Classification of Icelandic Watersheds and Rivers to Explain Life History Strategies of Atlantic Salmon

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A hierarchical classification system of Iceland's watersheds and rivers is presented. The classification is based on Iceland's substrate, climate, water, biota, and human cultural influences. The geological formations of Iceland are very different in character depending on their age and formation history. Three major types of formations occur: Tertiary, Plio-Pleistocene, and Pleistocene. These formations have different hydrological characters and different landscapes. There are also large differences in the climate within Iceland. Four major river types are found in Iceland: spring-fed rivers in Pleistocene areas, direct runoff rivers in Plio-Pleistocene areas, direct runoff rivers in Tertiary areas and wetland heath rivers in Tertiary areas. Eleven biogeoclimatic regions occur in Iceland, each having a different watershed type.

The classification together with life history theory can explain the distributions, abundances, and life history strategies of Icelandic salmonids. Oceanic conditions must also be considered to explain the life history patterns of anadromous populations. When the freshwater and marine habitat is stable, the life history

patterns of individuals in a population tend to be uniform, one life history form being most common. In an unstable environment many life history forms occur and the life span of one generation is long. The properties of the habitat can further explain which life history types are present. In the most stable and favorable rivers of Iceland resident life history forms are more common.

Such a classification of a river habitat greatly aids the understanding of the habitat and how it enables and constrains the salmonid populations within it. Consequently adaptations in life histories are better understood and conservation, utilization, and management of these valuable natural resources are made more coherent and efficient.

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INTRODUCTION

Rivers and streams and their biological systems are valuable resources and their value will without doubt increase in the future. Understanding of these ecosystems will help to insure their conservation and wise management.

Classification In order to understand nature, humans classify natural systems. Habitat classification is one way of understanding ecosystems. Many attempts to classify rivers and streams have been based on various chemical, physical, and biological variables, either in combination or alone (Huet 1959, Illies and Botosanenu 1963, Pennak 1971, Hynes 1970, Hawkes 1975, Binns and Eisermann 1979, Oswood and Barber 1982). There have been, however, few attempts to integrate these major groups of variables. The suitability of selected habitat variables has often been doubtful, even though success or failure of the stream inventory depends on this selection (Platts 1974).

Habitat view Habitat can be viewed as the template for the ecological strategies of biological organisms (Southwood 1977). Habitat at the level of the biological community can be viewed as all physical subsystems, while biological communities include all biological subsystems (Warren and Liss 1983). Communities are organized within habitats, which to a large degree enable and constrain populations, their distributions, life cycles, and food resources, as well as community organization and development (Hawkins 1983). At the population level, the habitat of one species includes other species.

Watershed as the fundamental unit Both lentic and lotic waters are parts of more incorporating systems. The surrounding watershed controls their characteristics and is therefore a basis for classifying freshwater systems. The importance of watersheds as a fundamental unit of study is widely accepted across various disciplines (Chorley 1969, Borman and Likens 1969, Black 1970, Curry 1972, Hynes 1975, Lotspeich 1980, Schumm 1977).

Contextualistic view There is a great need for an integrative systematic approach for understanding the considerable variability among and within freshwater systems and their biota (Hall and Knight 1981). Many authors have called for such an integrative approach to classification (Bailey, Pfister and Henderson 1978, Lotspeich 1980, Lotspeich and Platts 1982, Warren 1979, Warren and Liss 1983).

A comprehensive, integrative classification system for streams is needed to relate stream habitat to biogeoclimatic land systems (Frissel 1986, Lotspeich and Platts 1982, Warren 1979, Warren and Liss 1983). In developing such a classification system it is assumed that the organization and development of stream communities are determined by the structure and dynamics of the habitat, which in turn are controlled by the land-water system.

Capacity and performance To understand the structure of biological systems, they should be classified by their long-term capacities, rather than short-term performances (Warren 1979). A system potential capacity encompasses all of its possible developmental trajectories (Warren *et al.* 1979). A system develops from its potential capacity in response to a changing environment. While the capacity of a system can never be fully known, the concept of capacity helps us to understand the system in terms of its most general, invariant, and determining properties (Warren *et al.* 1979).

In classification based on capacity, variables that are most enabling and constraining should be chosen. The variables that appear to be the most enabling or constraining change with the spacio-temporal scale within which the system is viewed (Southwood 1976, 1977, Warren and Liss 1980).

Hierarchy A hierarchical view, in which the state of a higher level system enables and constrains the development of the lower level systems it embodies, recognizes this problem of scale. This kind of approach can be used for systems having subsystems that behave on heterogeneous time scales (Allen and Starr 1982).

Classification of stream systems These principles of capacities, enabling and constraining variables, and hierarchical control of system development can be applied successfully to stream systems. *Stream systems* can be viewed as hierarchically organized systems incorporating successively lower levels: *stream segment*, *reach*, and *microhabitat* subsystems (Frissel 1986). Similarly, a stream system is itself a subsystem in a broader *watershed system*, which in turn is a subsystem in a *biogeoclimatic region system* (Warren and Liss 1983).

Each level forms the environment of the level below.

The development of realized capacity and the performance of system at one level in hierarchy is therefore determined by the capacity and performances of the level above. Furthermore, because stream subsystems remain in the context of the watershed as a whole, their capacities and performances can be related to watershed events (Frissel 1986).

Processes of low frequency and high magnitude determine the capacity of a system high in the hierarchy, while relatively high frequency low magnitude events determine the capacity of a system low in the hierarchy (Frissel et al. 1985).

It is therefore important to initiate a classification at the highest levels in the hierarchy.

Adaptation Southwood (1977) developed a framework in which life history strategies of organisms are viewed in terms of temporal and spatial availability, predictability, and favorableness of habitats. An adequate hierarchical classification system can account for these habitat dimensions.

Present study The goal of this study is to develop a theoretically and empirically coherent and heuristically useful biogeoclimatic classification of Icelandic watersheds and rivers in relation to the ecology of the rivers, particularly the ecology of salmonid fishes, their distributions, abundances, and life history strategies.

ICELANDIC WATERSHEDS AND RIVERS

Domains of Icelandic watersheds

In order to classify Icelandic watersheds it is important to comprehend Iceland's substrate, climate, water, biota, and human cultural influences, which are considered as domains of classification. These domains and their capacities and performances as well as their interactions will be covered. In the next chapter, a classification system for Icelandic rivers based on these domains will be presented.

Human population, land use and geography

Iceland is situated in the North Atlantic Ocean, between 63° and 67° N latitude and 13° and 25° W longitude. Two-thirds of its 103,000 km^2 are over 200 m in elevation, and its highest peaks are about 2000 m above sea level (Figure 1).

Iceland was settled by Norwegian Vikings in the years 845 to 930 A. D. Through the ages, the human population size varied from 30,000 to 80,000 people, depending on how favorable conditions were (Thorarinsson 1953, Fridriksson 1969). Today, Iceland has a human population of about 250,000, which gives a mean density of 2.4 inhabitants per km^2. Half the population lives in and around the capital, Reykjavik. Outside the capital, the population is distributed along the coast and in the valleys all around the island. The central highlands are not inhabitated (Figure 2).

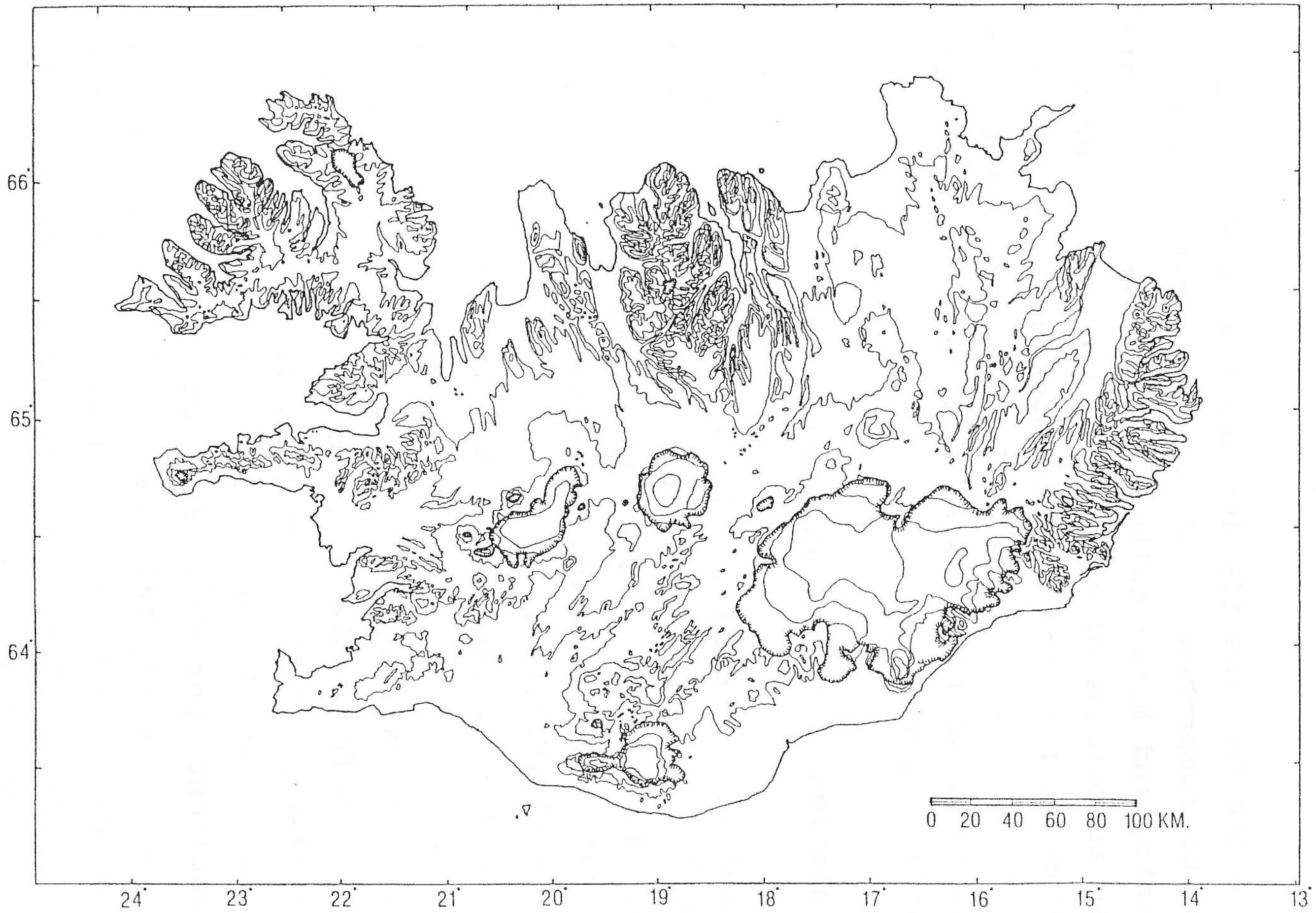

Figure 1. The topography of Iceland. (Lines at 300 m interval).

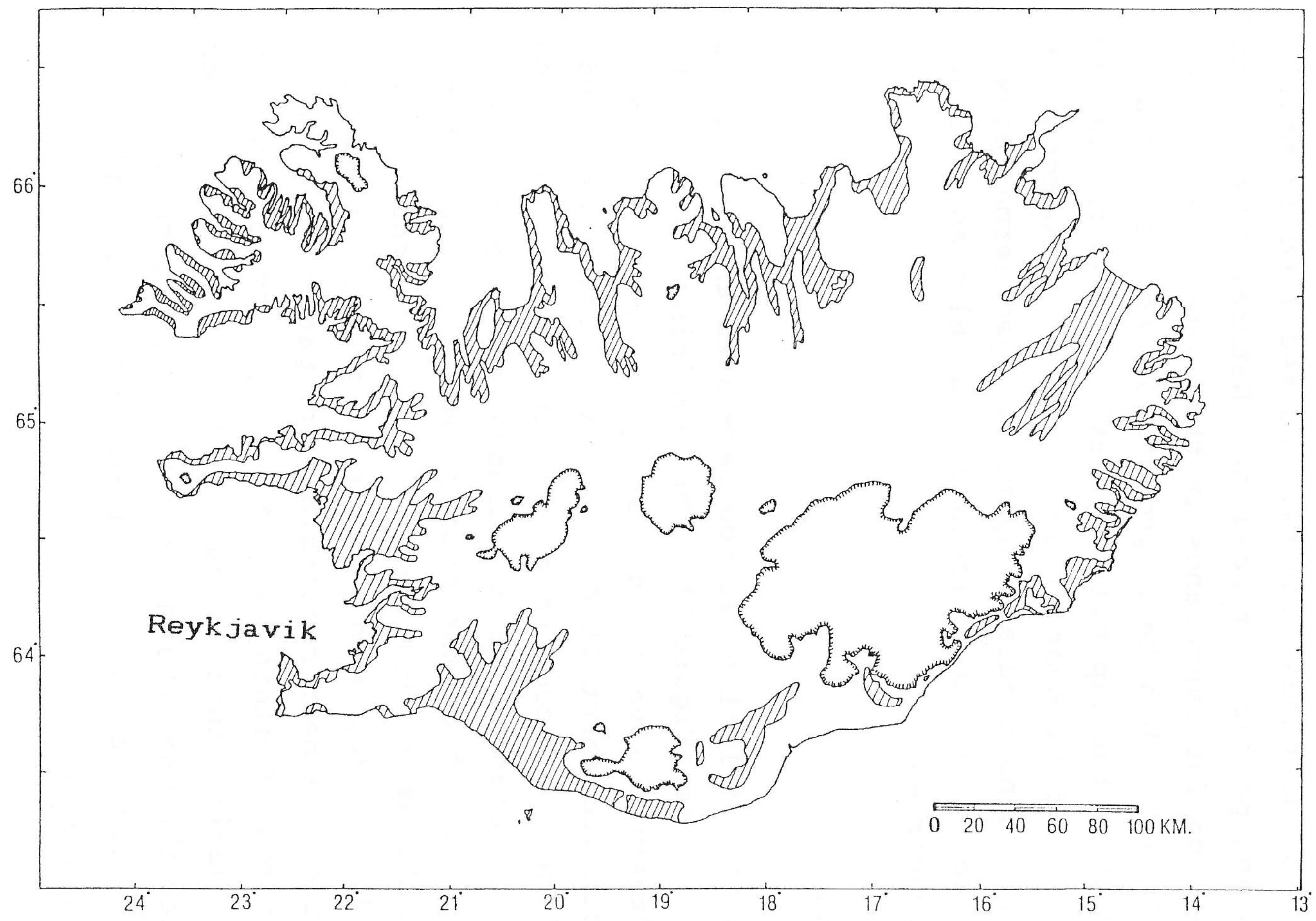

Figure 2. Inhabitated areas in 1980. (Gudbergsson 1984).

Fisheries and fish processing are the mainstay of the Icelandic economy. Agriculture, now consists almost entirely of animal husbandry (sheep, cattle and horses) and more than satisfies domestic needs. Land use is similar throughout the country. Farmed land is mainly hayfields and pastures or meadows. Naturally vegetated areas are used for rangelands in the summer, mainly for sheep. Industry has been growing in recent decades, particularly in the capital, Reykjavik, and in the larger towns. Iceland is poor in raw material resources but rich in energy, particularly hydro- and geothermal power. The standard of living in Iceland is as high as in other western countries.

Vegetation

Only 25% of Iceland is now vegetated and only 1% is covered by woods (Figure 3). The remaining 75% consists of sand deserts, lava fields, and glaciers. Because of cooling climate about 2500 B. P., vegetation declined. This decline was accelerated by settlement around 900 A.D. Woods changed to grasslands and heavy erosion began. About 60% of the country was vegetated at the time of settlement and about 30% of the country was covered with woods, mainly birch (Thorsteinsson 1981). Heavy grazing has been responsible for part of the change in vegetation. Draining of wetland by ditches has been extensive during this century and has in some cases accelerated the vegetation decline. Much effort has been put into stopping the resultant erosion, and some progress has been made.

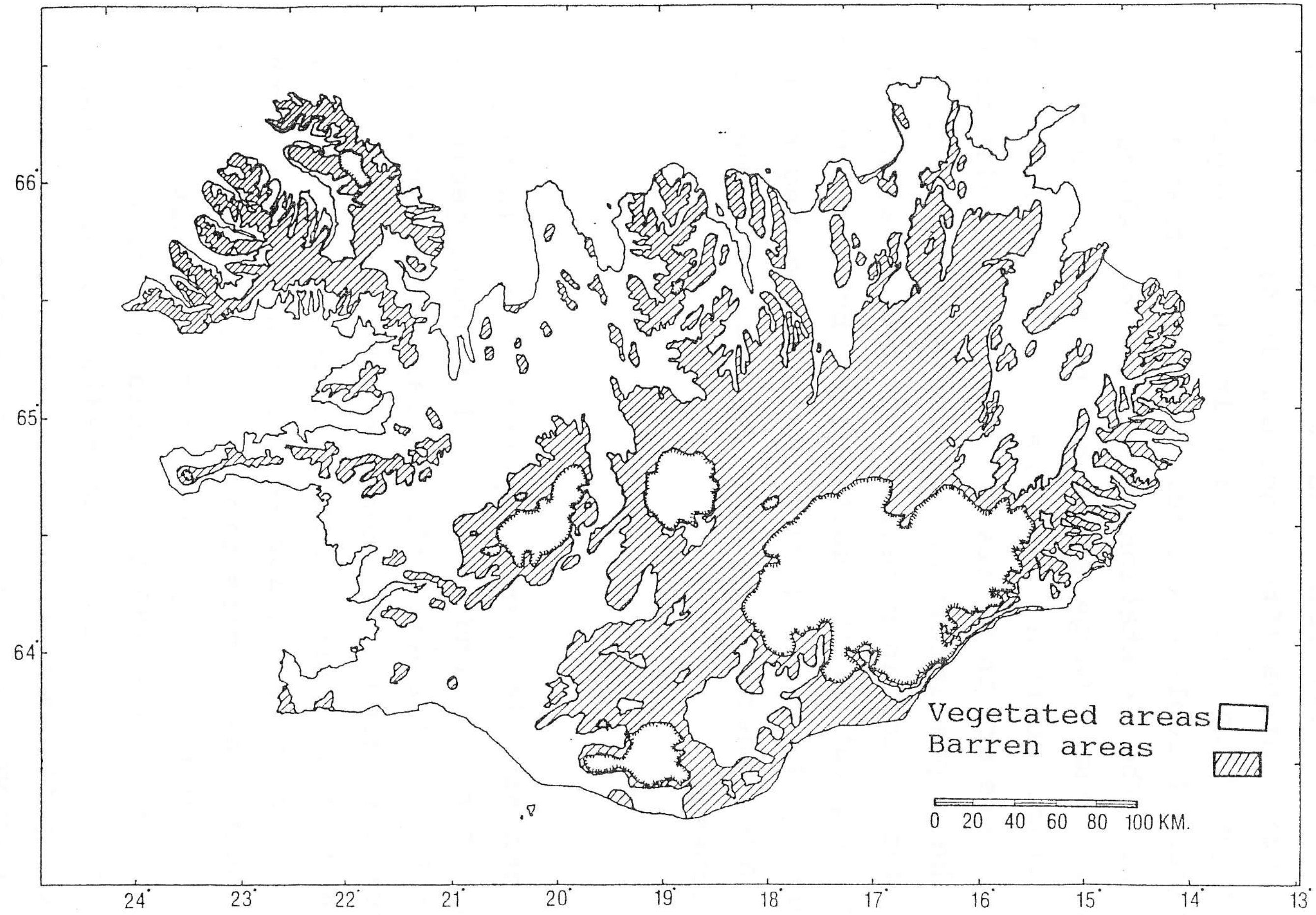

Figure 3. Vegetation in Iceland. (Thorsteinsson and Gudjonsson 1989)

The vegetation is subarctic with extensive grassland, mire vegetation, and heath vegetation with grass and dwarf shrubs (Steinthorsson 1974).

The vegetation and the soil in the geologically younger parts of Iceland are more sensitive than in the older parts. The vegetation is also more delicate at higher elevations. Large areas of the active volcanic zone are almost barren, and the remaining soil and vegetation there are in retreat. This is especially true in areas where precipitation penetrates deep into the porous ground. Aeolian material from the erosion areas can damage vegetation in nearby areas by covering the plants and by thickening the soil. The vegetation condition are generally better in areas outside the volcanic zones.

Geology

The geology is very important in classifying Icelandic watersheds and rivers. Different geological formations have different hydrological characteristics, and landscape is highly dependent on the geology.

Iceland is a young volcanic island (< 16 m.y.). Active volcanic zones run across the country in a north-east / south-west direction. Its bedrock is predominantly effusive igneous rocks. Basalt is the predominant rock type (80-85%), acid and intermediate rock constitute about 10%, and sediments of volcanic origin make up the rest (Saemundsson 1979).

It has proved convenient, because of major phases in Iceland's formation, to divide the geological history into four epochs: Tertiary (> 3.1 m. y.), Plio-

Pleistocene (0.7-3.1 m. y.), Pleistocene (< 0.7 m. y.) and Holocene (< 0.01 m. y.). These epoch do not correspond exactly with international time scales (Saemundsson 1979, Hjartarson et al. 1980). According to the theory of plate tectonics (Wegener 1915), Iceland is a hot spot on an ocean ridge and the active volcanism is due to change in direction of the Mid-Atlantic ridge (Jakobsson 1979, Kristjansson 1979). Like locations on other ocean ridges, Iceland is drifting outward from the volcanic zones in both directions (Vine and Mathews 1963). The continuous volcanism immediately fills up the gap between the plates (Le Pichon 1968, Morgan 1968). The drift rate is about 1 cm each year in each direction (Kristjansson 1979). At present, Iceland would be growing but for the erosion rate, estimated to be about equal the growth rate (Steinthorsson 1987). The rocks generally dip gently towards the center of the rift zone. The age of the bedrock reflects the outward drift. The rocks are youngest in the active volcanic zones and increase in age with distance from the zones (Saemundsson 1979). The actual rift zone of the ocean ridge cuts the island in a direction from SW to NE (Figure 4) (Saemundsson 1979, Steinthorsson 1981).

The rift zone has been displaced through time (Kristjansson 1979), this explaining rather complex distribution of rocks of different age and type (Saemundsson 1979). For example, the rift zone at Reykjanes - Langjokull (Figure 4) was initiated 6-7 m. y. ago when the rift zone jumped from the Snaefellsnes area to its present more southerly and easterly location. Volcanism during the Plio-Pleistocene (0.7 - 3.1 m.y.) was not confined to the present axial rift zone but

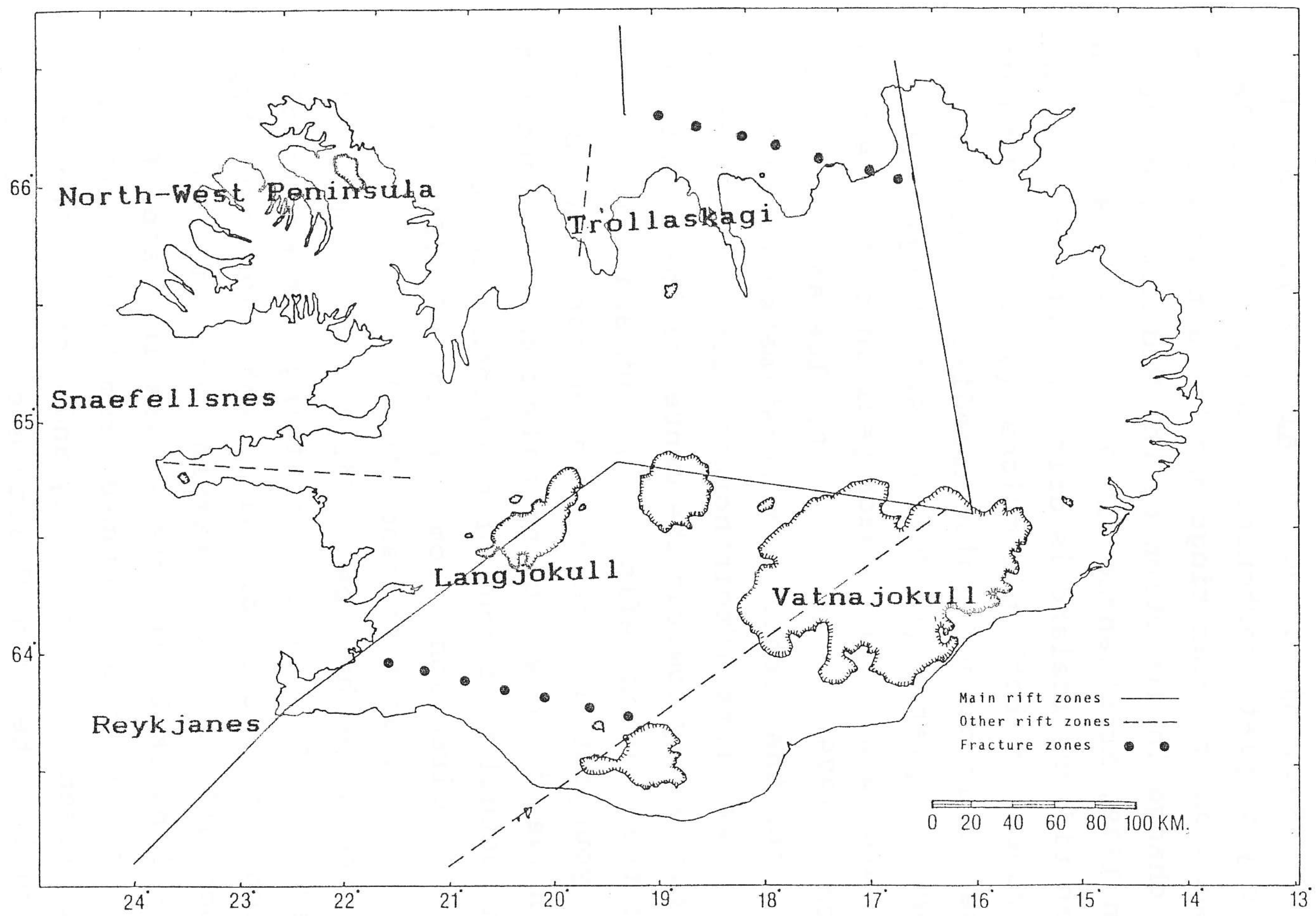

Figure 4. The mid-Atlantic ocean rift zone and Iceland.

occurred in other areas of Iceland, one perhaps older rift zone in Skagi in north Iceland, parallel to the present rift zone and now extinct and one zone at Snaefellsnes in west Iceland, transverse to the present rift zone and still active. Volcanism southwest of Vatnajokull began 2 m.y. ago and is parallel with the rift zone of Reykjanes - Langjokull. Since then these two parallel volcanic zones have been active in south Iceland (Figures 4 and 5). Different rocktypes originate from the actual rift zone (tholeiite series) than from volcanic zones outside the rift zone (transitional alkali and alkali series) (Jakobsson 1979, Steinthorsson 1981, Gudmundsson 1986). Active periods of volcanic systems have been found to vary from 300,000 years to 1 m.y (Saemundsson 1979). About 32 volcanic systems are considered to be active at present (Figure 6) (Gudmundsson 1986), 24 of which have erupted since deglaciation (Saemundsson 1979).

Earthquakes Movement of land and landslides are most likely to occur where there is some tectonic activity. In Iceland the tectonic activity is related to the mid-Atlantic plate boundary, especially to two major fracture zones, where the plate boundary is displaced. One of the zones is in south Iceland, the other in north Iceland and north of Iceland (Einarsson and Bjornsson 1979) (Figure 4). Faults often create waterfalls, which can inhibit movement of fishes. Such waterfalls are in some rivers in South Iceland.

In most regions, lava piles are tilted towards the present volcanic zone (Saemundsson 1979, Sigurdsson and Sigbjarnarson 1985).

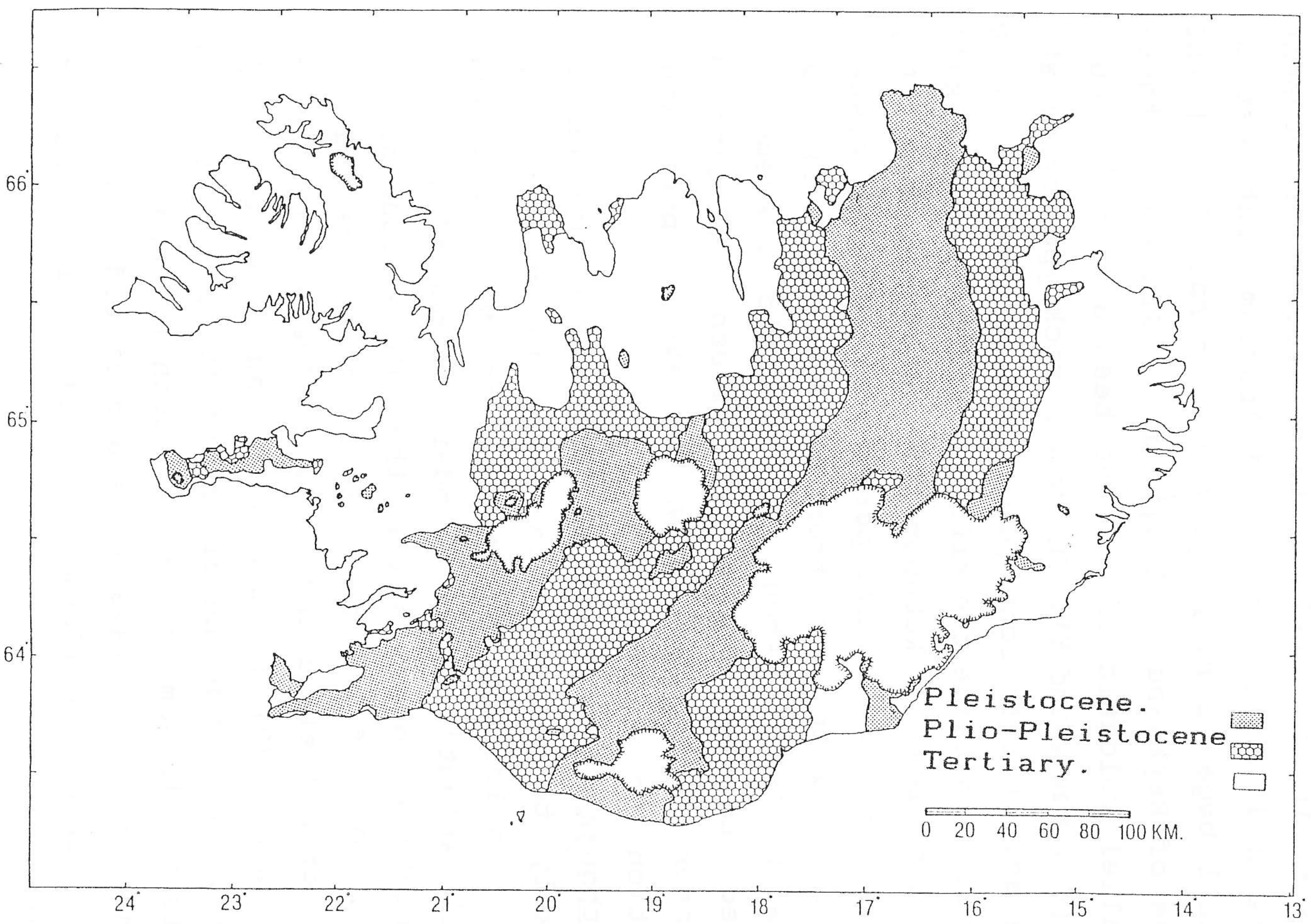

Figure 5. The age of geological formations in Iceland.

(Gudbergsson 1986).

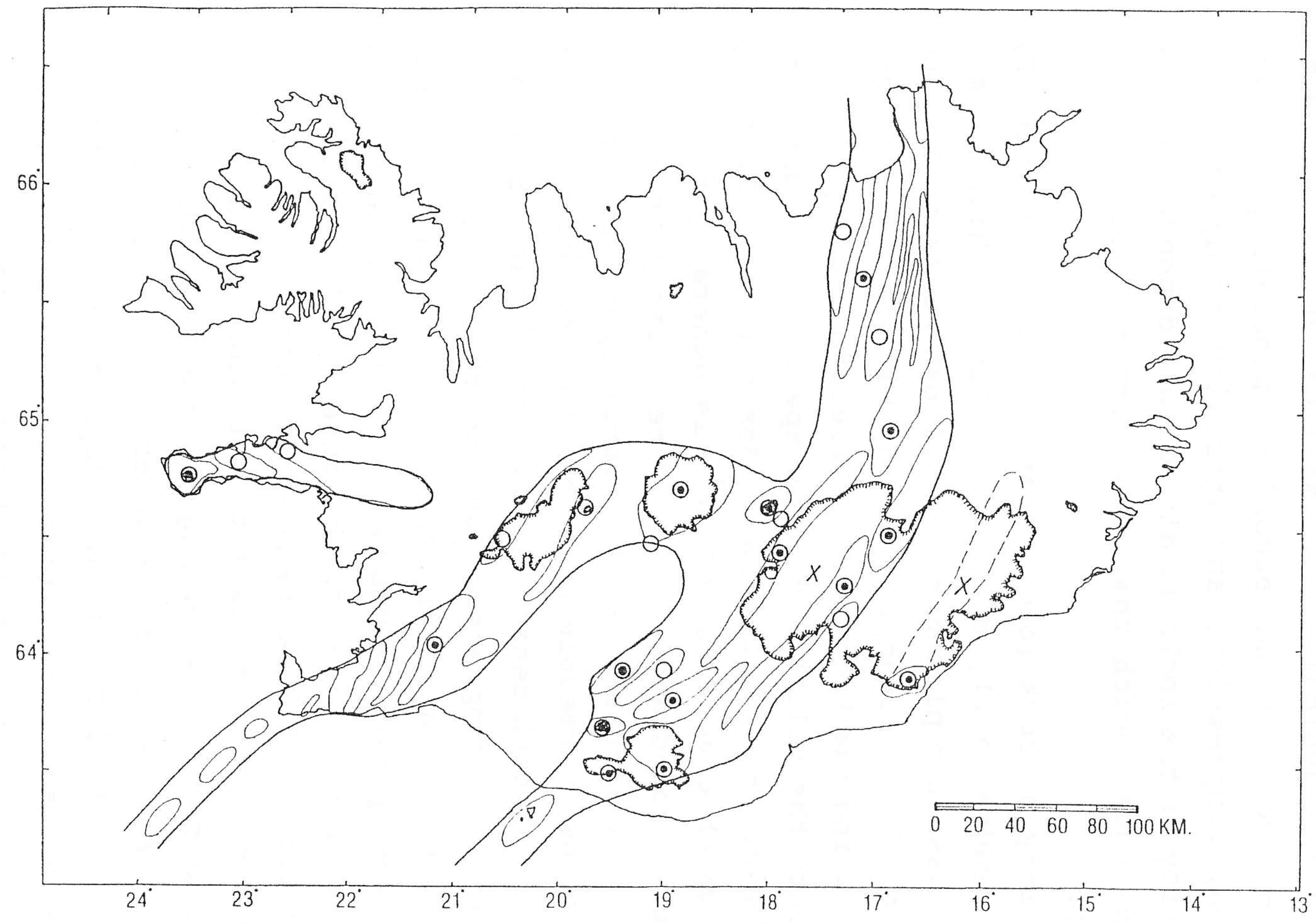

Figure 6. Active volcanic systems in Iceland. (Gudmundsson 1986).
Central volcanoes marked with dots.

Hydrogeology The interaction of land and water must be considered when watersheds and rivers are to be classified. The permeability and hydraulic conductivity of Icelandic geological formations decreases with increasing age, due to secondary mineralization and alteration, compression, and intrusion of dykes. The permeability of the rocks is also highly dependent on the conditions under which they were formed (Hjartarson et al. 1980).

Tertiary bedrock (older than 3.1 m. y.) (Figure 5) consists predominantly of basaltic lavas, which formed classical basaltic plateaus. The oldest rocks of Iceland are 16 m.y. old (Miocene). The basaltic plateaus changed markedly during the ice age (Plio-Pleistocene) by glacial erosion into the well known landscape of high mountains, deep valleys, and fjords (Saemundsson 1979). Tertiary bedrock, which covers 50,000 Km^2, is generally not very permeable. Groundwater divides are closely related to the topography (Arnason 1976). Tertiary bedrock in east Iceland is less permeable than that in west Iceland. The eastern pile is both denser and more zeolitised, probably because of more compression due to thicker icecap and longer ice age duration in the east than in the west. The north-west peninsula has markedly higher permeability than other Tertiary areas because of low secondary mineralization (Sigurdsson and Sigbjarnarson 1985). This affects the runoff characteristics in the Tertiary areas. Where the permeability is higher, the bedrock acts to store water and hence buffer water-flow, this resulting in lower fluctuations in discharge of the watershed. Dyke swarms and intrusions act as barriers for groundwater flow in some locations (Hjartarson et al.

1980).

Quaternary bedrock (younger than 3.1 m. y.) (Figure 5) is very heterogeneous in nature and was characterized by the cold climate of ice age under which it was formed. Glacial erosion also changed the bedrock's character. Typical lavas are not formed in subglacial eruptions. Eruption under thick ice or water forms pillow lava interstratified with various types of breccia and hyaloclastite, but eruption at shallow depth forms mostly tephra or tuff. Tephra is later metamorphosed into palagonite (Kjartansson 1943). Old palagonite is almost impermeable, while pillow lava is highly permeable. This affects the movement of water. The main differences between Plio-Pleistocene (0.7-3.1 m. y.) and Pleistocene (0.01-0.7 m. y.) rocks are that Plio-Pleistocene rocks are more eroded and have a higher degree of secondary mineralization than Pleistocene rocks and are, therefore, less permeable (Hjartarson et al. 1980).

Plio-Pleistocene areas cover 25,000 km^2 and lie between the Tertiary areas and the Pleistocene (neo-volcanic) zone (Figure 5). The topography is very different from the flat lava plains of the Tertiary formation. Subglacial volcanism created uneven topography with elongate ridges of hyaloclastite and pillow lava (Saemundsson 1979). These formations erode easily and have therefore been heavily eroded both by glaciers and later by water. The water has flowed overland, due to low permeability, and has made deep gullies and gorges in some areas. Gorges are also found in other places. Most of these are old river channels were formed during deglaciation by large glacial rivers fed by meltwater.

Pleistocene formations in the neo-volcanic zone cover about 30,000 km^2 (Figure 5). The volcanic rocks of the Pleistocene are of two types with regard to structure and morphology (Figure 7). One type includes extensive subaerial lava flows which erupted during interglacial periods. Glacial erosion later deprived these lavas of their surface features. The other type includes subglacial pillow lavas and hyaloclastite rocks (Figure 7). Many volcanic systems of the upper Pleistocene are still active (Figure 6) (Saemundsson 1979).

Deglaciation started earlier in west Iceland and in north Iceland (11,000 - 13,000 years) than in south-east Iceland, especially in the highlands there (9.000 years) (Einarsson 1968). Postglacial lava fields (Figure 8) in Iceland (Holocene, younger than 0.01 m.y.) are highly permeable, and almost all precipitation that falls on them penetrates into them. Vast amounts of water can be discharged from lava aquifers in a limited area. And vast amounts of water can be recharged, since rivers can partly disappear into lava (Hjartarson et al. 1980). Fissure swarms can have a strong influence on groundwater flow, and many of Iceland's largest springs are associated with fissure swarms (Hjartarson et al. 1980). In the volcanic zone, groundwater divides can be different from surface divides (Arnason 1976).

Soil and loose sediments Loose sediments in Iceland are in most places very thin. During the ice age, all sediments were swept into the sea. The outer part of the Icelandic shelf is made up of these sediments, which are several hundreds of meters thick (Kristjansson 1976).

Highly permeable loose sediments are fine and coarse

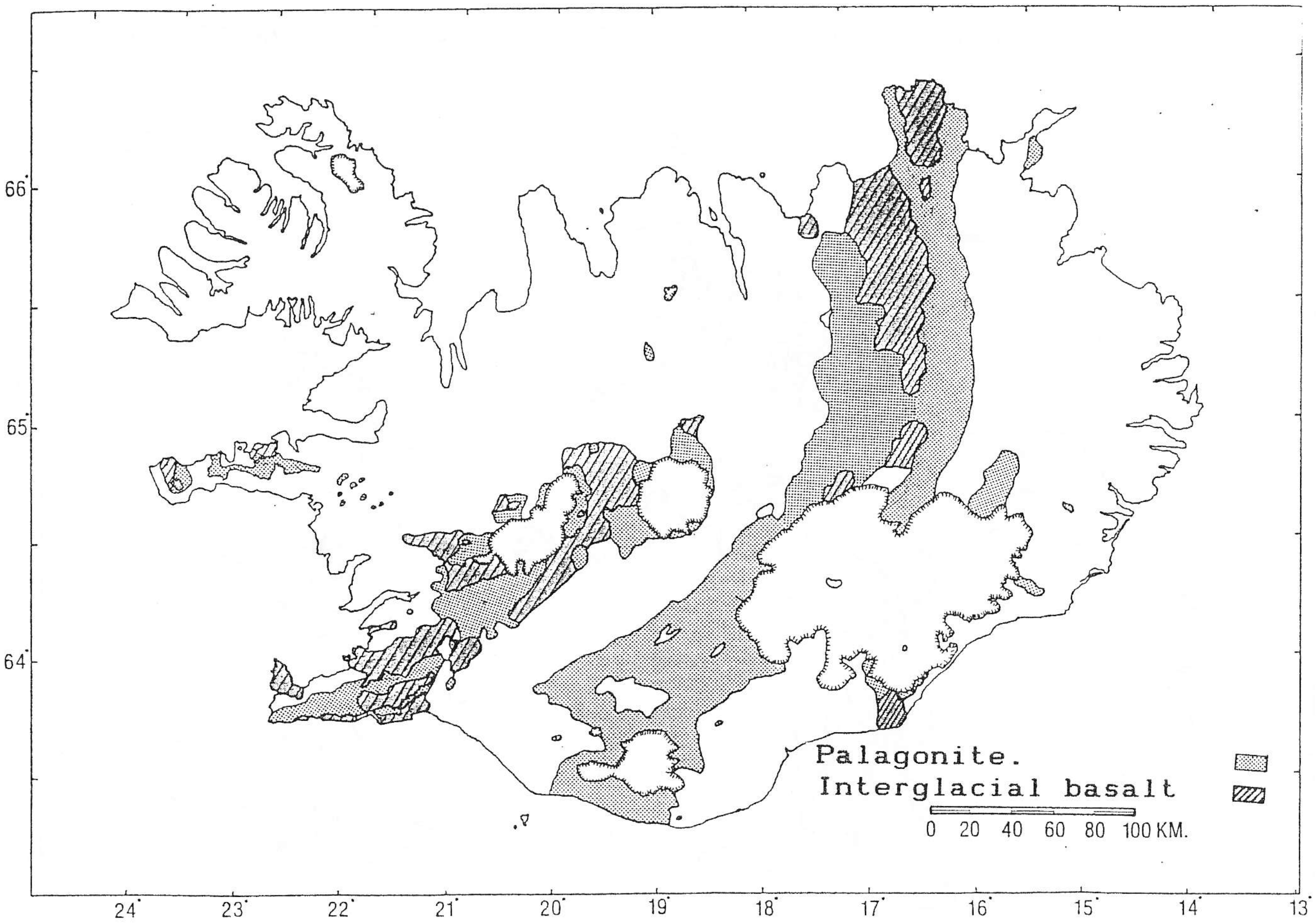

Figure 7. Pleistocene formations of Iceland. (Gudbergsson 1986).

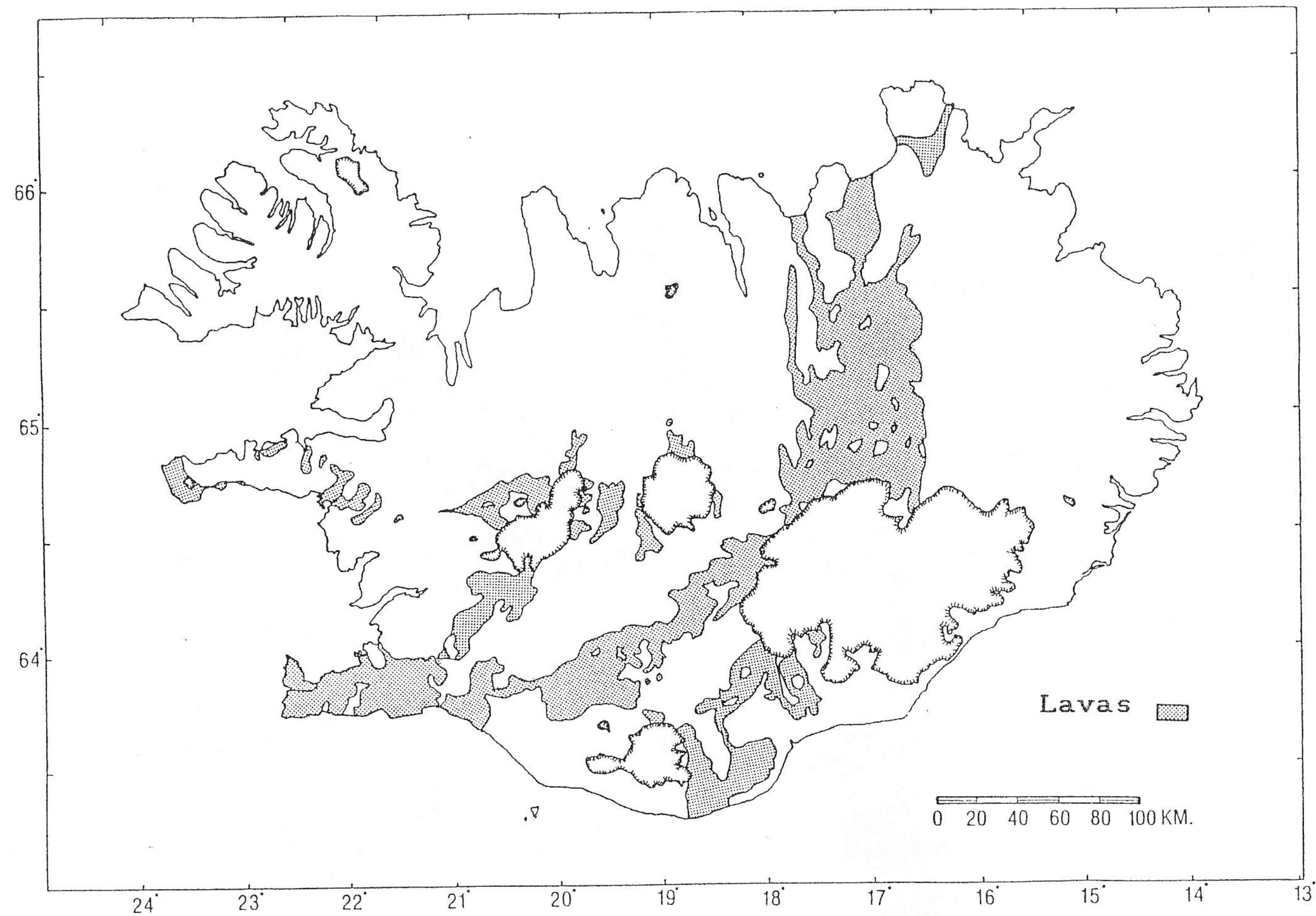

Figure 8. Neovolcanic formations of Iceland. (Gudbergsson 1986).

alluvium. Semipermeable loose sediments are moraines and valley fillings. Moraines vary in permeability, depending on the amount of clay and silt in them. A high fraction of silt and clay makes a moraine dense and impermeable. Glacial moraines and sediments play a large role in the hydrology of some flat heath areas in north Iceland. In the bigger valleys of the country, valley fillings were formed in interglacial and Holocene times. The valley fillings are rather heterogeneous sediments with variable but generally low permeability (Hjartarson et al. 1980). In south Iceland, alluvial and glacio-fluvial deposits are extensive (5,000 km^2). The majority of these deposits have come from glacial rivers, but the origin of large fraction of these sediments is volcanic ash from subglacial eruptions.

The soil cover in Iceland is discontinuous and delicate. The central highlands are more or less barren. The young volcanic areas are in a desert-like condition as water soaks into the porous ground. In Tertiary and Plio-Pleistocene areas the soils are more boggy and peat is extensively developed (Saemundsson 1979, Hjartarson et al. 1980).

Landscape

It is possible to divide Iceland into several topographical regions based on landscape. The landscape is the result of the type of geological formation and its erosional history.

In the Tertiary areas there are several types of landscape. Glacial erosion has incised the old basaltic plateaus. The typical fjord landscape is the dominant landscape. The fjord landscape is dominant in east Iceland as well as in the north-west peninsula. It is less clear, but still the dominant form, in north Iceland and west Iceland. Instead of fjords there are in some places deep valleys. Some of these are old fjords filled with fluvial sediments at their upper ends. Lowlands in the Tertiary areas are usually boggy and vegetated, and are in many places valuable farmlands. The mountains are usually mostly barren. The fjords and the valleys sometimes continue long distances underwater as submarine valleys.

There are two areas in north-west and north-east Iceland that differ from the typical landform. These areas are flat, old glacial moraines with some glacio-fluvial sediments in between. These areas are at an elevation of 300-600 m. above sealevel. They form vegetated flat heaths having moraine hills with numerous lakes and ponds in between. The rivers in these areas differ greatly in character from rivers in other Tertiary areas.

The Plio-Pleistocene areas lie between the Tertiary areas and the neo-volcanic zone. In some places there are no clear boundaries between these formations but rather a transition from one type to the other. The Plio-Pleistocene formations have lost their surface features because of glacial erosion. The land in these areas has usually been incised by water that has formed shallow valleys with ridges between the valleys. In some places deep gullies have been formed in these valleys. The rivers and the valleys, as well as the ridges, are generally lying in the same direction as the rift zone. This is indicative of an older row of volcanic formations, on a fissure in the direction of the rift zone, now deprived of their original surface characters. A river usually flows sooner or later into its neighboring parallel valley, and in this way there have been formed dense networks of rivers and streams in these areas. This is especially true in south Iceland. In north Iceland, where precipitation is lower, the landscape is flatter or it has the form of undulating hills like the Tertiary heaths. Still another form is like the deflation flats of the neo-volcanic formations. Direct runoff rivers are the dominant type, but springs are also found in some places where the ground is more permeable.

The neo-volcanic zones have a rather complex landscape. In most places, recent lava, often with rough surface (pahoehoe) but sometimes flat (aa), is the dominant feature. In some places no volcanic activity has occurred since deglaciation, and hence large areas are flat, barren, and sandy. These flat areas are often interrupted by volcanic mountains of several kinds. Volcanic craters usually lie in a row in the direction of the rift zone on a fissure swarm forming long ridges. Fissure systems usually have a central volcano (Figure 6). Large areas are without surface water, and deflation has destroyed vegetation and left large areas barren. Surface water exists in the flat sandy areas very temporarily in the spring, when the ground can be frozen and impermeable. Then mud streams may flow, but later nearly all the water penetrates into the ground. Large quantities of surface material are blown away in the sandy areas during dry periods. Areas with interglacial lavas are more stable and resistant to wind erosion, as are areas with recent lavas, even though all precipitation penetrates into these lavas (Figures 7 and 8). Spring-fed rivers are the dominant type in these areas. Some glacial rivers, having dense water-courses made of glacial silt and clay, run through these areas. These rivers are forced to run in the direction of the volcanic fissures, often between two volcanic ridges. The groundwater underneath can flow in a different direction (Arnason 1976).

It is possible in a more detailed fashion to divide the country into several regions based on landscape types (Preusser 1976). This does not, however, serve the purpose of this study.

Climate and ocean condition

Rivers are only one part of the hydrological cycle, and their characters depend heavily on the climate. The climate in Iceland is wet and cool. Oceanic influences on the climate are strong. A warm sea current, the Gulf stream, comes from the south and flows northward along the Norwegian coast. The Irminger current, a branch from the main stem, flows along the south coast of Iceland and goes clockwise around the island. In some years, this current does not reach to the sea north of Iceland. This causes failure in primary production in the sea north and east of Iceland. The East-Icelandic current, a branch of the cold East-Greenland current, flows to the east north of Iceland and then to the south, east of Iceland (Stefansson 1961) (Figure 9). In some years, this current along with other factors forces polar sea-ice to the north and east coast of Iceland. In these instances,

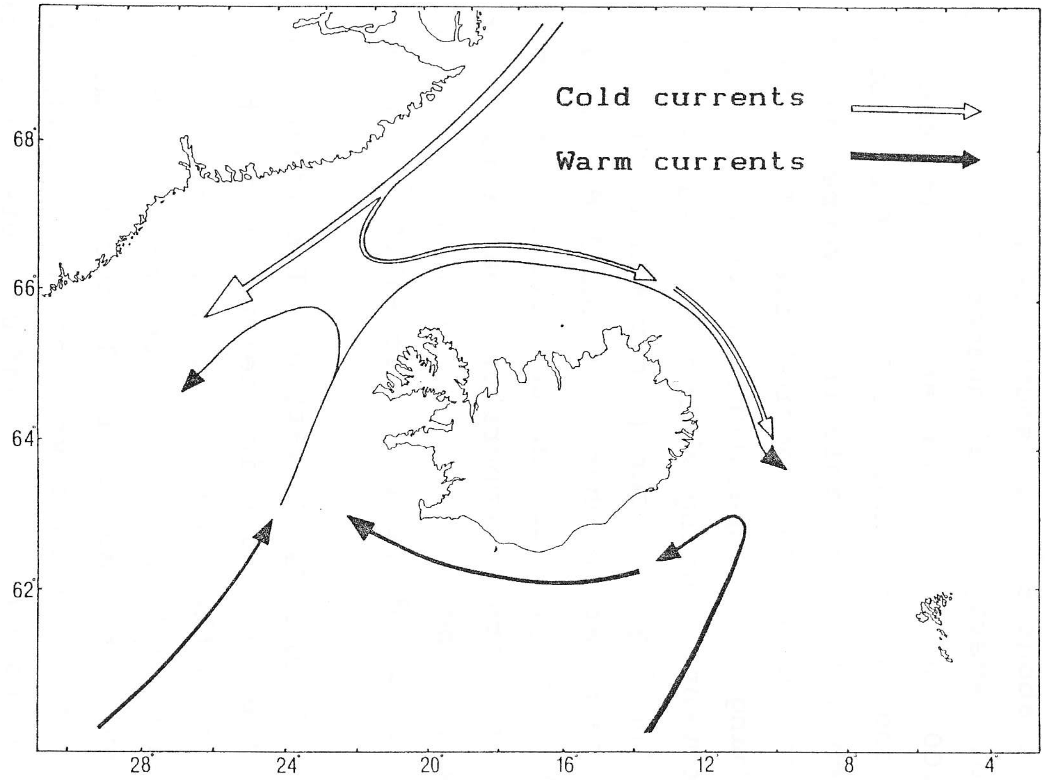

Figure 9. Sea currents around Iceland. (Stefansson 1961).

the polar ice has a depressing influence on sea and air temperatures (Bergthorsson 1969 and 1972, Einarsson 1976).

Temperature The climate of Iceland is oceanic near the shore, but more continental in the central highlands. The annual temperature range is narrow, with cool summers and mild winters (Figures 10 and 11). The annual mean temperature is about 5 ^{o}C in south Iceland and 3 ^{o}C in north Iceland. Average annual number of days of frost is around 100 in the south and 150 in the north (Eythorsson and Sigtryggsson 1971). The ground is usually frozen and impermeable from November to April. Frost is rare during the period from June to mid-September. Changes in temperature and wind direction and speed are frequent. During winter this causes frequent freezing and thawing to occur (Einarsson 1976).

Diurnal temperature change is small during winter (0.2-0.8 ^{o}C) but greater in the summer, especially inland. Common diurnal temperature change is 4 - 5 ^{o}C in the summer. The highest measured temperature in Iceland is 30.5 ^{o}C and the lowest is -37.9 ^{o}C (Einarsson 1976).

Sunshine and global radiation The length of the day from sunrise to sunset in Iceland is short in the winter and long in the summer. The shortest day in Reykjavik, south Iceland, is 4 hours and 8 minutes, and the longest day in the summer is 21 hour and 9 minutes. Respective numbers for Akureyri, north Iceland, are 3 hours and 5 minutes and 24 hours and 0 minutes (Einarsson 1976).

The amount of radiation is affected by the angle of the sun and the amount of cloudiness. The amount of

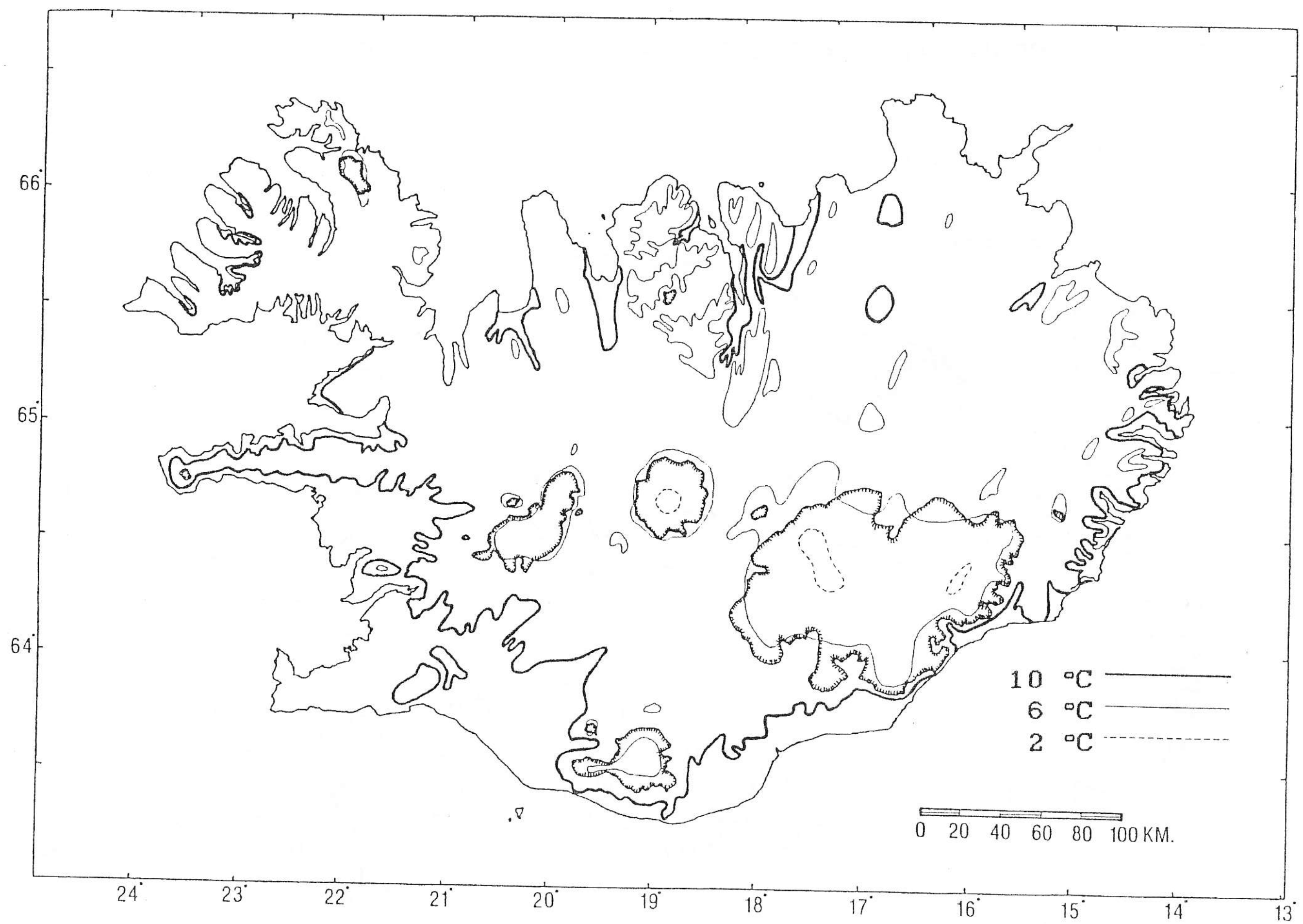

Figure 10. Average temperature in Iceland in July 1931-1960.

(Einarsson 1976).

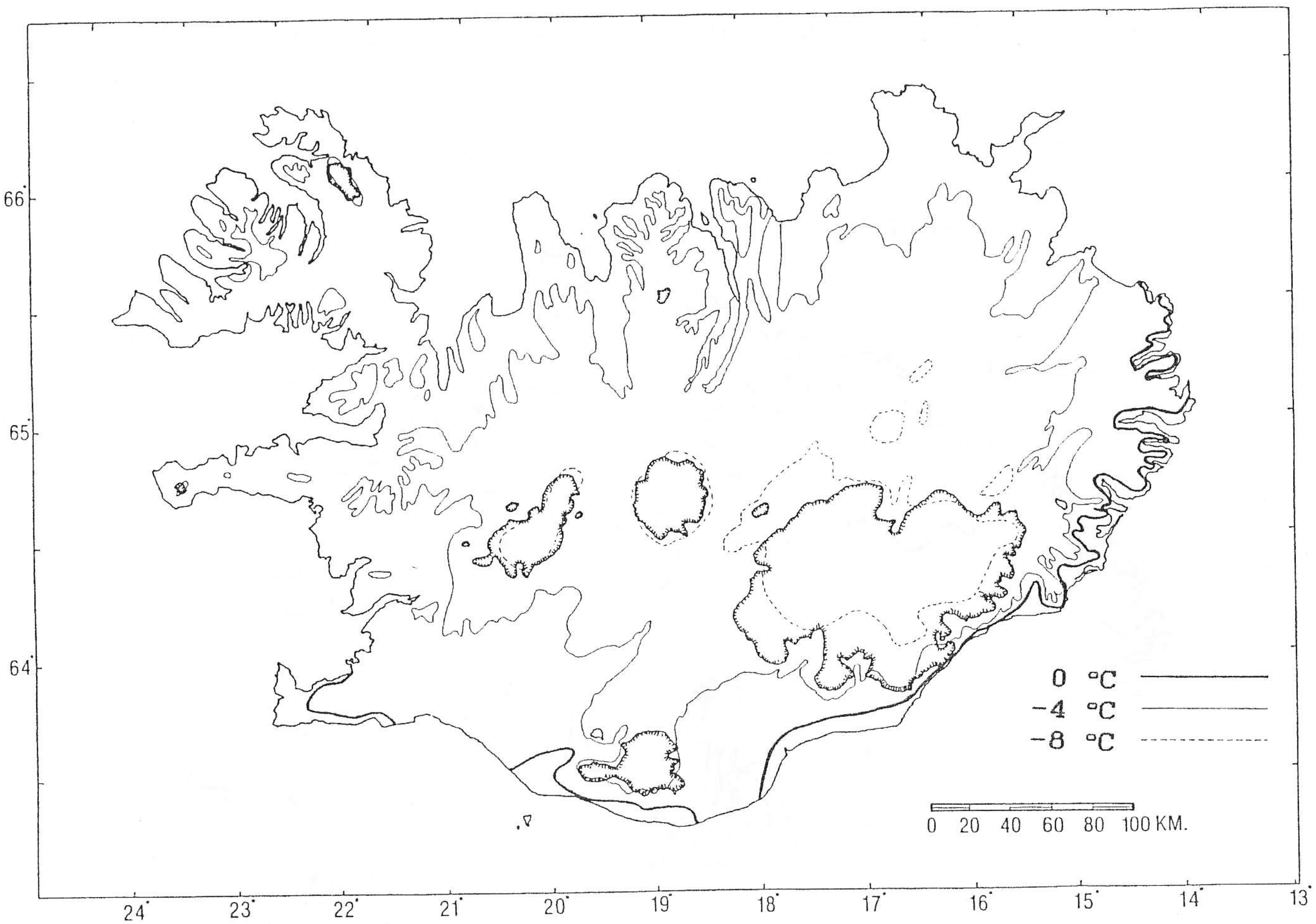

Figure 11. Average temperature in Iceland in January 1931-1960. (Einarsson 1976).

cloudiness and hours of sunshine have been measured in Iceland (Einarsson 1969, Berthorsson 1977). From these data the global radiation has been calculated (Figure 12) (Einarsson 1969). Radiation is very important in increasing the temperature of river waters in the summer.

Precipitation Iceland is in the route of maritime depressions, which are saturated with moisture. The most common wind directions are southerly to south-easterly. This causes high precipitation, especially in south-east Iceland. There precipitation is 1400 mm/year in the lowland and up to 4000 mm/year in the mountains. Precipitation of 1000 mm to 1600 mm/year is common in the south and in the west, while 400 mm to 600 mm/year is common in the north and the north-east (Sigfusdottir 1964, Einarsson 1976) (Figure 13).

The precipitation is generally highest in the fall and lowest in the spring. For the country as a whole, October has the highest precipitation, 12% , and May the lowest, 5% (Einarsson 1976).

More downpouring can be expected in south Iceland than in north Iceland, especially in south-east Iceland. There in the lowland, precipitation during 24 hours has been measured to be up to 120 mm (Berthorsson 1968).

A considerable part of the precipitation falls as snow, especially in the North. In south Iceland snow is 5 - 7% of the precipitation in the winter-months (October - April), while in the north about 50% of the annual precipitation is snow and 85 - 97% of the winter precipitation is snow. In west Iceland and east Iceland the proportion of snow in the precipitation is between that of south and north Iceland (Einarsson 1976). These measurements are from lowland stations. The proportion

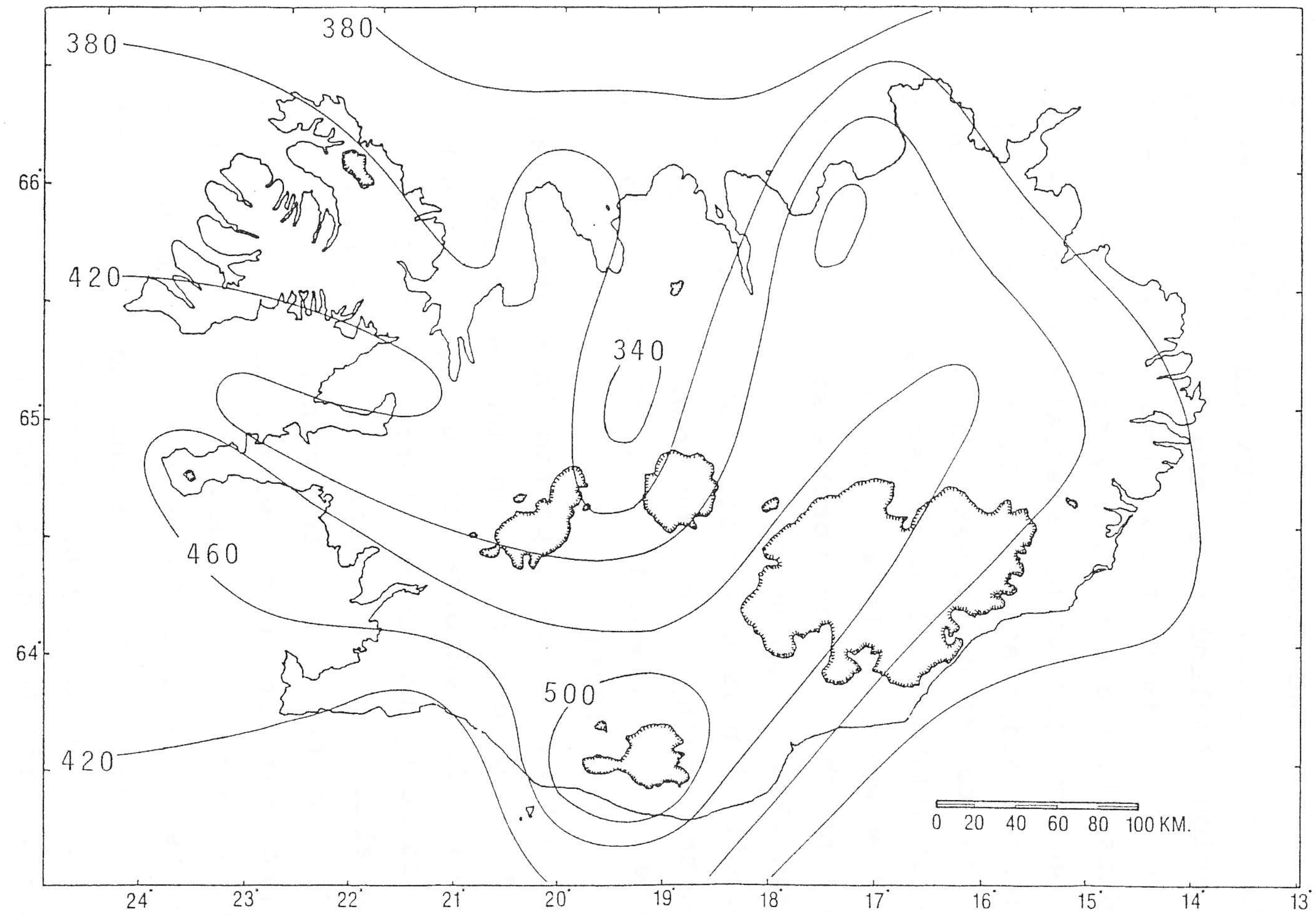

Figure 12. Distribution of global radiation in Iceland 1958-1967 in July, expressed in cal/cm² day. Lines at 40 cal/cm² day (Einarsson 1969).

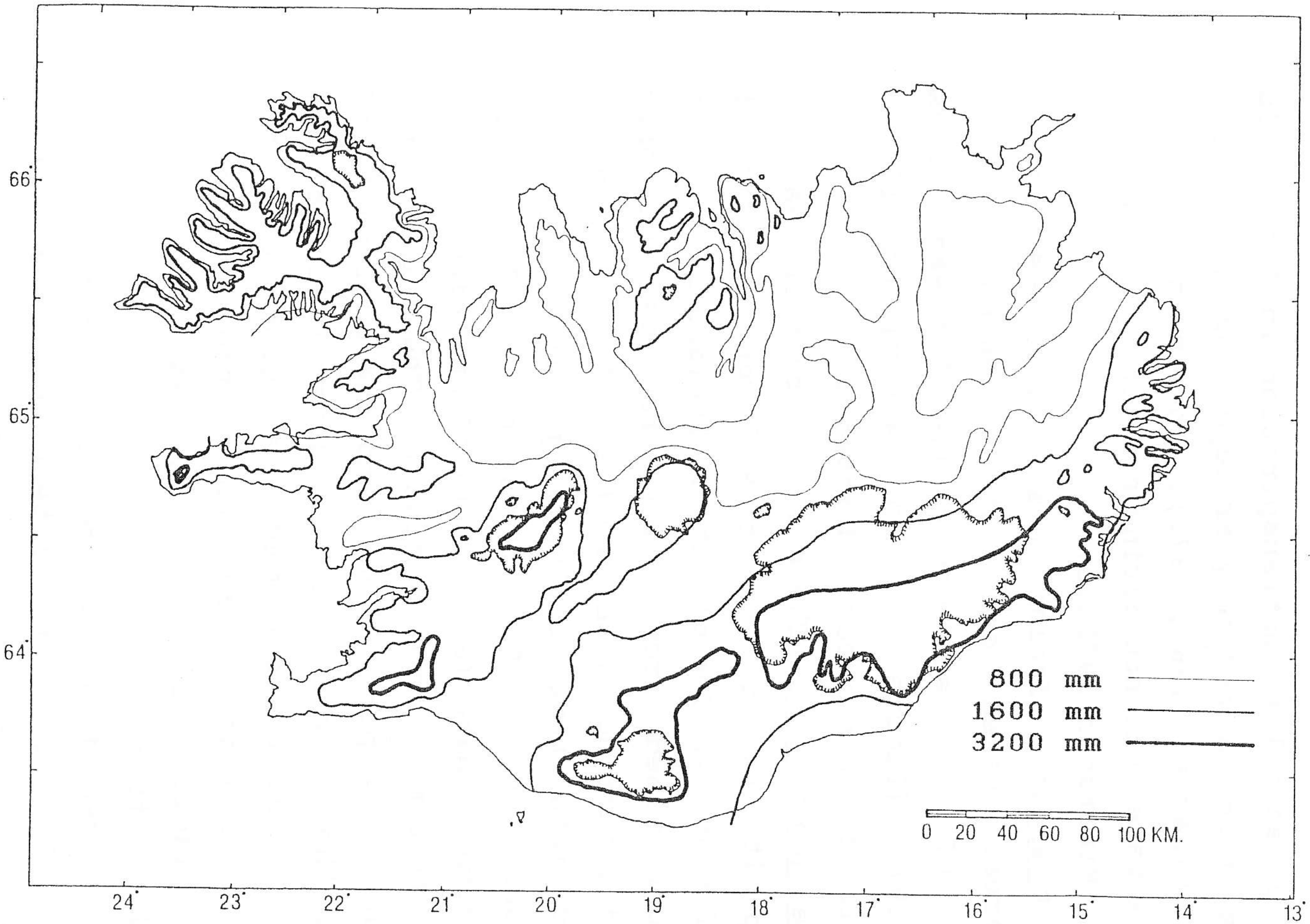

Figure 13. Average annual precipitation (mm) in Iceland 1931-1960. (Sigfusdottir 1964).

of snow is higher in the mountains. The snow appears earlier in the fall and melts later in the spring in north Iceland, and there is more snow depth (Einarsson 1976).

Annual potential evapotranspiration in Iceland is in the range of 360 to 560 mm/year depending on location (Figure 14) (Einarsson 1969, 1972). In some areas there is a negative water balance during some parts of the year (Figure 15) (Einarsson 1972a,b).

Forecast areas Iceland has been divided into 9 forecast areas based on weather conditions and correlation of weather conditions between areas (Einarsson 1978) (Figure 16). Such a division aids in classification of watersheds and rivers.

Climate in the past There is interest in learning climate capacity by looking at a larger numbers of weather performances. The climate in Iceland in the past has been determined from fossil records, historic records, and geomorphological studies. Major trends in Icelandic climate have followed global changes in climatic conditions. The earliest fossil records indicate a warm climate (average 10 ^{o}C and rare frosts) from 16 m.y. to 8 m.y. before present. The climate grew cooler during the upper Miocene, and the cooling trend continued in the Pliocene. In the lower Pliocene, the temperature of the coldest month was close to 0 ^{o}C. During the upper Pliocene and during the Pleistocene about 20 glaciations occurred, as seen from stratigraphical studies.

The Pleistocene floras became more and more like the present one. Two out of the latest three glaciations were most severe and ice covered all of the island except

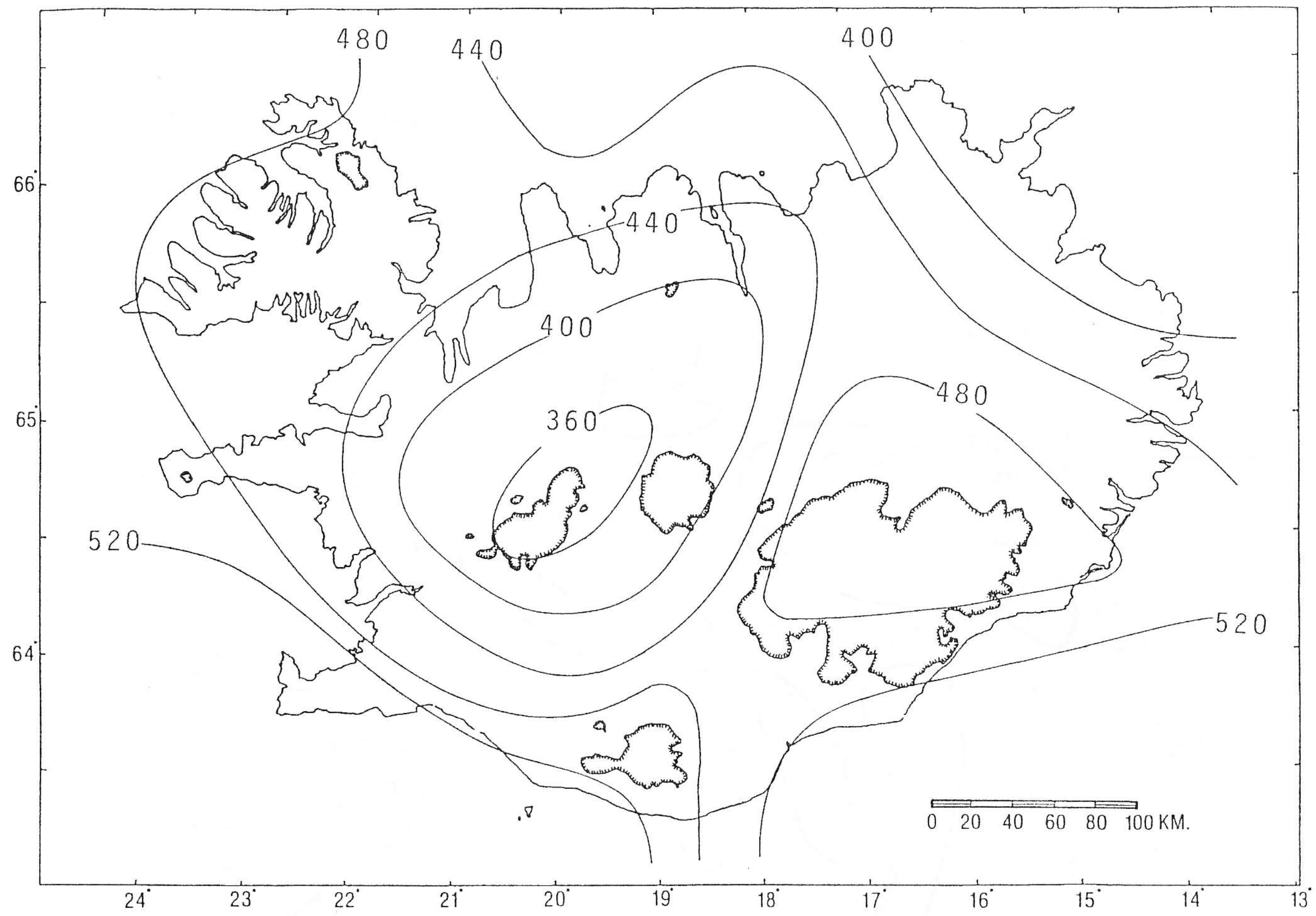

Figure 14. Distribution of potential evapotranspiration (mm) 1958-1967. Annual values. Lines at 40 mm intervals. (Einarsson 1972b).

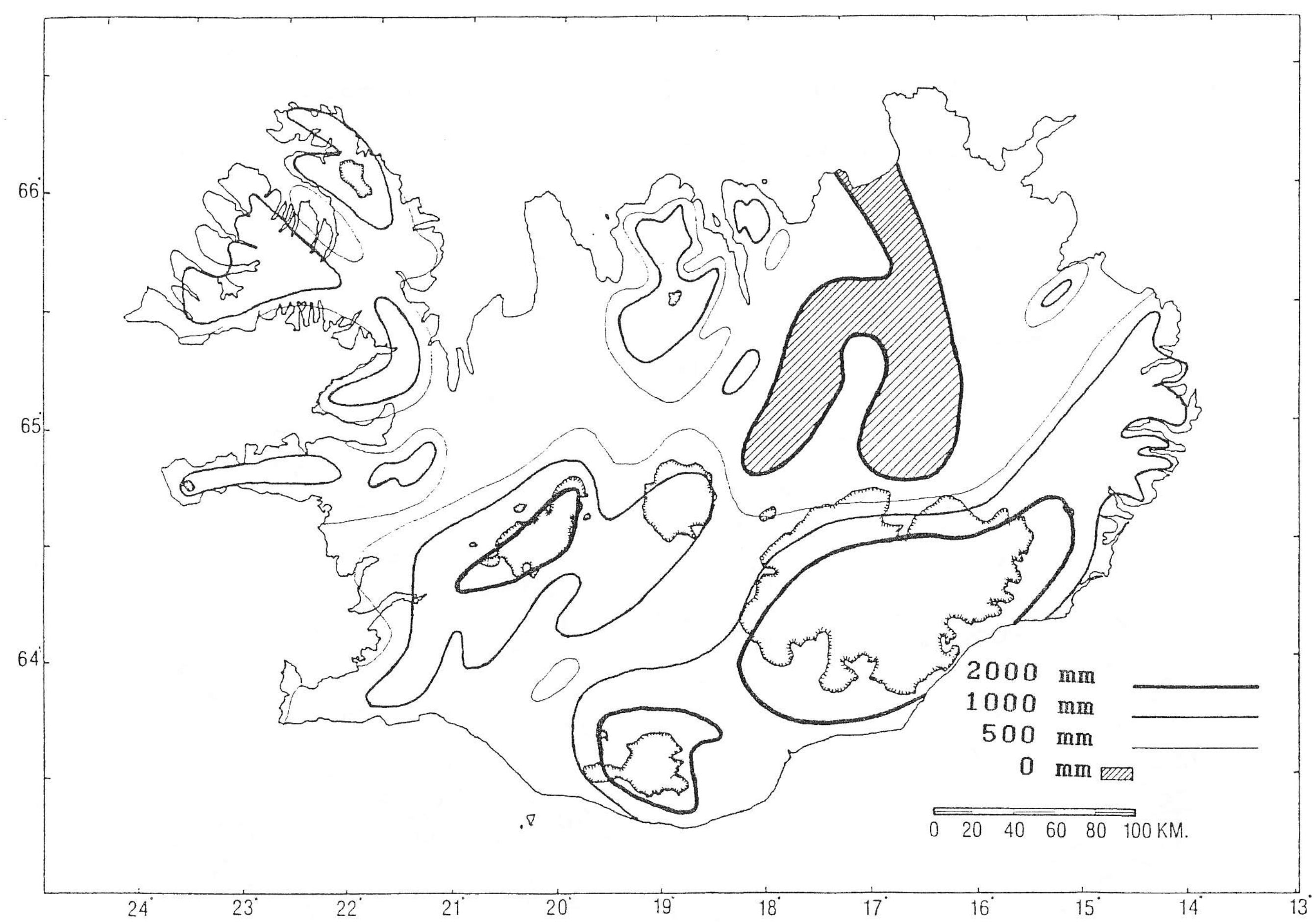

Figure 15. Potential water balance (mm). Annual values.

(Einarsson 1972b).

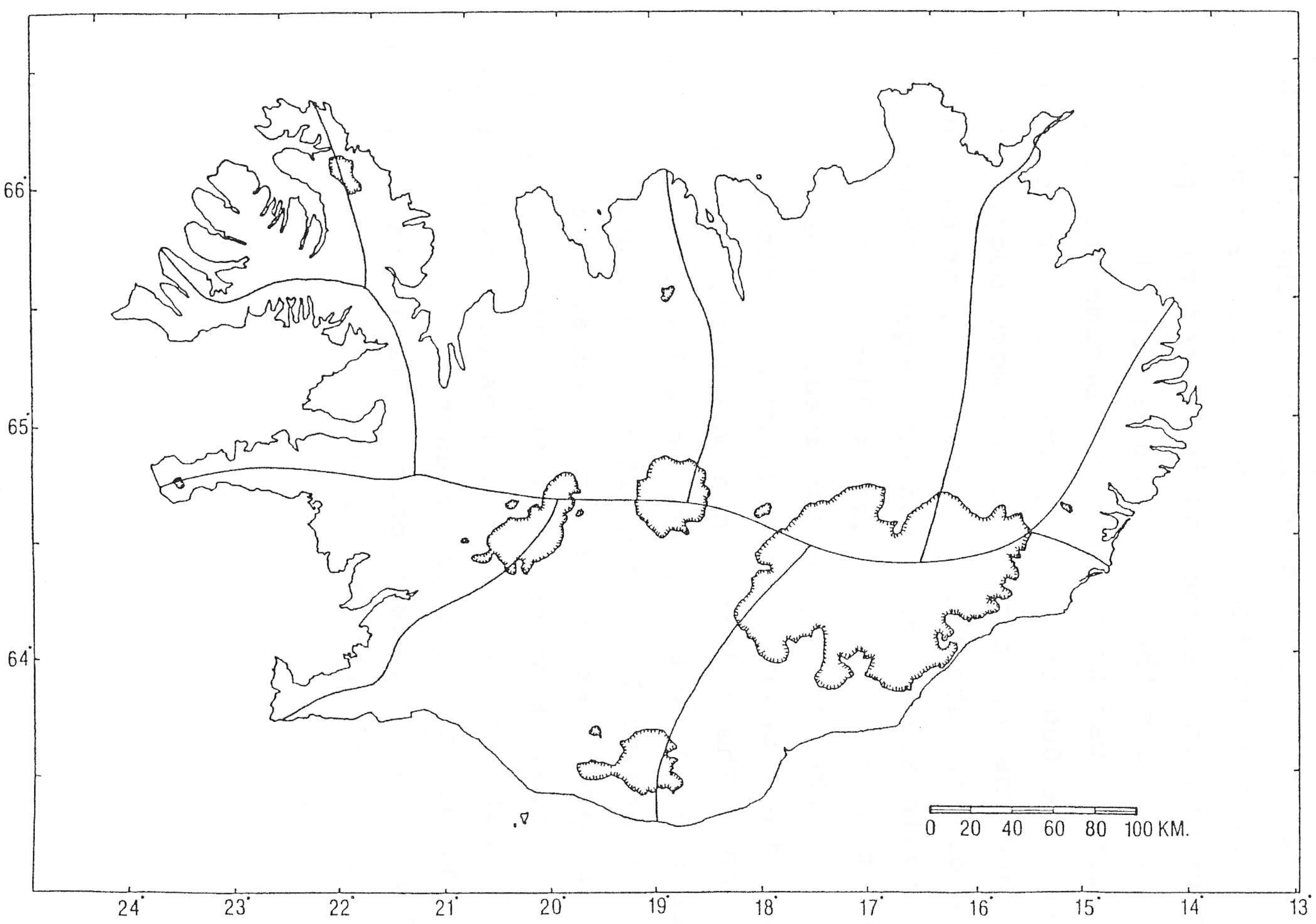

Figure 16. Weather forcast areas in Iceland. (Einarsson 1978).

for few nunataks (ice free mountains). The climate between the glaciation was similar to the present one (Simonarson 1979, Einarsson 1966, 1968).

The time after last glaciation is the time that salmonid fishes have been adapting and evolving in different rivers in Iceland and is therefore especially interesting. After the last glaciation (11,000 years ago) the climate was warm and birch became the dominant plant. About 6,000 to 7,000 years ago, precipitation increased and the vegetation became more boggy and new wetlands evolved. About 5,000 years ago, precipitation decreased again and a new birch era began. About 2,500 years ago the climate changed suddenly, temperature decreased, and precipitation increased. At the same time a new wetland era began. The country was settled around the year 900. The climate then was similar to today, until around 1200, when it became colder. It became still colder around 1600, and it was cold until 1920, when it became warmer again (Thorarinsson 1953, Berthorsson 1969, Einarsson 1976). There was more precipitation during the colder periods (Einarsson 1971), but the wind direction that brought the precipitation was similar to the present ones, this explaining the present location of glaciated areas.

ICELANDIC FRESHWATERS

Surface hydrology Average runoff per surface area is high in Iceland. Average annual runoff for the whole country is about 1730 mm. Surface runoff is highly dependent on the water balance (precipitation less evapotranspiration) and the permeability of the bedrock. The runoff is highest in south-east Iceland and generally high in south Iceland (1200 to 5000 mm). In north Iceland the runoff is generally lower (600 to 2500 mm) (Figure 17). In some areas there is no surface runoff due to high permeability of the ground (Rist 1956). The runoff measurements (Figure 17) and potential water balance (Figure 15) seem to be in good agreement in areas with dense bedrock.

Geothermal water Because of high geothermal activity in Iceland, there is widespread occurrence of geothermal springs. Areas with thermal water are generally classified into two categories: low temperature areas (<150 ^{o}C) and high temperature areas (>200 ^{o}C) (Fridleifsson 1979). Low temperature springs are usually associated with faults and dykes where water can reach geothermal heat only at great depth or in places with high heat flow (Bodvarsson 1961). High temperature springs are usually associated with recent intrusions and magma chambers in the volcanic zones (Arnason 1976).

Thermal water has considerable influence in some rivers in Iceland and a few rivers have almost pure geothermal water. However only about 3%. of Iceland's surface water is thermal water since most thermal water evaporates (Rist 1964). For the purpose of present study

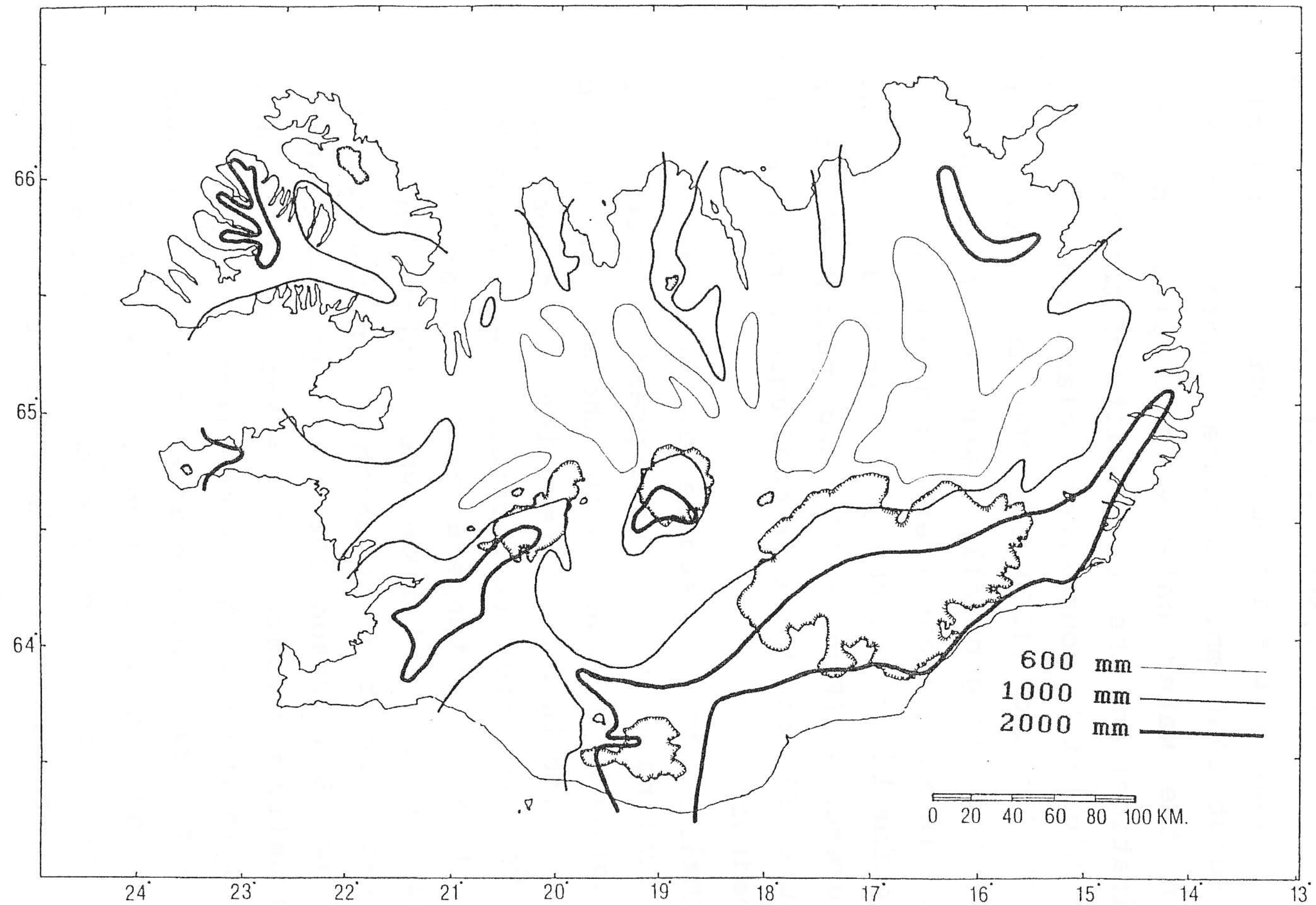

Figure 17. A drainage map of Iceland. Annual runoff in mm.

(Adapted from S. Rist 1956).

it is not important.

Glaciers. - About 11% of Iceland is covered by glaciers at present. All glaciers in Iceland are temperate and are dynamically active and responsive to climatic fluctuations. Glaciers in Iceland are of various type from small cirque glaciers to extensive plateau ice caps (Bjornsson 1979).

There are two main glacier regions in Iceland. The northern region comprises the north-west peninsula and a mountainous area in central north Iceland (Figure 1). In the north-west peninsula a glacier occupies the northern part of extensive basalt-plateau. About 115 cirque and valley glaciers are found in the alpine landscape of central north Iceland. The south and central region follows the water divide from west to east along the central highland. This includes several glaciers, some of them large, one of them, Vatnajokull, the largest glacier in Iceland (Bjornsson 1979).

Iceland became ice free at the end of the warm period from 8000 to 2500 B.P., except for small ice caps on the highest mountains. Glaciers grew during a cold and wet period after 2500 B.P. when present glaciers were formed. The glaciers expanded further after the cooling around 1200 and again during the cold period 1660 to 1920. Since 1920 the glaciers have been in recession (Bjornsson 1979).

Lakes Iceland has many lakes but only a few are large. Their basins are of various origins. There are 27 lakes larger than 5 km^2 and more than 80 lakes are larger than 1 km^2 (Rist 1975). About 1200 lakes are larger than 0.1 km^2. Lakes cover about 1.2% of the surface of Iceland (Adalsteinsson 1988). Apart from being important fish habitat, lakes are important in watersheds as buffers, stabilizing the runoff and the thermal regime of the outlet rivers.

The morphometry of the lakes is important, since shallow lakes have higher primary production with all the bottom producing as well as the water body. The content of dissolved solids is also important, higher concentrations increasing the production (Ryder et al. 1974). High primary production generally means higher secondary production, including fish production.

Wetlands and lakes are more common in the Tertiary and Plio-Pleistocene areas, there being few in the Pleistocene areas. Some of lakes are without visible in- or outflows. The water level in some of these lakes fluctuates with the level of the groundwater.

River types Icelandic rivers can be classified into three well defined classes based on the origin of the water. These types are glacial rivers, direct runoff rivers, and spring-fed rivers (Kjartansson 1945).

Glacial rivers originate in meltwater. Their flow fluctuates considerably with air temperature, and they reach peak flows late in the summer. Diurnal flow fluctuations also occur. Glacial rivers have large loads of suspended material. Glacio-fluvial deposits often occur in the slower flowing parts of the rivers due to fluctuations in flow. These cause the rivers to change their course (Rist 1956). Glacial rivers are often braided where their gradient is low. Some of the glacial rivers exhibit glacier burst (jokulhlaup) when glacier-dammed lakes burst out or because of subglacial geothermal or volcanic activity. Large quantities of water can be discharged in such a burst (several km^3), up to 200,000 m^3/sec. Glacier bursts usually only last one or two weeks, with sharp maximum peak flows (Rist 1956).

Direct runoff rivers occur where the bedrock is dense, in the Tertiary areas and in the Plio-Pleistocene areas. The flow of the direct runoff rivers is highly dependent on weather. The rivers swell rapidly during times of thaw and/or rain. River-water temperatures fluctuate closely with air temperature (Rist 1956).

Spring-fed rivers are mainly in the permeable Pleistocene bedrock areas and in recent geological formations. The flow in spring-fed rivers is even all year around as is the temperature of the water, which is close to the annual average air temperature (3-5 ^{o}C) (Rist 1956).

Runoff characteristics The flow patterns of Icelandic rivers depend on the permeability of the bedrock and the amount and the thermal condition of the precipitation. The permeability of the bedrock is very different between different formations.

There are mainly four types of discharge peaks in Iceland (Rist 1964, Rist and Sigvaldason 1968, Rist and Sigurdsson 1981, 1982, Rist and Thorsteinsson 1981). Most rivers have their maximum discharge in spring. Rivers at high elevation and rivers in North Iceland have their highest discharge peaks later in the spring than do southern and lowland rivers. Some rivers have discharge peaks in the fall, which is the time of highest precipitation. Then the ground can be frozen and less permeable, causing increased flow. Winter floods occur in some rivers, especially in the south and south-east when maritime depressions saturated with warm, moist air pass, these causing rain and snowmelt. The fourth type of discharge peaks occurs in glacial rivers in the fall, when melting of ice has reached its maximum (Rist 1968a, 1968b).

The Pleistocene areas (Figures 5, 7, 8) (neovolcanic zone) are generally very permeable (10^{-0} to 10^{-4} m/s) (Sigurdsson and Sigbjarnarson 1985) and most of the precipitation soaks into the ground. Water flows underground, sometimes long distances, until it reaches denser bedrock, often at lower elevations, where the water emerges in springs. Spring areas are sometimes on a beach or below sea level. Large areas are without surface water. Spring-fed rivers are thus the typical river type. The flow in these rivers is very even, only small changes occurring. Small peaks in the runoff can occur during winter and in spring during rain and thawing of snow, if the ground is frozen and thus less permeable. Then some overland flow occurs. However, in many porous areas, virtually no changes occur in the runoff (Kjartansson 1964). This is especially so in areas of recent lavas, in fissured areas, and in interglacial lavas (Figure 8). Runoff per surface area is highly dependant on the amount of precipitation and is, therefore, much higher in southern Pleistocene areas than in the northern areas.

The Plio-Pleistocene formations (Figure 5) generally have very dense bedrock and low permeability (10^{-2} to 10^{-6} m/s) (Sigurdsson and Sigbjarnarson 1985). In most places, loose sediments and soils are thin, so a large part of the precipitation runs overland. The permeability, which is almost entirely of capillary type, is reduced dramatically during frosts. The runoff in these areas therefore fluctuates greatly in the winter, especially in the south where the precipitation is greater and rain and thaw during winter are more frequent. The highest discharge peaks are in the spring when thaw and rain set in. Spring is earlier in the year in the south and in the lowlands than in the north and in the highlands. Small discharge peaks can occur at any time of the year. During summer the runoff is more stable, since water penetration into the ground is greater. The lowest discharge is usually late in the fall when frosts set in and the amount of precipitation is low.

The runoff characteristics in the Tertiary areas vary considerably, depending on the landscape, precipitation, and temperature. The Tertiary areas are generally mountainous and the bedrock is dense with low permeability (10^{-3} to 10^{-7} m/s) (Sigurdsson and Sigbjarnarson 1985). Soil cover is generally rather thin. The runoff, therefore, fluctuates throughout the year. The runoff pattern is similar to the Plio-Pleistocene areas except the fluctuations are generally not so large, soil, and vegetation, lakes, and ponds acting as buffers. This is especially true where the landscape is flatter as in the moraine heaths in western part of North Iceland.

<u>Influence of climate on flow pattern</u> Relatively small changes in temperature can have profound effects on the runoff pattern of Icelandic rivers. Cooling of a few degrees would cause the rivers in south Iceland to have higher discharges in the spring than today since snow would accumulate in the winter. The ground is generally less permeable during frosts, which would cause

overland flow during a larger part of the year than at present. Groundwater storage would decrease. During frosts, the decrease in permeability is especially large in some areas of the Plio-Pleistocene formations. Some rivers in the older part (Tertiary and Plio-Pleistocene) of the country would stop running during the winter because of frosts. Spring flood would be larger in all parts of the country, since more water would be stored in the form of snow. Flood danger during winter would increase because of sudden warming, snowmelt, and rain, as happens with the arrival of depressions loaded with moisture. Glacier growth would decrease flows of glacial rivers and some spring-fed rivers that depend on glacier melt-water that penetrates into the ground (Sigurbjarnarson 1967). Increase in precipitation has been associated with cooling, which would further change the flow patterns of Icelandic rivers.

Temperature increase of a few degrees would also alter flow patterns dramatically. Sudden thawing of snow during winter as maritime depressions arrive can cause winter discharge peaks in south Iceland, especially in rivers at low elevation. Such discharge peaks would become more common in all parts of the country, including highland rivers. Glacial rivers would have higher discharges and discharge peaks, especially late in the summer. Flows of spring-fed rivers that depend on glacier meltwater would increase. Small rivers and rivers in the north and at high elevations that are now frozen during winter would probably become perennial. It should, however, be born in mind that increase in temperature in the past has been associated with decrease in precipitation.

Chemical compositions of river waters Chemical concentrations in Icelandic freshwaters are generally low (Sigbjarnarson and Sigurdsson 1985). Chemicals in Icelandic freshwaters are derived from precipitation and rock weathering. Icelandic surface waters fall in the range of precipitation-rock dominance in the chemical classification of waters by Gibbs (1970).

The main ions in precipitation in Iceland are of marine origin (Halldorsdottir 1983), as in maritime regions elsewhere (Eriksson 1952). The main ions of marine origin are Cl^-, Na^+, Ca^{2+}, and Mg^{2+} in corresponding ratios. Concentrations of marine substances in the precipitation are highest in the winter months and lowest during the summer (Sigbjarnarson and Sigurdsson 1985), and highest near the shore but lower inland (Sigurdsson 1986, Arnason 1976, Gislason and Eugster 1987a). There is also higher content of marine substances in the precipitation in south and southwest Iceland than in north and east Iceland (Sigurdsson 1986). These differences in marine substances in the precipitation can be explained by the dominant air masses. The American-Atlantic air mass arrives in winter with south-westerly wind direction and is wet and windy. The Atlantic-European air mass arrives with south-easterly wind direction which is wet but not windy. The Arctic air mass arrives from the north and is windy but not excessively wet (Sigbjarnarson and Sigurdsson 1985).

The chemical concentration in Icelandic freshwaters can increase seasonally in a few locations because of high evapotranspiration and low precipitation, where there is low or negative potential water balance (Figure 15).

Geological chemical influences on freshwaters in Iceland are high in the younger areas of Iceland, especially the neo-volcanic (Pleistocene) zone and also in the Plio-Pleistocene areas (Sigurdsson and Sigbjarnarson 1985).

Gislason and Eugster (1987b) found that basaltic glass dissolved about 10 times faster than crystalline basalt. The rocks of the neo-volcanic zone and in the Plio-Pleistocene areas have high glass content (Sigbjarnarson and Sigurdsson 1985), explaining the high chemical content of freshwater in these areas. The chemical contents of freshwaters in the Tertiary areas are considerably lower (Sigurdsson 1986). Chemical erosion in Iceland is extremely high (98 tons per km^2 annually), especially in the younger parts of the country (Gislason and Eugster 1987a, Gislason and Arnorsson 1987a). On the average, 1000g of spring water in the neo-volcanic zone has reacted with 0.1 to 1 g of basaltic rock (Gislason and Eugster 1987b). The chemical content of spring water increases with increased temperature, as solubility increases.

In the older part of the country where the bedrock is basalt, geological influences on the chemical content of the water are less profound. In vegetated areas the chemical content of water is higher than in barren areas. Chemical content of water from wetland is usually high since high concentrations of CO^2 and various soil acids increase solubility in water.

There are some local industrial and agricultural chemical influences on precipitation and freshwaters. Exhalation from geothermal areas and mineral dust can locally add some ions to the precipitation (Gislason and

Eugster 1987a).

Electrical conductivity Electrical conductivity (also specific conductivity) or resistance is easy to measure and is a good indicator of the concentration of chemical ions in water. On a global basis, the concentrations of four major cations, Ca^{+2}, Mg^{+2}, Na^{+}, K^{+}, and four major anions, HCO_3^{-}, CO_3^{-2}, SO_4^{-2}, Cl^{-}, usually constitute the largest part of freshwater ionic salinity (Wetzel 1983).

River water has been analyzed chemically from all parts of Iceland (Armannsson 1970, Rist 1974, 1986, Halldorsdottir 1983). There is a strong positive linear association between electrical conductivity and total dissolved solids in Icelandic river-waters (Table 1), as described by the equation:

Conductivity (uS/cm) = -1.69 + 1.51 (Total dissolved solids (mg/l)).

The correlation coefficient, r = 0.89. The correlation is significant (0.0001). Fifty-three samples from all parts of the country were analyzed. It is generally assumed that electrical conductivity is a good measure for the total chemical content of freshwaters.

Table 1. Amount of dissolved solids in mg/l and specific conductivity in uS/cm (25 °C) for several Icelandic rivers.

River name	year	location	dissolved solids	conductivity
Ellidaar	1969	SW	58	86
Ellidaar	1973	SW	61	99
Ellidaar	1974	SW	55	81
Grafara	1973	SW	49	65
Laxa,Leirars	1973	W	46	73
Laxa,Leirars	1974	W	45	71
Andakilsa	1973	W	41	68
Andakilsa	1974	W	39	65
Grimsa	1973	W	57	89
Grimsa	1974	W	47	69
Flokadalsa	1973	W	65	89
Flokadalsa	1974	W	51	72
Hvita,upstream	1973	W	45	63
Hvita,upstream	1974	W	43	59
Hvita,downstream	1973	W	51	75
Hvita,downstream	1974	W	45	67
Stora-Thvera	1973	W	66	107
Stora-Thvera	1974	W	56	79
Thvera	1973	W	42	66
Thvera	1974	W	39	59
Nordura	1973	W	45	72
Nordura	1974	W	44	64
Orlygsstadaa	1973	W	48	55
Gilsa	1974	N	37	73
Gilsa	1974	N	51	94
Galtabol	1974	N	29	55
Thristikla	1974	N	23	35
Mjoavatn	1974	N	38	56
V-Fridmundarvatn	1974	N	43	61
A-Fridmundarvatn	1974	N	37	64
Seydisa	1975	N	36	63
Herdubreidara	1974	N	112	143
Hvannalindir	1974	N	75	111
Eidisvatn	1975	NE	93	165
Storilaekur	1975	NE	103	185
Logurinn	1974	E	56	102
Holmavatn	1975	E	47	55
Galtalaekur	1981	S	82	166
Thjorsa	1973	S	64	88
Hvita	1973	S	54	71
Hvita	1975	S	55	64
Fossa	1973	S	68	85
Stora-Laxa	1973	S	55	71
Tjarnara	1975	S	69	85
Svarta	1975	S	69	91
Jokulkvisl	1975	S	70	93
Tungufljot	1973	S	43	54
Bruara,upstream	1973	S	49	68
Bruara,downstream	1973	S	43	54
Laugarvatn	1975	S	69	83
Laugarvatn	1975	S	67	80
Sog	1973	S	51	78
Olfusa	1973	S	54	76

There is little change in specific conductivity in Icelandic rivers between seasons or years. The conductivity increases when the discharge is low and is lower during floods (Rist 1974, 1986). Conductivity measurements, by the present author and by others, have been compiled (Gudjonsson 1989a). These show that river water has high chemical concentrations in the Pleistocene areas (neo-volcanic zone) and the Plio-Pleistocene areas. Rivers in the Tertiary areas generally have low chemical concentrations, except for long rivers originating in vegetated lowlands and heaths, where the land is flat and retention time long.

Specific conductivity of precipitation in Iceland is in the range of 10 to 25 uS/cm, depending on location and season (Halldorsdottir 1983) as discussed previously. This gives a base line for comparison and evaluation of the chemical content of river water.

CLASSES OF ICELANDIC RIVERS

Gardarsson (1978, 1979) proposed a classification of Icelandic watersheds with emphasis on their conservation value. He suggested that such classification should be based on the geology and the landscape of the watershed as well as productivity and species distribution. The classification presented here is more extensive and detailed in development than the classification scheme of Gardarsson. This present classification, though in general agreement with Gardarsson, has some important differences.

On the basis of geology, topography, climate, runoff characteristics, and chemical properties, Icelandic rivers can be divided into several distinct classes. The present classification does this and results in several regions each having a distinct rivertype. It should be borne in mind that this is a regional classification. More detailed classification would be possible within each region and also within each watershed and river system (Frissel 1986). Other approaches to river and stream classification have been from an energetic standpoint in geomorphology (Curry 1972) and in biology, such as the nutrient spiralling theory (Newbold _et al._ 1981, Elwood _et al._ 1983), the river continuum concept (Vannote _et al._ 1980, Minshall _et al._ 1982), process modelling (McIntire and Colby 1978) and river zonation (based on gradient) (review by Illies and Botosaneanu 1963).

River-classes and the regions in which these classes of rivers are found will now be described. In the

Tertiary areas, there are two main river classes, direct runoff rivers and rivers originating in vegetated wetland heaths. Only direct runoff rivers originate in the Plio-Pleistocene areas. In the Pleistocene areas, the rivers are predominantly spring-fed. The drainage pattern of these river types are distinctly different (Figure 18).

Quaternary rivers

Both spring-fed rivers and direct runoff rivers are found in the younger parts of Iceland.

Spring-fed rivers Spring-fed rivers are characterized by the stability of their flow and thermal regimes. Their waters have high chemical content, especially if they have flowed long distances underground. Higher temperature of the water increases the chemical content. The specific conductance of spring-fed rivers commonly is in the range of 60-200 uS/cm. Springs at high elevation have lower chemical content since the water is colder and has not been in contact with the bedrock for long. The water in the springs, especially if the water has travelled long distances underground, can have high pH (9-10) and thus a low concentration of CO_2. The water is buffered by silica and carbon species and is distinctly different chemically from river water in the Tertiary areas (Gislason and Arnorsson 1987b). Spring-fed rivers are generally fertile. If water temperature gets high, as in long rivers and in lakes, the biological production in the river system is generally high. In the regions of spring-fed rivers, drainage density is low. It is not uncommon for spring-fed rivers to reach near full flow

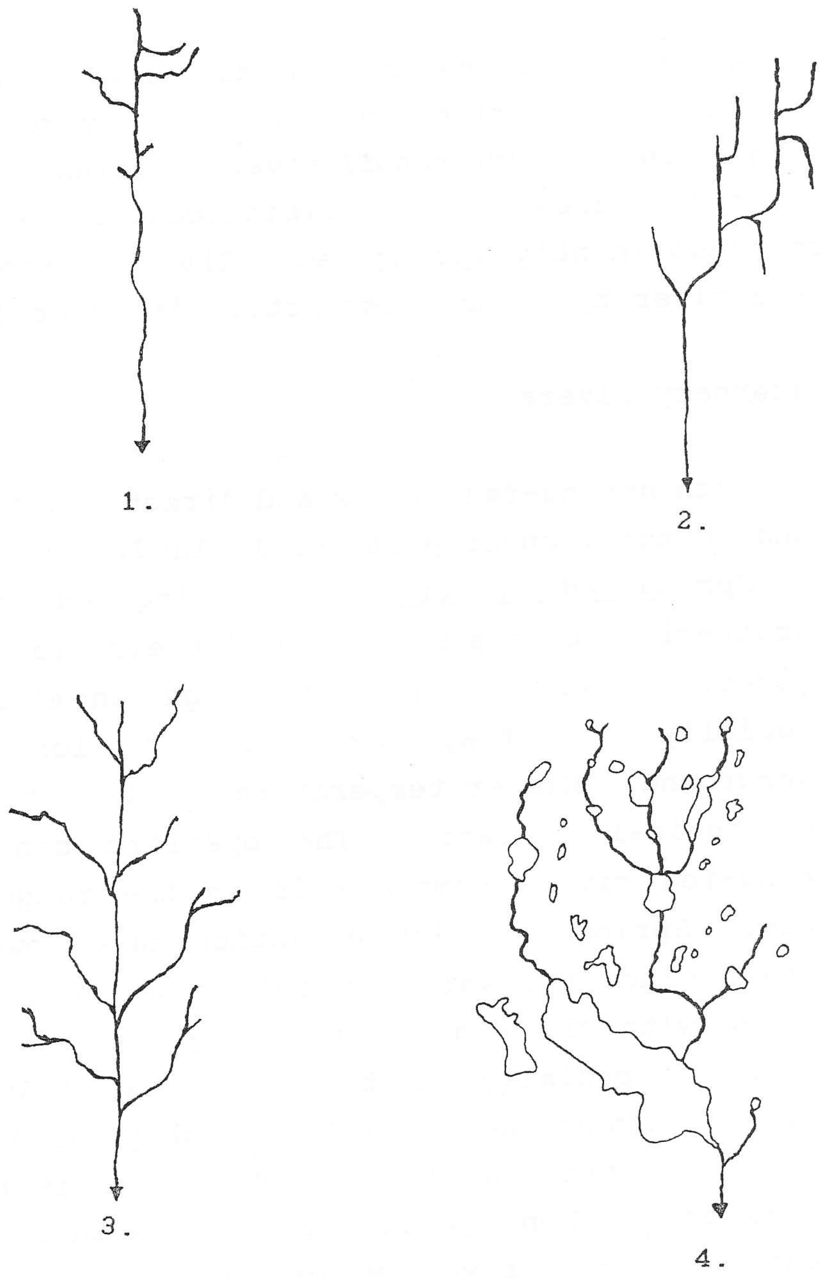

Figure 18. Drainage pattern of Icelandic rivers.

1. Spring-fed rivers.
2. Direct runoff rivers in Plio-Pleistocene areas.
3. Direct runoff rivers in Tertiary areas.
4. Wetland heath streams.

close to their origin, which can be one or more springs in a very limited area, such rivers then flowing directly to the sea. This drainage pattern is unique (Figure 18). Spring-fed rivers generally form a stable and productive environment.

Three major regions in Iceland are characterized by spring-fed rivers (Figure 19). Two of these are in South Iceland and one in North Iceland all in the Pleistocene (neo-volcanic) formation (Figure 5). Springs are near the edge of the neo-volcanic zone, where the bedrock is denser, as in the Plio-Pleistocene area in the lowland. Here buried horizonal lava strata reach the surface and allow water that has flowed underground along these strata to emerge.

There are differences in climatic condition between the spring-fed river regions being classified (Figure 10, 13, 16). The southeastern spring-fed river region is on the eastern neo-volcanic zone of the two parallel volcanic zones in south Iceland (Figure 19 1A). The amount of precipitation is high and the runoff per surface unit is also high. For this reason, there are fluctuations in runoff. Rivers and lakes are located in the small valleys between the axial ridges in a SW-NE direction. Since this area is not wide in a W-E direction, but is long in N-S direction, there are only a few large river systems in this area. In the lower middle part of the region, there are large springs draining large areas in the highlands. These springs form rather short, large rivers that flow in one channel, with a gentle slope, a short distance to the sea. These rivers are rather cold and can have high pH and low CO_2.

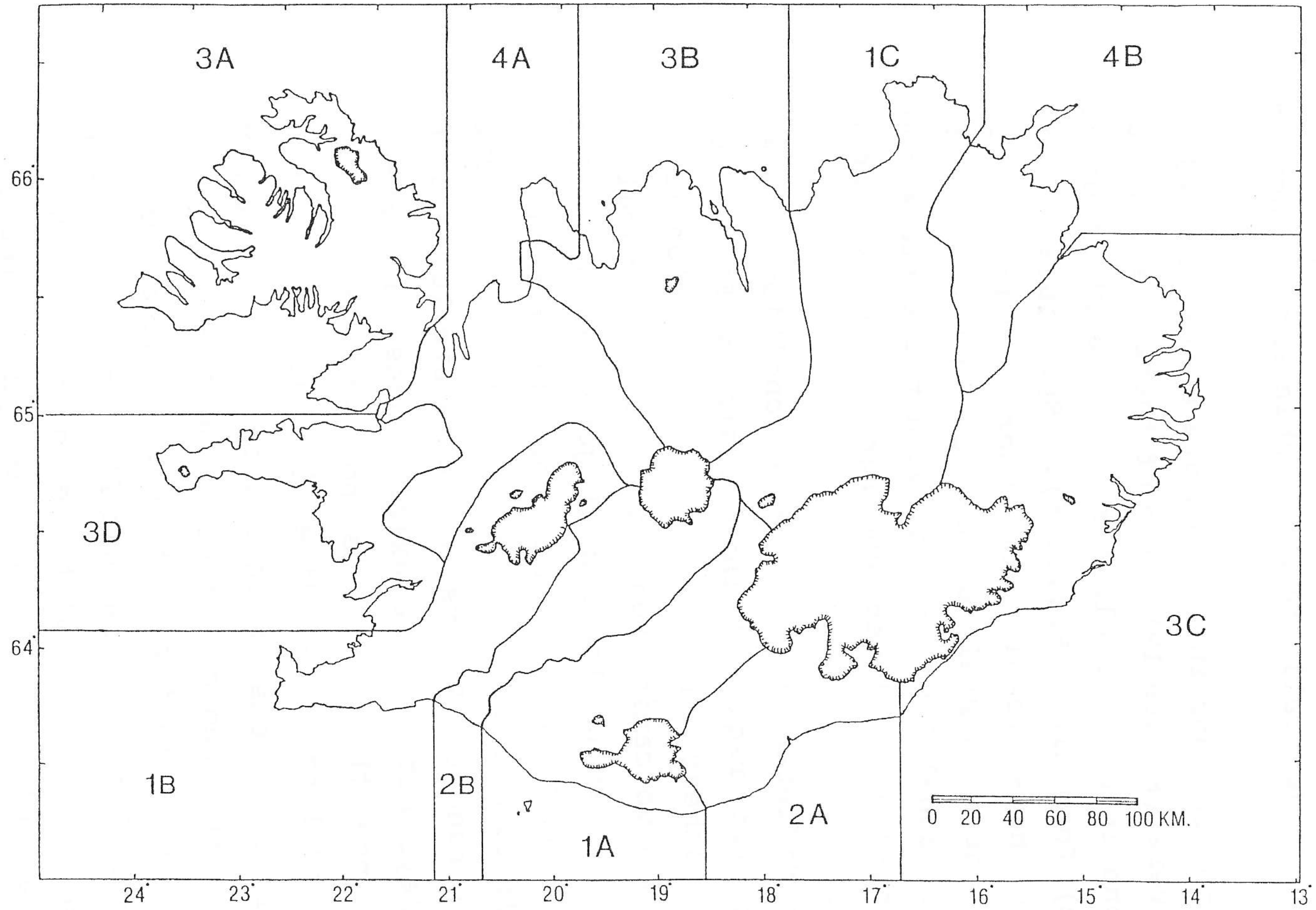

Figure 19. Classes of Icelandic watersheds and rivers.

1. Spring fed rivers. 2. Direct runoff rivers in Plio-Pleistocene areas. 3. Direct runoff rivers in Tertiary areas. 4. Wetland heath streams.

The south western spring area is in the western neo-volcanic zone in south Iceland (Figure 19 1B). It is large and a large part of the region has no surface runoff, most of the water reaching the sea underground, as in the Reykjanes peninsula. In the upper northern part of the region there are large spring-fed rivers that are the drainages of the highlands. There are also some spring-fed river systems flowing to the west. As in the other region of this type, the majority of the springs appear near the edge of the neo-volcanic zone on Plio-Pleistocene areas, where the bedrock is denser. Here, where sudden difference in elevation, emerges water flowing along buried surfaces emerges.

The north spring region (Figure 19, 1C) is on the neo-volcanic zone that crosses the northern part of Iceland. The southern part of this area has hardly any surface water apart from glacial rivers. There is a precipitation shadow in the south part of the region, north of the large glacier Vatnajokull. All precipitation soaks into the ground. Springs in this area are near the edge of the Pleistocene formation, where the bedrock is denser. Some water runs underground all the way to the sea. The runoff per surface unit in this region is lower than in other regions of this type, due to lower precipitation. There are small scattered areas of this type in the Snaefellsnes peninsula, west Iceland. The bedrock in this area is young as in other regions of this type.

Direct runoff rivers in Plio-Pleistocene areas The Plio-Pleistocene areas lie between the neo-volcanic zones and the Tertiary areas, with the exception of one area in south Iceland, which is between the two parallel neo-volcanic zones. Some Plio-Pleistocene areas are virtually taken over by spring-fed rivers. The dominant river type in these areas is, however, direct runoff rivers, which show certain similarities to spring-fed rivers. They originate on a similar type of bedrock, although the bedrock is older and denser. Rivers in the Plio-Pleistocene areas can have considerable part of their flows from springs. But the springs are smaller, since their permeable catchment areas are generally small and surrounded by denser bedrock. Rivers in these areas have rather high chemical content, the bedrock eroding easily. Their rather high specific conductivity is in the range of 50-100 uS/cm. The erosion can be seen in the deeply eroded gullies and canyons forming river channels. The river bottoms are formed by rather fine material, the rocks being easily broken into small grained material. The flow in these rivers fluctuates greatly, especially if the ground is frozen. Then it is impermeable and all water flows overland. Snowmelts occur into midsummer. The drainage density is high. During summer, some of the precipitation penetrates into the ground, this stabilizing the flow. The flow therefore depends highly on the weather, as does water temperature. Because solar radiation does not reach the water in the deep gullies, these rivers are generally cool. Although these rivers are rich in nutrients, their flow and temperature fluctuate and bedload is high, creating a very unstable environment limiting biological production.

There are two large regions and a few smaller areas characterized by this type of river. Both of the regions are in south Iceland. The western region (Figure 19 2B) is between the two parallel neo-volcanic zones in south Iceland. The drainage pattern is unique (Figure 18) as described earlier. There are few lakes in this region. In the eastern region (Figure 19 2A) most of the rivers run parallel to the old rift axis, as is the case in the western region.

There are also areas of this type in north Iceland and in West Iceland along the neo-volcanic zone, but these are almost completely taken over by spring-fed rivers. Some spring-fed rivers flow through these areas and join the direct runoff rivers to form rivers of mixed origin. The spring component in such rivers is usually larger than the direct runoff component. Some spring-fed rivers west of the western Pleistocene formation in south Iceland (1B in Figure 19) have a considerable direct runoff component. Due to lower precipitation in the north, the few rivers of this type are not distinctly different from rivers of the nearby Tertiary area. These areas in north Iceland are therefore not considered in this classification, but these should be considered for any more detailed classification of river systems on the borders of neo-volcanic and Tertiary areas in north and in west Iceland.

<u>Stability and productivity of the rivers in the Quaternary areas of Iceland</u> Rivers in the younger parts of Iceland are generally high in nutrients because of the high erosion rate. The spring-fed rivers generally form very stable environments. Direct runoff rivers are very unstable, limiting their production. Lakes in all these areas are generally very productive.

Tertiary rivers

Depending on the landscape, rivers in the Tertiary areas are of two types, direct runoff rivers and wetland heath streams. The rivers are buffered by carbon species (Gislason and Arnorsson 1987).

Direct runoff rivers in Tertiary areas Rivers of this type are common in Iceland. The Tertiary bedrock is dense and the soil cover is usually thin, so underground water storage is small. These rivers respond rapidly to changes in temperature and precipitation. Their chemical content is generally low, as they flow on dense bedrock and through thin soils, which are often unvegetated and nutrient-poor. Their specific conductance is in the range of 20 to 60 uS/cm. The rivers in the typical fjord landscape generally originate high in unvegetated mountains and flow a short way to the sea. Snow is melting during most of the summer, the retention time of the water in the rivers is short, and thus the rivers are cold. River flow is highly fluctuating, discharge being high in the spring during warming, rain, and snowmelt, but very low during frosts in the winter. Flow in smaller rivers and headwaters can stop completely in winter.

These rivers are therefore usually cold, steep, short, and unfertile. The environment in them is unstable and they are biologically unproductive. The drainage pattern is of the familiar dendritic type (Figure 18).

Three regions in Iceland have rivers of this type: the north-west peninsula, mid-north Iceland, and east Iceland (Figure 19). This river type is also found in other Tertiary regions.

In the northwest region (Figure 19 3A) the bedrock is not as dense as in the east, because glaciers in that area were not as thick as in the east and the duration of the ice-age there was shorter. The permeability of the bedrock there has some stabilizing effect on the flow of the rivers. Floods occur in early summer and very low discharges occur in late summer.

In the northern region (Figure 19 3B) there is not much precipitation and a large part falls as snow. The discharge is therefore low in winter, but floods occur early in the summer and snowmelt feeds the rivers all summer.

The bedrock is very dense in the eastern region (Figure 19 3C). There is much precipitation in this region, especially in the southern part. Highest runoff is in the fall during heavy rains and lowest in the latter part of the winter. Floods can be very big. The difference between annual lowest and highest discharge is large.

Rivers in the Tertiary areas that are longer and flow a long distance on lowland have higher chemical content and their temperature during the summer is higher. The specific conductivity in such rivers commonly is in the range 50-90 uS/cm. Lakes in the river system stabilize river flow and thermal regimes. The environment in such rivers is more favorable than in their shorter counterparts. This type of river, having long valleys and often a lake, is typical of a Tertiary region in west Iceland (Figure 19 3D). Rivers of this type are also found in other Tertiary regions.

Wetland heath streams This type of river originates on flat moraine heaths. Extensive wetlands with small ponds and lakes are between moraine ridges. The drainage pattern near the origin of these streams is unique (Figure 18) but downstream it resembles the pattern of other Tertiary rivers. The retention time of the water in such a system is long, since the water flows slowly through the wetland from one pond to another and then through several small lakes. The water has high chemical content as it starts to flow down through the extensive heathlands. The specific conductivity of these rivers is in the range of 60 to 160 uS/cm. The wetland and the lakes have stabilizing effects on the flow and thermal regime of these rivers. These rivers are biologically productive and rather stable.

There are two regions having this river type, both in north Iceland (Figure 19). The more western region (Figure 19 4A) is extensive and its drainages flow both to the north and to the west. A small area is divided from the main area on the tip of Skagi peninsula in the north (Figure 19 4A). The northeastern region (Figure 19 4B) is smaller and its drainages run both to the north and the east.

Flat areas in the Tertiary areas are also found elsewhere. But these are small and often at a much higher elevation. Snowmelt lowers the chemical content of the water in these rivers, which along with low temperature lowers biological production.

Stability and productivity of the Tertiary rivers

It is possible to rank the Tertiary rivers by their stability and productivity, from the most unstable and least productive to the most stable and productive: Short direct runoff rivers, short direct runoff rivers with lakes, long direct runoff rivers, long direct runoff rivers with lakes, and wetland heath streams. There is, of course, an intergrading from one type to the other.

DISTRIBUTION AND ABUNDANCE OF SALMONIDS IN ICELAND

Icelandic freshwater fauna

Icelandic freshwater flora and fauna are rather poor in species because of the geographic isolation of the island, its young age, and the adverse climatic conditions during glacial periods. Many invertebrate species in Icelandic freshwaters have a cosmopolitan distribution. This paucity of species is also reflected in the freshwater fish fauna. Only five freshwater species of fish are native in Iceland: European eel (*Anguilla anguilla*), three-spined stickleback (*Gasterosteus aculeatus*), and three salmonids, Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and arctic char (*Salvelinus alpinus*). Anadromous stocks of each these three species are found. Resident stocks of arctic char and brown trout but not Atlantic salmon occur.

The eel is mainly found in south and west Iceland. The stickleback is distributed all over Iceland. These two species both occur almost entirely in lentic waters.

Management of the freshwater fisheries

Fishing rights in Icelandic rivers go with the ownership of the farms adjacent to the rivers. Owners of the fishing rights in each river form an association, which manages the exploitation of the fish stocks within the laws. Usually the association rents or leases the fishing rights to anglers. Most of Iceland's rivers are used for sport fishing. There are strict regulations on the number of rods allowed in each river, the time fishing is allowed daily, and the time fishing is allowed annually. Fish are harvested from a few glacial rivers by net fishing. Net fishing is strictly regulated on the basis of fishing effort, by the number of nets, the fishing time, and the type of gear used. Regulations have kept the fishing effort rather constant (Gudjonsson 1978, Gudjonsson and Mills 1982). Fish associations keep accurate catch statistics, the sex and weight (at 0,5 kg intervals) of fish being recorded. Foreign ocean fishing on salmon is banned within Iceland's 200 mile fishing limit, and there is no significant ocean fishing by Icelanders (Isaksson 1980).

Fish populations in lakes are either exploited by recreational fishing or gill-net fishing. Only in a few lakes are fish harvested commercially. There are regulations limiting the fishing effort in lakes.

The fishery is broadly regulated by the Director of the Institute of Freshwater Fisheries. Fish in Icelandic rivers and lakes were harvested domestically until this century when commercial and sport fishing started to develop. Present day regulations of freshwater fisheries were established by law in 1932 (Gudjonsson 1978). Scarnecchia (1989) gave a good account of the history and development of freshwater fishery management in Iceland.

Habitat preferences of salmonid fishes

Of the three salmonid species, the Atlantic salmon inhabits the warmer, more productive rivers in Iceland. The arctic char is the dominant species in the coldest and harshest rivers. The brown trout has intermediate thermal and habitat preferences.

Apart from water quality and thermal preferences, there is selection of physical habitat by each salmonid species, although the three species have rather similar environmental demands (Allen 1969). Where these species occur within the same river system, there is a habitat selection and segregation, especially among juveniles. This is manifested in territorial behavior (Lindroth 1955, Keenleyside 1962, Keenleyside and Yamatoto 1962, Kalleberg 1958, Hartman 1963, Karlstrom 1977, Noakes 1980), which is influenced by food supply (Chapman 1966, Chapman and Bjornn 1969, Symons 1968, 1971) and because of different physical environmental needs (Elson 1975, Nilson 1963, Heggberget 1984). An account of sympatry of these three salmonid species in lotic water in northern Norway is given by Heggberget (1984), which is in good agreement with what Icelandic fish biologists have experienced. Spawning sites are often at the tail of a pool as it merges into a riffle. The river bed is usually fine gravel not mixed with fine sediment or very coarse substrate. The juveniles need cover from floods and predators as well as to lower their energy expenditure. This cover is often provided by coarse gravel, cobbles, and stones in the river-bed. Fry are generally in shallow slow moving water, where the river substrate is fine. As the juveniles grow to parr, they need coarser substrate for cover.

In general, salmon parr are further from river banks and in deeper water at higher velocities than the other two species. The char is in water having the lowest velocities. The brown trout is in water of intermediate velocities. When all species are present, each one is forced into the microhabitat to which it is best adapted (Heggberget 1984). When only one or two species are present, the habitat selection is broader. The habitat requirements of salmonids for spawning and rearing are broad, overlap, and lead to segregation when more than one species is present. This complicates the definition of the habitat preference of each species.

These three salmonids can utilize lakes for nursery habitat. If all species are present there is habitat segregation. Salmon juveniles can use shallow stony littoral areas, so long as an inlet or an outlet stream provides spawning area. This applies also to the brown trout, but if salmon are present the trout is pushed further offshore in the lake. The char can spawn at sites with very slowly flowing water. If the other two species are present, the char is generally pushed into the deeper water where it sometimes becomes pelagic, especially in deeper lakes. Lakes are important for salmon production in some water systems in Iceland (Einarsson 1987), as is also known in Canada (Chadwick and Green 1985, Ryan 1986).

Distribution and abundance of salmonids in relation to the classification

The distribution and abundance of the salmonid species in Iceland can be explained by the classification system presented.

Atlantic salmon stocks are found in all parts of Iceland. Distribution, however, is limited to the warmer, more productive rivers. Waterfalls act as barriers and limit access of salmon to the upper parts of some watersheds. The salmon is the dominant species in spring-fed rivers with lakes near their origin, and at the lower end of the longer spring-fed rivers (Areas 1 in Figure 19) (Table 2). It is also the dominant species at the lower end of the longer direct runoff rivers in the Plio-Pleistocene areas (Areas 2, especially 2B, in Figure 19). In the Tertiary areas, salmon are common in lowland rivers and at the lower end of long rivers. The salmon is thus the dominant species in many rivers in west Iceland (Areas 3D in Figure 19), but in very few rivers in the north-west Peninsula (Area 3A in Figure 19), in the Trollaskagi Peninsula, north Iceland (Area 3B in Figure 19) and in east Iceland (Area 3C in Figure 19). The salmon is the dominant species in almost all wetland heath rivers (Areas 4A and 4B in Figure 19) (Table 2).

The brown trout is found throughout Iceland. It is the dominant species in many rivers of the younger part of the country and is common in lakes. Anadromous stocks occupy many direct runoff rivers of the Plio-Pleistocene areas (Areas 2A and 2B in Figure 19) and spring-fed rivers (Areas 1A and 1B in Figure 19) in south Iceland. Resident stocks are also common in these areas as well as in spring-fed rivers in the north (Area 1C in Figure 19) (Table 2).

The arctic char is found in all parts of Iceland. It is the dominant species in short spring-fed streams as well as in the upper parts of spring-fed rivers (Table 2). It is also the dominant species in many colder rivers of the older parts of the country (Areas 3, especially in 3A, 3B, 3C in Figure 19) (Table 2). Anadromous char stocks are common. The char is also commonly the dominant species in lakes as well as in the slower flowing sections of rivers.

Fish are more abundant in the more productive rivers, but the physical habitat as well as the stability of the fluvial environment also play an important role.

Table 2. Distribution of salmonids in the rivers of Iceland. ( ) means that river type is not common in the region.

River type	Region as in Figure 19	Main species
<u>Quaternary rivers</u>		
Short spring-fed rivers and springs	1ABC	Arctic char
Longer spring-fed rivers	1A(BC)	Brown trout
Long or lake-fed spring-fed rivers	1BC(A)	Atlantic salmon
Short direct runoff rivers	2AB	Arctic char
Longer direct runoff rivers	2B(A)	Brown trout
Lowland or long direct runoff rivers	2B(A)	Atlantic salmon
<u>Tertiary rivers</u>		
Short direct runoff rivers	3ABCD	Arctic char
Long lowland or lake-fed direct runoff rivers	3D(ABC)	Atlantic salmon
Wetland heath rivers	4AB	Atlantic salmon

ADAPTATION OF SALMONIDS TO THE ENVIRONMENT--
LIFE HISTORY STRATEGIES OF SALMONIDS

Review of ideas

The action of natural selection depends on the net effects of all selective pressures acting, which are seldom known in detail (Sheppard 1960). Selection does not need to be constant, and can be disruptive. There are limitations to what extent organisms can respond to selective pressures, since they are constrained in the flexibility of their morphological, physiological, and behavioral features and by the limitations of the mechanisms of inheritance.

Teleost fish employ a wide variety of life history strategies favoring their progeny reaching sexual maturity. This adaptation to the environment, through natural selection, by each species or population is expressed in a characteristic combination of biological traits, such as fecundity, size at maturity, size and number of offspring, reproductive lifespan, and spawning season and pattern (Mann and Mills 1979).

Three major theories of life history strategies have been developed in the last two decades: the r-K selection theory, the bet hedging theory, and the cost of reproduction theory (Wooton 1984).

Until recently r- and K-selection was the most influential of these three theories. Life history pattern is described as being either r- or K-selected (MacArthur and Wilson 1967). Selection in unstable environments where population size is controlled largely by density-independent factors is termed r-selection. Life history tactics include early maturity and high reproductive effort, even though it may result in high adult mortality. K-selection, on the other hand, describes selection in stable environments where the population size is controlled by density-dependent factors. Life history tactics include late maturity, multiple broods, larger but fewer offspring, and low reproductive effort (Pianka 1970, Stearns 1976). There exists a r-K continuum of traits, between the two extremes (Mann and Mills 1979). In recent years, the r-K classification has not proved to be especially helpful, since there are many species and populations that do not fit into the classification, and serious contradictions have been identified (Ito 1980). The r-K theory is not detailed enough to account for covariation in life history traits observed in nature (Schaffer 1979, Wooton 1984). For example, salmonids have relatively few large eggs compared to other freshwater fishes, contrary to what the r-K theory predicts relative to other life history traits of salmonids and the environment in which salmonids live. Neither does the theory include details of age specific fecundities and mortalities, this having major implications for the interpretation of life history patterns (Charlesworth 1980). Another example is the combination of life history traits of both types in some species. The threespined stickleback and the mosquitofish (Gambusia affinis), have combination of r and K selected traits (Wooton 1984, Stearns 1983a, 1983b). But r-K theory has been useful in stimulating new ideas of life history tactics.

The bet-hedging theory assumes that the crucial factor determining the best adapted life history is the stability of the environment. If juvenile survival is variable, a life history is favored in which the animal is iteroparous with relatively low fecundity and long life span. If juvenile survival is more certain, life history traits such as early age of maturity, high fecundity, and short life span will be favored (Stearns 1976). One difficulty with this theory is that mortality is not invariantly age-specific, even in the same population. This theory has been useful and merits further application where both juvenile and adult survival is known (Wooton 1984).

The cost of reproduction theory deals explicitly with a life history aspect that the other two theories do not account for. Both imply that only certain combinations of life history traits can occur -- for example, early maturation and high fecundity are correlated with short lifespan (Wooton 1984). The cost of reproduction theory assumes that any current breeding attempt imposes a cost, decreasing expected future reproductive successes (Bell 1980, 1984a, 1984b). Selection should then favor a life history pattern tending to maximize the sum of present and expected future successful reproductive outputs (Schaffer 1974, Schaffer and Rosenzweig 1977). Age-specific mortality can greatly influence whether the organism will be semelparous (at low juvenile mortality) or iteroparous (at high juvenile mortality). In this respect, this theory will lead to the same prediction as the bet-hedging theory (Wooton 1984). The concept of reproductive effort gives some insight into the trade-off between present reproduction and future expected reproduction. Reproductive effort is defined as the proportion of the total resources available allocated to reproduction (Gadgil and Bossert 1970).

This theory can thus be viewed as employing optimization principle (Lotka 1922, Rozen 1967, Cody 1974). Foraging is then viewed as a problem of energy acquisition. Natural selection operates to optimize the energy that can be allocated for progeny (Ware 1982). According to this, organisms would tend to gain as much food as possible at the least expense. And various morphological, physiological and behavioral adaptations would result. Optimal life history theory assumes that, within the limits imposed by physiological considerations and the mechanism of inheritance, there is selection for energy allocation yielding the highest reproductive value (Schaffer 1974, Ware 1982).

From this point of view, recruitment prediction requires understanding of the relationship between parents and their offspring and the effect of environmental factors (Ware 1982). Beverton and Holt (1957) formulated recruitment to increase asymptotically in relation to the size of the mature stock. Ricker (1958) suggested that mortality rate of the prerecruitment stage was density-dependent, this resulting in recruitment reaching maximum at some intermediate mature stock size. If the energy each individual accumulates per unit of time decreases with higher stock abundance or lower food supply, widespread occurrence of density-dependent growth in immature fish would be explained. Surplus power for reproduction may be as strongly density-dependent as growth rate. Reproductive effort would then vary with stock density

(Ware 1982). Brown trout are able to reabsorb some of their eggs under starvation conditions, and many fish species such as rainbow trout (Oncorhynchus mykiss) do not develop all their oocytes when food is limited (Scott 1962). It has also been shown in several fish species that, under limited food condition, only eggs near the main blood vessels in the ovaries obtain optimal amounts of nutrition (Meien 1940 and Anokhina 1960, quoted by Mann and Mills 1979). Annual differences in fecundity are known in several salmonid species. This is pronounced in pink salmon (Oncorhynchus gorbuscha), the differences being correlated with sea temperature (Rounsefell 1957). Examination of catch data from Icelandic rivers reveals the size of the grilse and salmon to vary from year to year, depending on oceanic conditions. When oceanic conditions are favorable, the fish are more abundant and are larger in size (Scarnecchia 1984b). Since fecundity is size dependent, variation in fecundity of fish of the same age can be expected from year to year. Annual variations in fecundity have been reported for Atlantic salmon (Pope, Mills and Shearer 1961, Thorpe, Miles and Keay 1984) and other fish-species, such as the capelin (Mallotus villosus) (Nakashima 1987). Evidence of reduced reproductive effort in relation to available food resources tends to support Ware's explanation of the various stock-recruitment relationships. These relationships can be viewed as special applications of optimal life history theory.

Life history traits and their interaction

Salmonid fishes are interesting for study of life history strategies, because of large number of semi-isolated populations within species and because of large diversity of reproductive strategies within and between species (Schaffer 1979). Salmonids are opportunistic, phenotypically plastic generalists, having quite variable life history strategies also within species (Thorpe 1986). The precise homing of these fishes provides the mechanism for development and maintenance of adaptation through reproductive isolation, thus maintaining the distinctiveness of populations. Migratory behavior and life histories are closely linked. Life history traits appear to co-evolve to form strategies best suited for the biology and the environment of a given taxon (Hutchings and Morris 1985). Life history traits interact and should be viewed in the context of the entire life history of the organism (Warren and Liss 1980). It is useful to look at these life history traits and their interaction in Atlantic salmon. Generally, tendencies in the life history of Atlantic salmon occur in the other two Icelandic salmonid species.

Incubation time No stock difference have been observed in the incubation time of eggs of Atlantic salmon (Wallace and Heggberget 1988). The time is controlled by temperature and can be described by a single power equation (Crisp 1981) over a wide range of temperatures (Wallace and Heggberget 1988). Efficiency of converting yolk to body tissues differs among stocks, and the temperature at which maximum yolk conversion efficiency occurs varies (Beacham and Muray 1987).

Time of spawning Time of spawning varies between stocks of Atlantic salmon (Heggberget 1988). Different stocks, appear to have adjusted their time of spawning to the thermal regime of the river during incubation of the eggs, so that the alevins will hatch and the fry will start feeding at a good time for survival. Information from hatcheries in Iceland that rely on wild broodstock indicates that time of spawning varies between rivers. In colder rivers the spawning occurs earlier.

Egg number and size Conflicting selection pressures act on the size and the number of eggs. Increased number of eggs is important to overcome the effects of predation and to fully utilize available nursing grounds. Suitable spawning habitat for salmonids does not always coincide with suitable nursery habitat. Agonistic territorial behavior in salmonid fry favors full utilization of suitable habitat within the normal dispersion distance from the spawning grounds. On the other hand larger egg will result in larger fry (Mann and Mills 1979) with larger yolk sacs, these fry being less sensitive to starvation and other physiological stress (Hunt 1969, Ivlev 1961, Adelman, Bingham and Maatch 1955). These two selective pressures result in some compromise between size and number of eggs, which depends on the prevailing environment.

Egg number in Atlantic salmon increases with parental size (review by Thorpe, *et al*. 1984). Many authors have also reported that egg size also increases by parental size (Thorpe *et al*. 1984). In general, egg size appears to increase directly with egg number (Prouzet, Le Bail and Heydorff 1983 cited in Thorpe *et. al.* 1984, Dahl and Somme 1944, Pope *et al*. 1961). A compromise between the growth to larger size to obtain higher fecundity and increased mortality while obtaining larger size would seem to occur. There are differences in both egg number and egg size of salmon at the same length between different stocks of salmon (review by Thorpe et. al. 1984, Randall 1989), as elsewhere in Icelandic salmon (Gudjonsson, Gudbergsson and Johannsson unpublished data). Differences in egg size in the same stock between years have been observed (Pope et. al. 1961, Thorpe et. al. 1984).

Thorpe et. al. (1984) found that egg number and egg size was correlated within river-year groups, but not sea- year group in Scottish salmon. Large eggs gave rise to large first-feeding fry, small eggs to smaller fry. This difference in fry size was not maintained, since rapid growth was associated with progeny of small eggs of young spawners, while progeny of large eggs of older parents had initial territorial dominance but slower growth rates. Thorpe et al. (1984) further correlated these findings with differences in developmental rates at other stages in life. They suggested that multiple-age structure of spawners was maintained by counter-balancing advantages. Size of alevins and fry is not only influenced by initial egg size but also by the temperature regime during incubation and development.

Freshwater age Where the river habitat is stable and favorable in relation to the sea or the ocean outside, resident stocks may have advantages over anadromous stocks. Nevertheless, anadromy opens the way to utilization of new habitats. Marine growth of anadromous salmonids is evidence that oceanic habitat can be very favorable. Anadromous migrations can also be important in the distribution of the species.

There is large variation in the freshwater age of anadromous salmonids. Smolts of Atlantic salmon have been found to be from 1 to 8 years old, while smolts of brown trout have been found to be from 1 to 6 year old (review by Randall, Healey, and Dempson 1987). Arctic char stay 1 to 8 years in fresh water before they first migrate to sea (Dempson and Kristoffersson 1987).

Results from many studies have indicated that there is an inverse relationship between smolt age and sea age of salmon (review by Randall and Leger 1986). On the other hand, sea age and river age seems to be independent in some salmon stocks in Canada (Bielak and Power 1986, Robitaille et al. 1986).

There is large variation in size of a year-class in some Icelandic salmon stocks, especially where the environment is unstable. The size of a year-class is not always related to the magnitude of parental spawning, but rather to environmental conditions. Whether an year-class is to be large or small in the river is evident after the first winter of life. If it is large after the first winter, then it will stay large. This has been learned from annual field surveys (electro fishing) in rivers in north and north-east Iceland. Hunt (1969) found that the size of brook trout parr (Salvelinus fontinalis) at the end of their first summer was important for overwinter survival. Larger fry suffered lower mortality and mortality was lower when the mean size of 0+ parr, in the fall, was large. This is also the experience of the author for salmon in Iceland. Low growth rate of salmon fingerling, during their first summer of life is related to higher mortality rates of the 0+ parr. Year classes emerging and growing during cold springs and summers are often small in numbers. Such environmental effects on cohort size are also known for other freshwater fishes (Mills and Mann 1985).

There is also large annual variation, in some stocks, in the proportion of each year class that smolt at a certain age. There is general latitudinal cline in age at smolting in Atlantic salmon, this increasing at higher latitudes on both sides of the Atlantic (Dahl 1910, Power 1981). Saunders and Schom (1985) showed the importance of the variation in this life history parameter of Atlantic salmon. Individuals of a given year class can smolt at different times over a period of several years and spawn over a still longer period, and thus breed with salmon from many other year classes. Stocks of Atlantic salmon are often small. This will help to maintain genetic variation in such stocks. Moreover, such a stock can better survive through several successive years of poor reproduction. Such stocks are more resilient than stocks with uniform life histories. The importance of this variation in fluctuating environments has been demonstrated for other fish species such as the Pacific sardine (Sardinops caerula) (Murphy 1967). Other herring-like fish show a similar adaptation -- that is longer reproductive life spans in more fluctuating environments (Murphy 1968). This is the case in the American shad (Alosa sapidissima) (Legget and Carscadden 1978).

The duration of freshwater residency is both environmentally and genetically induced (Randall et. al. 1987). Developmental plasticity has been shown in the rates of growth, smolting, and maturation during the river phase. These rates co-vary within many salmonids (Alm 1959. Thorpe 1977, Thorpe and Morgan 1978, 1980, Thorpe Talbot, and Villareal 1982, Thorpe et al. 1983).

Smolting Bimodality is evident in the frequency distribution of fork length in sibling juvenile Atlantic salmon at the end of their first growing season in fish culture. The upper modal group represents potential one-year smolts, while the lower modal group consists of parr that do not become smolts when one year old (Simpson and Thorpe 1976, Thorpe 1977, Thorpe and Morgan 1978, Thorpe et al. 1980, Bailey, Saunders and Buzeta 1980).

The proportion of smolts entering the upper mode can be influenced by environmental factors affecting growth (Power 1986), such as temperature (Kristinsson, Saunders and Wiggs 1985) and density (Thorpe 1977). Thorpe (1977), Bailey et al. (1980), and Thorpe et al. (1983) have demonstrated that the proportion entering the upper modal group is strongly influenced genetically. The male parent seems to most influence the rate of development, while the female parent appears to most influence body size (Thorpe and Morgan 1978). The time of divergence into two groups as well as the size at which it occurs, varies between families (Thorpe et al. 1980).

Thus bimodality is seen both in hatchery reared salmon and in wild fish. Variable growth rate leads to separation of each year class into different size groups, which results in various age at smolting. In colder river the same year class can smolt over several years. During colder periods, the range in smolt age as well as the mean smolt age of the same year class increases, while in warmer periods the range and the mean smolt age decrease. This can be seen in the colder rivers of

Iceland, for example in the north-east. The importance of this variation is evident, as mentioned earlier, and the variation becomes more important during colder, harsher periods.

Time and size at seaward migration The time of outward migration of smolts varies among stocks of different rivers. This emigration, as well as smolting, is stimulated by various environmental factors such as temperature and photoperiod (Eriksson and Lundqvist 1982, Thorpe 1988). This timing, as well as the size of the smolts, seems to be genetically influenced. Icelandic salmon stocked as fry in Sandy brook, a tributary to the Connecticut River, USA, migrated later and at smaller size than smolts from a nearby stock that were also stocked as fry (Orciari, Mysling, and Leonard 1987).

The general trend in Iceland is that in the southernmost rivers smolts migrate early (May-June) while smolts in north-eastern rivers migrate later (June-July). These times coincide with the appearance of spring condition in the sea outside these rivers (Gudjonsson 1988a). There is little variation in the size of smolt in Iceland (Einarsson 1987a, T. Tomasson, Institute of Freshwater Fisheries 1988 pers. comm., Poe 1975, Kristjansson 1987, Gudjonsson 1988a, Antonsson and Gudjonsson 1989). Smolts in Iceland are generally smaller than Atlantic salmon smolts elsewhere (Einarsson 1987a).

Age at maturity There is large variation in the size and age at which Atlantic salmonid mature. In some stocks of Atlantic salmon in Iceland, most fish return to spawn after one winter at sea (grilse), while in other stocks there are also fish returning after two or more years at sea (salmon) (Scarnecchia 1983). Such variation has been observed in salmon stocks around the world (Rounsefell 1958, Ricker 1972, Dahl 1916, Power 1981).

There are also considerable differences in age at maturity between the sexes. In general, males tend to reach maturity at an younger age. Males do not have to invest as much energy in reproductive tissues as females (Jonsson 1977), which may make maturity at an younger age possible. Differences in reproductive energy expenditures may also be reflected in the fact that mature males are larger than mature females of the same age in rivers of Iceland. Sexually mature males are of two major types. One is large migrant males that spend one or two years at sea (3 and 4 is also known but rare). The other type is mature male parr, often called precocious males, which mature without a migration to the sea.

Mature male parr occur in different proportions in different populations (Jones 1959, Myers, Hutchings, and Gibson 1986). There is evidence that males destined to mature as parr have faster initial growth rates than male parr destined to smolt (Saunders, Henderson and Glebe 1982, Thorpe et al. 1983). It has been suggested that in order to smolt, parr must reach a threshold in size and/or developmental stage, a higher threshold being required for reach sexual maturation as parr (Bailey et al. 1980, Thorpe et al. 1980, Saunders et al. 1982). This may explain the widespread occurrence of mature male parr in the more productive Icelandic rivers. Available data suggest that mature male parr are favored in the more stable rivers of Iceland where nonanadromous stocks of char and brown trout also appear to be favored.

Migrant males fight for females, and size becomes important in determining mating success, which depends in part on proximity to the nest excavated by the female. The male closest to the nest, in a linear dominance hierarchy, has the best chance to fertilize the eggs, the male second closest the second best, and so on. Grilse males spend only one year at sea and thus are smaller than salmon, which spend two or more years at sea. In some rivers almost all males spend one year at sea, while in other rivers there are also males that spend two or more years at sea. Grilse males are more common where the river environment is stable. High mortality at sea during a second year at sea would also favor grilse males.

Mature male parr sneak to the nest in order to fertilize the eggs. The best sneakers are small since they can be unnoticed. But there is competition among mature parr for the best hiding places near sexually mature females, so the larger precocious males may be favored. Mature male parr can mate successfully with females in the absence of anadromous males (Myers and Hutchings 1987). Therefore, both forms may be strongly size selected by counter-balancing forces, there appearing to be two or more optimal sizes for males at maturity in many salmon stocks (Leonardsson and Lundberg 1986, Myers 1986, Gross 1985). Some mature male parr can smolt the year after spawning, go to sea, and return as full-sized males (Thorpe and Morgan 1980, Bagliniere and Maisse 1985), thus achieving the advantages of both reproductive forms. Observations by the author on smolts in rivers in north-east Iceland have shown that some of the male smolts have spawned before as parr. Mature male parr also have the capacity to spawn more than once as parr.

Salmonid females put more energy into their reproductive tissues than do males. It may therefore be more important for females than for males to reach larger size in order to gain higher reproductive effort. In anadromous stocks of Atlantic salmon, females generally migrate to sea. A possible exception is in the southernmost part of the distribution of the species (France), where there are reports of mature female parr (Bagliniere and Maisse 1985). Others have explained such females as rare unsuccessful mutations (Hindar and Norland 1989).

Females generally spend one, two, or three winters at sea. Delayed maturity can result in larger reproductive effort, but also in higher mortality. Larger fish appear better able to ascend long, fast rivers. Higher age and larger size at maturity can be adaptations to the difficulties of upstream migration (Schaffer and Elson 1975). Larger fish spawn larger eggs, which can result in larger fry perhaps better able to survive in a larger, faster, colder, and harsher rivers. This would also favor delayed maturity. But the advantages of delayed maturity depend heavily on the rate of mortality and the rate of growth during the second year at sea (Schaffer and Elson 1975). Female grilse are most likely to be favored where smolt survival is high and nonfluctuating.

Most salmon stocks in Iceland are essentially semelparous. In some stocks, however, a considerable proportion of the fish are iteroparous (spawn more than once. Some salmon spawn first as grilse (1 sea winter) or as salmon (2 or more sea winters), then migrate to the sea the following spring and return later that same summer to spawn again or return after one whole year at sea. There are, thus, several life history patterns of iteroparous salmon.

Theoretical studies indicate that fluctuating environmental conditions causing variable mortality rates of immature fish will favor reproduction over several years (iteroparity) (Murphy 1968). When prereproductive survival is uncertain, a tradeoff between lower reproductive effort and greater longevity will occur (Stearns 1976). On the other hand, when fluctuations occur in the mortality rate at the sexually mature stage, then increased reproductive effort and consequently shorter life span will be favored(Schaffer 1974). In populations of American shad (Alosa sapidissima), the southernmost populations are semelparous, while northern populations are iteroparous (Legget and Carscadden 1978), possibly because of more fluctuating survival of the young in northern rivers. Some anadromous populations of brown trout in Iceland are iteropareous, while many anadromous char populations are semelparous. Nonanadromous populations of these species are often iteropareous. The advantages of iteroparity must also depend on available recovery habitat for post-reproductive adults in the river, as well as, on distance to areas in the sea with food sufficiently available for large fish from year to year.

As noted earlier, most Icelandic stocks of salmon are essentially semelparous, with high reproductive effort and fecundity. But individuals in each yearclass become sexual mature at different ages, this realizing advantages of a sort of populations yearclass iteroparity (Mann and Mills 1979). Schaffer (1974) predicted that a population of semelparous organism with variable prereproductive mortality would respond by only a fraction of the population reproducing annually. Age at maturity of salmon in more fluctuating environments in rivers in Iceland is more heterogeneous than in the more stable rivers. True iteroparity in salmon stocks in Iceland is found only in rivers having good recovery sites for spawned fish.

There are strong indications that the period shortly after the smolt migrate to sea is the most critical in respect to the survival of the fish. This is seen in that large part of the variation in the run of salmon can be predicted by the variation in the grilse run one year earlier (Kristjansson 1982, Scarnecchia 1984a, Scarnecchia, Isaksson and White 1989a). There is large variation in the survival of coho salmon smolts (Oncorhynchus kisutch) depending on the degree of upwelling (review by Fisher and Pearcy 1988). Poor feeding opportunities for the outmigrating smolts appears to result in poor survival. Also in food-poor years predation on smolts may be heavy because of lack of alternative prey for predators (Fisher and Pearcy 1988). Sea conditions fluctuate more and are more unpredictable in the sea north and east of Iceland than south and west of Iceland (Asthorsson, Hallgrimsson and Jonsson 1983). This may affect food production and the survival of smolts in Icelandic stocks of salmon, more so in North Iceland than in South and West Iceland (Scarnecchia 1984b, Scarnecchia, Isaksson and White 1989b). This appears to also affect the abundance of other fish species. Weight, growth, and survival of cod (Gadus morhua), capeline, and other fishspecies of particular yearclasses are affected by these fluctuation in oceanic condition (Malmberg 1986).

Variable smolt survival could partly explain higher and more heterogeneous age at maturity of salmon in northern rivers. For fish that survive this critical period, it can be advantageous to stay an extra year at sea to gain higher fecundity, if subsequent mortality rate is relatively low and growth rate is high. It seems that there is higher growth rate at sea in stocks in north Iceland than stocks from south and west Iceland. From the catch records, it is seen that both grilse and salmon in north Iceland are generally larger in size than in west Iceland, even though the smolts are similar in size. The higher gain in weight at sea could further make it advantageous to stay an extra year at sea in north Iceland.

Unfavorable oceanic conditions and heavy smolt mortality would also favor selection of precocious male parr, especially if the river environment is stable. Smolt mortality can be very high during downstream migration (Larson 1985) where there are long migration routes to the sea.

The sea age at maturity seems to be determined in freshwater. In some Canadian stocks, ovarian development stage was found to be more advanced in emigrating smolts in grilse stocks than in stocks spending multiple winters at sea (Chadwick, Randall and Leger 1986). There is also an inverse relationship between ovarian development in Atlantic salmon smolts and parental sea age (Chadwick, Claytor and Leger 1987). Other findings tend to support this. There is a linear association of grilse and salmon in the same smolt cohort in salmon stocks in Iceland, despite varying oceanic condition (Kristjansson 1982, Scarnecchia 1984a, Scarnecchia, Isaksson, and White 1989). These findings further strengthen the view that life history pattern is in part genetically determined in salmonids. Life history is partly environmentally induced, and variations in the environment can alter it.

Life history strategies

Life history strategies can best be understood with reference to the entire life history pattern of each stock. Knowledge about its habitats will aid in understanding the selecting pressures and the adaptation of the stock, as seen in its life history pattern.

The various stocks of Atlantic salmon have evolved so that they can best survive in the habitats they live in. Habitat itself is constantly evolving. A stock of salmon is therefore of transitory nature, since it is constantly adapting to its changing environment. Knowledge about the habitat and understanding of its development should greatly facilitate understanding of the patterns of evolution operating on the organism within it.

By knowing the habitat dimensions of the species or populations under study, it should be easier to detect the most enabling and constraining environmental features, which in most cases should also be the most selective pressures. In this respect the usefulness of a comprehensive habitat classification is apparent. A hierarchical view is necessary both to classify the habitat and to understand interspecific and intraspecific variation in adaptation to the environment, including variation in life history traits. It is therefore valuable to relate the various biological traits of an organism to various environmental conditions.

LIFE HISTORY PATTERNS OF ICELANDIC SALMON IN RELATION TO THE CLASSES OF ICELANDIC WATERSHEDS AND RIVERS

Life history data

The general trends in life history tactics of Atlantic salmon have now been described. The dominant features of different classes of Icelandic rivers have also been revealed. It is now of interest to look at the life histories of different salmonids inhabiting different classes of Icelandic rivers. Most informations on the life histories are availible for Atlantic salmon, but in some cases also for the brown trout and the arctic char. The main emphasis is therefore on the life history of the Atlantic salmon. Oceanic conditions and fluctuation in the favorableness of the sea to outmigrating smolts have also been discussed. The oceanic conditions of the sea outside different parts of Iceland are important to consider when the life history strategies of anadromous stocks are viewed.

Life history data from Icelandic watersheds are of several types. Accurate catch statistics are available, since the catch each year as well as sex and weight of each fish is recorded for nearly all rivers. Long series of such catch statistics as well as fairly constant fishing effort make these catch statistics unique. Grilse and salmon can be separated by use of weight frequencies. Each smolt cohort was treated separately, so the grilse of year n were considered to be in the same cohort as salmon of year n+1. There is a problem with the catch data where there are repeat spawners. A salmon that is going to spawn for the second (or third or fourth) time is likely to be considered as a salmon that has been 2 or 3 years at sea. This will distort the grilse-salmon ratio as seen from these data alone. Data are also taken from numerous scale analyses, which also aid in the separation of the grilse from salmon. Field surveys provide important data on smolt age as well as on the occurrence of mature male parr. In a few instances, age data were available from adult and smolt traps.

Some of these data are published, mainly in the reports of the Institute of Freshwater Fisheries in Iceland. Other unpublished date were collected by the Institute.

Life history tactics in spring-fed rivers

Spring-fed rivers offer a stable habitat. The thermal regime and the physical habitat in each river in large part determine what species can occur. Many of these rivers have resident trout and char stocks. Anadromous stocks are often present, but part of such a stock may be resident. Climatic conditions as well as the oceanic conditions outside these regions differ, and it is of interest to see how the stocks respond in each region.

<u>Spring-fed rivers in south Iceland (1A)</u> Oceanic conditions outside this area (Figure 19 1A) do not fluctuate much. Volcanic activity has, however, disturbed the biota in two of the largest rivers in recent years. There is little information on life histories of salmonids in this area. Brown trout is the

dominant species, anadromous populations of brown trout being common, but resident fish are also known. The smolt age seems to be uniform and the fish spawn several times over their life span. Arctic char, both resident and anadromous are also in this area, but salmon are rare.

Spring-fed rivers in south-west Iceland (1B) Some rivers in this area have a lake near their origin. Rivers in this area flow to the west, south, and north of Iceland (Figure 19 1B). Salmon is the dominant species. The life history pattern is uniform, one life history type being dominant (3 years in freshwater and 1 year at sea) (Table 3). The density of juveniles is high in these productive and stable rivers. Mature male parr are found here, as in many productive rivers in Iceland. This indicates that the maturing of male parr in freshwater is favored where food is abundant and the river environment stable. Mortality from smolt stage to returning adult is always high. In River Ellidaar, S.W. Iceland, outmigrating smolts have been tagged and the return rate measured. From those studies the mortality was 80% in the 1975 smolt run (Isaksson, Rasch and Poe 1978), 90% in the 1985 smolt run (Kristjansson 1987) and in the 1988 smolt run the mortality was 85% (Gudjonsson and Antonsson unpublished data). This high marine mortality together with the favorable river environment favors the mature male parr.

There are some repeat spawners. Weight frequencies in catch data are mainly used to separate grilse from salmon. Repeat spawners are therefore likely to be considered as salmon (2 years at sea) in the catch statistic data. The salmon component is thus lower than

Table 3. Several life history traits of salmon stocks of spring-fed rivers in south-west Iceland (1B in Figure 18).
SW = Sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of cacth records used written below average catch.

River name	Males: Mature parr	Males: 1 SW %	Males: 2 SW %	Males: 3 SW %	Females: 1 SW %	Females: 2 SW %	Females: 3 SW %	Repeat spawners %	Smolt age in years: 1	2	3	4	5	6	7	8	Average catch no	%SD	References
Ellidaar	#	94.6	5.3	0.1	93.3	6.7		5		*	D	*	+				1440 (1968-1986)	26	Fridriksson 1940 Poe 1975 Gudjonsson 1978 Gardarsson 1983 Kristjansson 1987 Inst.Freshw. Fish. Unp. data
Ulfarsa	#	95.6	4.4		95.2	4.8		1		*	D	+					277 (1949-1986)	52	Tomasson 1975 Inst. Freshw. Fish.Unp. data
Leirvogsa	#	90.4	9.5	0.1	87.6	12.4		1		+	D	*					400 (1974-1986)	39	Gudjonsson 1986a, 1986b, 1987a, Inst. Freshw. Fish. Unp. data
Sog	#	69.4	25.2	5.4	57.3	38.4	4.3	15		*	D	*					441 (1975-1986)	30	Johannsson 1976 Fridriksson 1940 Gudjonsson 1978 Inst. Freshw. Fish. Unp. data
Grimsa and Tungua	#	85.8	12.1	2.1	77.3	21.1	1.6	2		+	D	+					1009 (1958-1986)	59	Gudjonsson 1978 Inst. Freshw. Fish. Unp. data

the numbers indicate (Table 3). This is especially apparent in River Sog, which has high proportion of repeat spawners (15%). The time shortly after the smolt migrate to sea seems to be especially critical. Fish that once reach maturity seem to have a good chance to spawn more than once in these rivers. This is because the fish have good opportunity to survive after spawning, especially in the larger rivers and in lakes (River Sog, River Ellidaar), and then recover at sea. In this regard, the sea south of Iceland (River Sog) is more predictable and favorable than elsewhere around Iceland.

There are rivers flowing north from this region, which join a large glacial river. These spring-fed rivers are at high elevation (500-600 m. above sea-level). Arctic char is the dominant species in these drainages, such as in River Seydisa. Some of the char are resident and some sea run. The anadromous char juveniles leave the river after 2 to 4 years and migrate to the sea, more than 100 km. The char generally stay 2 summers at sea (1 and 3 also known) before returning to River Seydisa, where most of the char seem to spawn 1 to 3 years later. The char always spend the winter in freshwaters, but immature char do not necessarily spend the winter in the home river. A high proportion of males do not go to sea. The river environment is stable and both juveniles and adults are present in the river for several years, this favoring persistence of the stock even though unfavorable oceanic conditions north of Iceland last for some years (Gudjonsson 1989a).

Spring-fed rivers in north Iceland (1C) These rivers are fairly stable but oceanic condition outside fluctuate greatly from year to year (1C in Figure 19). Atlantic salmon is the dominant species. The juveniles smolt at relatively young age. The largest part of the same year-class smolts over a period of about 3 years (Table 4). In this way, an entire yearclass will not be virtually lost if smolts find unfavorable oceanic conditions on entering the sea. Smolt of the same cohort will mature at different times over a period of 3 years and some of the fish will spawn more than once. Together these tend to ensure that unfavorable oceanic condition will have less adverse effect on the stock. In this respect, these stocks have both real iteroparity and the advantages of a sort of iteroparity resulting from a yearclass maturing at different times. Such multiple life history patterns can be viewed as a sort of polymorphic adaptation to different conditions in time, even though polymorphic adaptation to different condition in space is better known.

Life history in Quaternary direct runoff rivers

Rivers of this type are in two regions, both in south Iceland. The thermal regime of the rivers governs what species are dominant. The rivers in the east area (2A) are generally shorter and colder than rivers in the west area (2B). Brown trout is the dominant species in the east area while Atlantic salmon is dominant in the west area. These species respond differently in their life histories to similar environments. These rivers are unstable in flow and temperature. The rate of juvenile survival is thus uncertain.

Table 4. Several life history traits of salmon stocks of spring-fed rivers in north Iceland (1C in Figure 18).
SW = sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of catch records used written below average catch.

River name	Males: Mature parr	Males: 1 SW %	Males: 2 SW %	Males: 3 SW %	Females: 1 SW %	Females: 2 SW %	Females: 3 SW %	Repeat spawners %	Smolt age in years: 1	2	3	4	5	6	7	8	Average catch no	%SD	References
Laxa í Adaldal	+	50.9	37.4	11.7	19.6	73.8	6.6	5		*	*	*	+				523 (1949-1986)	42	Fridriksson 1940 Karlstrom 1972 Tomasson 1987a, 1988a, Inst. Freshw. Fish. Unp. data
Reykjadalsa	*	85.4	14.3	0.3	32.0	67.7	0.3	2		*	*	*	+				328 (1974-1986)	52	Tomasson 1984, 1986a Inst. Freshw. Fish. Unp. data
Ormarsa	#	70.9	26.3	2.8	30.3	67.7	2.0	2		+	*	*	*	+			154 (1974-1986)	62	Inst. Freshw. Fish. Unp. data
Deildara	#	63.4	35.8	0.8	39.3	59.4	1.3			*	*	*					147 (1970-1986)	61	Inst. Freshw. Fish. Unp. data

Quaternary direct runoff rivers in south-east Iceland (2A) Rivers in this area (Figure 19 2A) are generally unstable, but oceanic conditions in the sea outside are stable. Brown trout is the dominant species. Arctic char are also common, but salmon are rare. The brown trout here are usually anadromous. The juveniles smolt when 2-3 years old and go to the sea. Many of these rivers flow into spring-fed and glacier-fed rivers, which offer stable environments in the estuaries for large juveniles. Some juveniles spend their last 1 or 2 freshwater years near the estuary of the river. After staying at sea 2 or 3 summers the brown trout reach sexual maturity. They spawn each year after that up to 5 times (M. Johannsson Institute of Freshwater Fisheries 1988 pers. com.). Brown trout always overwinter in freshwater, but immature fish do not necessarily overwinter in their home water (Gudjonsson 1989a).

The life histories of these brown trout stocks show that the freshwater phase is relatively short but the adult stage is long and the stocks are iteropareous. This is a good adaptation to unstable river conditions and stable oceanic condition. Post-juveniles form the main portion of the stocks, and the rivers are only used for spawning and for the first 1 or 2 years of life (1 year in the estuary of the main river).

Quaternary direct runoff rivers in south Iceland (2b) The rivers in this area (Figure 19 2B) are unstable but the oceanic condition are stable. Atlantic salmon is the dominant species in most of the rivers, but brown trout also occur. The juveniles generally smolt at a young age (2 to 3 years old) (Table 5). In some rivers, the juveniles leave their home river earlier and spend

Table 5. Several life history traits of salmon stocks of Quaternary direct runoff rivers in south Iceland (2b in Figure 18).
SW = Sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of catch records used written below average catch.

River name	Males: Mature parr	Males: 1 SW %	Males: 2 SW %	Males: 3 SW %	Females: 1 SW %	Females: 2 SW %	Females: 3 SW %	Repeat spawners %	Smolt age in years: 1	2	3	4	5	6	7	8	Average catch no	Average catch %SD	References
Stora Laxa	+	57.6	36.3	6.1	18.7	75.9	5.4	15		*	*						295 (1973-1986)	61	Johannsson 1978 Fridriksson 1940 Inst.Freshw. Fish. Unp. data
Litla Laxa	+	Sparse data						*		*	*								Inst. Freshw. Fish. Unp. data
Kalfa	#	Sparse data						*		*	*								Inst. Freshw. Fish. Unp. data

their last year in a mainly spring-fed river, which many of these rivers flow into (M. Johannsson Institute of Freshwater Fisheries 1988 pers. com.). The fish reach sexual maturity at different sea-ages (Table 5). Furthermore, a considerable proportion of the fish spawn more than once (Table 5). Mature male parr exist in the smaller lowland drainages of this type. In the highland drainages mature male parr are very rare. Maturation of males at the parr stage from River Stora Laxa was very low when reared in a hatchery, but hatchery rearing of other stocks induced high degree of sexual maturation in male parr. Large proportions of the fish in these stocks are in the post-juvenile stage. This adaption is similar to the adaption of brown trout in the same type of rivers in south east Iceland. Differences in how these two species respond to similar environments are also apparent.

Life history in Tertiary rivers

Rivers in the Tertiary areas are generally harsh and unproductive. The presence of lakes and the altitude are the most influential factors. Rivers in extensive, flat, vegetated areas at relatively low altitude are the most stable and productive ones.

Life histories, depending on the environmental character, are very different in these rivers from those in rivers of other types.

Direct runoff rivers in north-west Iceland (3A) Conditions in the rivers and in the sea outside the river in this area (Figure 19 3A) are unstable. Arctic char, often anadromous, is the dominant species in the region.

Anadromy opens the possibility to utilize more dependable and productive environments in the sea. Food abundance in the inshore areas the char utilize are not highly dependant on oceanic condition. Data on char life history are poor. It is likely that for the first time the char generally migrate to sea very young. Salmon occupy only a few rivers, mostly lake-fed ones or ones with long lowland drainages. Strengths of yearclasses are highly variable, depending on climatic conditions. In cold years, fry emerge late and suffer higher mortality during their first winter. Salmon in each year class smolt over a period of many years (Table 6). Smolt age and range in smolt age of a yearclass increases during periods of cold years. The fish reach maturity after one or two years at sea. Thus many life history patterns exist in salmon stocks in this region. This is an adaption to this unstable environment. Progeny of a single female spawn over period of many years. This favors persistence of the stock during harsh periods, either in the river or in sea. Mature male parr are generally rare, apparently an evolutionary result of the harsh and unstable river environment. In systems with lowland lakes, rivers are more favorable and stable and mature male parr more common. Repeat spawners are very rare. There is little chance to survive in the river after spawning, and chances to recover at sea the following spring are presumably slim and unpredictable.

<u>Direct runoff rivers in north Iceland (3B)</u> The rivers in this region (Figure 19 3B) are unfavorable for Atlantic salmon, and the oceanic condition in the spring are fluctuating and unpredictable. Only a few of these rivers support salmon. Arctic char is the dominant

Table 6. Several life history traits of salmon stocks of direct runoff rivers in north-west Iceland (3A in Figure 18). SW = sea winter, D = dominant, * = common, # = fairly common, + = rare. Years of catch records used written below averge catch.

River name	Males				Females			Repeat spawners	Smolt age in years								Average catch		References
	Mature parr	1 SW	2 SW	3 SW	1 SW	2 SW	3 SW		1	2	3	4	5	6	7	8	no	%SD	
		%	%	%	%	%	%	%											
Laugadalsa	#	76.5	23.0	0.5	51.2	47.7	0.5										311 (1954-1986)	58	Inst. Freshw. Fish. Unp. data
Langadalsa	+	63.8	34.9	1.3	30.9	68.8	0.3	0			*	*	*	*	*		177 (1957-1986)	70	Jonsson 1984a Einarsson 1986a, 1987b, 1988a, Inst. Freshw. Fish. Unp. data
Hvannadalsa	+	65.4	32.9	1.7	42.4	55.0	2.6	0			*	*	*	*			76 (1969-1986)	64	Jonsson 1984a Einarsson 1986a, 1987b, 1988a, Inst. Freshw. Fish. Unp. data

species, both anadromous and resident forms being present. The resident form is mainly confined to lakes. The anadromous char presumably migrates generally to the sea very young for the first time. Many life history forms of char occur in these and other unstable rivers. The life history patterns of salmon here are similar to those in the direct runoff rivers of the north-west (Table 7). Fish in a yearclass smolt and become mature over a long time period. Mature male parr are rare and so are repeat spawners. The same constraints affect the salmon stocks in this area as in other areas having unstable freshwater and marine environments.

Direct runoff rivers in east Iceland (3C) The oceanic conditions off this area (Figure 19 3C) are very unpredictable. Moreover, the rivers are unstable. Arctic char is the dominant species, and is often anadromous. Salmon are rare. The life history pattern of salmon stocks in this area is similar to life history pattern in rivers of this type in other regions. Mature male parr are rare and so are repeat spawners (Table 8). The total age span of salmon is broader than in rivers of this type elsewhere. This adaptation to very unstable environment is similar to those rivers having similar environments.

Direct runoff rivers in west Iceland (3D) Rivers in this area (Figure 19 3D) are heterogenous. Some are typical direct runoff rivers, but many are stabilized by lakes. Lakes and extensive lowlands in west Iceland make many of the rivers more favorable salmonids environments. Oceanic conditions here are more predictable than in north Iceland. Atlantic salmon is the dominant species in many of the rivers. The life history patterns in the

Table 7. Several life history traits of salmon stocks of direct runoff rivers in north Iceland (3B in Figure 18).
SW = Sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of catch records used written below averge catch.

River name	Males				Females			Repeat spawners	Smolt age in years								Average catch		References
	Mature parr	1 SW %	2 SW %	3 SW %	1 SW %	2 SW %	3 SW %	%	1	2	3	4	5	6	7	8	no	%SD	
Fljotaa	+	64.4	31.9	3.7	28.7	68.5	2.8	0		*	*	*	+				155 (1969-1986)	47	Inst. Freshw. Fish. Unp. data
Fnjoska	+	50.5	48.0	1.5	18.1	81.1	0.8	0		+	*	*	+	+			282 (1969-1986)	46	Tomasson 1988b Inst. Freshw. Fish. Unp. data

Table 8. Several life history traits of salmon stocks of direct runoff rivers in east Iceland (3C in Figure 18).
SW = Sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of catch records used written below averge catch.

River name	Males				Females			Repeat spawners	Smolt age in years	Average catch		References
	Mature parr	1 SW	2 SW	3 SW	1 SW	2 SW	3 SW		1 2 3 4 5 6 7 8			
		%	%	%	%	%	%	%	D=dominant age, *=common +=rare	no	%SD	
Breiddalsa	+	76.6	23.3	0.1	55.3	44.3	0.4	1	+ * * * + + +	123 (1971-1986)	89	Inst. Freshw. Fish. Unp. data
Lagarfljot	Sparse data							1	+ * * * +			Inst. Freshw. Fish. Unp. data

more favorable and stable rivers here are similar to those in spring-fed rivers in south-west Iceland (Table 9). There is a uniform life history pattern with one dominant smolt age and a high grilse component of the mature stock. In the more unstable rivers, multiple smolt ages occur and a wider range in age at maturity. Mature male parr are common in many of the more stable rivers of this type. In these rivers, some of the fish spawn more than once.

Wetland heath stream in north-west Iceland (4A) These rivers are productive and relatively stable. They flow both to the west and to the north (Figure 19 4A). Atlantic salmon is the dominant species in most of these rivers. Arctic char, often anadromous, are also common in the slower flowing sections of the rivers.

Oceanic conditions in the west are more stable than in the north. Consequently, the stocks of salmon in rivers flowing west (River Thvera and River Laxa i Dolum) have more uniform smolt age than stocks in rivers flowing north (Table 10). This is apparently because smolt survival is more stable from year to year at sea west of Iceland than north of Iceland. Mature male parr are found in high numbers in the most favorable rivers. Repeat spawners are found in some number in some of the rivers, where there are good possibilities to survive after spawning, as in lakes or in slow flowing river sections. There is also a wide range in the age of maturity in these stocks, favoring stock persistence through several years of unfavorable oceanic conditions. The life history is most uniform in the most stable and favorable rivers. During colder harsher periods, in the river, yearclasses are smaller, the smolt age increases,

Table 9. Several life history traits of salmon stocks of direct runoff rivers in west Iceland (3D in Figure 18).
SW = Sea winter, D = dominant, * = common, # fairly common, + =rare.
Years of catch records used written below averge catch.

River name	Males				Females			Repeat spawners	Smolt age in years								Average catch		References
	Mature parr	1 SW	2 SW	3 SW	1 SW	2 SW	3 SW		1	2	3	4	5	6	7	8	no	%SD	
		%	%	%	%	%	%	%											
Laxa i Kjos	#	77.5	22.1	0.4	71.0	28.7	0.3	5		*	*	*					1311 (1959-1986)	25	Gudjonsson 1978 Inst. Freshw. Fish. Unp.data
Bugda	#	85.6	14.1	0.3	82.1	17.8	0.1			*	*	+	+				230 (1957-1986)	45	Einarsson 1987a Inst. Freshw. Fish. Unp. data
Laxa i Leirarsveit	#	79.2	19.6	1.2	70.8	29.0	0.2			+	D	*					933 (1955-1986)	49	Jonsson 1981 Inst. Freshw. Fish. Unp. data
Andakilsa	#	85.3	14.1	0.6	79.3	19.9	0.8			*	D						174 (1971-1986)	47	Tomasson 1978 Inst. Freshw. Fish. Unp. data
Nordura	#	77.6	21.4	0.9	56.3	43.1	0.6	2		+	D	*	+				1702 (1969-1986)	28	Gudjonsson 1978 Fridriksson 1940 Jonsson 1982, Inst. Freshw. Fish. Unp. data
Langa	#	88.1	11.5	0.4	78.8	20.9	0.3	3		*	D						1542 (1971-1986)	40	Isaksson 1985 Inst. Freshw. Fish. Unp. data
Alfta	#	78.4	20.5	1.1	64.6	34.3	1.1				D Sparse data						301 1972-1986)	30	Einarsson 1987c, 1988b, 1989a, Inst. Freshw. Fish. Unp. data
Mida	No data	71.9	27.3	0.9	58.1	41.2	0.7		No data								149 (1970-1986)	34	Inst. Freshw. Fish. Unp. data
Haukadalsa	No data	71.8	27.0	1.2	54.9	44.2	0.9		No data								609 (1948-1985)	44	Inst. Freshw.

Table 10. Several life history traits of salmon stocks of wetland heath rivers in north-west Iceland (4a in Figure 18).
SW = sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of catch records used written below averge catch.

River name	Males				Females			Repeat spawners	Smolt age in years								Average catch		References
	Mature parr	1 SW %	2 SW %	3 SW %	1 SW %	2 SW %	3 SW %	%	1	2	3	4	5	6	7	8	no	%SD	
Thvera	#	71.4	24.9	3.7	51.7	46.3	2.0	5		+	D	+					1683 (1957-1986)	39	Gudjonsson 1978 Einarsson 1989b Inst. Freshw. Fish. Unp. data
Laxa i Dolum	+	72.7	47.9	2.6	49.5	47.9	2.6	0		+	*	D	+				880 (1972-1986)	61	Jonsson 1979, 1984b Gudjonsson 1984 Einarsson 1986b, 1987d, Inst. Freshw. Fish. Unp. data
Laxa i Hrutafirdi	+	75.0	24.3	0.7	37.5	60.8	1.7			+	*	*	+	+			46 (1961-1986)	93	Einarsson 1986c, 1986d, Inst. Freshw, Fish. Unp. data
Hrutafjardara and Sika	+	66.4	32.1	1.4	33.7	65.1	1.2	0		*	*	*	+	+			270 (1971-1986)	33	Einarrsson 1982, 1987e, Inst. Freshw. Fish. Unp. data
Miðfjardara	+	63.2	35.0	1.8	34.2	64.3	1.5	1		+	*	*	+				1255 (1956-1986)	45	Gudjonsson 1978 Inst. Freshw. Fish. Unp. data
Vididalsa and Fitja	+	56.9	35.7	7.3	23.1	68.9	8.0	2		*	*	*	+	+			1064 (1948-1985)	36	Gudjonsson 1978 Tomasson and Gardarsson 1985 Tomasson 1986b,1988c Inst. Freshw. Fish. Unp. data
Vatnsdalsa	+	67.2	28.6	4.2	22.1	75.9	2.0	2		*	*	*	+	+			996 (1974-1986)	33	Gudjonsson 1983 Gardarsson and Tomasson 1985 Tomasson 1987b 1988b Inst. Freshw. Fish. Unp. data
Laxa a Asum	#	79.8	19.0	1.2	62.5	36.4	1.1			+	*	*	+				1237 (1968-1985)	40	Kristjansson 1982 Tomasson 1986c, 1987c, 1988e Inst. Freshw. Fish. Unp. data
Blanda	+	49.6	49.7	0.7	24.5	74.8	0.7	0		+	*	*	+				1433 (1974-1986)	41	Gudbergsson and Gudjonsson 1986 Gudjonsson 1986c, 1987bc, Gudjonsson and Vidarsson 1988ab

as does the range in smolt age.

Wetland heath streams in north-east Iceland (4B)

Rivers in this region (Figure 19 4B) are stable but oceanic conditions are unstable. Atlantic salmon is the main species. Life history adaptations in these rivers are similar to those in rivers in north west Iceland, but the life span is longer apparently in response to more fluctuating oceanic conditions (Table 11). Repeat spawners are common and so are precocious male parr. Some of these later migrate to sea, as observed in a smolt trap in River Vesturdalsa.

The life history strategies of Icelandic stocks of salmonids in relation to the classification

The classification system presented aids understanding of the physical constraints in the habitat on the life histories of the salmonids. When habitat capacities and performances are viewed, both in the rivers and in the sea outside, along with the capacities and performances of the fish populations, understanding of adaptations to habitat through different strategies in life history is enhanced.

The rivers of Iceland present very different environments for salmonids. The stability of the environment is variable and favorableness in terms of food availability is variable. Food availability depends on the fertility and the thermal regime of the river water. The physical habitat within and between rivers is mainly dependent on the slope of the watershed and the type of the geological formation. Both the type of the physical habitat and the thermal regime of the river

Table 11. Several life history traits of salmon stocks of wetland heath rivers in north-east Iceland (4b in Figure 18).
SW = sea winter, D = dominant, * = common, # = fairly common, + = rare.
Years of catch records used written below averge catch.

River name	Males				Females			Repeat spawners	Smolt age in years								Average catch		References
	Mature parr	1 SW %	2 SW %	3 SW %	1 SW %	2 SW %	3 SW %	%	1	2	3	4	5	6	7	8	no	%SD	
Svalbarðsá	+	57.9	36.9	5.3	16.2	80.8	3.0	1		*	*	*	*	*			135 (1971-1986)	58	Benediktsson 1987 Inst. Freshw. Fish. Unp. data
Sandá	+	60.6	34.7	4.7	22.4	73.4	4.2	1		*	*	*	*	*			207 (1964-1986)	66	Inst. Freshw. Fish. Unp. data
Midfjardara and Kverka	+	74.4	22.9	2.7	24.2	74.7	1.1	1		+	*	*	*	+			117 (1970-1986)	61	Odinsson 1988 Inst. Freshw. Fish. Unp. data
Sela	+	61.7	35.4	3.0	31.9	65.9	2.2	1		+	*	*	*	*	+	+	410 (1975-1986)	95	Kristjansson 1982 Gudjonsson 1988b Inst. Freshw. Fish. Unp. data
Vesturdalsa	+	66.7	31.6	1.7	36.7	62.6	0.7	1		+	*	*	*	*	+	+	216 (1956-1986)	66	Gudjonsson 1988a Inst. Freshw. Fish. Unp. data
Hofsa	+	64.6	31.4	4.0	16.8	79.1	4.1	1		+	*	*	*	*	+		494 (1948-1986)	90	Gudjonsson 1988c Inst. Freshw. Fish. Unp. data

water affect the distribution of the salmonid species.

The life histories of salmonids in the rivers of Iceland vary depending on the stability of the river habitats and the oceanic condition outside. In the most stable and productive rivers, salmonids tend to be resident (Table 12). In the case of Atlantic salmon, female of which are always anadromous in Iceland, mature male parr are common in such rivers. This is also true where the oceanic condition are harsh and unpredictable. Where oceanic conditions are more stable and predictable, anadromous stocks tend to have uniform life histories (Table 12). If the river presents an unstable and harsh environment in relation to the sea outside, anadromous stocks are common. The freshwater phase is then often short and the stock reserves are in multiple forms of adults or semi-adults at sea (Table 12). The fish then spend different times at sea and some may spawn more than once, if there are recovery sites in the river for spent fish (lakes, slow sections). If both freshwater and oceanic conditions are unstable, multiple life history forms are present (Table 12).

The fish always tend to be in the life forms where the chances of surviving, growing, and reproducing are best. From this point of view, the bet-hedging life history theory (Stearns 1976) can be applied to the salmonids in Iceland. The life history seems to be adapted so that the population can survive even though heavy mortality can occur at certain life stages from time to time. One such life stage is the first winter of life for salmon in many of Iceland's rivers, especially in the colder and more unstable rivers where juveniles can suffer high mortality. If salmon eggs

Table 12. Summary of life history patterns of salmonids in Icelandic rivers in relation to the stability of river and oceanic environments.

River environment	Ocean environment	Rivers in region as in Figure 19	Life history patterns
Unstable	Unstable	3ABC	Multiple patterns in years at sea and in freshwater
Unstable	Stable	2AB (some in 3D)	Short river duration, many patterns in years at sea including repeat spawning
Stable	Stable	1AB (some in 3D, 4A)	Uniform life history pattern, one dominant life history pattern, resident forms more common
Stable	Unstable	1C, 4AB	Many patterns in years in freshwater and years at sea including repeat spawning, resident forms more common

hatch late in the summer and growth during the first summer is poor heavy mortality can occur the following winter. Another such life stage is the time when smolts go to the sea. If unfavorable ocean conditions exist then, heavy mortality occurs. This is the case, in some years, in the northern rivers of Iceland.

The populations have adapted their life histories to such constraints. In the examples above, juveniles from the same year-class smolt over a period of some years, so the entire yearclass will not be lost if the smolts are confronted with harsh conditions. Furthermore, the smolts that survive through this critical period will return over a period of several years and therefore spawn in different years.

Other adaptations are seen where the river habitat is very unstable but oceanic condition stable. There the freshwater phase is short but different individuals of a yearclass mature and spawn over a period of several years. Where there is suitable habitat within the river system for spawners to recover after spawning, some fish may spawn more than once. A different adaptation is seen in the most stable and favorable rivers in Iceland, where resident life forms are favored.

As seen from these examples, it is neccessary to know the habitat of the population in question and how it constrains and enables the population, if its life history tactics are to be understood. With such understanding, the management of the populations, the fish stocks, is made more coherent and effective. By constantly adapting life history to habitat, salmonids persist in and coevolve with constantly changing habitat. Salmonid research and management should always take this into account.

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