four alleles were observed, of which two were not found elsewhere. The reason for the increased variation at this locus in the populations of Leynavatn and Loch Mealt is not clear.

Lack of morphological and ecological polymorphism in the Arctic charr of Leynavatn fits well with evolutionary and ecological scenarios proposed for the origin and maintenance of two or more sympatric Arctic charr morphs (for overviews see: Skúlason *et al.*, 1992; 1999; Gíslason *et al.*, 1999; Jonsson and Jonsson, 2001). In essence, it is anticipated that morph diversification takes place particularly in large and deep lakes, featuring two or more different and spatially distinct habitats with accompanying differences in food bases, and where interspecific competition is absent or very weak. Lake Thingvallavatn, Iceland, featuring four very different Arctic charr morphs, is a clear example of a lake where such criteria are met (Sandlund *et al.*, 1987; Jonsson *et al.*, 1988; Malmquist *et al.*, 1992; Snorrason *et al.*, 1994b; Skúlason *et al.*, 1999;). By contrast, Leynavatn is quite small and, despite being relatively deep, the concave basin form is such that the size of the littoral benthic habitat is very small relative to the pelagic habitat. Furthermore, Brown

trout, and by now Atlantic salmon, co-exists with Arctic charr in the lake (Larsen *et al.*, unpubl).

Compared to Arctic charr, the trophic morphology of Brown trout appears much less variable and studies hereof are relatively limited (Hanken and Hall, 1993). A notable exception are the three sympatric Brown trout morphs in lake Lough Melvin, Ireland (Ferguson and Mason, 1981; Ferguson, 1986; Elliott, 1994). The present study demonstrates small but significant differences in morphology among the populations studied. The fact that trout in Leynavatn has a more curved snout than trout in the other lakes may constitute a character displacement resulting from interspecific interactions with Arctic charr, forcing the trout towards a more strictly benthic life style. The forked caudal fin of the trout in Toftavatn may also relate to their feeding behaviour, being more inclined towards pelagic and epibenthic animals than in the other lakes (see also Jeppesen *et al.*, 2002b). The above differences in the diet of Brown trout are congruent with expectations based on different functional trophic morphology of fishes and, hence, differences in their feeding behaviour and efficiency (see e.g., Alexander, 1967; Liem and Kaufmann, 1984; Thompson, 1994).

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Food Web Interactions in Five Faroese Lakes tracked by Stable Isotopes

Føðsluskipanin í fimm føroyskum vøtnum
kannað við støðugum isotopum

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Úrtak

Fyri at lýsa etimynstrið og vistskipanina hjá fiski í fimm føroyskum vøtnum vórðu kanningar av støðugum kolevnis- og køvievnis isotopum (stable isotope kanningar) gjørdar. Sum heild vóru nærur ongi kolevni (lægr $\delta^{13}\text{C}$) í ryggleysum botndjórum í profundala økinum og djóraeti í pelagiska økinum í mun til ryggleysu botndjórini í strandaøkinum, serliga í teimum djúpu vøtnunum. Talið av $\delta^{13}\text{C}$ í vøddavevnaðinum á fiski var ymiskur í teimum ymisku vøtnunum. Í Leynavatni, har bæði sjósíl (*Salmo trutta*) og bleikja (*Salvelinus alpinus*) liva, var meir $\delta^{13}\text{C}$ í sjósíli av øllum støddum enn í bleikju. Hetta bendir á, at tey bæði fiskasløgini hava bytt føðigrundarlagið sínamlum. Harafturimóti vísu $\delta^{13}\text{C}$ kanningarar í vøtnum, har sjósíl og kombikk (*Gasterosteus aculeatus*) liva saman, at sjósílið serliga leitar sær føði úti á vatninum og í profundala økinum. Í vøtnum, har bara bleikjur vóru, sást onki til, at tær valdu sær serlig øki at finna sær føðina á. Kanningarar vísu eisini, at sjósíl < 30-40 cm, fóru djúpari at leita eftir føði, tess størri sílini vóru. Harafturimóti leitaðu fiskietandi sjósíl > 40 cm meira ímóti vatnbakkaðkjunum. Kombikk vóru bara fingin í Toftavatni og Sørvágsvatni, og bendu kanningarar á, at hetta fiskaslagið sum heild var stöðufast. Í $\delta^{15}\text{N}$ kanningunum var ongin greiður munur funnin á ryggleysum botndjórum í profundala økinum og strandaøkinum. $\delta^{15}\text{N}$ í ryggleysum ránsdjórum (súgvarar og vatnmottur) var 1,1-2,6 ‰ hægri enn í plantu- og detritus etandi ryggleysum djórum (í miðal 0,5 stig hægri í vistskipanini, tá $\delta^{15}\text{N}$ verður hildið at vaksa 3,4 ‰ frá einum stigi í vistskipanini til tað næsta).

Í fiski var $\delta^{15}\text{N}$ 1-3 stig hægri í vistskipanin enn í botndjórunum á fyrsta stigi í føðiketuni. $\delta^{15}\text{N}$ stigið var hægst í sjósíli > 40 cm, ið vísir, at hesi eta fisk. Nakrir minni fiskar, eisini kombikk, hava eitt fitt innihald av $\delta^{15}\text{N}$, ið vísir, at tey eta fisk ella ryggleys ránsdjór. Tó ótu sjósíl og bleikja < 40 cm, sambært innihaldið av $\delta^{15}\text{N}$, í høvuðsheitum ryggleys djór. Henda niðurstøðan samsvaraði við magakanningar av fiskinum.

Abstract

Stable isotope analyses of carbon and nitrogen were used to identify foraging habitats of fish and food web interactions in five Faroese lakes. Benthic invertebrates in the profundal and zooplankton in the pelagic zone were overall depleted in carbon (lower $\delta^{13}\text{C}$) relative to benthic invertebrates in the near-shore littoral zone of particularly deeper lakes. Levels of $\delta^{13}\text{C}$ in fish muscle tissue differed among the lakes. In Leynavatn, where brown trout (*Salmo trutta*) occurred in sympatry with Arctic charr (*Salvelinus alpinus*), the $\delta^{13}\text{C}$ of trout of all size classes was higher than of charr, suggesting niche segregation among the two species. By contrast, in lakes with trout and sticklebacks (*Gasterosteus aculeatus*), the $\delta^{13}\text{C}$ data suggested that trout forage particularly in the open water or profundal zone, while no clear habitat preference was found in the charr-only lake. We found a tendency to, and for some lakes a significant, size-dependent variation, in the $\delta^{13}\text{C}$ values of brown trout, indicating that trout < 30-40 cm forage increasingly at deeper sites with increasing size. Yet, piscivorous trout

Table 1. Some lake characteristics. For further details see Landkildehus *et al.* (2002) and Jensen *et al.* (2002).

	Lake area (km ²)	Max. depth (m)	Mean depth (m)	Total phosphorus (µg P l ⁻¹)
Eystara Mjáavatn	0.03	7	3.0	16
Leynavatn	0.18	33	13.7	3
Sørvágsvatn	3.56	59	27.5	5
Toftavatn	0.52	22	5.8	11
Saksunarvatn	0.08	17	6.5	6

> 40 cm had a more littoral signal. The $\delta^{13}\text{C}$ of the few three-spined sticklebacks caught in only Toftavatn and Sørvágsvatn indicated that this species is mainly stationary. We found no clear difference in the $\delta^{15}\text{N}$ of benthic invertebrates between the profundal and littoral zones. The $\delta^{15}\text{N}$ of predatory invertebrates (leeches and water mites) was 1.1-2.6 ‰ higher than for herbivorous-detritivorous invertebrates (on average 0.5 trophic level higher, as $\delta^{15}\text{N}$ is assumed to increase 3.4 ‰ from one trophic level to the next). The $\delta^{15}\text{N}$ of fish was 1-3 trophic levels higher than that of benthic primary consumers, most pronouncedly for trout > 40 cm, indicating that these large trout were obligatory piscivores. However, some of the smaller fish, including several sticklebacks, also exhibited a relatively high $\delta^{15}\text{N}$, suggesting that they were piscivorous or fed on predatory invertebrates. Yet, the majority of trout and charr < 40 cm were confined to invertebrate prey as inferred from $\delta^{15}\text{N}$ data and a parallel conducted study of gut contents.

Introduction

Carbon and nitrogen stable isotope ratios are often used to identify food web interactions and energy flow in lakes. Nitrogen isotope ratios become enriched up through the food web, permitting estimation of consumer trophic positions (Minagawa and Wada, 1984; Fry, 1988; Cabana and Rasmussen, 1996). Carbon ratios can be used to identify carbon sources as they often differ markedly among primary producers and habitats, while only minor fractiona-

tions occur from one trophic level to another (Vander Zanden and Rasmussen, 2001). In addition, primary consumers in the pelagic zone often have a markedly different signal from those in the littoral zone, because phytoplankton discriminates against $\delta^{13}\text{C}$ more than benthic algae do, and consumers conserve these differences (Hecky and Hesslein, 1995; Vadeboncoeur *et al.* submitted). This allows identification of the preferred feeding habitat of potentially migrating organisms such as fish. Therefore, analyses of stable isotopes may be a useful supplement or an alternative to investigations of stomach, the contents of large-bodied consumers as they provide information on food intake over a prolonged time period (Maruyama *et al.*, 2001). Here, we present stable isotope data from five Faroese lakes with contrasting mean depths and fish community structures.

Materials and methods

In August 2000 we collected benthic invertebrates in the surface sediment, on stones and in macrophyte-covered areas with hand-held dip nets in the littoral zone. In the pelagic zone, we used a benthic sledge

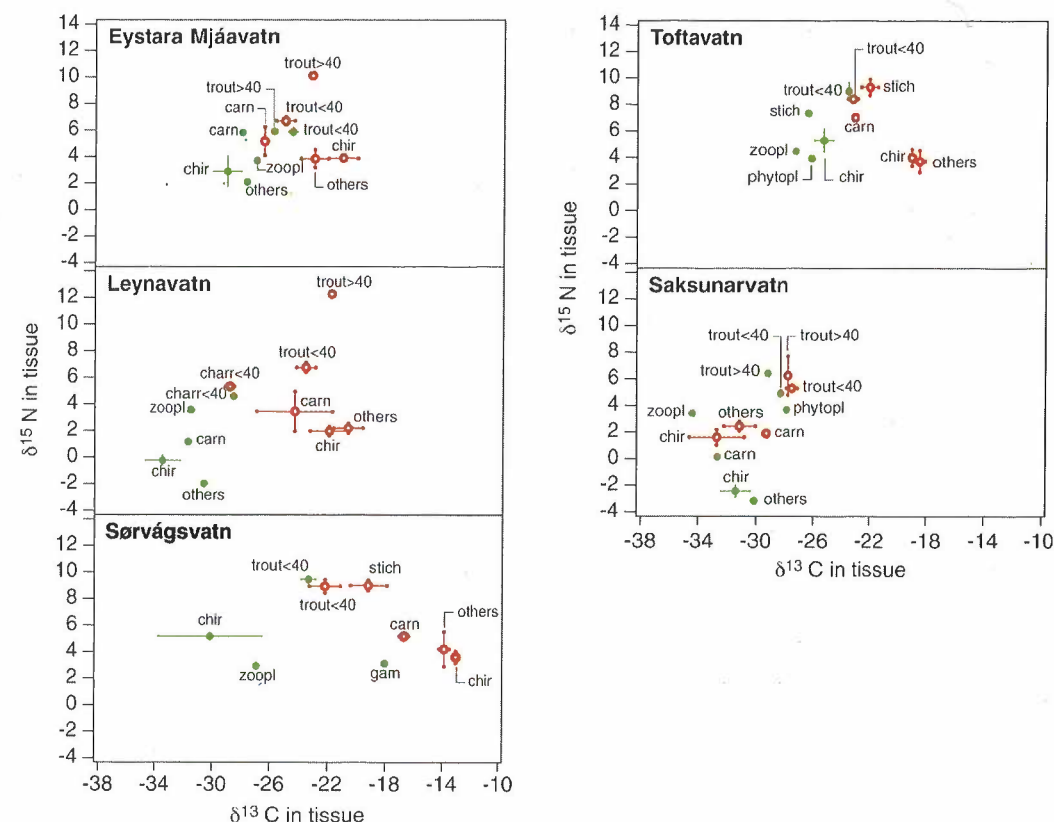


Fig. 1. Isotope fractions of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) (mean $\pm$ SD) in phytoplankton, zooplankton, various benthic invertebrates and fish muscle sampled in the littoral zone and offshore in the five study lakes. Legends to data points: Prefixes; l= littoral (circle); p= profundal (dot); Legends; phytopl = phytoplankton, chir = chironomids, carn = carnivorous macroinvertebrates, gam = *Gammarus* sp., others = other macroinvertebrates, zoopl = zooplankton, >, < 40 = fish fork length >, < 40 cm, charr = Arctic charr, trout = trout, stich = three-spined sticklebacks.

to collect benthic invertebrates and a 140 μm net to collect zooplankton and phytoplankton. Collections included small suspended particles by hauling with a 10 μm net (pre-filtered through a 50 μm net to remove zooplankton). Fish were caught in multi-mesh sized gill nets (14 different mesh sizes from 6.25–75 mm) placed overnight in the littoral zone parallel to the

shore at 1.5 m depth and at the bottom in the pelagic zone (Jeppesen *et al.*, 2001). In some lakes pelagic nets were also set at half the depth at the sampling station. The number of nets ranged between 4 and 9 per lake depending on size and depth. All samples were stored frozen, dried at 75 $^{\circ}\text{C}$ for 48 h, and ground into a fine powder using mortar and pestle. Dry sample ma-

terial was packed into 4 x 6 mm tin capsules for subsequent isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous flow isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility, USA. Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material; $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ = $([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. A more positive (less negative for carbon) isotopic value is said to be isotopically enriched, meaning that the sample contains proportionally more of the heavy stable isotope (${}^{13}\text{C}$ or ${}^{15}\text{N}$). The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (both standards have a value arbitrarily set at 0).

By using primary consumers as the baseline trophic level, consumer trophic position can be calculated from the formula: trophic position-consumer = $((\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4 + 2)$ (Vander Zanden *et al.*, 1997).

Unless otherwise indicated, we employed a non-parametric statistical test (NPARWAY, SAS, 1989) with a 5 % significance level.

Results

Morphometric and chemical data for the five lakes are outlined in Table 1 and described in detail in Landkildehus *et al.* (2002) and Jensen *et al.* (2002). All study lakes are generally nutrient-poor, but varied considerably as to lake area and depth.

Except for Saksunarvatn, $\delta^{13}\text{C}$ of benthic invertebrates tended to differ among species caught in the littoral and profundal zones, not least in the two deepest lakes, Sörvágsvatn and Leynavatn (Fig. 1). As expected from previous studies (e.g. Hecky and Hesslein, 1995), the littoral zone invertebrates of these lakes were depleted in carbon relative to the profundal zone. Because of a low number of invertebrates analyzed, a statistical test could only be performed for chironomids (all lakes – littoral versus profundal) and for chironomids versus other invertebrates (except predators) in the littoral zone in three lakes.

In all lakes but Saksunarvatn, the $\delta^{13}\text{C}$ of chironomids was significantly ($p < 0.05$) lower in the profundal zone, while $\delta^{15}\text{N}$ was only significantly different for Leynavatn. No significant differences were found in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between chironomids and the other benthic invertebrates in the littoral samples from the three lakes (Eystara Mjáavatn, Saksunarvatn and Leynavatn). Pooling data from all benthic invertebrates per habitat, apart from the predators, yielded the same results as when testing littoral vs. pelagic profundal data for chironomids. The $\delta^{13}\text{C}$ signal of predatory invertebrates (*Hydracarina*, *Helobdella*) from the littoral zone tended to be lower than that of their potential prey, suggesting that they were not restricted to the littoral zone. Except for Saksunarvatn, the $\delta^{15}\text{N}$ of predatory invertebrates was 1.1 to 2.6 ‰ (average 1.8 ‰ or 0.5 trophic positions) higher than for the consumers, respectively (Table 2). In Saksunarvatn, $\delta^{15}\text{N}$ was on average 0.1 ‰ lower for consumers in the

Table 2. $\delta^{15}\text{N}$ and trophic position (in parenthesis) of primary consumers (benthic + zooplankton), invertebrate predators and fish. When no significant differences were found in $\delta^{15}\text{N}$ among the two habitats (littoral zone versus pelagic/profundal zone, the data were pooled for the selected groups. In Leynavatn and Saksunarvatn, trophic position is given as a range for the two habitats. Litt = littoral zone, pel = pelagic and profundal zone.

	Eystara Mjáavatn	Leynavatn	Sørvágsvatn	Toftavatn	Saksunarvatn
<i>Invertebrates</i>					
<i>Primary consumers</i>					
litt		2.1±0.6 (2)			2.0±1.0 (2)
litt+pel	3.5±1.1 (2)		4.1±1.1 (2)	4.4±1.3 (2)	
pel		0.8±1.0 (2)			-2.6±0.7 (2)
<i>Predators</i>					
litt		3.5±2.1 (2.4)			1.9 (2)
litt+pel	5.4±1.1 (2.6)		5.2±0.2 (2.3)	7.0 (2.8)	
pel		1.2 (2.6)			0.2 (2.8)
Brown trout <40 cm	6.2±0.8 (2.8)	6.8±0.9 (3.4-3.8)	9.3±1.11 (3.5)	8.6±0.8 (3.2)	5.4±1.2 (3.0- 4.4)
Brown trout >40 cm	10.1 (3.9)	12.3 (5.0-5.3)			
Arctic charr <40 cm		5.4±0.9 (3-3.4)			
Three-spined stickleback <3 cm				7.1±0.2 (2.8)	
Three-spined stickleback >3 cm			9.3±0.9 (3.5)	10.2±0.3 (3.7)	

profundal zone and 2.8 ‰ higher in the littoral zone, respectively.

$\delta^{13}\text{C}$ of zooplankton and phytoplankton was generally on a par with the level for benthic invertebrates in the profundal zone, while $\delta^{15}\text{N}$ and the trophic position of these invertebrates revealed no clear pattern (Fig. 1). In the few lakes for which both phytoplankton and zooplankton data are available, the trophic position was largely identical (Toftavatn and Saksunarvatn).

No significant difference ($p>0.3$) was observed in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of brown trout

caught in the littoral zone and in the open water in any of the lakes (Fig. 1). In Sørvágsvatn, Toftavatn and Eystara Mjáavatn, $\delta^{13}\text{C}$ generally lay between the values of invertebrates in the littoral and profundal/pelagic zones, suggesting that the fish forage in both habitats. In Leynavatn, however, which hosts also Arctic charr, $\delta^{13}\text{C}$ of trout approximated the levels of littoral invertebrates. By contrast, $\delta^{13}\text{C}$ of charr approached the values of invertebrates in the pelagic zone (zooplankton) and the profundal benthos. In Saksun-

arvatn, however, $\delta^{13}\text{C}$ of trout was comparable to the levels found in Leynavatn and Eystara Mjáavatn, but remarkably higher than of invertebrates from both the littoral and the profundal zones in the lake (Fig. 1).

Apart from Saksunarvatn, $\delta^{15}\text{N}$ of trout muscle tissue from fish with a fork length (hereafter called size) < 40 cm was 2.8-5.2 ‰ (mean 4.2 ‰) or 1.2 trophic levels higher than the averages of benthic and zooplankton consumers, while $\delta^{15}\text{N}$ in the two large trout found in Leynavatn (61 cm) and Eystara Mjáavatn (41 cm), were 10.9 ‰ and 6.6 ‰ (or 3 and 1.9 trophic levels), respectively, higher than in the consumers, suggesting that they were piscivorous (Table 2). In Saksunarvatn, $\delta^{15}\text{N}$ of trout < 40 cm was 3.4-8 ‰ higher than in consumers in the littoral and pelagic zone, respectively.

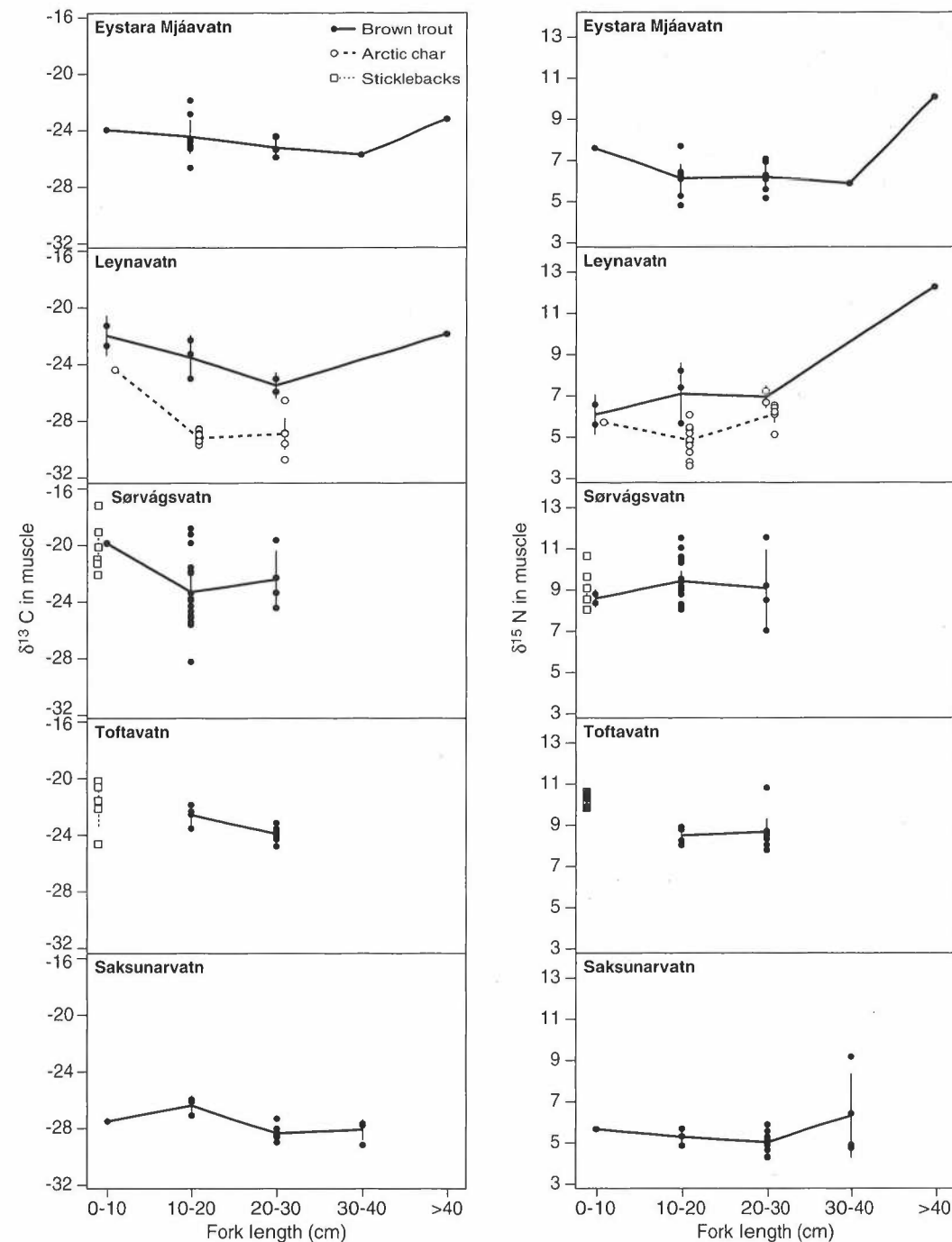
For trout < 40 cm, $\delta^{13}\text{C}$ showed a decreasing trend with increasing size (Fig. 2), the signal being, however, only significant for Leynavatn (linear regression, $\log_e$ -transformation of $\delta^{13}\text{C}+40$ ($p<0.005$, $r^2=0.6$), Toftavatn ($p<0.007$, $r^2=0.53$) and Saksunarvatn ($p<0.02$, $r^2=0.31$). The few trout > 40 cm from the littoral zone showed a $\delta^{13}\text{C}$ signal comparable to that of the smallest fish caught there (< 10 cm). For all lakes, except Leynavatn, $\log_e$ -transformed values of $\delta^{15}\text{N}$ in trout were not significantly related to the log-transformed size for fish < 40 cm. In Leynavatn, $\delta^{15}\text{N}$ increased significantly with size ($p<0.05$, $r^2=0.22$). In lakes with large-sized trout (> 40 cm), i.e. Eystara Mjáavatn and Leynavatn, $\delta^{15}\text{N}$ levels were 3-6 ‰ higher than

the average for smaller fish in these lakes. Apart from this, a few other fish had elevated $\delta^{15}\text{N}$ levels (Fig. 2). For charr occurring in Leynavatn, $\delta^{15}\text{N}$ was not significantly correlated to fish size. Charr in the 10-20 cm size range had a significantly ($p<0.05$) lower $\delta^{15}\text{N}$ than trout within the same size interval (Fig. 2).

$\delta^{13}\text{C}$ values of three-spined sticklebacks (sticklebacks) caught in the littoral zone of Toftavatn and Sørvágsvatn were comparable to those of benthic invertebrates from the littoral zone, while the only specimen caught offshore (in Toftavatn) exhibited a profundal/pelagic zone signal (Fig. 1). Sticklebacks > 3 cm had a high $\delta^{15}\text{N}$ (10.2 ± 0.3 ‰), which was significantly higher than in both littoral and pelagic trout, while $\delta^{15}\text{N}$ of sticklebacks < 3 cm was comparable to the level of the invertebrate predators (Table 2). By contrast, no significant difference was found in $\delta^{15}\text{N}$ between large sticklebacks (4-5.5 cm) and trout in Sørvágsvatn.

Discussion

The study of food web interactions in the five lakes showed several similarities, but also some differences. In Leynavatn, where brown trout and charr live in sympatry, the C isotope fractionation suggests niche segregation between the two species. Trout $\delta^{13}\text{C}$ levels indicated littoral food species, whereas the $\delta^{13}\text{C}$ levels of charr ranged in-between the levels recorded for littoral and profundal/pelagic invertebrates. This also explains the lower $\delta^{15}\text{N}$ of charr compared to trout of similar size, since the average $\delta^{15}\text{N}$ of the primary consumers in the



profundal benthos was significantly lower than in the littoral zone (Fig. 1). Habitat segregation is often the result when brown trout and Arctic charr occur in sympatry (Nilsson, 1963; Nilsson and Pejler, 1973, L'Abée-Lund *et al.*, 1993; Hammar, 1998). Brown trout remains in the littoral habitat exploiting the declining summer resources of macroinvertebrates, whereas Arctic charr more profitably utilizes the peak summer resource levels of small zooplankton in the pelagic (Hammar, 1998). The competition becomes even stronger in reservoirs where the littoral zone is less well-developed. In such environments, brown trout has been driven close to extinction, whereas small-sized charr thrive feeding on zooplankton and profundal benthic invertebrates (Grimås, 1961; Nilsson, 1961; Hammar 1998). The charr in Leynavatn was apparently not confined to zooplankton, as zooplankton $\delta^{15}\text{N}$ was only 1.8 ‰ and thus only 0.5 trophic levels lower than that of charr. Therefore, the isotope data indicate that the Leynavatn charr derived C and N from a mixture of zooplankton and benthic invertebrates, both profundal and littoral, but fed mainly in the pelagic/profundal zone (Fig. 1). The gut content of 53 Leynavatn charr, also sampled in 2000, consisted mainly of zooplankton (primarily *Daphnia* sp.) and benthic invertebrates such as chironomids

(Tanypodinae) and mussels (*Pisidium* sp.) (Malmquist *et al.*, 2002). In an earlier study of Leynavatn, Gydemo (1983) found that the preferred food item of charr was benthic cladocerans (*Eurycercus*), and only in rare cases *Pisidium* and chironomid larvae dominated. The trout of Leynavatn (< 40 cm) were 1.3 trophic positions above the littoral benthic primary consumers and 0.3 above the invertebrate predators (Table 2), while they were 1.8 and 1.6 trophic positions, respectively, higher than in the same taxa from the profundal zone. This suggests that the trout mainly fed on littoral benthic invertebrates. The gut content of 39 trout of this size class sampled in 2000 consisted mainly of larvae and pupae of chironomids (Tanypodinae) and the benthic, littoral cladoceran *Eurycercus lamellatus* (Malmquist *et al.*, 2002).

The $\delta^{13}\text{C}$ levels of trout in the four other lakes without charr indicate that trout foraged opportunistically in both principal habitats, the littoral and profundal/pelagic. We infer this from two facts. First, despite clear differences in $\delta^{13}\text{C}$ of potential food resources between the habitats no significant differences were found in the $\delta^{13}\text{C}$ signal of fish caught there. Secondly, $\delta^{13}\text{C}$ of the trout in all lakes except Saksunarvatn (see discussion of this lake below) ranged between the values of the food resources in the littoral and the profundal/pelagic zones. The isotope data (Fig. 1, Table 2) indicated and the stomach analyses confirmed that trout < 40 cm mainly fed on invertebrates (Malmquist *et al.*, 2002). In Sørvgásvatn, the gut content mainly consisted of *Eurycercus* and Chironomidae larvae, while

Fig. 2. Isotope fractions of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) in muscle of fish of different size classes in the five study lakes. Samples from the littoral and offshore catches are pooled.

adults and pupae of various chironomids dominated in Eystara Mjáavatn. By contrast, the stomach content of most trout specimens in Toftavatn differed, zooplankton (*Daphnia* sp.) accounting for a large proportion. Also, water mites and caddisflies constituted significant proportions (Malmquist *et al.*, 2002). The importance of predatory water mites may help explaining the high trophic position of trout < 40 cm in this lake compared to Leynavatn and Eystara Mjáavatn. The trophic position of trout was also high in Sörvágsvatn, but unfortunately stomach data were not available for this lake.

For all lakes, we found a tendency to, and for some lakes a significant, decline in $\delta^{13}\text{C}$ with increasing size of trout < 40 cm, whereas obligate piscivores (as judged from the $\delta^{15}\text{N}$) were enriched in $\delta^{13}\text{C}$ corresponding to that of the smallest fish. This indicates that fish from an early start in the littoral zone migrate towards deeper sites with increasing size, although the obligate piscivorous brown trout (> 40 cm) seem to return to the littoral zone where they feed on littoral trout rather than on pelagic charr (having a pelagial C signal). Also, the only analyzed large trout from Eystara Mjáavatn was enriched in carbon. In an isotope study of Loch Ness, where charr and brown trout live in sympatry, Grey (2001) also found trout > 40 cm to be piscivorous and an increasing $\delta^{15}\text{N}$ and decreasing $\delta^{13}\text{C}$ with fish length < 40 cm. Yet, contrasting our results, piscivorous trout in his study did not show a littoral C signal, which corroborates several comparative studies showing large trout to feed

mainly on pelagic charr in lakes where they live in sympatry (Nilsson, 1964; Aass *et al.*, 1972; Hammar and Filipsson, 1988; review in Hammer, 1998). The mainly littoral habitat choice of large trout in our study must, however, be interpreted with caution as only few specimens were analysed. Only few other data on the habitat choice of trout in Faroese lakes are available. Brattaberg (1995) found that large specimens tended to migrate extensively, while small individuals stayed near the shore.

In all lakes except Leynavatn, $\delta^{15}\text{N}$ of trout and charr did not change significantly with size for fish < 40 cm, suggesting that trophic position is independent of size in this range, which is also confirmed by the stomach analyses (Malmquist *et al.*, 2002). The observed increase in Leynavatn with size should be interpreted with care, as the result is based on data from only seven fish. In a recent investigation, Overmann and Parrish (2001) argued that the $\delta^{15}\text{N}$ of walleye (*Stizostedion vitreum*) increases with size irrespective of the diet, which is critical for the use of the N isotope as indicator of trophic position. Our $\delta^{15}\text{N}$ data for brown trout (except maybe those from Leynavatn) and Arctic charr contrast their findings.

The isotope data from Saksunarvatn were atypical and deserve some discussion. In this lake, the $\delta^{13}\text{C}$ of trout was generally less depleted than in benthic invertebrates caught in both the littoral and the pelagial/profundal zones, but resembled the level of trout found in the nearby lake, Eystara Mjáavatn. The gut content analyses (Malmquist *et al.*, 2002) revealed that trout

in Saksunarvatn consumed mainly chironomids (primarily Tanypodinae larvae), *Eurycercus* and leeches, which in our investigations showed a more depleted C signal than in fish collected in both habitats. Our samples of benthic invertebrates from the littoral zone cannot, therefore, be generally representative for this habitat in the lake. The contradictory results are further underlined by the fact that the $\delta^{13}\text{C}$ signal of the littoral zone invertebrates from this lake corresponds to that of profundal zone specimens in the lake, while being far from the values detected in the littoral zone of the other four lakes. Whether this reflects that the littoral benthic samples were taken too close to the major inlets of the lake cannot be ruled out, as we do not have any data on the C and N isotope fractions of inorganic and organic N in the inlet water.

The few data available on three-spined sticklebacks (caught in Toftavatn and Sörvágsvatn only) suggest that they foraged mainly in the littoral zone. Accordingly, sticklebacks were caught primarily in the littoral gill nets (Jeppesen *et al.*, unpublished data). Yet, the only analyzed stickleback from the open water was depleted in C, indicating a more stationary behaviour than recognized for trout. In another study of a Faroese lake (Ryskivatn), three-spined sticklebacks were mainly confined to the benthic zone offshore (Brattaberg, 1995).

Assuming that the average $\delta^{13}\text{C}$ of the primary consumers is representative for the food selected by the fish, a rough estimate can be reached of the relative proportion consumed in the two habitats for the diffe-

rent fish species and size classes (Vander Zanden and Rasmussen, 1999). For simplicity, we will restrict ourselves to the size classes presented in Fig. 1. Based on this assumption, charr in Leynavatn consumed 69 % of their food in the pelagic/profundal zone, while trout < 40 cm mainly fed in the littoral zone (78 %). By contrast, the littoral consumption by trout < 40 cm ranged between 56 % in Eystara Mjáavatn to 33 and 39 % in Toftavatn and Sörvágsvatn, respectively, while trout > 40 cm exclusively fed in the littoral zone. The larger share of pelagic/profundal food in Toftavatn corresponded well with the gut analyses showing a higher proportion of zooplankton in the food in this lake. The isotope data indicate that this is also the case in Sörvágsvatn, which seems likely considering the large depth of the lake. Unfortunately, no stomach analyses were made for this lake. The littoral sticklebacks consumed between 56-57 % of their food in the littoral zone in the two lakes in which they were recorded, while the only open water stickleback found fed exclusively here. The isotope-based estimation of habitat choice thus supports the explanation of the observed morphometric character displacement (a more curved snout indicating benthic feeding) of brown trout in Leynavatn, as well as in Toftavatn where trout had a more forked caudal fin (indicative of a more pelagic foraging manner) (Malmquist *et al.*, 2002).

No difference in $\delta^{15}\text{N}$ between zooplankton and phytoplankton was observed. This may indicate that the zooplankton do not solely base their energy uptake on

phytoplankton but perhaps also consume allochthonous organic matter, as suggested by Hessen *et al.* (2002) based on a multi-lake analysis of data from oligotrophic Norwegian lakes. By contrast in eutrophic Danish lakes with higher phytoplankton abundance, Jeppesen *et al.* (unpublished data) found $\delta^{15}\text{N}$ to be 2.3 ‰ (or 0.8 trophic positions) higher in zooplankton than in the phytoplankton fractions indicating that zooplankton mainly consume phytoplankton in eutrophic lakes. Our results from the Faroese lakes must, however, be interpreted with caution, because both the zooplankton and phytoplankton hauls included other organic (e.g. picoplankton) and inorganic particulate matter.

In conclusion, stable isotope analyses have proved to be a valuable tool to identify food web interactions and fish habitat choice in Faroese lakes characterized by simple food web structures. They have provided a more integrated picture of the feeding habitats and predation pressure of fish than can be obtained by snapshot gill net sampling with subsequent gut content analyses. However, because of overlap in C and N isotope fractions among the different potential prey items, isotope analyses can hardly stand alone, but ought to be supplemented with gut content analyses to fully elucidate food web interactions in the lakes.

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Ecology of Five Faroese Lakes: Summary and Synthesis

Vistfrøði á fimm føroyskum vøtnum: Samandráttur og samanrenning

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Úrtak

Tíðliga í august 2000 varð ein vatnlívfrøðilig kanning gjørd av fimm føroyskum vøtnum við lítlum taðfalli (Sørvágsvatni, Toftavatni, Leynavatni, Saksunarvatni og Eystara Mjáavatni). Granskarar úr Føroyum, Danmark, Íslandi, Svørki og Noreg vóru við í kanningini. At Føroyar eru staddar á markinum millum arktiska økið og evropeiska meginlandið, skuldi havt við sær, at eitt stórt tal av ymiskum sløgum var at finna í føroysku vøtnunum. Men úrslitini vísa, at sløgini í føroysku vøtnunum bert vóru eitt lítið sindur fleiri enn í grønlenskum vøtnum, á leið tað sama sum í íslenskum vøtnum, og gjøgnum alla vistskipan færri enn í vøtnum í Bretlandi og Skandinavia. Helst kemst hetta av, at Norðuratlantshavið rundan um oyggjarnar virkar sum ein forðing fyri spjaðing, sum saman við lítlu støddini, oyggjarnar hava, hevur við sær, at oyggjarnar liggja avbyrgdar og tí ikki hava ta mongdina av ymiskum sløgum ella lutfall millum sløgini, sum væntast kund. Kanningarnar staðfestu, at stórir munur var á vistskipanini í ymiskum vøtnunum. Hetta var helst orsakað av, at munur var á fiskastovnunum í ymsu vøtnunum, og vøtnini vóru eisini ymisk bæði náttúrulegafrøðiliga og evnafrøðiliga. Í Leynavatni, har bleikja (*Salvelinus alpinus*) og sjósíl (*Salmo trutta*) liva í samljóði, sá út til, at sera nógv djóraeti varð etið. Hetta sást serliga, tí bert ein lítill partur av Cladocera-sløgum vóru av slagnum *Daph-*

nia. Tó kann hetta eisini vera orsakað av landa- og evnafrøðiligum viðurskiftum. Í teimum báðum vøtnunum, har sjósíl og kombikk (*Gasterosteus aculeatus*) liva í samljóði, var etitrýstið av rovdýrum miðal, meðan lægsta etitrýstið av rovdýrum var í vøtnunum, har einans sjósíl vóru at finna. Hesar eygleiðingar vóru staðfestar av kanningum av stöðugum isotopum, sum vístu eitt greitt bólkabýti í vøtnunum við sjósíli og bleikju, eitt minni eyðsýnt uppbýti í vøtnunum við sjósíli og kombikki og minst uppbýti í bólkar í vøtnunum, har einans sjósíl vóru. Stóri munurin á samanseting av fiskasløgum og djóraeti hevði einans eina lítla ávirkan á einkynnaðu djórini, men ávirkaði týðuliga samansetingina av plantuæti. Framleiðslan av plantuæti var lítill í øllum vøtnunum, og hetta vísir, at føðsluevnini vóru avmarkaði. Smáverubólkarnir vóru eisini í høvuðsheitum stýrdir av føðsluevninøgðunum, men teir eru helst ein týðandi partur av føðini hjá djóraætinum. Okkara niðurstøða er tí, at føroysku vøtnini hava eitt sera áhugavert plantu- og djóralív, har eyðkenni frá bæði arktiskum, sub-arktiskum og temperaðum økjum eru umboðaði, og at vøtnini eru løtt at ávirka við nýggjum sløgum úr útlandinum ella úr øðrum føroyskum vøtnum.

Abstract

A limnological investigation of five oligotrophic Faroese lakes (Sørvágsvatn, Toftavatn, Leynavatn, Saks-

Table 1. Selected physico-chemical and biological variables from five Faroese lakes. Data sources: Landkildheus *et al.*, 2002; Jensen *et al.*, 2002; Lauridsen and Hansson, 2002; Brettum, 2002.

	Sørvágsvatn	Toftavatn	Leynavatn	Saksunarvatn	Eystara Mjáavatn
Morphometrics					
Lake area (km ²)	3.56	0.52	0.18	0.08	0.03
Mean depth (m)	27.5	5.8	13.7	6.5	3
Max depth (m)	59	22	33	17	7
Catchment/lake area (km ²)*	35.2	3.6	16.6	12.3	1.8
Cultivated (%)	6	2	1	1	0
Physico-chemical characteristics					
Total phosphorus (TP, µg l ⁻¹)	5	11	3	6	16
Total nitrogen (TN, µg l ⁻¹)	318	220	168	114	252
TN:TP by weight	64	20	56	19	16
Chlorophyll <i>a</i> (µg l ⁻¹)	0.8	1.1	1.3	1.3	1.7
Secchi depth (m)	12.5	5.8	10.0	8.8	4.3
Biota					
Zooplankton biomass (µg DW l ⁻¹)	26	162	72	518	1173
Phytoplankton biomass (µm ³ l ⁻¹)	84	163	135	210	195
Chlorophyll:TP	0.16	0.10	0.43	0.22	0.11
Phytoplankton biomass:TP (µm ³ µg ⁻¹)	17	15	45	35	12

*including the lake

unarvatn, Eystara Mjáavatn) was undertaken in early August 2000 by researchers from the Faroe Islands, Denmark, Iceland, Sweden and Norway. Despite the location of the islands on the climatic border between the Arctic and the European continent, which suggests a potential high species richness, the species richness of the lakes was only a little higher than that in Greenland, similar to that in Iceland but low at most trophic levels compared with lakes in the United Kingdom and Scandinavia. This is most likely due to the function of the North Atlantic Ocean surrounding the islands as a dispersal barrier, which in conjunction with the smallness of the islands lead to isolation and thus sub-optimal and disharmonic species abundance. Major differences in the trophic structure of the lakes, attributed to variations in the fish community composition and differences in physico-chemical factors of the lakes, were observed. In Leynavatn, where Arctic charr (*Sal-*

velinus alpinus) and brown trout (*Salmo trutta*) live in sympatry, charr control of zooplankton seemed high, as indicated by a particularly low share of *Daphnia* among the cladocerans, though the latter may also be influenced by physico-chemical factors. In the two lakes where brown trout occurred in sympatry with three-spined sticklebacks (*Gasterosteus aculeatus*), the predation pressure was intermediate, the lowest pressure being recorded in trout-only lakes. These findings were confirmed by stable isotope analyses that demonstrated a strong niche segregation in charr-trout lakes, a less pronounced segregation in trout-stickleback lakes and the least significant segregation in trout-only lakes. The marked differences in the community structure of fish and zooplankton seem to only weakly affect protists, but apparently impacted the phytoplankton composition. Phytoplankton production was low in all lakes, indicating nutrient limitation. Also the microbial com-

munities seemed largely controlled by nutrients, but probably served as an important food source for the zooplankton. We conclude that Faroese lakes host a highly interesting flora and fauna exhibiting elements from arctic, sub-arctic as well as temperate climates and that the lakes are sensitive to introduction of foreign aquatic species as well as to transplantation of, for instance, fish among local lakes.

Introduction

Faroese lakes are interesting objects of study for several reasons. First, from a limnological point of view the lakes are virginal as, up to now, only few and not particularly detailed studies have been undertaken (reviewed by Christoffersen, 2002). Second, the Faroe Islands are geographically isolated by their position in the North Atlantic Ocean and are relatively small, which influences the dispersal potential from Iceland and other regions. The lakes are consequently well-suited for studies of biogeography. Third, the low species diversity conditioned among other factors by the isolation and the great inter-lake differences in fish species composition make the lakes interesting objects for studies of food chain interactions. Finally, they are of considerable interest to the current climate debate, both because they constitute an important link in studies along lati-, longi- and altitude gradients, and because seasonal temperature variations are relatively small due to their location in a region exhibiting mild winters and cool summers. This final chapter presents a summary and synthesis of the studies of the five lakes.

Results and discussion

Lakes, catchments and climate

The Faroe Islands are located at 62°N, 7°W with the Shetland Islands to the SE and Iceland to the NW as the nearest foreign coasts. The climate is greatly influenced by the warm North Atlantic Current and by the passage of frequent cyclones (Cappelen and Laursen, 1998). Consequently, the climate is humid, unsettled and windy, with mild winters and cool summers (average seasonal variation in air temperature: 3.2–10.5 °C). The precipitation varies considerably, being around 800 mm at the outer coastal areas and rising to above 3200 mm in central coastal areas (Hvalvík, Klaksvík), and occasionally even to 5000 mm in central mountain areas (Cappelen and Laursen, 1998; Mortensen, pers. comm.).

The Faroe Islands are the remnants of a large low relief plateau of Tertiary flood basalts resulting from volcanic eruptions almost 60 million years ago prior to the opening of the North Atlantic Ocean basin. The Faroe basalt plateau is built up by layers of near horizontal basalt flows from mainly rift volcanism. The Tertiary landscapes with aligned low relief depressions trending northwest-southeast set the physical topographic environment for the glaciations of the Quaternary period. The glacial processes reshaped the former plateau to a high relief landscape exaggerating directional trends of the earlier drainage system. Deep valleys with steep sides and flat bottoms evolved, preserving the general northwestern-southeastern direction of the previous landscape (Mortensen, 2002). As glaciation covered the entire Faroes, al-

though small islands may only have supported small glaciers, if any (Mortensen, 2002), the present biological community evolved during the past approx. 11,000 years.

The five lakes range in size and average depth from 0.03 km² and 3.0 m (Eystara Mjáavatn, hereafter called Mjáavatn) to 3.56 km² and 27.5 m (Sørvágsvatn) (Landkildehus *et al.*, 2002). The catchment area to lake area ratio varies almost three-fold, from 60 (Mjáavatn) to 154 (Saksunarvatn), whereas the agricultural area of the catchments varies only negligibly, ranging between 0 % and 6 % (Table 1). Moreover, the sewage input is low and the lakes are accordingly all oligotrophic with low total phosphorus (TP) and total nitrogen (TN) levels and high TN:TP ratios (Jensen *et al.*, 2002). A slightly higher concentration of nitrogen was recorded in Sørvágsvatn, most likely due to runoff from the defrosting chemicals at the Vágar airport (Jensen *et al.*, 2002). The low TP values result in low chlorophyll *a* (0.8–1.7 µg l⁻¹) and high water transparency (Secchi depth: 4.3–12.5 m). In all lakes, the water was well oxygenated and well buffered with pH values near neutral.

Species composition and richness

Compared to lakes of similar nutrient levels in the United Kingdom and at similar latitudes on the European continent, the five lakes studied are characterized by low species richness. Only three fish species were recorded, with brown trout (*Salmo trutta*) occurring in all lakes, three-spined stickleback (*Gasterosteus aculeatus*) in

two lakes and Arctic charr (*Salvelinus alpinus*) in only one lake. Generally, brown trout and three-spined stickleback are well represented in Faroese lakes, while Arctic charr only occurs in a few lakes, and naturally so only in Leynavatn (Malmquist *et al.*, 2002b). In some coastal lakes, also eel (*Anguilla anguilla*) can be found and nine-spined stickleback (*Pungitius pungitius*) has been recorded in a few lakes (Jeppesen *et al.*, unpubl. data). In former investigations, also Atlantic salmon (*Salmo salar*) was observed in Leynavatn (Gydmo, 1983).

The rarity of Arctic charr in the Faroe Islands, despite its commonness in Iceland, Greenland and northern Norway, is probably climatically conditioned, as optimum growth conditions for charr occur at temperatures around 10–12 °C (Jobling, 1983). At higher temperatures, the allocation of energy for charr growth becomes less efficient and the risk of diseases increases (Jobling, 1983; Malmquist *et al.*, 2002a). In early August 2002, the mean surface temperatures in the lakes (12.0–15.0 °C, Jensen *et al.*, 2002) exceed the preferred temperature for charr. Moreover, because of the strong winds combined with relatively low summer temperatures and high winter temperatures, the lakes are most likely un- or only temporarily stratified during summer, rendering it difficult for charr to find cold refuges in the lakes. A notable exception is Leynavatn where the hypolimnion temperature is relatively low (9.2 °C; Jensen *et al.*, 2002) and thus close to the optimum temperature for charr. Brown trout has a higher temperature optimum (Elliott,

Table 2. The number of taxa recorded in the study lakes. Note that the benthic invertebrates have not yet been fully identified to species level, so the taxa aggregation level is from species to order and thus underestimates the actual species richness. Data sources: Brettum, 2002; Lauridsen and Hansson, 2002; Malmquist *et al.*, 2002a,b; Schierup *et al.*, 2002; Jeppesen *et al.*, unpubl., n.d. = no data. In Leynavatn only two fish species were found. However, in earlier investigations also Atlantic salmon (*S. salar*) was recorded. Therefore 3 in parenthesis.

Number of species/taxa	Sørvágsvatn	Toftavatn	Leynavatn	Saksunarvatn	Eystara Mjáavatn
Phytoplankton	35	31	26	16	20
Zooplankton	10	11	8	7	7
Cladocerans in sediment samples	n.d.	11	10	10	8
Cladoceran remains in the surface sediment (0-1 cm)	11	12	8	10	10
Zoobenthos excl. cladocerans in the littoral zone	n.d.	19	20	21	21
Fish	2	2	2(3)	1	1
Zoobenthos excluding cladocerans in the littoral zone	n.d.	12	12	13	13
Submerged macrophytes	10	14	10	14	10

1994), which may explain its larger success in Faroese lakes (Malmquist *et al.*, 2002a). The absence of other species commonly occurring in cold temperate regions, such as whitefish (*Coregonus lavaretus*), smelt (*Osmerus eperlanus*) and Eurasian perch (*Perca fluviatilis*), must be ascribed to the isolation of the islands from the continent.

The zooplankton community was species-poor and included six cladocerans (numerically dominated by *Bosmina longispina*, *Daphnia* sp. and *Holopedium gibberum*), three cyclopoid copepods (one *Cyclops* and two *Eucyclops* species) and eight rotifers (dominated as in other arctic lakes by *Polyarthra* sp.) (Lauridsen and Hansson, 2002). No calanoid copepods were found. Calanoids are also absent from North-East Greenland lakes, while *Limnocalanus minutus* of American origin (Hrbáček *et al.*, 1967), is abundant in West

Greenland lakes located close to the American continent (Lauridsen *et al.*, 2001). Also, *Leptodiptomus minutus* and *Diaptomus glacialis*, whose main distribution is in Europe and Asia, occur in Icelandic lakes (Malmquist *et al.*, 2002b). The absence of calanoids is somewhat puzzling, but may be caused by a low dispersal potential as seen elsewhere (Keller and Yan, 1998)

Besides the pelagic forms, an additional seven species of benthic cladocerans were observed in the benthic samples (Malmquist *et al.*, 2002b), of which in particular *Alona* spp., *Alonopsis elongata* and *Eurycerus lamellatus* were abundant. Analyses of cladoceran remains in the surface sediment of the five lakes showed that the cladoceran species number ranged between 8-12 (mean=10) (Table 2), which is higher than in 21 Icelandic lakes (4-10, mean =

8.3), but considerably lower than in southern Scandinavia and mid-Europe (14-26, mean=21). (Jeppesen *et al.*, unpubl. results). Interestingly, *Macrothrix hirsuticornis* was not found in the sediment samples or as remains in the surface sediment, although the species is widely distributed in North and North-East Greenland and Iceland, as evidenced by analyses of sediment remains (Jeppesen *et al.* 2001; Jeppesen *et al.*, unpubl.).

A few pelagic invertebrate predators occurred in the lakes, for example water mites and leeches (Malmquist *et al.*, 2002b). However, a number of potential important predators known from the temperate zone are missing. These include *Chaoborus* spp. and *Leptodora kindtii*, which often have a significant structuring effect on the pelagic food chain in temperate lakes. Also noteworthy is the absence of *Notostraca*, the omnivorous but mainly predatory *Lepidurus* spp. and the filter-feeding *Branchinecta*. *Lepidurus arcticus* is widespread in North and East Greenland, Iceland, Svalbard and on Bear Island, and it has also been recorded further south in West Greenland and northern Scandinavia.

The taxa composition of macrobenthos in the five Faroese lakes was relatively similar to the records from Iceland, with some notable exceptions, however (Malmquist *et al.*, 2002b). The four trichopteran species identified (*Polycentropus flavomaculatus*, *Tinodes waeneri*, *Agrypnia obsoleta* and *Mesophylax impunctus*) have not been recorded in Iceland, but occur in Scandinavia and in the United Kingdom.

Also gammarids, represented by *G. lacustris* in two of the study lakes, and in other Faroese lakes and ponds also by *G. duebeni* and *G. pulex* (Poulsen, 1928), have not been found in Iceland. By contrast, the chironomid sub-family *Diamesinae*, which is widespread in cold oligotrophic lakes and streams in Iceland, was not recorded in the study lakes, most likely because of too high temperatures and possibly also competitive exclusion (Malmquist *et al.*, 2002b). As in Arctic lakes (Røen, 1962), ostracods were abundant in the Faroese lakes (Malmquist *et al.*, 2002b). Since the macrobenthos was only partly identified to species level, species richness cannot be fully evaluated, although it remains clear that it is low compared to findings in European lakes at similar latitude.

The phytoplankton species richness varied between 16 (Saksunarvatn) and 35 (Sørvágsvatn) (average 25.6, Table 2), which is lower than in comparable Norwegian lakes, where the species number in samples from late July and early August (the time of sampling in the Faroe Islands) typically ranges between 30 and 50 (Brettum, 2002). As in the Norwegian lakes, the species richness was greatest among chrysophytes and cryptophytes, but in some lakes also chlorophytes and diatoms contributed significantly to the diversity.

The study of aquatic plants also included Sandsvatn at Sandoy. A total of 24 species were found, including six isoetids, 13 elodeids, one nymphaeid and four charophytes (Schierup *et al.*, 2002). Four species are new to the Faroe Islands (*Callitriche palustris*, *Tolypella nidifica*, *Potamogeton*

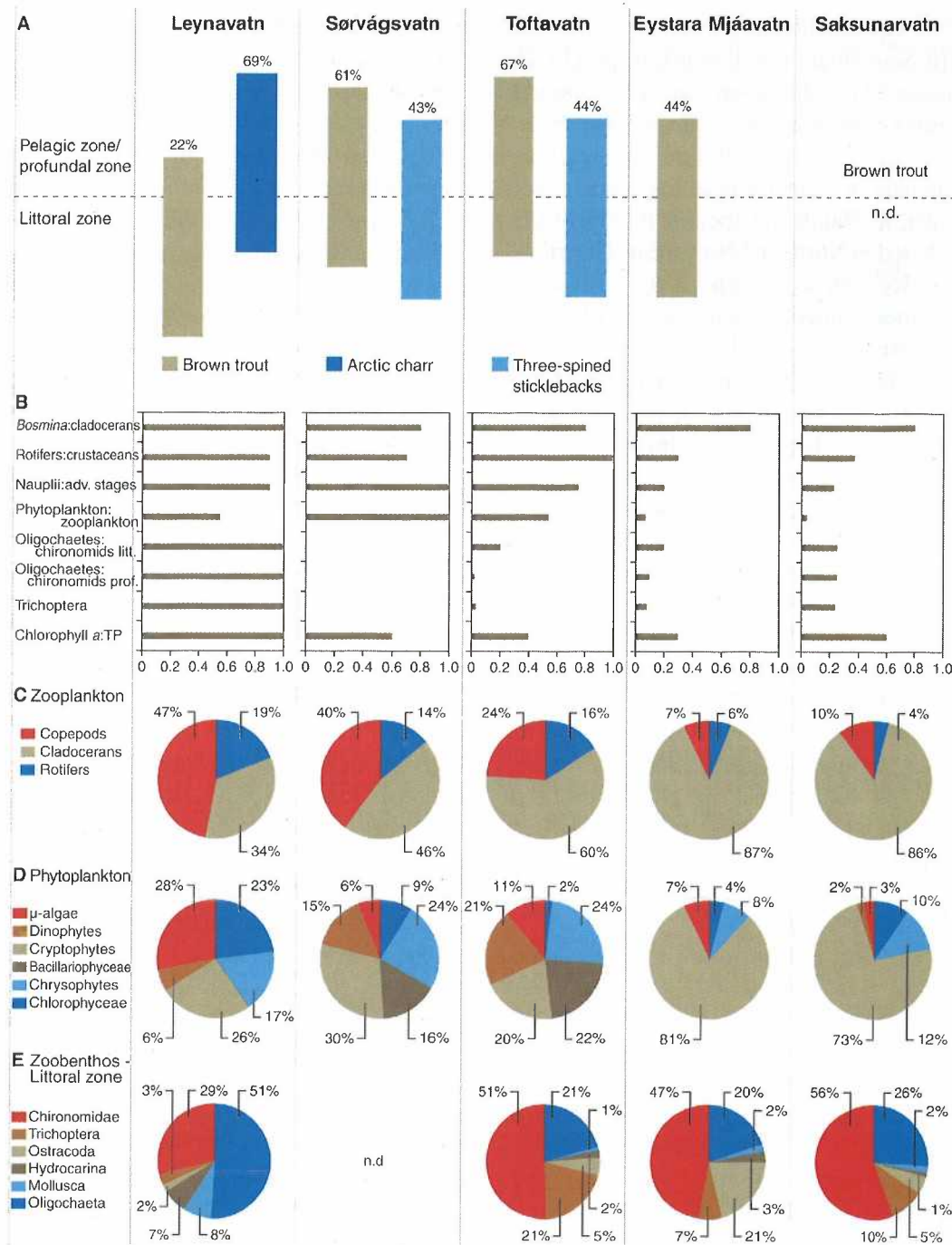


Fig. 1. Aspects of trophic dynamics in the five study lakes.

Panel A: The share of food consumed by fish with a fork length < 40 cm in the pelagic zone/profundal sediment and the littoral zone. The survey is based on analyses of stable isotopes of prey items and fish muscles (Jeppesen *et al.*, 2002). Note that the share of brown trout from the two environments changes markedly with fish community composition. Trout forage mainly in the littoral zone when living in sympatry with Arctic charr and in the pelagic zone/profundal zone when living in sympatry with three-spined stickleback, while they are more indifferent in trout-only lakes. Reliable data on Saksunarvatn are not available (see discussion in Jeppesen *et al.*, 2002).

Panel B: A number of predation indicators based on data from Tables 1 and 3. The different indicators are set to 1 (high predation pressure) in the lake exhibiting the highest values, data being normalized to this value for the other lakes. The trout-only lake distinguishes itself as to most variables, the trout-stickleback lakes lie in-between these and the trout-charr lakes closest to the latter.

Panels C and D: The relative contribution of various groups to total zooplankton biomass and of various phytoplankton taxa to phytoplankton biovolume in the five lakes. Also here, trout-only lakes differ significantly from the other lakes, the contribution of cladocerans and of chrysophytes being particularly low in the trout-charr lakes.

Panel E: The relative contribution of various taxa of benthic invertebrates in the littoral zone of four of the study lakes. Note the high percentage of oligochaetes in Leynavatn. No data were available for Sørvágsvatn.

obtusifolius and a hybrid), of which two, *C. brutia* and *T. nidifica*, are rare in Scandinavia. Toftavatn, Sørvágsvatn and Saksunarvatn exhibited the highest species richness (14), while the three other lakes hosted less species (10) (Table 2). The isopods, especially *Isoëtes lacustris* and *Littorella*

uniflora, dominated in the shallow areas, while the charophyte *Nitella opaca* was the most dominant species and often formed dense beds from 0.5 to 10–11 m depth. The plant species richness seems not to differ markedly from similar lake types in northern Europe. Considerable variation was found in plant coverage between the lakes, mainly reflecting that Faroese lakes have steep slopes. Coverage was particularly low in Leynavatn and highest in Toftavatn. The plants were overall small and only a minor part of the water volume in the plant-covered area actually hosted plants (< 3 %, and frequently only ca. 1 %) (Schierup *et al.*, 2002).

In summary, the species richness for all the studied biota, with the possible exception of aquatic plants, was generally lower in the Faroe Islands than in comparable lakes on the European continent, but at the same level or slightly higher than in Icelandic lakes. The higher richness found in Faroese lakes than in Icelandic and North-East Greenland lakes may be ascribed to a warmer climate in the Faroe Islands and possibly a closer contact with the European continent.

Trophic interactions

Differences in fish stock composition and abundance seem to have a marked impact on the degree of predatory control of invertebrates (Fig. 1). In Leynavatn, where Arctic charr and brown trout live in sympatry, predator control on zooplankton by fish seemed particularly high. The share of *Daphnia* of total *Daphnia* and *Bosmina* abundance was thus only 10 % in Leyna-

Table 3. Selected fish predation indicators in the five Faroese lakes. Data sources: Lauridsen and Hansson, 2002; Malmquist *et al.*, 2002b. n.d. = no data.

	Sørvágsvatn	Toftavatn	Leynavatn	Saksunarvatn	Eystara Mjáavatn
<i>Bosmina</i> :cladocerans by number	0.75	0.74	0.90	0.47	0.74
Rotifers:crustaceans by number	8.7	12.5	10.9	3.9	3.6
Nauplii: copepodids+adults by number	0.8	0.6	0.7	0.2	0.1
Zooplankton:phytoplankton calculated on dry weight basis	1.1	3.5	1.8	8.5	20.5
Oligochaetes:chironomids in the littoral zone by number	n.d.	0.4	1.8	0.4	0.4
Oligochaetes:chironomids in the profundal zone by number	n.d.	0.08	5.9	0.6	1.1
Trichoptera ind m ⁻²	n.d.	2672	95	974	1220

vatn compared to 25-53 % in the other lakes (Table 3). Such low ratios are often attributed to size-selective predation on large-bodied cladocerans (e.g. Brooks and Dodson, 1965; Jeppesen *et al.*, 2002). A significant predatory control by fish may also be exerted on zoobenthos in Leynavatn, as evidenced by a much lower abundance of macroinvertebrates in both the profundal and the littoral zone, abundance being about three times lower than in the other lakes (Malmquist *et al.* 2002b; no data are available from Sørvágsvatn, however). Likewise, the oligochaetes:chironomids ratio was pronouncedly higher (1.8) in the Leynavatn littoral zone than in the other three lakes (all 0.4) where studies of the benthic invertebrate community were conducted, the same pattern being observed in the profundal zone. Thus, brown trout, Arctic charr and three-spined stickleback prefer chironomids over oligochaetes (Berg *et al.*, 1994, authors' unpublished results from Greenland and the Faroes).

Also the low abundance of Trichoptera may point in the same direction. However, the low densities of benthic macroinvertebrates in Leynavatn may also be attributed to physico-chemical features of the lake (Malmquist *et al.*, 2002b). For example, Leynavatn is the most oligotrophic of the lakes and the littoral zone seems to be least suitable as a habitat for invertebrates, as judged by the quite extensive bottom area characterized by sandy substrate and a very poorly developed macrophyte vegetation. The chironomids generally thrive better in stony and vegetated habitats than in sandy areas (Weatherhead and James, 2001). In accordance with the relatively poor food conditions in Leynavatn, the growth rates of brown trout and Arctic charr were lower here than in the other study lakes.

The stable isotope carbon data give further support for high predation control of invertebrates in Leynavatn (Jeppesen *et al.*, 2002). In Leynavatn, $\delta^{13}\text{C}$ analyses of fish muscle tissue indicate a strong niche

segregation between Arctic charr and brown trout, with charr feeding mainly on invertebrates in the open water and the profundal zone (69 % of consumption), while trout of the same size mainly feed on benthic invertebrates in the littoral zone (78 %) (Fig. 1). Moreover, the Leynavatn trout had a more curved snout than in the other three lakes, which may be a character displacement resulting from interspecific competition with charr (Malmquist *et al.*, 2002a). In accordance herewith, benthic food constituted a larger part of their diet here than in the other lakes (Malmquist *et al.*, 2002a). Arctic charr did not show any signs of morphological or ecological polymorphism, as often seen in sub-arctic and arctic lakes where charr is the sole fish species (Hammar, 1989; Langeland *et al.*, 1991; Malmquist *et al.*, 1992; Snorrason *et al.*, 1994; Riget *et al.*, 2000). In correspondence herewith, their diet was, irrespective of age, of mixed origin deriving from both the pelagic and the benthic habitat.

In two of the lakes, brown trout occurs in sympatry with three-spined stickleback (Sørvágsvatn and Toftavatn) and predator control of zooplankton appears to be higher here than in the trout-only lakes (Mjáavatn and Saksunarvatn), but lower than in Leynavatn. Thus, though there were no clear-cut differences in the *Bosmina*:*Daphnia* ratio, the rotifer:crustacean ratio was considerably higher in lakes with both sticklebacks and brown trout than in trout-only lakes (8.7-12.5 versus 3.6-3.9), and also the nauplii:copepodids ratio was higher (0.6-0.8 versus 0.14-0.20) (Table 3, Fig. 1). These differences most likely reflect

that fish by preying upon the advanced stages of copepods (copepodids + adults) and cladocerans favour otherwise small but inferior competitors such as rotifers and nauplii. Also, the zooplankton:phytoplankton biomass ratio was substantially lower in Toftavatn and Sørvágsvatn (1.1-3.5) than in the trout-only lakes, where it was in fact very high (8.5-20.5) (Table 3, Fig. 1).

The stable isotope analyses of carbon showed that trout in Toftavatn and Sørvágsvatn forage more in the pelagial/profundal zone (61-67 %) than they do in the trout-only Mjáavatn (44 %) (Fig. 1), even though the littoral zone is relatively large in Toftavatn. However, the $\delta^{13}\text{C}$ analysis indicates that three-spined sticklebacks to a larger extent than brown trout are confined to the habitat, littoral or pelagial, in which they were caught. Therefore, niche segregation among the two species is apparently not as strong in trout-stickleback lakes as in the trout-charr lake, which may be the reason for the apparently stronger top-down control in Leynavatn (Table 3, Fig. 1).

From both the stable nitrogen and stomach analyses it appears that only few of the fish are piscivorous (Jeppesen *et al.*, 2002; Malmquist *et al.*, 2002a). The $\delta^{15}\text{N}$ analyses indicated that trout with a fork length > 40 cm are obligate piscivores, but only few trout reach this length. Some smaller trout and Arctic charr may also be partly piscivorous, while most trout mainly consumed invertebrates and relied on benthic food items. The trophic position of trout in the lakes with stickleback, Toftavatn and Sørvágsvatn, tended to be somewhat higher than in the other lakes

(Jeppesen *et al.*, 2002), maybe reflecting a certain predation on sticklebacks in these lakes, and in Toftavátn on water mites as well (Malmquist *et al.*, 2002a). The overall low degree of piscivory in these Faroese lakes may to some extent be ascribed to the apparent scarcity of sticklebacks, the low nutrient state and thus low primary production (Christoffersen *et al.*, 2002; Jensen *et al.*, 2002), resulting in a relatively slow growth of salmonid fish and a somewhat stunted nature of the fish populations. By contrast, as seen in both Arctic charr and brown trout populations in lakes where sticklebacks seem to be abundant, the salmonids may improve their final size and growth rate, and even their longevity, considerably by shifting from benthic or pelagic food items to sticklebacks (Malmquist *et al.*, 1992; Jonsson *et al.*, 1999; Riget *et al.*, 2000).

The marked differences in community structure of fish and zooplankton seem to only weakly affect the biomass of protists and bacterioplankton (top-down control). Chlorophyll *a* varied only negligibly (0.8–1.7 µg chlorophyll *a* l⁻¹) despite major differences in the zooplankton:phytoplankton ratio (Tables 1 and 3) and hence most likely in the zooplankton grazing pressure on phytoplankton. Also the phytoplankton production varied little among the lakes (estimated to 3–7 g C m⁻² yr⁻¹) (Christoffersen *et al.*, 2002). By contrast, biomasses of phytoplankton, ciliates, heterotrophic nanoflagellates and bacterioplankton in the five lakes were related to the concentration of total phosphorus (Christoffersen *et al.*, 2002; Jensen *et al.*, 2002), indicating re-

source control (bottom-up control) rather than grazer control (top-down control). This is also supported by a long turnover time of the phytoplankton population of 6–24 days (Christoffersen *et al.*, 2002). Yet, the chlorophyll *a*:TP ratio tended to be higher in Leynavátn where top-down control on phytoplankton grazers was assumed to be highest. Also the phytoplankton biovolume:TP ratio was highest in this lake and high in Saksunarvátn as well (Table 1). The indications of overall low grazer control of phytoplankton biomass correspond well with a cross-analysis of data from Greenland and European lakes showing low cascading effects of fish on phytoplankton biomass in oligotrophic lakes, while strong cascading effects are generally observed in eutrophic lakes (Jeppesen *et al.*, in print).

By contrast, changes in zooplankton composition and abundance seem to have a profound effect on phytoplankton composition. In the trout-only lakes where the zooplankton:phytoplankton ratio was high and cladocerans dominated the zooplankton community, cryptophytes dominated the phytoplankton community, accounting for 73–81% of biomass as compared to 20–35% in the three two-species lakes (Fig. 1). This difference cannot be related to the difference in lake morphometry or nutrient state among the lakes, as Toftavátn and Saksunarvátn are the most similar lakes as to morphometry and nutrient state, but with highly contrasting phytoplankton communities. Prevalence of cryptophytes in lakes with low fish predation and dominance of large-bodied cladocerans have

been seen in many experimental studies (Bergquist and Carpenter, 1986; Kerfoot, 1987; Schriver *et al.*, 1995) and following removal of zooplanktivorous fish (Hansson *et al.*, 1998). Apparently, dominance of *Daphnia* and cryptophytes in the trout-only lakes resulted in low species richness of zooplankton and phytoplankton. These results must, however, be interpreted with care, because the chances of recording rare species are likely to be smaller in samples dominated by a few species.

In units of carbon biomass it was obvious that the protozoan populations (heterotrophic nanoflagellates and ciliates) contributed less to the microbial community than both bacteria and picoalgae (Christoffersen *et al.*, 2002). The average bacterial production rates of 0.9 µg C l⁻¹ d⁻¹ would yield 1 to 5 g C m⁻² yr⁻¹ corresponding to 14–80 % of the phytoplankton production. Since phytoplankton primary production was low, pico- and nanoplanktonic organisms are suggested to serve as important food sources for large-sized ciliate populations as well as zooplankton and thus support higher trophic levels (Christoffersen *et al.*, 2002).

Conclusions

Faroese lakes are situated on the climatic border between the Arctic and the European continent whose lakes differ considerably both as to taxonomic composition and abundance of organisms. Hence, the Faroese lakes may potentially be viewed as a “meeting point” for organisms with completely different adaptations, but with physiological features permitting survival

in Faroese lakes. This might suggest a particularly high species diversity in Faroese lakes, but this is evidently not the case according to our investigation and other studies. An explanation may be that the North Atlantic Ocean surrounding the islands functions as a dispersal barrier, leading to isolation and sub-optimal species abundance. The fauna and flora of Faroese lakes have features in common with both arctic and continental systems, but for most trophic levels overall species diversity is lower than in continental lakes but higher than in arctic lakes. Certainly, more species would have the potential of developing populations in the Faroe Islands were they not limited by natural dispersal barriers. The nature of Faroese lakes make them highly sensitive to intentional or accidental introduction of new species by humans.

We conclude that Faroese lakes host a highly interesting flora and fauna exhibiting elements from arctic, sub-arctic and temperate ecosystems. This and the low species richness, the notable absence of some key structuring organisms, like several invertebrate predators and fish species, and the relatively cold climate make Faroese lakes particularly interesting objects for comparative studies of ecosystem structure and function and for the evaluation of climatic effects on lakes.

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