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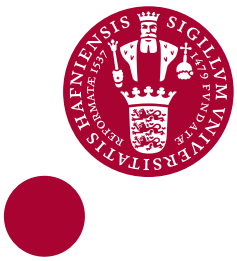

Lowland river systems - processes, form and function

Pedersen, M. L.; Kronvang, B.; Sand-Jensen, K.; Hoffmann, C. C.

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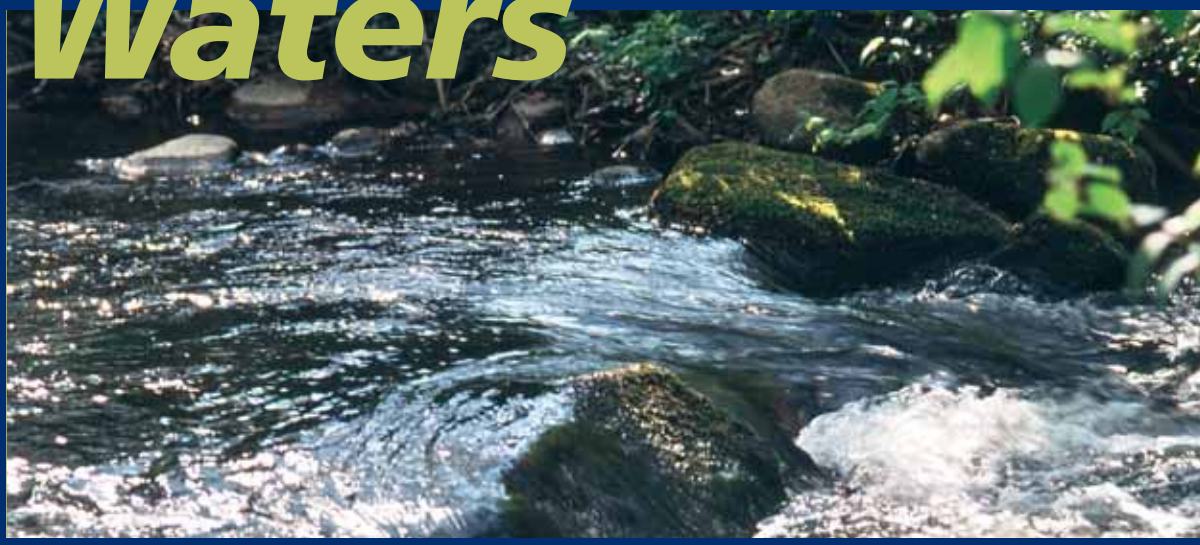

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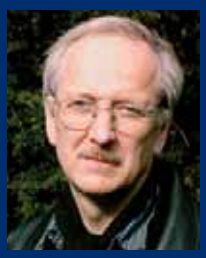

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EDITORS: Kaj Sand-Jensen, Nikolai Friberg & John Murphy

Running Waters

Historical development and restoration of lowland Danish streams

National Environmental Research Institute
Ministry of the Environment · Denmark

Running Waters
Historical development and restoration of lowland Danish streams
by Kaj Sand-Jensen, Nikolai Friberg & John Murphy (editors)

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Foreword

Many people are fascinated by the dynamic nature and heterogeneity of streams. Nothing is exactly the same from one second to the next and from one stream site to another. For scientists, however, the dynamic nature of streams is a constant challenge. To study streams and provide an accurate and reproducible description of the physical and chemical environment, and the biological life it supports, is a difficult, though rewarding, task. Among all the variability there are regular patterns and constraints which are possible to determine and use in practical management.

Stream flow is a permanent downstream movement – turbulent and unpredictable. A small quiet and slowly flowing stream can rapidly turn into a roaring river eroding the banks and transporting many tons of sediment following a few days of heavy rain. The stream can change direction and location if it is allowed to do so or has uncontrollable forces. Streams have this shifting gentle and angry face which we appreciate but also a temper we want to be able to predict to prevent unpleasant surprises.

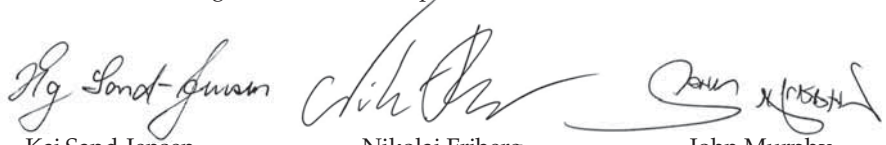
According to ancient Nordic mythology, the troll found a home in the cold water of streams when the glaciers melted under him 13,000 years ago. Ever since, he has remained the spirit of the stream who from time to time became furious and takes a toll from the carriages, horses and drivers passing a stream. The gods, the prophets and their disciples who later occupied the country have been unable to drive him out of his hide in the pool under the bridge. Only here, out of sight and out of reach, is he safe, though doomed to stay in the wet element.

We have made a great effort to describe and display important physical processes and biological creatures along and within the streams. Many people have helped us with photos. Fortunately they have never caught the image of the troll, which could have raised an omnivorous anger among his many hidden cousins distributed in the streams and rivers over the entire Earth.

In the spirit of the Enlightenment this has become a book on the visible, predictable and comprehensible nature of Danish streams which can help us attain understanding and sensible management. The National Environmental Research Institute, Denmark, and director of research Kurt Nielsen have supported us with funds for printing and time for exceptional technical assistance from Juana Jacobsen and Kathe Møgelvang. We are deeply indebted to photographers, the research institution and the three persons above.

We would also like to thank Jon Bass, John Davy-Bowker, Mike Furse, Iwan Jones, Martin Neale and Mattie O'Hare of the UK Natural Environment Research Council Centre for Ecology and Hydrology for their help in reviewing and improving the book.

Hillerød, Silkeborg and Dorchester, April 2006



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Great Belt
Zealand
Copenhagen
SWEDEN
Bornholm
Baltic Sea
Falster
Lolland
GERMANY
0
50
100 km

Introduction

This book was in its original Danish version written for Danes with a general interest in nature or a specific interest in streams and their biology. Whatever background, however, they were all Danes and as such familiar with our small country. Now we want to reach an audience outside our borders and have therefore made this introduction, which gives a brief background to Denmark beyond streams, macrophytes and macroinvertebrates.

Figure 1
Map of Denmark with the main regions, largest cities and three largest rivers.

Running waters focuses on geomorphology, hydrology and ecology of streams and rivers in Denmark and all anthropogenic impacts acting upon them. The book was initially published for a Danish audience, but when we showed it to colleagues in England, New Zealand, Estonia and Lithuania they asked for an English version. They were impressed by the quality of illustrations and layout and wished to learn more about Danish lowlands; knowlegde streams which would be applicable to lowland streams in their own countries. Moreover, they wanted to know more about the Danish policy on pollution control of industrial and domestic sewage and the initiatives taken to bring channelised streams in the farmland back to their original meandering form.

To meet this interest, we have produced an English version and John Murphy has kindly helped us editing it. However, to fully appreciate the book and facilitate its reading, we will briefly introduce you to the basic geology and geography of Denmark and the typology and public administration of Danish water courses.

Denmark is a small, lowland country (43,000 km^2) with more than 403 islands. Nowhere in Denmark does the distance to the coast exceed 50 km and the coast line is very long (> 7,300 km). The peninsula, Jutland is connected to the European continent, while the island of Funen and the large island of Zealand are interconnected via bridges (Figure 1). Zealand is separated from Sweden by the narrow strait, Øresund, connecting Kattegat and the Baltic Sea. Southwest of Zealand are two other main islands, Falster and Lolland, while the island of Bornholm is located far to the Southeast in the Baltic Sea.

Denmark is a densely populated and intensely cultivated country, inhabited by about 5.3 million people (approx. 125 persons/km^2). The capitol, Copenhagen, is located in northeastern Zealand, on the Øresund, and about 2 million people live in the greater Copenhagen area. More than 80% of Danes live in urban areas and the other densely populated regions in the

Box 1 Danish terms for running waters

"Vandløb" is both a technical and common Danish word for running waters of all kinds. To distinguish different sized watercourses in Danish we use the words "kilde" for spring, "kildebæk" for small brooks, "bæk" for brooks, "å" for streams and rivers and "flod" for very large rivers. The Thames and the Rhine would be "flod" to Danes, while the two largest rivers, River Skjern and River Gudenå are "å" to us because they are not sufficiently big to become a "flod". You may notice that bæk is equivalent to beck used in Yorkshire and Scotland as a remnant of the influence of Scandinavian settlers in the Viking period. Å is used throughout the Nordic countries, i.e. Sweden, Norway, Iceland and the Farao Islands as the common name for large streams.

country are mid-Funen around Odense and eastern Jutland around Kolding, Frederica, Vejle, Horsens and Århus. The western and northern parts of Jutland have fewer people.

Denmark is very suitable for agriculture as the climate and soils are optimal for cultivating crops. The climate is temperate Atlantic with fairly mild winters (0 ºC), not too hot summers (17 ºC) and an average annual precipitation of 720 mm approximately evenly distributed over the year. Only the island of Bornholm consists of bedrock in some parts, while all other parts of Denmark have sandy and loamy moraine soils. Therefore, almost every part of Denmark has been cultivated. Today the dominant land-use is agriculture (63%), while forests (mainly plantations) cover about 12% and other nature areas cover about 10%. Lakes and streams cover only about 1% of the country.

There is a long history of landscape alteration in Denmark. Deforestation began early; by about 2,000 years ago approximately 50% of forest cover was lost. At the beginning of the 19th century the area covered by forest reached a minimum of less than 4% and the substantial deforestation resulted in increased groundwater levels and flooding. Increased sand erosion in coastal areas blocked streams and further exacerbated the impacts of increased water levels. To counteract the effects of increased water levels and secure agricultural production, meadows were drained and streams channelised and culverted. The agricultural area in Denmark peaked in the 1930s at 76%.

Agricultural production is very efficient with dense stocks of pigs and dairy cows and intensive use of fertilisers and pesticides. In 2005 there were about 13 million pigs in Denmark with an annual production of about twice that number. The main fertiliser is livestock manure, and the main nutrient sources of nitrogen (> 80%) and phosphorus (approx. 50%) to inland and coastal waters derive from agriculture. Intensive agriculture and livestock production, mostly pigs, are dominating in western part of Denmark i.e. in Jutland.

All Danish water courses are small and short. Only River Skjern, River Gudenå and River Storå in Jutland are sufficiently large to deserve the predicate river (Box 1). All other Danish water courses are small streams, brooks and springs. Of the ten largest Danish streams, eight are located in Jutland, which has the largest surface areas and receives the most precipitation, while Funen and Zealand hold one large stream each.

Over very short distances in their upstream parts, a few Danish streams may have relatively steep slopes (> 100 m/km), but true mountain streams do not exist as there are no mountains in Denmark. The highest point is only 173 m above sea level. The majority of streams, therefore, have very shallow slopes (< 5 m/km).

Denmark's surface geology consists of soft sediments of clay, sand and gravel left by the two latest glaciations. During the second last glaciation, the entire country was covered by ice. During the last glaciation, ending some 13,000 years ago, the ice sheet glaciers covered all the islands and the northern and eastern parts of Jutland. The glaciers stopped in a prominent front, whose two parts ran west-east from the present North Sea coast to mid-Jutland and north-south from mid-Jutland to the current German border (Figure 1). Only the south-western part of Jutland was left un-glaciated. Large rivers ran from the glacier front towards the south-west between relatively shallow sandy hills left over from the former glaciation. The glacial rivers left gravel and sand in West-Jutland while clay was deposited further to the west in the central part of the present North Sea.

The glacial history, therefore, explains the topography and surface geology of Denmark, and to some extent the distribution of animals and plants. West-Jutland is dominated by well-leached and carbonate-poor deposits of sand and gravel. East-Jutland is dominated by poorly-leached and more carbonate-rich moraine deposits of clay, sand and gravel. The

islands of Funen, Zealand, Lolland and Falster are dominated by less-leached and carbonate-rich deposits of predominantly clay.

Denmark is known for implementing the first Ministry of Environmental Protection (1971). Relatively intense ecological monitoring of streams also started around 1970 and was intensified even further around 1990. Today, it is the responsibility of the 14 Danish counties covering all Denmark to set quality objectives for streams and rivers. Each County Council politically decides quality objectives, which range from stringent objectives in streams of specific scientific interest to streams with eased objectives i.e. heavily impacted streams. It is also the counties responsibility to monitor the quality of streams in their region to ensure that they fulfill the objectives set. Monitoring is based on macroinvertebrates and the regional network comprises in total more than 10,000 sites. In addition to regional monitoring activities, a national monitoring programme for the aquatic environment, including streams, was launched in 1988 with revisions in 1992, 1997 and 2003. The programme is jointly undertaken by the Danish EPA, the National Environmental Research Institute (NERI), the Geological Survey of Denmark and Greenland (GEUS), the National Forest and Nature Agency and the 14 Danish counties. The counties undertake stream sampling but data storage, analysis and reporting are the responsibility of NERI. Today, the programme encompasses more than 800 monitoring stations covering all stream types in Denmark and monitoring includes three biological quality elements (macrophytes, macroinvertebrates and fish) as well as physico-chemical features and hydromorphological elements. From 2007 the counties will be closed as part of a large-scale structural reform and regional, as well as national, monitoring activities will be transferred to the state.

To summarise: Danish landscapes are intensely utilised almost everywhere and the historical and contemporary agricultural influence on the morphology, management and ecological quality of streams is very strong. Most streams are small, but more prominent streams and rivers exist in Jutland. Their biodiversity and abundance of flowering plants, macroinvertebrates and fish, mainly brown trout, can be very high making Danish streams very important for sport fishing, recreation and overall biological quality among European lowland streams.

Giant ice sheets and melt water have formed the landscape and river valleys.

1 Lowland river systems – processes, form and function

Present day river valleys and rivers are not as dynamic and variable as they used to be. We will here describe the development and characteristics of rivers and their valleys and explain the background to the physical changes in river networks and channel forms from spring to the sea. We seek to answer two fundamental questions: How has anthropogenic disturbance of rivers changed the fundamental form and physical processes in river valleys? Can we use our understanding of fluvial patterns to restore the dynamic nature of channelised rivers and drained floodplains in river valleys?

Danish rivers, their floodplains and river valleys – formation and characteristics

During the last Ice Age the forces of flowing water and erosion by glaciers created the river valleys. The Danish islands and eastern and northern parts of Jutland were covered by a gigantic ice cap during this Ice Age. Underneath the ice, water was flowing in melt water rivers from the base of the ice cap to the glacier fronts. Melt water flowed in the valleys of the glaciated landscape, thereby enhancing the landscape features (i.e. hills and valleys) already present. On its way to the glacier front, the fast-flowing melt water eroded deep valleys, while the slower-flowing waters deposited sand, gravel and stones as ridges (hills). The outcome can be seen in the Danish landscape today, for example in the deep valleys of eastern Jutland where the River Gudenå and its tributaries flow. In addition, the melting of large ice blocks, left in the valley following the retreat of the ice cap, created lakes such as those in the River Gudenå valley.

At the glacier front in mid-Jutland, the melt water concentrated in several large rivers that flooded the moraine landscape in western parts of Jutland. The glacial melt water created large washout plains where sand, gravel and stones were deposited. Today these washout plains are heath plains acting as wide river valleys between the old moraine hills. The heath plains are river valleys for some of the large contemporary rivers in Denmark. The river with the greatest discharge in Denmark, the River Skjern, runs west from Nørre-Snede between Skovbjerg and Varde moraine hills and enters the sea in a large delta in Ringkjøbing Fjord.

Since the last Ice Age rivers and streams have eroded the pristine moraine landscape and have formed floodplains and valleys along the rivers and streams (Figure 1.1). On the moraine hills exposed during the last Ice Age in western Jutland, the streams have had approximately 100,000 years to interact with the surrounding landscape. This long period explains why

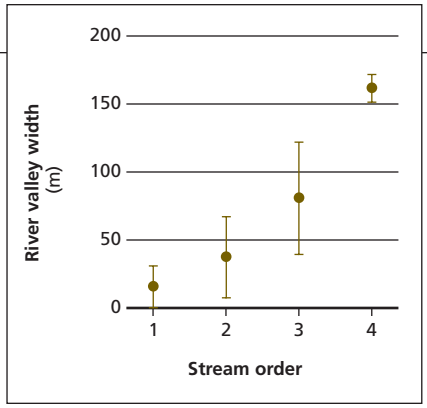
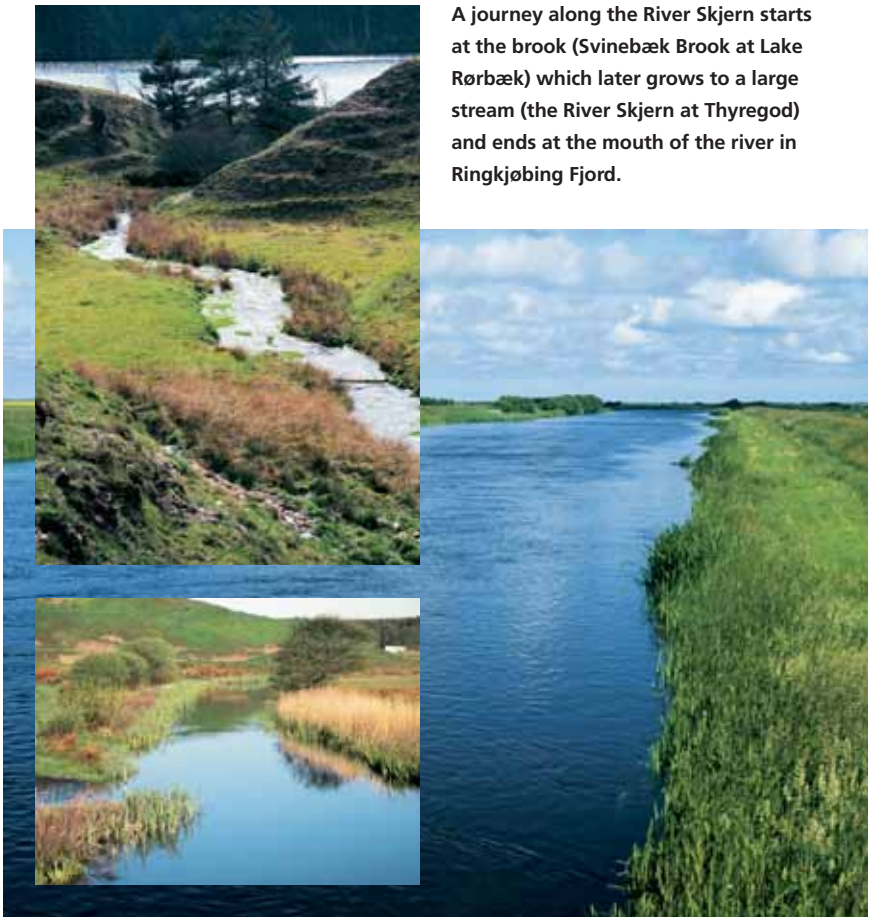


Figure 1.1 The river valleys increase in width from the source to the sea – just as rivers do. Here is an example from the Brede Stream catchment in southern Jutland.

the valleys and floodplains are wider in western Jutland than in the relatively young moraine landscape of eastern Denmark.

In northern Jutland the post-glacial rise in sea level (Yoldia Sea) created marine deposits near the shores. These have subsequently been exposed by the tectonic upheaval of the landmass. They form the present-day wide river valleys, bordered by former sea cliffs that now stand out as steep eroded hillsides, in this part of the country. A good example of this is the Skals Stream, north of Viborg. As a consequence of postglacial landmass movement, land subsidence in the southern part of Jutland has created special conditions where the present-day rivers are flowing in marine deposits and continuously adjust their morphology to the rising sea level. On the island of Bornholm, the presence of bedrock creates an in-stream environment different from anywhere else in Denmark.



A journey along the River Skjern starts at the brook (Svinebæk Brook at Lake Rørbæk) which later grows to a large stream (the River Skjern at Thyregod) and ends at the mouth of the river in Ringkjøbing Fjord.

The river valley – intimate interactions between river and floodplain

Rivers are naturally in a dynamic equilibrium with their valley and floodplain. The stream slope and flowing water create the energy needed for transporting eroded soil particles from stream banks and hillsides in the catchment to the sea. Erosion is most prevalent in the upper river system, where many small streams are in close contact with the surrounding landscape. Groundwater and drainage water from the catchment also supply vast quantities of dissolved substances to the streams. These are also subsequently transported to the sea.

In the lower part of natural, unmodified river systems, flooding of the river valley occurs regularly at high-flow events. During flooding vast quantities of sediment and organic debris are deposited on the floodplain. Close to the stream bank most of the sand is deposited as levees. Finer sediment and organic particles are deposited further away from the stream. The flooding waters, sediment and organic material are an important renewing source of nutrients to the floodplain. In natural systems these supplies of nutrients and sediment are essential for the growth and development of natural floodplain vegetation. In this way nature has created a buffer

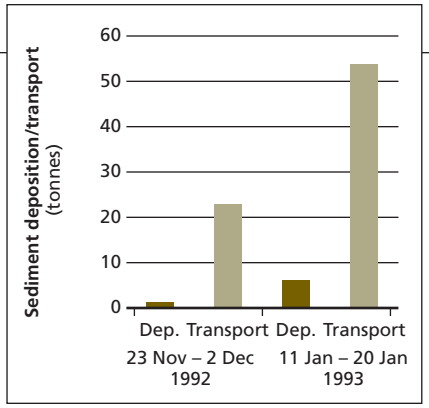


Figure 1.2 Floodplain sediment deposition during high flow events can reduce the sediment transport to the sea. During two 9-day flooding events in the lower part of the Gjern Stream (catchment area: 110 km²) between 6% and 11% of the transported sediment was retained on the floodplain [1].

system delaying the loss of nutrients and sediment to the sea and enhancing the recycling of nutrients within the catchment. A substantial proportion of the suspended material being carried by floodwaters can be deposited on the floodplain and hence retained within the catchment (Figure 1.2).

Streams in undisturbed lowland landscapes will naturally wind or meander through the river valley. A stream moves from side to side within the river valley by eroding sediment on the outside of meanders and depositing the sediment on the inside of meanders further downstream. It is a slow physical process, which evolves over decades or centuries. In some cases the stream erodes at the base of the valley sides, thereby slowly widening the floodplain. The constant lateral movement of rivers and streams occasionally leaves meanders cut off and isolated on the floodplain as small oxbow lakes. Vegetation and deposited material from the stream will eventually fill the lakes and create small wetlands on the floodplain. Oxbow lakes have a characteristic mixed vegetation assemblage, different from that on the rest of the floodplain, and are quite distinct features in our natural river valleys.

The structure and composition of floodplain soils are highly variable. The Brede Stream valley in southern Jutland has alternating layers of sandy stream deposits, peat and organic material on its valley floor (Figure 1.3). Deposits of organic origin generally dominate soils in Danish river valleys. Decomposed coarse plant material makes up peat layers and fine particulate organic matter and diatom shells deposited in shallow waters make up the gytja layers.

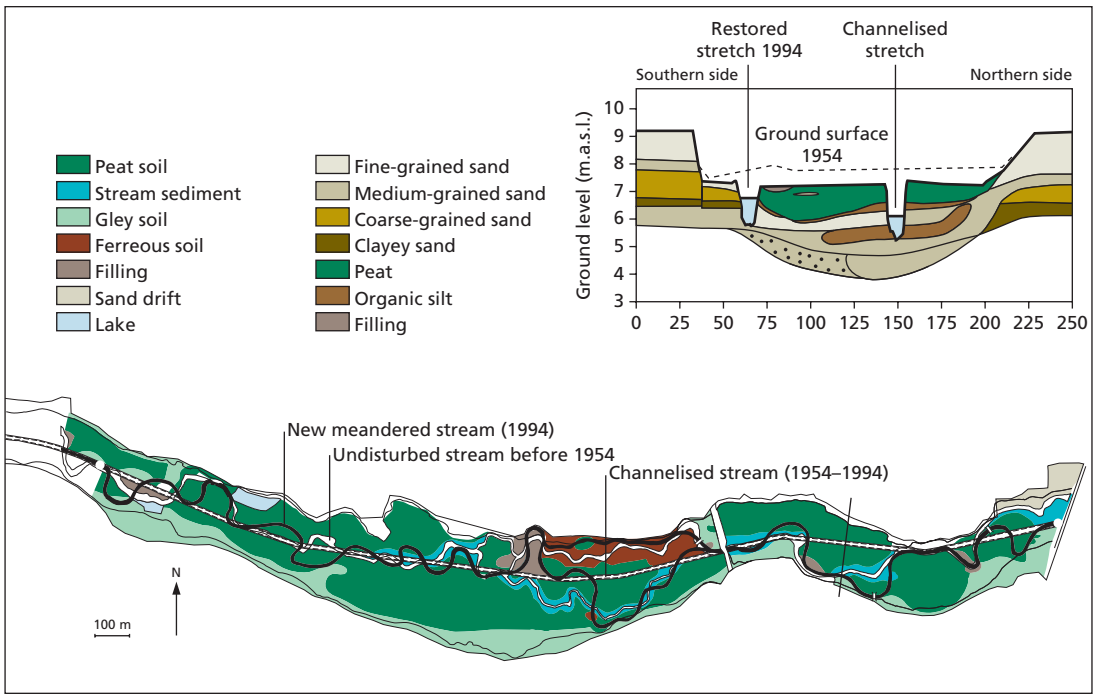


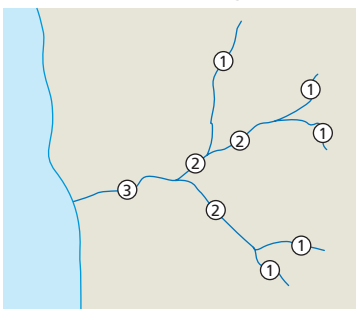
Figure 1.3 The diversity of soil types in the river valley of the Brede Stream is considerable. The channel of this 4-km reach was re-meandered in 1994 in an initiative by the County of Southern Jutland. The river valley was drained and the river was channelised in 1954. Oxidation of the organic soil layer has caused a 0.5 m subsidence of the floodplain over the period of 40 years [2].

During high flow events the natural unregulated watercourse floods the river valley and sediment and nutrients are deposited on the flood plain.

Box 1.1 Stream order

The systematic pattern of longitudinally connected reaches increasing in size at confluences can be presented as a hierarchical system determined by origin and downstream connection – this is known as the Stream Order [3].

Stream order according to size



In total, 6,700 km^2 (15%) of Denmark's area consist of such poorly drained soils rich in organic layers. These soils are primarily found in the river valleys and on raised seabed deposits in northern Jutland and in the salt marsh areas in southern Jutland. These soils have been in high demand because when drained they provide excellent nutrient-rich soils for agriculture.

Streams – a network of unidirectional flow

River systems form a finely branched network of many small, headwater streams that meet to form fewer and larger streams that finally merge into one large river reaching the sea (Box 1.1). From upstream brooks to the downstream river, water is continuously received from the surrounding land. The influence of the catchment landscape on stream morphology depends on soil type, topography, terrestrial vegetation and land use. Streams therefore form a unique ecosystem because of the linear connections within the network, the unidirectional flow and the intimate contact with the land.

Many brooks are formed by springs located near the base of steep slopes, where water leaves the groundwater reservoir. The confluence of several springs forms a spring brook, which is characterised by stable discharge and water temperature. Further downstream the confluence of spring brooks forms a stream, usually 0.5–2 m wide. Streams increase in size as they flow downstream becoming larger, 2–4 m wide. Even further downstream at the confluence of the larger streams, the river is formed.

There is never a long distance to the sea from anywhere in Denmark. Rivers, in the strictest sense, are therefore not very common. Denmark has only two large rivers: the River Gudenå, which is the longest river and the River Skjern, which has the highest discharge (Box 1.2).

Flow and substrata from spring to river

With increasing distance from the spring, the stream usually becomes wider, deeper and transports more water (Figure 1.4 and 1.5). Large rivers often originate in mountains, run down the mountain slopes and across plains towards the sea. Along the course, the slope decreases [4]. This is generally also the case in the short river systems in Denmark, where the steepest slopes are usually found in the springs and brooks, and the lowest slopes in the rivers close to the outlet [5, 6]. However, on the local scale Danish streams follow a more irregular course with shifting reaches of steep or low slopes. This is primarily due to the presence of lakes, which act as hydraulic thresholds and re-set the natural dynamics of the flowing streams. Because of the local irregularities reaches with steep slopes and high physical stress may occur anywhere along the course.

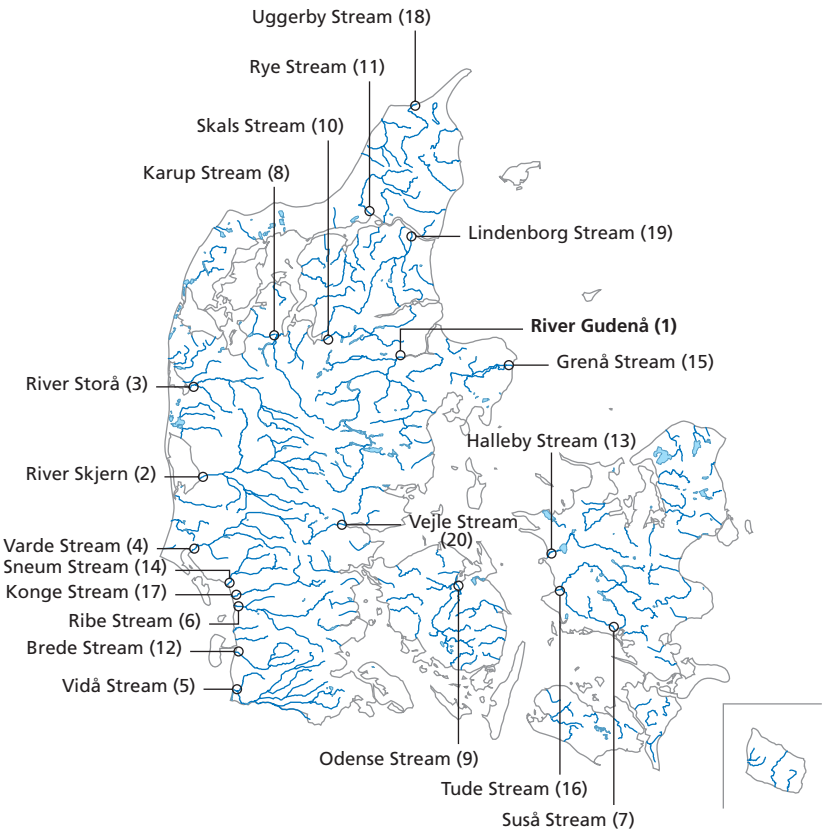
Gravity, acting on the slope of the water surface, drives the downstream flow. The mean current velocity along reaches also depends on the resistance to flow exerted by the streambed, banks and plant surfaces. Since upstream brooks are shallow and narrow, water flows in intimate contact with the streambed and banks. So in spite of a steeper slope, the mean current velocity is usually lower in small Danish brooks than in large rivers [3, 4].

Box 1.2 Danish watercourses: length and location

We have many both naturally and artificially created watercourses in Denmark. The vast majority of watercourses are of 1st and 2nd order – these are called brooks. Medium-sized watercourses (3rd to 5th order) – the streams – are fewer in numbers and we only have a few large watercourses. The longest Danish watercourse, River Gudenå, is 176 km long. Based on physical appearance and biotic communities only the River Gudenå, River Skjern and River Storå can be classified as large rivers.

Watercourse	Total length
Small watercourses (Width: 0–2.5 m)	48,000 km
Medium-sized watercourses (Width: 2.5–8.0 m)	14,500 km
Large watercourses (Width: >8 m)	1,500 km
Total	**64,000 km**

The map shows the 20 largest watercourses in Denmark measured by catchment area.



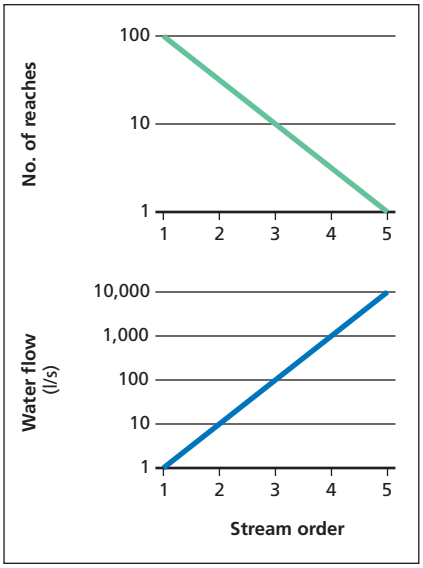
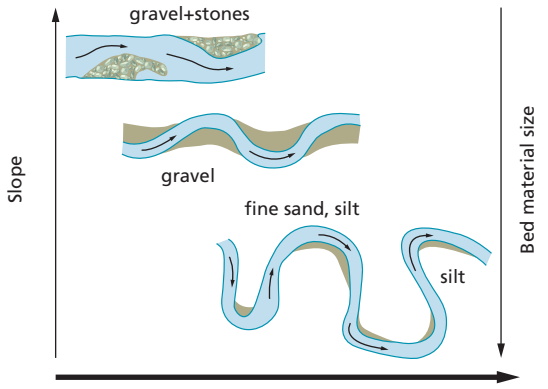


Figure 1.4 Idealised graphs illustrating how the large number of small headwater streams gradually merge into fewer streams of higher order (top), and higher discharge (bottom).

Box 1.3 Lowland channel patterns

Classification of channel patterns in lowland streams. The channel pattern is the result of many processes interacting at many scales, and a classification scheme provides an overall insight into the dominant processes and parameters (modified from [5]).



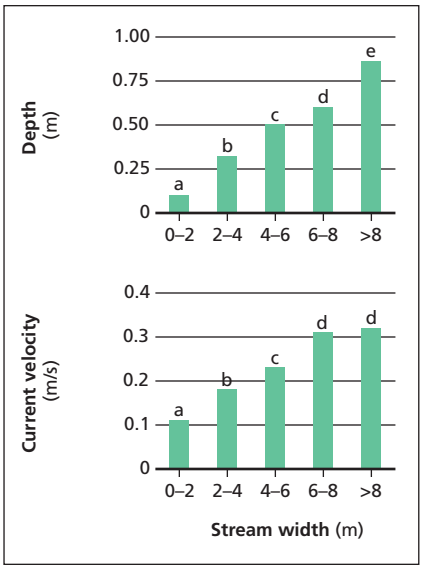


Figure 1.5 There are systematic changes in mean depth and current velocity along the river continuum from source to outlet. Summer measurements in 350 Danish stream reaches illustrate the overall patterns. Different letters mark statistically significant differences.

Local flow conditions above the streambed regulate erosion and sedimentation of particles. Although we may intuitively assume that steep headwaters have coarse gravel and stone substrata while large rivers have fine-grained sand and mud, this does not apply to Danish lowland streams – neither in their original unregulated state nor in their contemporary regulated state. In a nationwide study of 60,000 plots (25 × 25 cm) in 350 reaches across 75 streams, we did not observe systematic changes in the main substrata along the stream courses. Sand was the most common bottom substratum in both small and large streams (approx. 40% of all plots). In streams less than 2 m wide, gravel and stones were found in 30% of the plots, while 23% of the plots in streams more than 8 m wide had sediments dominated by gravel and stones. Mud was also frequent in small (32%) and large streams (23%).

Channel patterns – fundamental principles of river morphology

Stream slope, water discharge, sediment supply and grain size distribution of transported sediment, control the channel planform pattern in rivers and streams. Since these parameters change systematically through the river channel system, the same would be expected from the channel planform pattern. In the following section we examine how the link between channel form and physical processes generates the distinct channel patterns.

Stream channel patterns have traditionally been classified as straight, sinuous or meandering [3, 7, 8] (Box 1.3). The straight and sinuous channels are generally found in the upper parts of the lowland river systems where the channel slope is high and discharge is low. These streams are often found in the moraine landscape and the stream bed substratum is dominated

The channelisation of Danish streams increased the slope of new straightened stretches. Trapezoid weir-like constructions were built in many streams, to dissipate energy from the increased slope over short segments of the stream. Unfortunately these constructions also act as obstructions limiting the free migration of fish and macroinvertebrates. Today many of these obstacles have been transformed into riffles by local water authorities.

equally by sand and gravel/stones with scattered fine sediments. Erosion dominates in this part of the river system and material is continuously added to the stream from bank erosion and overland flow. The combination of sandy moraines and addition of material ensures also a continuously high proportion of sand on the stream bed. Stream power is insufficient to remove the coarse material, and the stones and gravel are left in channel, whereas clay, silt and sand are transported further downstream as suspended solids in the water. Within the streams, sidebars of coarse material are formed, with areas of fine-grained sediment deposited in between. In streams with very steep slopes the streambed is made up of a series of steps dominated by gravel and stones and finer sediments in pools between the steps. As discharge increases, stream power also increases despite the lower slope, and the stream can transport a wider range of sediment sizes, resulting in significant sediment transport along the streambed. This in turn leads to the development of riffles and pools characteristic of the sinuous channel. Further downstream, with greater stream power, the characteristic lowland meandering channel is formed. In natural sinuous and meandering streams erosional zones occur at regular intervals. Along the outside of the meander bends sediment is eroded and deposition occurs further downstream on the inside of meanders. Various sediment sizes can be transported, depending on the strength of stream power. Fine sediments such as clay, silt and fine sand are transported in the water column as suspended solids, whereas coarse sand and gravel are transported along the stream bed. Coarse sediment is concentrated in the riffles, where flow divergence cause stream power to decrease locally, leaving the flow incapable of moving coarse particles such as gravel and stones. Fine sediment can be captured between the large particles forming a very compact riffle structure typically found in lowland streams [8]. The fine sediment is deposited on the inside of meanders where current velocity decreases – the depositional areas on the inside of meanders are known as point bars.

The cross section

Channel pattern and cross sectional profile change as you travel down through the river system. With increasing distance from the source, depth, width and current velocity vary as a function of discharge (Box 1.4). These relationships are known as the hydraulic geometry of the stream and vary depending on geological and geomorphological conditions in the catchment

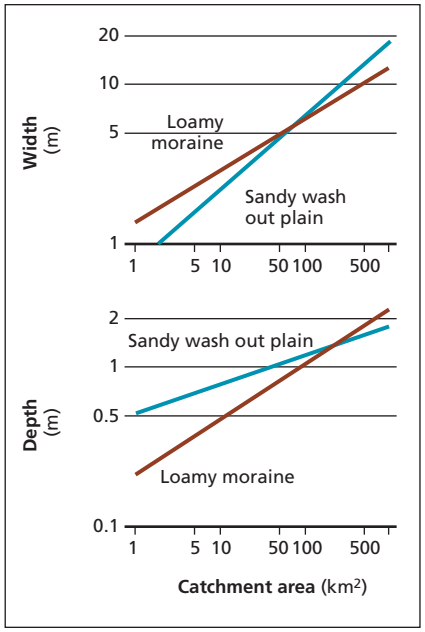


Figure 1.6 Natural channel geometry as a function of catchment area varies between different landscape types in Denmark [9]. The smaller streams on the sandy wash out plain in western and southern Jutland are generally deeper and less wide than the streams on the loamy moraine soils in eastern Jutland. For streams in catchments larger than approx. 100 km² the relationships are reversed.

and variations in climatic conditions [1]. Since geology affects the ability of the soil to be eroded, and climate and groundwater conditions affect the amount of water drained through the channel, the hydraulic geometry relationships can be expected to vary significantly among streams in different parts of Denmark.

On the sandy washout plains of western Jutland, streams receive a large proportion of groundwater all year round. These streams tend to be deeper and less varied in their depth than

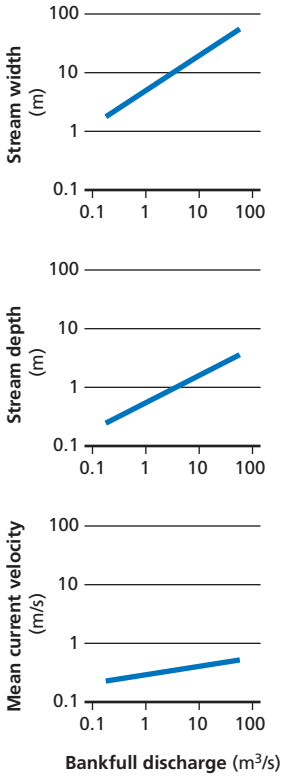
Box 1.4 Hydraulic geometry

Systematic variations in the physical properties of the channel and flow through the river system can be described using a set of equations, known as the hydraulic geometry relationships [3].

$w = aQ^b$ $d = cQ^f$ $U = kQ^m$
$w = aA^b$ $d = cA^f$ $U = kA^m$

Where: **w** is the bankfull width, **d** is the bankfull depth and **U** is the mean current velocity at bankfull discharge, **Q** is the bankfull discharge, **A** is catchment area, **a**, **c**, **k** are constants and **b**, **f**, **m** are exponents. Note that for any given relationship **b** + **f** + **m** = 1 and **a** × **c** × **k** = 1.

The relationships are indicated as log-log plots of the dependent variable width, depth or mean current velocity as a function of the discharge (or catchment area). The constants and exponents reflect properties of the catchment from where the stream water is drained. Different river systems in different parts of the world will thus have different constants and exponents reflecting differences in climate, geology and geomorphology.



	Exponents b	f	m	Reference
Upland river (Appalachians, USA)	0.55	0.36	0.09	[9]
Great-plains river (Mid-western USA)	0.50	0.40	0.10	[3]
Lowland river Denmark (River Skjern)	0.48	0.44	0.08	[10]

streams in the moraine landscape, as the catchment area increases. Furthermore, moraine streams are generally wider for any given catchment area (Figure 1.6). These generalities persist up to a certain catchment size, after which the relationships between catchment area and depth and width are shifted.

Such general relationships can be used to design channels with natural dimensions in Danish river restoration schemes. The hydraulic basis for the functioning of different river ecosystems can be compared, using constants and coefficients from hydraulic geometry relationships. These provide a valuable tool for assessing the variations in overall physical habitat conditions at the river system or catchment scale. However, if we want to know anything about the actual habitat conditions within the stream we have to look at finer scales (Box 1.5).

In-stream habitats – predictable and variable

Running water actively forms the physical habitats within streams. We have already shown how substratum composition varies through the river system from source to sea. Now we take a closer look at the variations at a finer scale, within a given stretch of stream.

In all lowland stream types, from straight to meandering, the stream habitats alternate between sections of high and low current velocity. In areas of high current velocity, coarse sediment dominates, whereas fine sediment dominates in areas of low current velocity. The longitudinal distance between successive areas of high current velocity is approximately 5–7 times the width of the stream. The ultimate development of this habitat variation is the riffle and pool sequence, which is a dominant feature of all meandering streams (Box 1.5)

Riffles and pools are distinctly different habitats with respect to substratum, depth and current velocity (Figure 1.7). These fundamental physical differences are also reflected in the species composition and abundance of macroinvertebrate communities in the two habitats [12].

At an even finer scale, there are significant variations in substratum, depth and current velocity within the distinct habitats and the varied nature of small-scale habitat features underlines the heterogeneous nature of lowland stream (Box 1.6). However, local habitat structure within any stream reach still depends in part on large-scale conditions such as flow regime, and local conditions such as river valley slope, meandering and riparian vegetation structure. Variations in these controlling factors potentially influence the

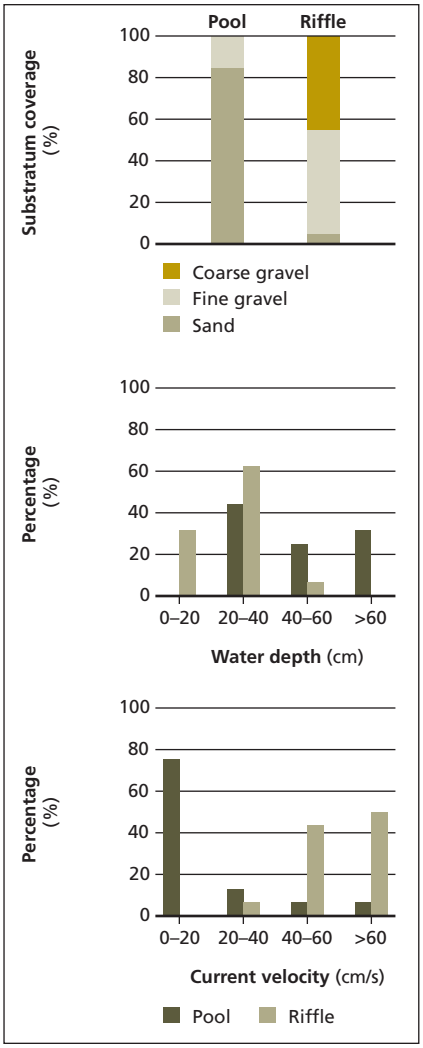
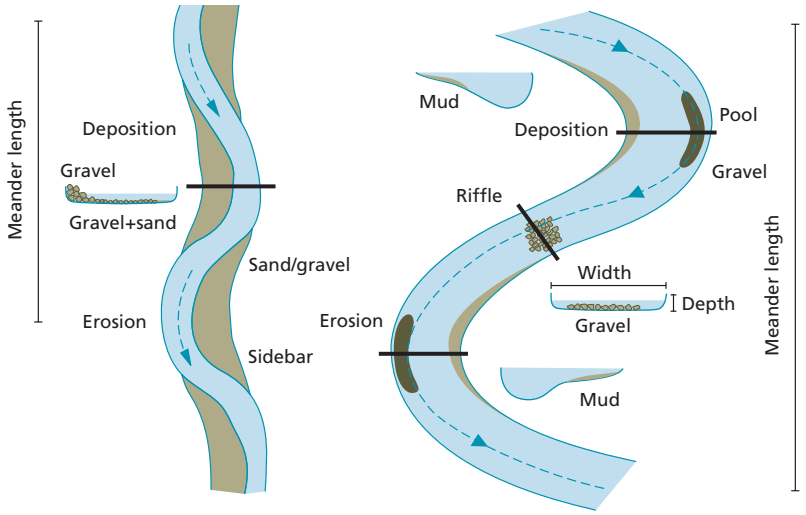


Figure 1.7 Substratum, depth and current velocity of riffles and pools in a lowland stream in Denmark. Pools are deeper areas in the streams with low current velocity and fine substratum. In contrast riffles are the fast velocity and shallow areas dominated by gravel substratum.

Box 1.5 Channel morphology

Current velocity, depth and streambed substratum vary in a predictable manner in natural stream channels. The distance between two neighbouring riffles in a meandering channel is 5–7 times the channel width. Straight channels exhibit identical alternating patterns.

The channel sinuosity is defined as the length between two points along the deepest part of the channel (known as the thalweg) divided by the distance along a straight line between the points. Natural straight or sinuous channels in the upper parts of the river systems have sinuosities between 1.05 and 1.5 and naturally meandering channels have sinuosities higher than 1.5. The sinuosity of the streams in Denmark has been used to quantify the total length of natural channels in all river systems [11]. The total estimated length of channels in Denmark was found to be approximately 2,000 km. Almost half of these natural streams are found in the western and southern part of Denmark.

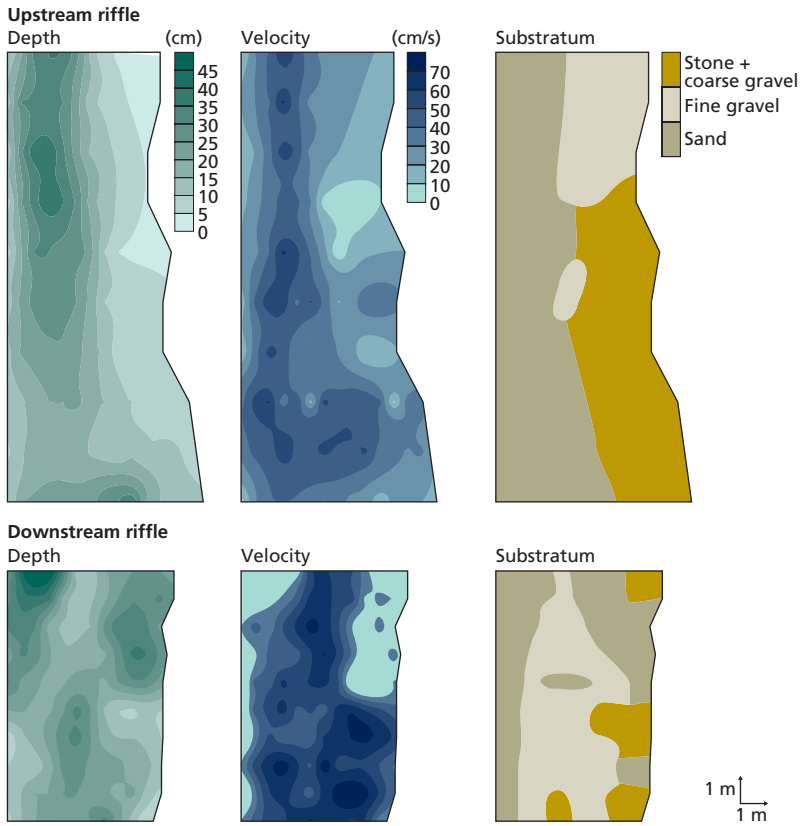


habitat structure between any riffle in a stream and cause significant differences in the micro-habitat structure both within and among riffles. These small-scale differences in habitats clearly affect the composition and abundance of the local biotic communities [13].

At first glance lowland streams are physically homogenous with consistent and predictable variations in their physical features from source to sea. Local hydrological, geological and landscape conditions influence the general pattern of channel sinuosity. At the channel reach-scale, riffles and pools alternate, creating different environments. Within these distinct habitats there is considerable fine-scale variability in habitat conditions. And yet despite this small-scale heterogeneity, we are capable of predicting general patterns in habitat structure and biotic communities throughout the river system from source to sea.

Box 1.6 Small-scale variability in riffles

Variations in substratum, depth and current velocity in riffles are considerable in lowland streams when surveyed in detail, as here from the Tange Stream, Denmark. Small-scale variations are part of the dynamic environment that characterises in-stream habitats in streams around the world. Large-scale characteristics of the individual habitats (riffle/pool) usually hide considerable variations at smaller scales.



Human impacts on Danish rivers, floodplains and valleys

River valleys and streams cut through the countryside as corridors connecting the land and sea by supplying a green vein for transport of water, sediment, nutrients, plants and animals. Streams, river valleys and floodplains have been extensively exploited since the first humans inhabited Denmark after the last Ice Age. In the beginning, river valleys acted as ideal places for settlements because of the possibility of combining fishing and hunting. Later, streams and rivers became valuable sources of energy for water mills. Dams that were constructed on many watercourses now obstruct the free flow of water from source to sea. Larger streams and rivers were important means of transport, e.g. barge transport from Silkeborg to Randers on the River Gudenå during the 18th and 19th century, and are still widely used for recreational canoeing today. Fish farms were established in many river valleys during the 20th century and they used the stream as a source of water for breeding and rearing trout.

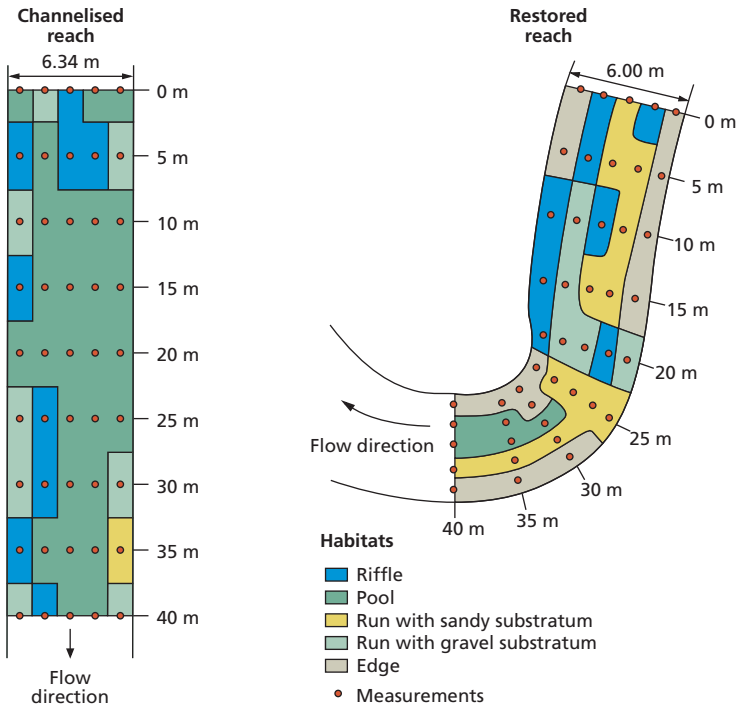
However agriculture has caused the most radical changes to the rivers and floodplains. For centuries floodplains were used for cattle and horse grazing and also for haymaking, used for winter fodder. Over the past 100 years

Streams are highly variable over small scales.

Box 1.7 Habitats in channelised and restored reaches

In channelised rivers and streams uniform cross sections with steep banks have replaced the natural irregular cross sections. The uniform physical conditions have reduced in-stream habitat diversity in many Danish streams. The dredging activities have removed coarse substratum (gravel and stones) from the stream and fish spawning grounds have been lost. The combination of these actions has reduced the available habitats for macroinvertebrates and fish.

The habitats are more varied in a restored reach of the Gelså Stream compared to an upstream channelised reach [14].



agricultural practices have intensified, primarily due to increased crop production. This has resulted in drainage and construction of ditches in river valleys and the straightening and channelisation of many streams, to increase drainage efficiency. Advanced technology increased the development of drainage schemes, in particular by means of tile drainage throughout eastern parts of Denmark. Many small streams in the upper river systems were culverted in order to ease the use of agricultural machinery. Physical changes to the river valleys have altered hydrological conditions and affected both vegetation and animals. As a consequence of the drainage schemes carried out during the last century, Denmark has now almost no pristine streams and river valleys. Channelisation and straightening have physically modified more than 90% of the stream network of 64,000 km (Box 1.7).

The extensive floodplain drainage has caused significant subsidence of river valleys soils. This phenomenon is caused by decomposition of the peat layers when exposed to atmospheric oxygen. Subsidence levels of 0.5 m are very common in many river valleys and levels of up to 1 m have been measured in the lower part of the River Skjern system, even though this area was drained as late as the 1960s [15]. As a consequence of the subsidence, the beds of ditches and streams have had to be further lowered and tile drainage has been renewed.

Large-scale channelisation and straightening of streams has increased sediment erosion and mobilisation. In order to maintain drainage capacity in channelised streams, excess sediment had to be removed from the streambed, causing continuous disturbance to stream conditions. This maintenance is currently still required in many streams. The recurring need for removal of sediment from the streambed has profound consequences for stream flora and fauna. Streams have gradually become wider and deeper than they would have been under natural conditions. At the same time straightening of the streams has reduced the stream length, which leads to an increase in stream bed slope. In order to compensate for the increased slope weirs were constructed in the streams, whereby most of the energy was concentrated in a few large weirs. These weirs have acted as obstructions to the free movement of animals and

plants. Over 140 such obstructions were found within a restricted area such as Sønderjylland County (3,940 km^2) in the late 1980s.

The repeated disturbances caused by dredging helps to increase sediment transport both in terms of suspended transport and transport along the streambed. Over a period of 3 months following maintenance work on the Gelså Stream, sediment transport increased by 370 tonnes of which 280 tonnes was registered as bed-transported material [16]. An increase of this magnitude can have devastating effects on the stream biota due to sand intrusion into salmonid spawning grounds and general habitat degradation for macroinvertebrates.

River Skjern is the largest restoration project until now.

What initiatives are needed to reverse the physical degradation of rivers and floodplains?

Public interest in restoring the natural dynamics of streams and floodplains has been growing over the past 15 years. The best example of a completed project is the restoration of meanders along the River Skjern and the re-establishment of wetlands on its floodplain. Prior to these initiatives, vast sums of money had been invested in improving water quality in Danish rivers and streams. As water quality has improved it has become increasingly clear that it is now primarily the physical degradation of the rivers and floodplains that limits biological diversity.

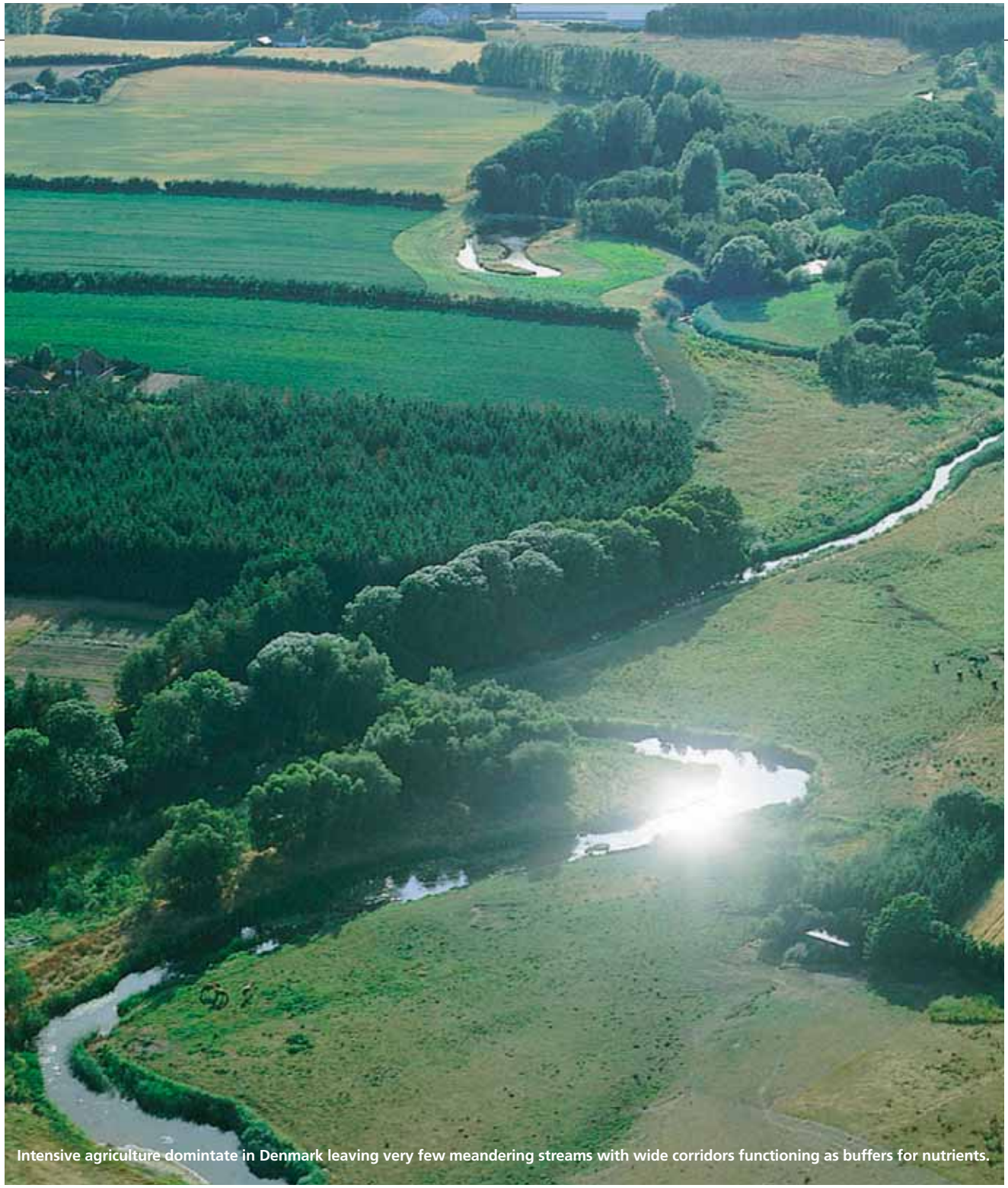
Over the last 20 years hundreds of projects have focused on removal of obstructions in streams. These projects have enhanced the opportunities for salmonoid fish to reach their upstream spawning areas. Unfortunately, these efforts have not been supported by restoration of spawning grounds that were lost during the period of continuous dredging of stream sediments. The effective lack of restoration of spawning grounds is made very difficult by the defeatist attitude towards the excess continuous transport of sand into the streams, which causes rapid siltation of the gravel beds. It is obviously necessary to track down, identify and combat the excess sediment delivery and thereby reduce the sediment transport. Actions could encompass a more effective enforcement of the existing compulsory 2 m-wide uncultivated buffer strips along streams or the establishment of wider buffer strips, with no agricultural production, to prevent sediment reaching the channel.

The only possible way to re-establish more natural physical and biological conditions in the thousands of kilometres

of streams is to change maintenance procedures, including timing, frequency and intensity of dredging and weed cutting. Future maintenance must include gentle procedures in those parts of the river systems where the potential for the development of diverse floral and faunal communities exists. Over the past 20 years maintenance procedures in many streams administered by municipalities and counties, have been changed towards gentle and selective weed cutting that leaves some vegetation in the channel and on the banks, and dredging activities have been reduced. Documentation detailing the procedures that have the most positive effect on biodiversity is, however, still lacking. There is an urgent need for experimental studies in different Danish stream types to determine which maintenance procedures are most successful at sustaining and improving stream biodiversity.

In order to proceed from here, a holistic approach to river and floodplain restoration is required. We need to see the river valley, the floodplain and the stream as one unit in a landscape mosaic. Information on the physical diversity of the river valley and its streams therefore needs to be integrated in a system allowing classification of rivers and river valleys according to geomorphology, hydrology and geological setting. The ultimate goal of our restoration efforts should be based on physical and biological data on the structure of the few remaining undisturbed streams in Denmark.

The river and river valley classification systems in combination with the established biological reference conditions of our streams in different parts of the country will be an important tool for future decisions on how and where to implement restoration schemes. We also need to gather both short-term and long-term information on how the river and floodplain ecosystems respond to the restoration. The future success of our restoration effort will rest on our ability to document ecosystem responses to past restoration efforts and subsequently to improve our methods based on this knowledge.



Intensive agriculture domintate in Denmark leaving very few meandering streams with wide corridors functioning as buffers for nutrients.

2 Hydrology, sediment transport and water chemistry

The physical and chemical quality of Danish streams has been entirely altered by the dramatic changes in anthropogenic pressures occurring over the last 150 years. Large-scale drainage schemes for reclamation of agricultural land, organic wastes from an increasing urban population, soil and bank erosion giving rise to excess sediment transport, leaching of nutrients and organic micropollutants are among the suite of anthropogenic pressures affecting the streams. The last three decades have been spent on introducing several Governmental and Regional Action Plans for combating these pressures and improving stream ecology.

Pollution history of streams

Less than forty years ago the main pollution problem in Danish streams was the discharge of organic matter from inefficient sewage treatment plants, and from industries, freshwater fish farms and small settlements without treatment facilities. Another pollution problem was the spill of liquid manure from agricultural farms that could accidentally kill all life in a watercourse.

Increasing public awareness of water pollution problems resulted in the establishment of the Danish Ministry of Environment – the first ministry of its kind in the world. The Danish regional authorities were selected as responsible for surveying the chemical and biological quality of groundwater and surface water and they were committed to establish regional plans for water quality objectives and to provide an overview of the ecological state of all streams and lakes every four years. Substantial investments in improved water pollution control resulted in decreased discharges of organic matter to surface water from larger point sources (>30 person equivalents) during the 1970s and early 1980s in most Danish River Basins (Figure 2.1).

Hydrological monitoring of Danish streams was initiated already in 1917 where the first gauging stations for daily recordings of water stage were installed, which, combined with bimonthly discharge measurements permits estimates of daily discharge. Since then the hydrologic network has become denser and currently more than 400 hydrological stations are in regular operation [1]. Monitoring of water chemistry in Danish streams did not begin until the mid-1960s as part of the first Hydrological Decade. Monthly sampling was initiated in four large rivers in different regions of Denmark. During the 1970s and early 1980s, several stations for monitoring water quality were established by the Danish regional authorities in order to measure the state and trend in water chemistry, and the main pollution sources of nutrients and organic matter.

Major implemented measures to diffuse nutrient pollution

1985 NPO Action Plan
- Elimination of direct discharges from farms
- Livestock harmony at the farm level

1987 Action Plan on the Aquatic Environment I
- 9-month storage facility for slurry
- 65% winter green fields
- Crop and fertiliser plans

1991 Plan for Sustainable Agricultural Development
- Standard nitrogen fertilization values for crops
- Standard values for nitrogen in animal manure
- Required utilisation of nitrogen in animal manure (30-45%)
- Fertiliser accounts at farm level

1998 Action Plan on the Aquatic Environment II
- Demands for an overall 10% reduction of nitrogen application to crops
- Demands for catch crops
- Demands for transforming 16,000 hectares farmland into wetlands
- Reiterated demands for utilisation of nitrogen in animal manure (40-55%)

2003 Action Plan on the Aquatic Environment III
- Halving of the Danish P surplus before 2015
- Establishement of 50,000 ha buffer zones to reduce P losses from agricultural fields
- Reiterated demands for catch crops and utilisation of N in animal manure

Table 2.1 List of Governmental Action Plans implemented in Denmark to reduce nutrient losses to the aquatic environment.

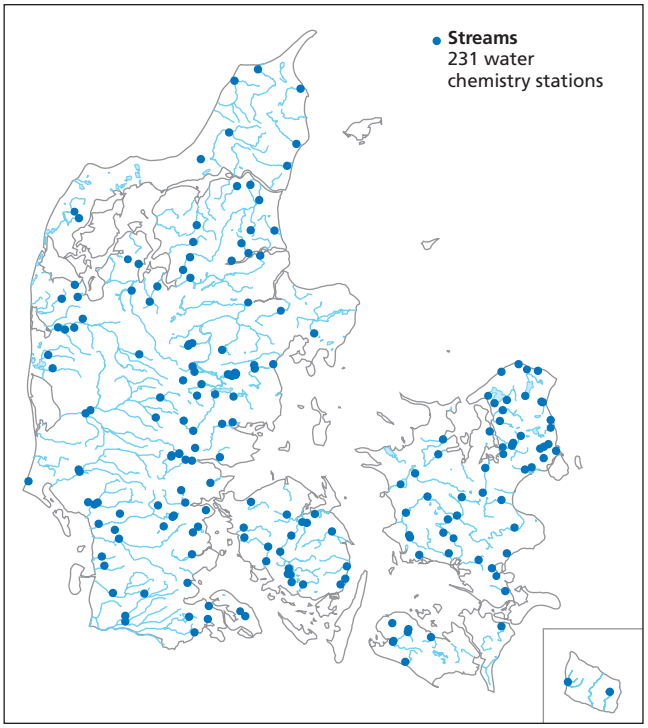
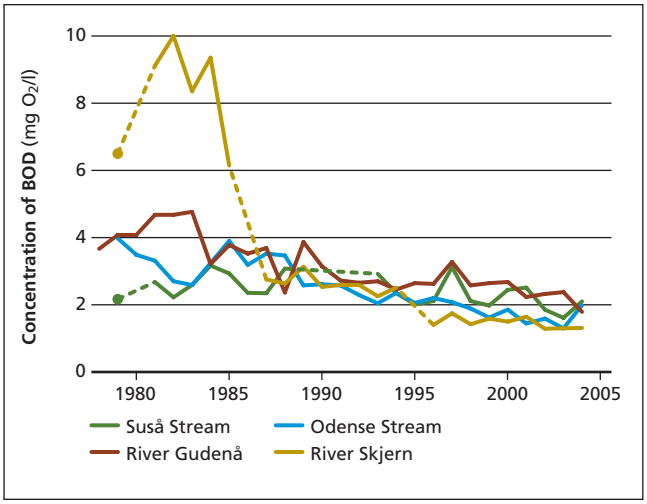


Figure 2.2 Map showing the Danish stream monitoring network for measuring hydrology and water chemistry according to a regular sampling protocol.

Figure 2.1 Trends in the concentration of BOD in the largest Danish streams during the period 1978–2004.



The distribution of water quality stream stations in Denmark were, however, very sparse and not well distributed geographically until 1987 when around 50 stations were in regular operation.

The Danish Parliament has adopted several plans for improving the quality of water bodies since the early 1980s (Table 2.1). Following the first Action Plan in 1987 a national monitoring network was established covering all water bodies. The monitoring network was put into operation in 1988. The plan was to regularly monitor hydrology and water chemistry at more than 270 stream stations throughout the country (Figure 2.2). The monitoring network enabled the Danish regional and national authorities to establish a nationwide state of the hydrology and water chemistry of Danish streams and assess the temporal trends and effects of the various Environmental Plans adopted [2].

Box 2.1 Draining of agricultural land

Approxymately 50% of the agricultural land in Denmark is drained and on loamy soils with tile drains.

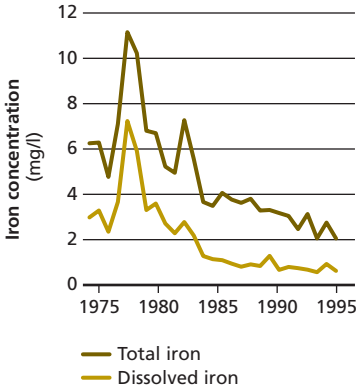
Large amounts of ammonium, dissolved reactive phosphorus, sulphate and iron are leached from former wetland areas when these are drained for agricultural purposes. Leaching of substances is highest just after draining and declines during the following years when mineralisation rates decline and the soil level shrinks.

The two examples show reclamation of agricultural land on the floodplains of the large River Skjern, which was straightened and channelised in the early 1960s.

Net leaching of ammonium, iron, sulphate and dissolved reactive phosphorus from a newly tile-drained wetland area along the large River Skjern.

Following drainage work along the main river channel the concentration of total and dissolved iron increased dramatically in the artificial, excavated drainage channel that received pumped water from the reclaimed floodplain rich in pyrite. The elevated concentrations of iron decreased slowly during the post drained period.

	Before draining	After draining
Ammonium (NH_4-N) (kg N/ha)	0.06	114
Total iron (Fe) (kg/ha)	–	536
Sulphate (SO_4-S) (kg S/ha)	28	1,875
Orthophosphate (PO_4-P) (kg P/ha)	0.04	0.20



The changing landscape

The Danish landscape has undergone major changes during the last 100–150 years. These changes dramatically altered the physical conditions, hydrological regime and water chemistry of the streams. Sewerage systems and sewage treatment plants were installed in most Danish towns during the 20th century but in the beginning only with mechanical treatment and the waste water were discharged into the nearest water body, typically streams, thereby creating excess organic pollution for kilometres downstream. The intensification of agricultural production in rural areas triggered large scale drainage of most of the Danish land area through major drainage schemes that led to straightening and channelisation of more than 90% of all Danish streams (see chapter 1). Moreover, numerous 1st order streams were culverted to facilitate easier access to fields for farm managing. Detailed drainage schemes, including excavation of ditches in the predominantly sandy riparian areas and installation of tile drains in the predominantly loamy riparian areas, broke the natural interaction between groundwater and surface water in riparian areas. Moreover, the intense drainage activity created water quality problems in streams due to enhanced mineralisation of organic matter releasing excessive nitrogen and phosphorus to surface waters. Another major ecological problem in Danish streams was created by drainage in riparian areas with a high content of pyrite. Here soluble iron was formed in the former anoxic but now oxic soil layers and transported to streams giving severe problems due to acidification and precipitation of iron oxy-hydroxides, ochre (Box 2.1). Currently more than 400,000 ha of former wet riparian areas have been artificially drained and are

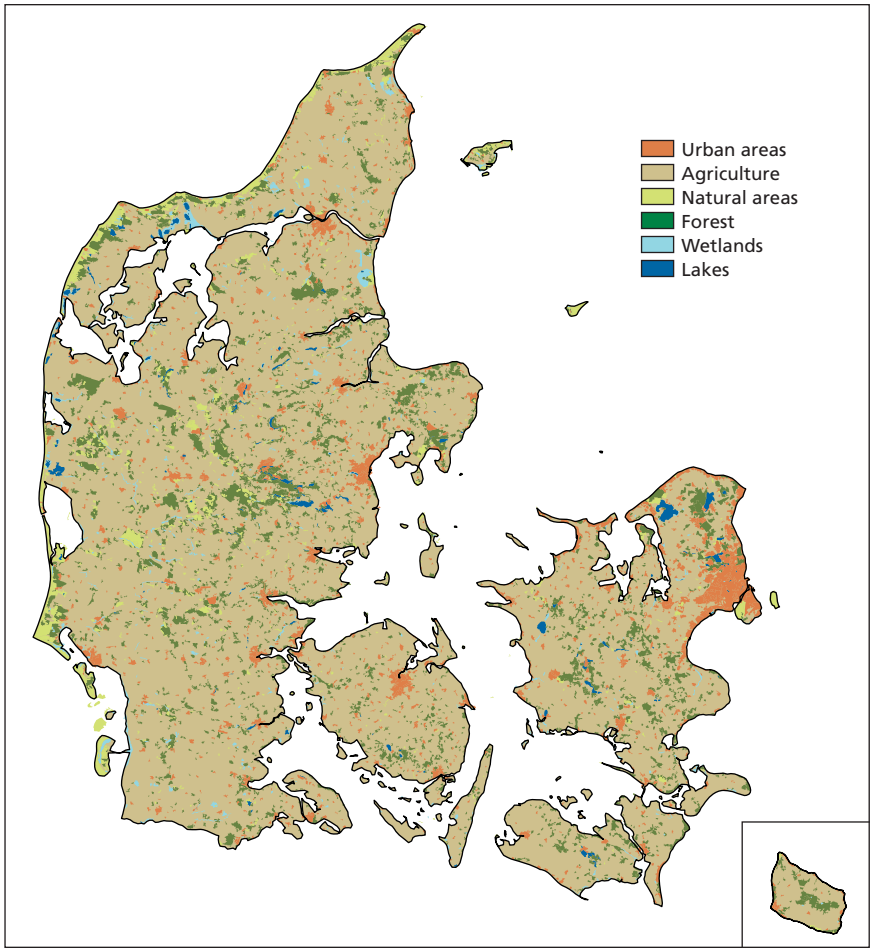


Figure 2.3 Land use in Denmark is classified in 6 main classes. Agriculture is the main land use all over the country.

in agricultural production. Agriculture mainly as arable land, now occupies more than 60% of the Danish land area (Figure 2.3).

The hydrological cycle

Although Denmark is a small country there is a large west-east gradient in precipitation from an annual precipitation of more than 1,200 mm in western Jutland to an annual precipitation of less than 600 mm on the island of Zealand. Figure 2.4 shows the water balance in Denmark. The precipitation gradient results in a decreasing average and minimum runoff in the streams from west to east in Denmark (Figure 2.5). The west-east gradient in the water balance also has a strong impact on the median minimum runoff in Danish streams which is very low on south-eastern Zealand and Bornholm, reducing the ability of streams to dilute discharges of pollutants from point sources, re-aerate the water and ensure the biological quality during summer. Streams in eastern Denmark are therefore very sensitive to drought years and many small 1st order streams (see box 1.1) are at risk of drying out. This

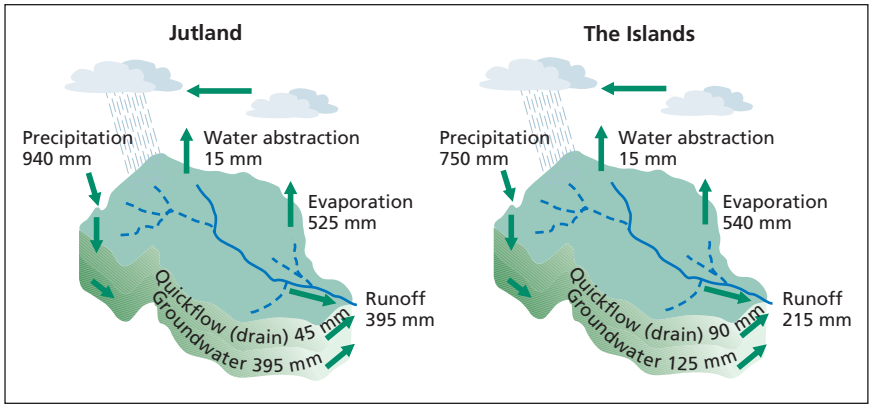


Figure 2.4 Water balance for Jutland and the islands during the period 1971–2000. Streams in Jutland receive most water and have the largest interaction between groundwater and surface water. Streams on the islands are more dominated by water discharging from the unsaturated, often tile-drained zone.

phenomenon has locally been accelerated by abstraction of groundwater for water supply to large cities, especially around the capital of Copenhagen.

Danish streams have been categorised into 5 different hydrological regime types based on differences in hydrology (Table 2.2). The categories include 2 small stream types and 3 larger stream types and the regime types are clearly distributed according to region. The stable hydrological regime is mostly found in the northwestern part of Jutland, the moderately stable regime in central and eastern Jutland and the unstable flashy stream types on the islands of Funen, Zealand, etc. to the east [1].

The hydrometric stations having been in operation since 1920 in Danish streams show a general upward trend in average annual runoff during the last 100 years (Figure 2.6). This trend can be explained by a simultaneous upward trend in annual precipitation during the same period. Changes in land use, drainage of agricultural land and extraction of drinking water from groundwater have also influenced the hydrology of Danish streams. An example is Århus Stream near the largest city in Jutland where extraction of drinking water has reduced annual average runoff during the last 100 years (Figure 2.7).

Most climate scenarios predict a wetter and warmer climate in Denmark for the next 50–100 years [4]. Such a climate change will alter the water balance and the runoff in Danish streams. An estimate of the importance of climate change has been calculated by using a precipitation-runoff model, a modelled downscaled (25 km grid) 30-year time series of climate data for a reference period (1961–1990), and modelled data for the period 2071–2100

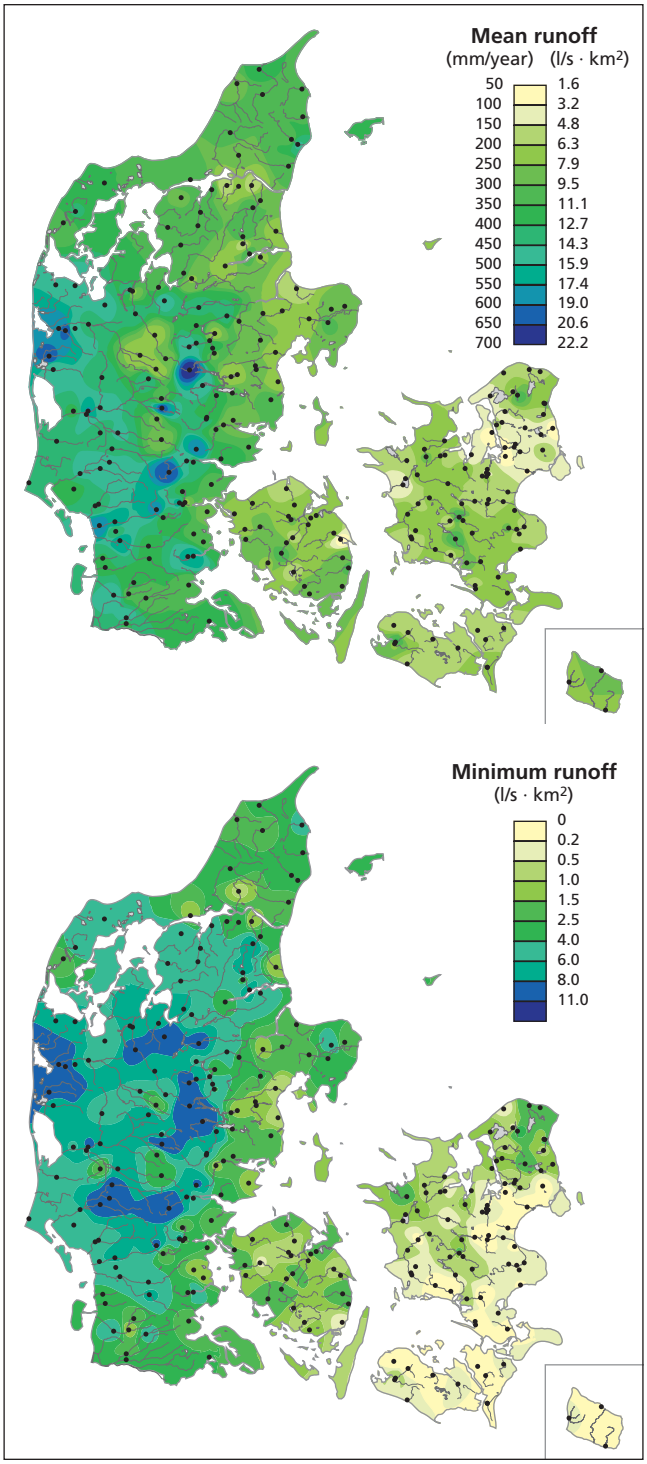


Figure 2.5 Maps showing the average annual runoff and median minimum runoff in Danish streams during the period 1971–1998 [1].

	Small streams		Large streams		
	Stable hydrological regime	**Unstable hydrological regime**	**Stable hydrological regime**	**Moderate stable hydrological regime**	**Unstable hydrological regime**
Region	Jutland	The Islands	Northwestern Jutland	Central and southern Jutland	The Islands
Mean catchment area (km^2)	82	59	834	394	472
Mean discharge (l/s)	717	406	11,300	5,400	4,100
Average frequency of daily discharge being more than 7 times higher than long-term median discharge (times per year)	1.4	4.9	0	0.2	1.5
Average annual duration of daily discharge being 7 times higher than long-term median discharge (days)	1.9	6.5	0	1.1	6.7
Frequency of daily discharge being lower than the long-term median minimum discharge (times per year)	2.2	2.2	2.1	1.5	2.2
Average annual duration of daily discharge being lower than the long-term median minimum discharge (days)	10.1	6.7	10.1	13.0	6.3
Long-term median maximum discharge divided by the median discharge	6.7	18.8	2.7	5.0	7.7
Long-term median minimum discharge divided by the median discharge	0.38	0.12	0.61	0.70	0.59

Table 2.2 Examples of the different hydrological regime types of Danish streams [1].

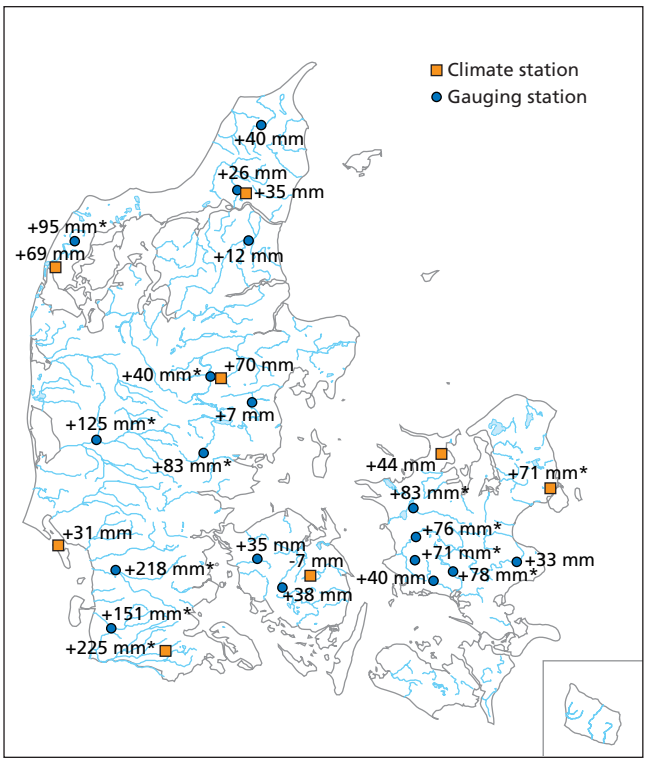
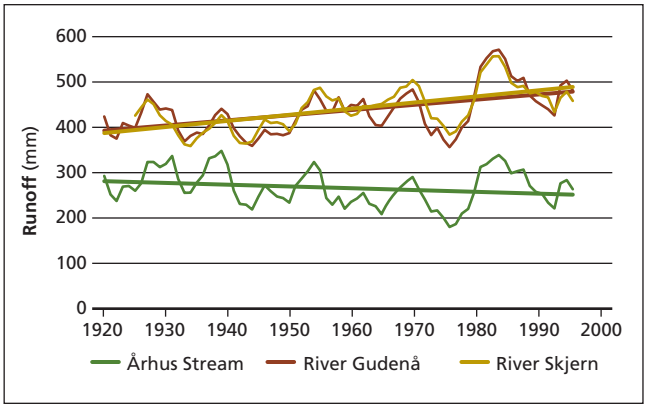


Figure 2.6 Trend in annual precipitation at climate stations and annual average runoff in 16 large Danish streams at gauging stations during the recent 75 years. Stars indicate significant increase. [3].

Figure 2.7 Trends in annual average runoff in three streams in Jutland, Denmark from 1920–1996 shown as 5 years running averages. The line shows the upward trend in River Gudenå and River Skjern and the downward trend in Århus Stream the latter being influenced by water abstraction.



using the HIRHAM model and the IPCCa2 scenario [5]. Table 2.3 shows the predicted differences between the two 30-year periods in terms of precipitation, temperature, potential evaporation and runoff parameters for 10 smaller Danish streams situated all over country. Average annual precipitation increases cause a higher average annual runoff because the main increase in precipitation is in autumn and winter. The predicted climate and hydrological changes will increase sediment transport as well as delivery of nitrogen and phosphorus to the streams if the agricultural production and practices remain unchanged [5].

Stream	Annual runoff Control period (1961–1990) (mm/yr)	Annual Runoff Scenario period (2071–2100) (mm/yr)	Difference in runoff (mm/yr)	Change in runoff (%)
Odderbæk Brook, N. Jutland	191	226	35	18
Bolbro Brook, S. Jutland	524	602	78	15
Østerbæk Brook, N. Zealand	71	81	10	14
Ellebæk Brook, W. Jutland	275	325	50	19
Maglemose Stream, Zealand	83	90	7	9
Ølholm Brook, E. Jutland	344	391	47	14
Lyby-Grønning Stream, N. Jutland	151	180	29	20
Lillebæk Brook, Funen	179	214	35	20
Højvads Rende Stream, Lolland	141	188	47	34
Bagge Stream, Bornholm	262	292	30	11

Table 2.3 Forecast of the impact of climate change on annual and seasonal runoff in Danish streams based on downscaled predictions from the climate model HIRHAM. The scenario involves a doubling of CO_2 concentrations.

Sediment transport

The sediment input to Danish streams derives from a variety of sources among which erosion of stream banks, soil erosion and surface runoff and sediment delivery via tile drainage pipes have been found to be the most important (Box 2.2). The importance of stream bank erosion as a sediment source for Danish streams was also documented in a survey of soil and bank erosion along 33 agricultural fields in 15 small Danish streams [6].

Transport of suspended sediment in Danish lowland streams is generally low when compared to other regions of the world with mountains and steeper slopes (Box 2.2). However, the transport of suspended sediment varies considerably from stream to stream depending on the hydrological regime. The inter-annual variation in the transport of suspended sediment in a stream is also very high as shown for 14 small streams for the period 1993–2000 where the transport of suspended sediment was measured utilising flow-proportional or time-proportional sampling

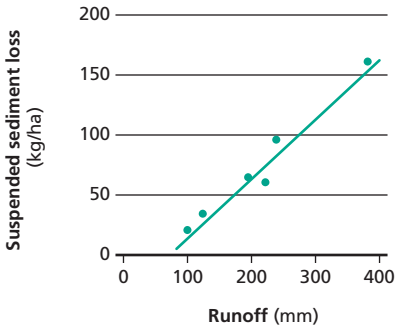
Ripples composed of sand an silt-size sediments are typically found in must Danish lowland streams, as a sign of excess sediment bedload.

Box 2.2 Sediment transport in Danish streams

A sediment budget showing the sources of suspended sediment to a small stream in eastern Jutland, Denmark, reveals that although bank erosion is the main source, soil erosion and tile drains also deliver a substantial proportion of sediment to the stream. The sediment budget will show great year-to-year variations due to the tight relationship between climate and erosion. For example, rill erosion on arable fields in Denmark has been shown to vary 10–20-fold between wet and dry years.

Suspended sediment yields in Danish streams are low when compared to other regions of the world. The suspended sediment transported in Danish streams is very fine-grained and is therefore of importance as carrier of environmentally harmful adsorbed substances, such as phosphorus, heavy metals, certain pesticides, PAHs, etc. The transport of suspended sediments in Danish streams varies considerably from year to year, and the majority of the annual suspended sediment yield is often transported during a few days with rain or snow melt.

The movement of coaser sediment on the stream bed (bed load) is seldom measured in Danish streams because it is extremely difficult to obtain precise measurements [7]. However, the few existing quantitative measurements show that the bed load is considerably higher in the dominantly groundwater fed streams in western Jutland as opposed to streams in eastern Jutland and on the islands.



	May 1993 to April 1994	May 1994 to April 1995
Subsurface tile drainage water	15%	11%
Soil erosion and surface runoff	19%	0%
Stream bank and bed erosion	66%	89%

Estimated contribution of subsurface drainage water, surface runoff and stream bank and bed erosion to total suspended sediment export from the 11 km² Gelbæk Stream catchment in central Jutland, Denmark (adopted from [8]).

Stream	Catchment area (km²)	Measurement period	Suspended sediment load (tonnes/km² per year)	Sediment bed load (tonnes/km² per year)
Vorgod Stream	455	1976,1977	7.1	< 5.0
River Skjern	2,220	1976,1977	6.4	12.4
River Skjern	2,220	1994,1995	7.9	10.2
Grindsted Stream	238	1970,1974,1975	18.7	22.8
Ansager Stream	138	1970,1974,1975	9.5	19.7
Varde Stream	598	1974,1975	9.4	< 1
Brede Stream	292	1968	6.2	14.7
Grønå Stream	603	1968,1981	6.8	10.3
River Gudenå	1,787	1974	3.4	< 1
Mattrup Stream	88	1974	2.2	< 1
Århus Stream	120	1986–1987	14.3	< 1
Lyngbygaard Stream	126	1986–1987	28.4	< 1
Tude Stream	146	1970,1971	5.4	< 1
Suså Stream (upstream)	42	1978,1979	7.7	< 1
Suså Stream	601	1978,1979	5.6	< 1

Average annual suspended sediment load and sediment bed load in different Danish streams [7, 9].

programmes (Box 2.2). Such accurate knowledge on the transport of suspended sediment in streams is valuable as fine sediment is an important carrier of phosphorus, heavy metals and micro-pollutants.

The bed load of sediment in Danish streams has been less intensely studied and the majority of information available is related to large streams in western Denmark with a stable hydrological regime and thus a high sediment transport capacity during the entire year. Large differences in the bed load of sediment in Danish streams have been measured for the different stream types (Box 2.2).

Even though sediment transport is low in Denmark compared to most other countries, high delivery of sediment to streams from unstable stream banks causes ecological problems because of accumulation of sand and mud on the stream bed during low-flow periods. Straightening and channelisation of most Danish streams have triggered both a higher sediment input to the streams and a lowering of the transport capacity, thereby forcing stream managers to excavate streambed sediment as part of stream maintenance. The natural physical conditions in Danish streams are therefore severely impacted.

Acidification

Acidification because of acid rain or enhanced nitrification caused by agricultural practice affects sensitive water bodies located in carbonate-poor soils with limited buffer capacity to neutralise acidic compounds. In areas of low buffer capacity, acid rain and drainage water also release aluminium from soils into lakes and streams, generating toxic conditions for aquatic species.

High alkalinity and pH in streams are associated with calcareous soils in the catchments in eastern Jutland and on the islands where glacial till deposits from the last glaciation period prevail (Weichsel 14,000 years ago). Such soil types have a natural buffering capacity, reducing the risk of acidification. Western Jutland in contrast, has mineral weathered 140,000 years old moraines from the Saale glaciation, and coarse textural soils on the outwash plains from the Weichsel period. Both soil types are low in carbonates and vulnerable to acidification. Moreover, smaller areas with windblown deposits along the west coast of Denmark and in some central parts of Jutland are also low in carbonates and vulnerable to acidification.

Most Danish streams generally have a high or very high buffering capacity (>0.1 mmol HCO_3^-/l) against acidification. A buffering capacity of 0.02–0.1 mmol HCO_3^-/l can be found in smaller Danish streams in vulnerable areas, whereas a low buffering capacity of 0.01–0.02 mmol HCO_3^-/l is rarely found [10]. Thus, the majority of Danish streams have, on average, an annual pH exceeding 6.5 and should not suffer any biological damage owing to acidity (Figure 2.8). However, streams and lakes of low or very low buffer capacity have been documented to show a downward trend in pH during the period 1977–1989. The strong recent decline in the emission of acidifying gases (mainly sulphure oxides) to the atmosphere has decreased the potential problem with acidification of Danish streams. However, the large emission and deposition of ammonia from Danish agriculture is currently as important as acid precipitation and may locally acidify Danish streams of low buffering capacity.

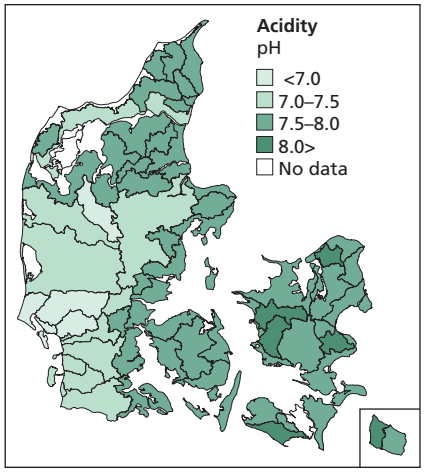


Figure 2.8 pH in Danish streams illustrated as annual means for streams in 67 larger river catchments during the period 1989–1998.

Ochre

Ochre ($Fe(OH)_3$) and ferrous iron (Fe^{2+}) can damage the flora and fauna in streams. High concentrations of ferrous iron (>0.5 mg/l) are toxic for fish and macroinvertebrates, and precipitated ochre on spawning gravel, plant surfaces and animal gills can physically inhibit their organisms. Ochre is ferric (Fe^{3+}) oxy-hydroxides that precipitate under aerobic conditions at pH higher than 4 in surface water because of the input of soluble ferrous iron and ferric iron (pH<3) from soil water and groundwater. Ferrous iron is found naturally in some deep anaerobic groundwater aquifers, but the main source of ferrous iron in Danish streams is from oxidation of natural deposits of pyrite (FeS_2) in waterlogged soils. The water level in these soils has in many cases been lowered due to reclamation of agricultural land. Land drainage has reduced the groundwater

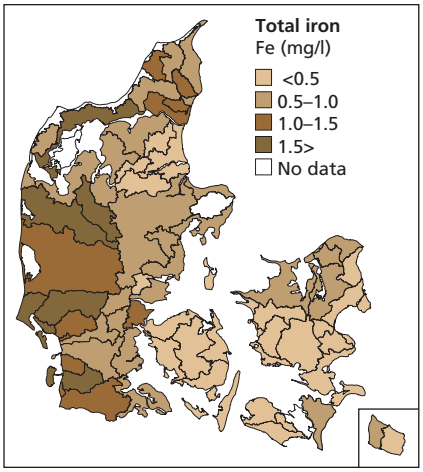


Figure 2.9 Concentrations of total iron in Danish streams as annual means for streams in 67 larger river basins during the period 1989–1998.

Application of slurry from an increasing pig production is now adays done in the spring due to the increase in storage facilities (9 months) demanded by the 1st Action Plan on the Aquatic Environment.

table and caused oxidation of pyrite to ferrous iron, sulphate and protons that escape with the drainage water to surface waters (see Box 2.1). Deposits of pyrite in Danish soils are mainly found along coastal areas and floodplains in Jutland where old brackish or marine deposits exist. A survey of low-lying areas in south-western and northern Jutland showed that 25% of almost 500,000 ha low-lying soils have a potential for releasing ferrous iron and cause ochre problems in surface waters. The concentration of total iron in Danish streams reflects these conditions as the concentrations are highest in western Jutland and lowest on the islands (Figure 2.9).

Nutrients

The quantity of nitrogen and phosphorus exported to the streams and lakes in Denmark and their sources has been calculated for the period 1989–2002 (Box 2.3). The amount of nitrogen and phosphorus discharged to water from point sources has been reduced by 70% for nitrogen and 84% for phosphorus during the same period. Thus, nitrogen and phosphorus losses from diffuse sources and the losses from agriculture in particular, have become increasingly important.

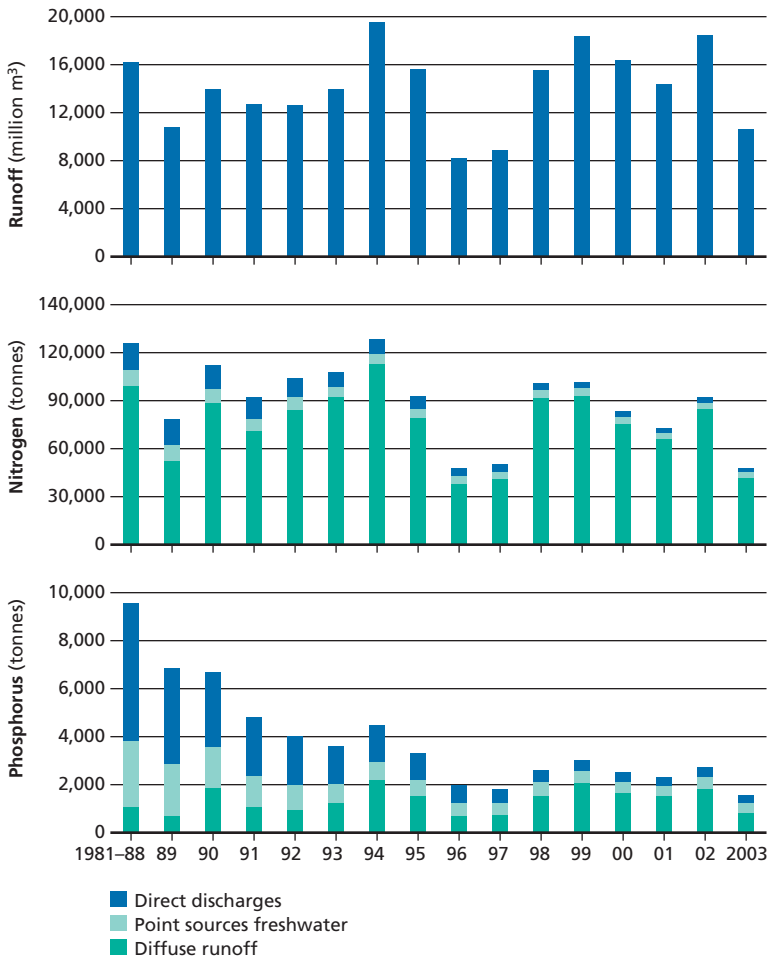
Important indicators of the pollution potential from agricultural production are the consumption of chemical fertiliser and the production of animal manure on arable land. Several scientists have documented a positive relationship between the consumption of chemical fertiliser in agriculture and the resulting concentration or transport of nutrients in streams [11]. The nitrogen and phosphorus input to Danish arable land reached a maximum in the early 1980s, following a strong increase in the consumption of chemical fertilisers during the 1960s and 1970s (Box 2.4). The consumption of nitrogen and phosphorus in chemical fertiliser has decreased in Denmark since the mid-1980s due to the implementation of four major Danish Action Plans on the Aquatic Environment. The Action Plans have posed several restrictions on Danish farmers, especially regarding their storage facilities for liquid manure, application times of liquid manure on the soils, demands for utilisation of nitrogen in animal manure, reductions of livestock densities and reductions of quota for allowed use of nitrogen for crops [12].

Nitrogen and phosphorus cycling in Danish agriculture has been monitored since 1989 in five small agricultural catchments by use of questionnaire surveys at the field level and measurements of nitrogen and phosphorus in

Box 2.3 Sources of Nitrogen and Phosphorus

Sources and transport of total nitrogen and total phosphorus through Danish streams to coastal waters have changed considerably during the period 1989–2003. Discharges of nitrogen and phosphorus from point sources (especially sewage treatment plants) have been greatly reduced and consequently the diffuse sources have gained in significance during this 14-year period.

The weather, particularly precipitation, is of great importance for the diffuse loadings of nitrogen and phosphorus to Danish coastal waters as can be seen from the relationships between annual nutrient loadings and annual runoff during the period 1989–2003.

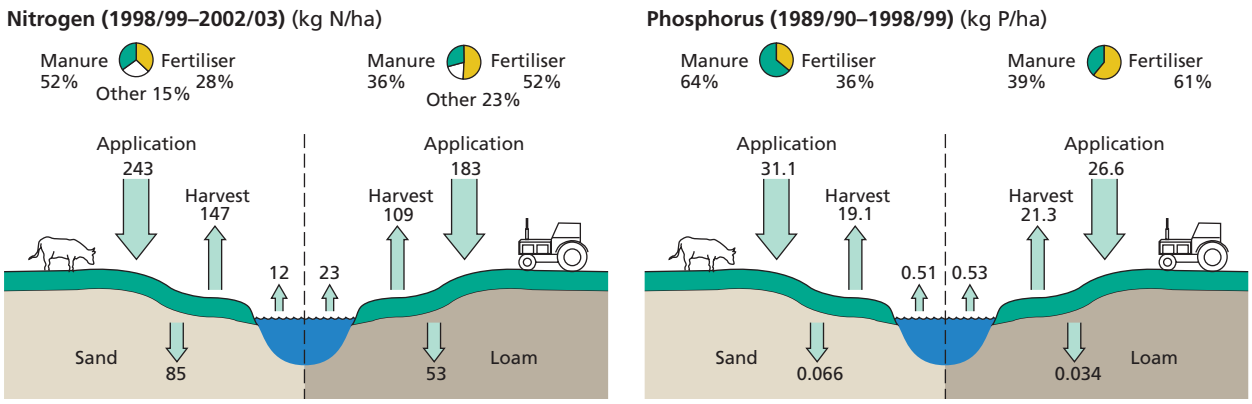


soil water, drainage water, groundwater and stream water [2]. The five catchments represent typical Danish farming systems ranging from crop production on the predominantly loamy soils on the islands to animal production on the sandy soils in Jutland. The data collected can be used to establish overall nitrogen and phosphorus budgets for small catchments, revealing the major input and outputs of nutrients (Box 2.4).

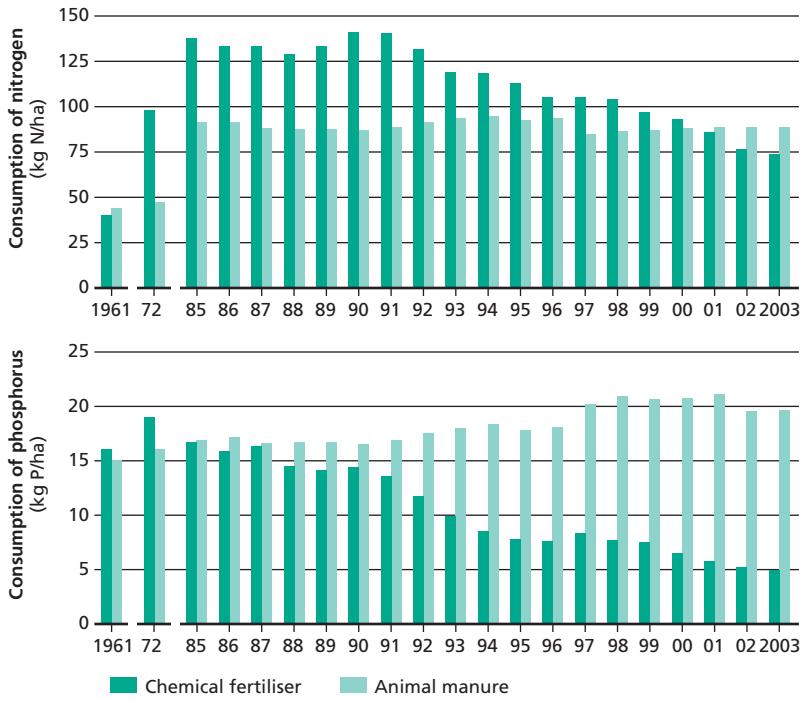
Dissolved inorganic nitrogen is responsible for the main transport of nitrogen in Danish streams that drain catchments dominated by agricultural land use (80–90%). Nitrate-N (NO_3^--N) is the main constituent (78–85%). The average annual loss of total nitrogen from agricultural land in small catchments was nearby two times higher from loamy catchments (23 kg N/ha) than sandy catchments (12 kg N/ha) during the monitoring period 1998–2003 (Box 2.4). In comparison, the average annual loss from predominantly forested catchments was 2.3 kg N/ha during the same period.

Dissolved reactive phosphorus (inorganic) constitutes on average 38% of the total phosphorus in streams draining loamy and sandy catchments in Denmark. Particulate phosphorus associated with inorganic and organic matter is of great importance in Danish streams. The speciation of the phosphorus export from small agricultural catchments implies that the pathways are linked partly to the movement of water in the soil column and partly to erosional processes. The average annual export of total phosphorus from loamy (0.53 kg P/ha) and sandy agricultural catchments (0.51 kg P/ha) was almost identical during the monitoring period 1989–1998 (Box 2.4). In comparison, the average annual export

Box 2.4 Nitrogen and Phosphorus losses from Danish agriculture



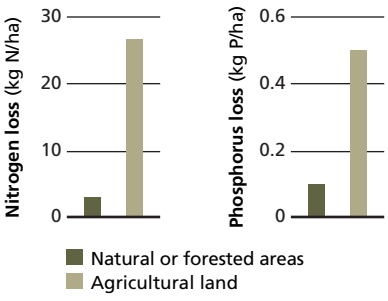
The consumption of nitrogen and phosphorus in chemical fertilisers in Danish agriculture increased after World War II and peaked in the early 1980s for nitrogen and mid-1970s for phosphorus. Since then a dramatic reduction has taken place due to the adoption of several Danish Action Plans to reduce nutrient loadings of the aquatic environment.



Large differences are observed in the nitrogen and phosphorus cycling within two main types of Danish agricultural catchments. The nitrogen and phosphorus surplus is exceedingly higher in sandy catchments in Jutland due to high livestock density and application of manure. The resulting nitrogen leaching is also highest in the sandy catchments, whereas the resulting riverine nitrogen transport is highest in the loamy catchments. That higher amounts of N escape to streams from loamy catchments than from sandy catchments – although nitrogen leaching is highest in sandy catchments – must be ascribed to differences in the hydrological cycle of the two catchments types. Thus, a much larger part of net precipitation falling on loamy catchments is rapidly discharged to streams due to infiltration through macropores to tile drains linked to the streams, as opposed to sandy catchments, where most of the net precipitation infiltrates to groundwater resulting in long residence times. The nitrate passing the redox zone in groundwater is also subdued to denitrification due to biogeochemical processes which transform nitrate to gaseous nitrogen

(N_2 or N_2O). In the case of phosphorus, the sorption potential for dissolved inorganic phosphorus in the topsoil and subsoil compartments is important for the amount of phosphorus leached through the soil. Usually only a small part of the phosphorus surplus is lost from the topsoil due to leaching. The soil can, however, be overloaded with phosphorus and for specific threshold of phosphorus saturation, depending on soil type, leaching of large quantities of phosphorus will commence. This situation has been confirmed in some Danish fields, and especially drained organic soils are very vulnerable to phosphorus leaching because of their much lower phosphorus sorption capacity. Transport of phosphorus in streams draining agricultural catchments is much higher than normal phosphorus leaching from agricultural soils. Therefore, other hydrological pathways are important for the delivery of phosphorus to streams, mainly due to soil erosion and surface runoff, stream bank erosion and the loss of particulate phosphorus from the soil surface via macropore-flow [13].

The loss of nitrogen and phosphorus from agricultural areas is much higher than background losses as measured in small streams draining predominantly forested catchments.



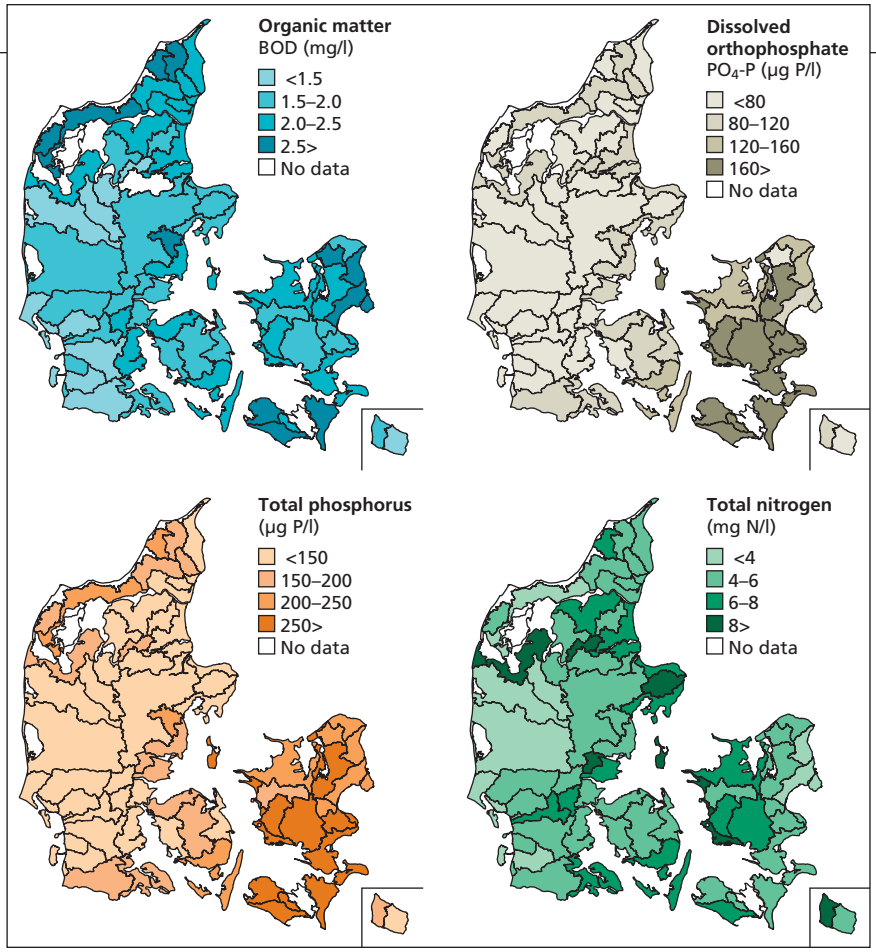


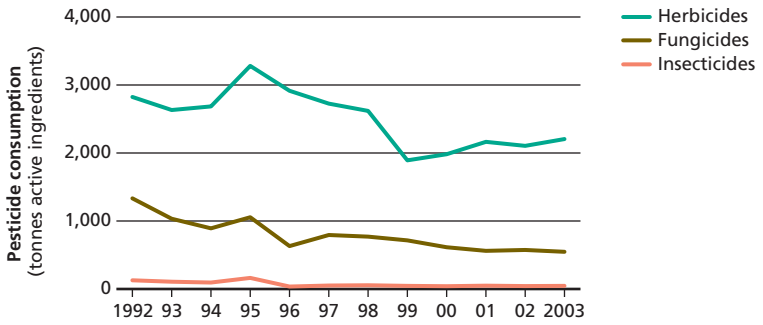
Figure 2.10 Maps showing the average annual concentration of BOD, total nitrogen, total phosphorus and dissolved reactive phosphorus during the period 1989–1998. The maps are constructed based on measurements in streams within 67 larger basins.

Compound	Number of streams monitored for heavy metals	Range of maximum concentrations observed in 4 larger Danish streams	Limit values for discharges to Danish freshwater
Arsen (Ar)	2	1.4–3.1	4
Cadmium (Cd)	3	0.04–0.16	5
Chromium (Cr)	2	2.9–12	10
Cobber (Cu)	4	3.3-21	12
Mercury (Hg)	1	0.008*	1
Lead (Pb)	1	7.0*	3.2
Nickel (Ni)	5	2.9–34	160
Zink (Zn)	4	18–81	110

Table 2.4 Concentration of heavy metals in larger Danish streams draining mixed agricultural and urban catchments (data from the year of 2000).

Box 2.5 Pesticides

The consumption and application of pesticides in Danish agriculture has been reduced since the late 1980s.



Many pesticides are detected in Danish streams and normally there is a relationship between amounts of active substances applied and the frequency of detection in the streams. Herbicides are generally detected more often than fungicides and insecticides, as many of these pesticides are more hydrophobic and are thus sorbed in the soils or in stream sediments. Fungicides and insecticides are detected in stream sediments and sometimes in very high concentrations that are damaging to the fauna [14]. The concentration of pesticides in Danish streams is very low and usually below the detection limits (1–10 ng/l). However, high concentrations of newly applied pesticides are occasionally detected in small streams draining agricultural catchments, especially during spates where pesticides are transported by surface runoff or macropore-flow directly to streams.

Detection of pesticides in 25 smaller Danish streams draining dominantly agricultural catchments during the year of 2000. (Number of water samples analysed = 189)

Compound	Detection frequency (%)	Average concentration (ng/l)	Median concentration (ng/l)	Maximum concentration (ng/l)
Glyphosate (H)	73.9	132	77	1,400
Dimethoate (I)	2.1	46	27	120
Bentazone (H)	37.0	61	20	1,200
Ioxynil (H)	5.9	75	20	440
Pirimicarb (I)	3.8	23	26	42
Fenpropimorph (F)	1.6	49	27	110
Ethofumesate (H)	5.4	187	65	920
Diuron (H)	23.8	57	25	360
Terbuthylazine (H)	32.3	72	29	1,260
Propiconazole (F)	6.4	138	20	1,400
Pendimethalin (H)	11.1	75	38	580
Esfenvalerate (I)	0	-	-	-

(H) = Herbicide; (F) = Fungicide; (I) = Insecticide.

***: Only 62 water samples analysed for in the case of esfenvalerate.**

was 0.079 kg P/ha from undisturbed catchments.

A statistical analysis of changes in flow-adjusted nitrogen concentrations in 63 Danish streams draining agricultural catchments without major point sources, has shown a general downward annual trend of 27% during the period 1989–2002. The downward trend was higher in loamy catchments than in sandy catchment because of higher livestock densities and longer residence times in groundwater in sandy areas [12]. A similar statistical trend analysis has not shown significant changes in phosphorus concentrations in 38 smaller Danish streams in agricultural catchments.

In spite of successful adoption of several Action Plans for combating nutrient pollution from point sources and diffuse sources, the concentrations and loads of nitrogen and phosphorus in Danish streams are still very high, causing eutrophication of many water bodies (Figure 2.10).

Heavy metals and organic micropollutants

One of the first major pollution stories hitting the Danish newspaper headlines in the late 1960s was the finding of excessive amounts of mercury in fish and sediment in the Varde Stream in south-western Jutland. The mercury pollution was caused by discharge of sewage from an industrial plant using inorganic mercury in their production of chemicals for use in industrial products. Heavy metals are now generally detected in low concentrations in Danish rivers and do not create immediate concern about their ecological impacts (Table 2.4). The reason is the strong decrease in the use of most poisoning heavy metals, such as mer-

cury, cadmium and lead in households, industrial production and chemical fertilisers. Moreover, the introduction of phosphorus precipitation in most Danish sewage treatment plants has increased the treatment efficiency for heavy metals by more than 50%. The concentrations of heavy metals in outlet water from sewage treatment plants are currently below the stipulated quality objectives required for the aquatic environment. However, there are still some doubts about the importance and fate of nickel, zinc and copper in animal manure, which is applied in great quantities to agricultural areas and thus can be transported to streams. Moreover, the presence of naturally high concentrations of heavy metals in deeper, reduced groundwater (arsenic) or in groundwater where water abstraction has lowered the groundwater table (nickel) could locally pollute surface water with heavy metals where deeper groundwater enters the streams.

A major reduction in the use of pesticides in Danish agriculture has been documented (Box 2.5). The decrease is mainly due to the introduction of new modern pesticides that are applied in much smaller quantities than old pesticides. The occurrence and concentration of pesticides in streams have been monitored every year since 1999 in 25 streams draining agricultural catchments. The occurrence and concentration of the most important pesticides detected are shown in Box 2.5. Even though some pesticides and metabolites are detected frequently, the concentrations of pesticides in streams are low. During certain periods of the year (spraying season with either low flow or spates) the maximum concentrations of certain pesticides surpass the threshold concentration. Strict regulation of pesticide application on agricultural land has certainly helped to reduce pesticide loss to surface waters in Denmark.

The presence of other organic micro-pollutants has been measured in five larger Danish streams since 1998 (Table 2.5). Among the most frequently detected substances are PAHs (Polycyclic aromatic hydrocarbons) derived from exhaust gas from cars and other combustion processes. Among the most discussed harmful substances are those with hormone disturbing effects, for example nonylphenols, DEHP, biphenol A and natural estrogens in the aquatic environment.

Feminisation (intersex) of fish was found for the first time in watercourses near the city of Århus, Jutland [15]. This phenonenon is probably caused by natural hormones discharged with domestic sewage into the aquatic environment and to a lesser extent by hormones originating from the synthetic substances.

Regaining the natural retention processes in river basins

The last two Danish Action Plans (1998 and 2003) for reducing nutrient pollution of the aquatic environment involved measures to combat nutrient pollution by increasing the nutrient retention capacity in the landscape. The main measures are rehabilitation of former riparian wetlands and wet meadows by closing down drainage schemes where surface water is pumped away, re-meandering of streams to re-establish the natural hydrological interaction between the stream channels and their floodplain, recreation of former lakes, and establishment of uncultivated buffer zones along watercourses. The philosophy is to regain some of the natural nutrient sinks in the landscape through denitrification of nitrate, sedimentation of organic nitrogen and particulate phosphorus and sorption of dissolved phosphorus in the rehabilitated areas. Research has proven that the efficiency of natural systems to remove nitrogen and retain nitrogen and phosphorus is very high in some natural systems (Box 2.6).

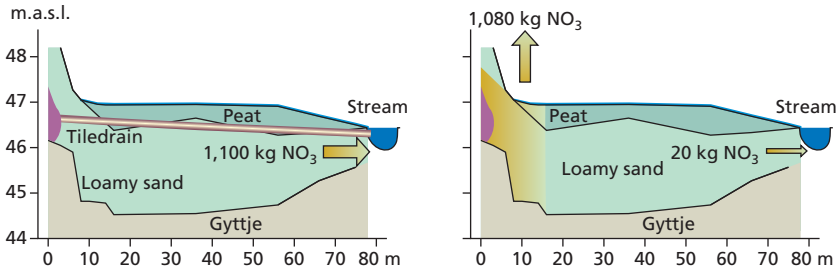
Improved nutrient managing at the source (farmer) can be supported by measures to rehabilitate the natural conditions in catchments by, for example, reinstating naturally vegetated buffer zones along river channels, restoring river channels and floodplains and reinstating wetlands and lakes (Box 2.7).

Table 2.5 Concentrations of organic micropollutants detected most often in Danish streams.

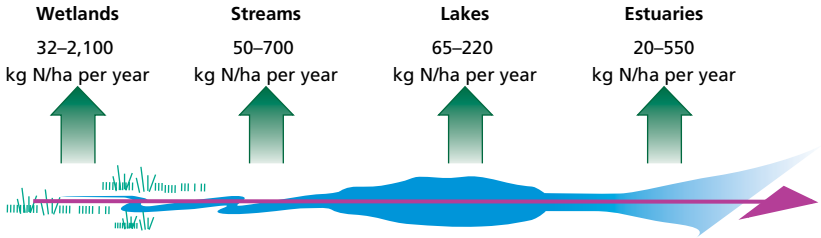
Environmental pollutants	Number of detections	Mean values (µg/l)	Max. values (µg/l)
Trichlor-ethylene	12	0.285	1
Acenaphthene	6	0.0085	0.025
Flouranthene	7	0.0105	0.033
Pyrene	8	0.0115	0.031
Linear alkyl benzene sulphonate (LAS)	6	1.75	14

Box 2.6 Nutrient retention

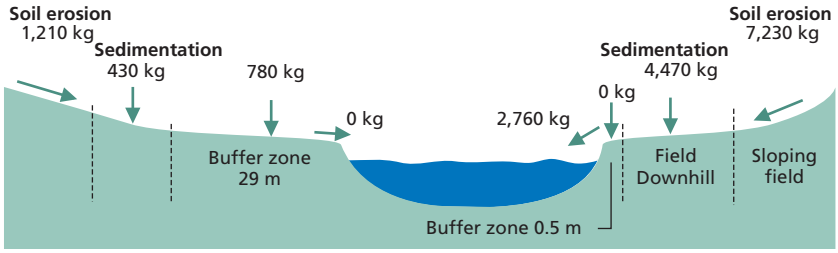
Undrained riparian areas can remove substantial amounts of nitrate through denitrification whereby – under anaerobic conditions through the use of organic carbon (biologically) or pyrite (chemically) – nitrate is transformed to gaseous N. If the riparian area is tile-drained instead nitrate will pass through the area without being reduced.



The removal of nitrate via denitrification is a process that takes place under anaerobic conditions in all soils and water compartments where nitrate exists.



Wide non-cultivated buffer zones along stream channels can function as an effective filter for nutrient-rich soil particles mobilised through soil erosion processes and transported with surface runoff towards the streams.



Soil erosion can deliver huge quantites of sediment and phosphorus to aquatic ecosystems.

Perspectives and future threats

We have gained great insight into the hydrological and chemical conditions in Danish streams during the last 15–20 years. Research has helped us to understand many of the processes governing the hydrochemistry of streams and catchments, especially the threats from acidification, ochre and nitrogen pollution. However, we now face a new era where treatment of point source discharges alone cannot solve the problem of achieving good ecological quality surface waters as demanded in the EU Water Framework Directive. Thus, we need to improve the understanding of physical processes that regulate transport of substances from agricultural fields to streams, and biogeochemical processes that remove, transform or store substances during the transfer from land to sea. This information is required by managers in order to target pollution problems in surface waters and it is necessary for preparing new and better hydrochemical models to predict possible future changes in the aquatic environment of regional management schemes and climate change.

Box 2.7 Restoring rivers and floodplains

Rehabilitation of river and floodplains is one of the important management schemes that can be used by river basin managers to reduce diffuse nutrient pollution. The effect of rehabilitating streams, wetlands and lakes in a 100 km^2 catchment in Jutland, Denmark was simulated by the TRANS model [16]. The effect measured as increases in nitrogen removal and phosphorus storage in streams, lakes and floodplains following rehabilitation, was very high.

	Nitrogen removal (tonnes)		Phosphorus storage (tonnes)	
	Pre-restoration	Post-restauration	Pre-restoration	Post-restauration
Watercourses	5.2	21.6	0.24	–0.08
Lakes	33.5	28.0	–1.39	0.09
Floodplains	0.13	31.3	0.35	0.89

The springbrook is the first part of the river system.

3 From spring to river – patterns and mechanisms

A river system consists of a branched network of streams, but how do environmental conditions and the distribution of organisms vary along the system? The depth, width, discharge and mean age of the water increase from source to mouth and the physical and chemical characteristics of the water gradually become more influenced by contact with the atmosphere and in-stream processes. Species composition and diversity also change along the stream. These patterns are influenced by the location and site-specific characteristics of the reaches. In addition, they are influenced by the dispersal of organisms between reaches making the biota at each site dependent on the biota at neighbouring sites.

Streams – a network with unidirectional flow

As described in chapter 1, streams form a unique ecosystem because of the linear connection in the network, the unidirectional flow and the intimate contact with the land. The network generates a finely branched connection transporting water and matter from the terrestrial areas to the sea. These aspects are incorporated in models for transport of organic matter and nutrients and for transformation of oxygen and carbon, and they are integrated in the River Continuum Concept (Box 3.1).

Species composition and richness at the individual stream reaches are often treated as if they were independent of conditions at neighbouring reaches even though organisms are extensively dispersed throughout the stream network.

Flow and substrata from spring to river

With increasing distance from the spring, the stream usually becomes wider, deeper and transports more water (Figure 3.1 and 3.2). Slope, temperature and CO_2-concentration also change downstream.

Along the course, the slope decreases [2]. Denmark has no mountains, however, and its streams follow more irregular courses, shifting between reaches of steep or low slopes, interspersed with stagnant lakes with long water retention. Nonetheless, the steepest slopes are usually found in the springs and brooks, and the lowest slopes in rivers close to their outlet [4, 6]. However, due to irregularities, reaches with steep slopes and high physical stress may occur anywhere along the course of a river.

A comparison of 208 Danish stream reaches during summer showed a doubling of the mean water velocity from

Box 3.1 River Continuum Concept (RCC)

The RCC was formulated by American stream ecologists to conceptualise general patterns of input and conversion of organic matter along the stream course [1]. Some of the original concepts were able to withstand later tests while others had to be abandoned [2, 3].

Streams receive large amounts of terrestrial organic matter along the entire course from their source to their mouth. Thus, streams usually decompose more organic matter than they produce by photosynthesis. The net balance of the system metabolism in streams is said to be heterotrophic because the combined annual respiration of all organisms exceeds the photosynthesis of algae and plants. The ratio of annual photosynthesis to annual respiration (P/R) may be close to 1 in desert streams because they receive little terrestrial material. In spring, when irradiance is high and bank shading low and while the terrestrial input of organic matter is low and respiratory degradation is restricted by low temperatures, photosynthesis may also exceed system respiration in small Danish streams [4]. On an annual basis, however, system respiration surpasses photosynthesis at all reaches in Danish streams and in most other streams worldwide.

The original RCC proposed systematic changes in photosynthesis, respiration and the ratio between these along the stream course but both processes depend on local organic inputs, water depth and turbidity, stream bed stability and terrestrial shading.

The original North American descriptions of gradual changes in the photosynthesis to respiration ratio from very low values in the upper sections (P/R << 1), highest values in the mid-sections (approaching 1) and lower values in downstream sections (e.g. 0.2–0.8) presuppose that the upper sections are highly shaded by forests, the mid-sections are unshaded and that photosynthesis in the lower sections is constrained by light attenuation in deep water.

Recent studies have revealed that organic inputs from the floodplain in the lower sections had been underestimated, especially during flooding [2]. Neither has there been any verification of two other RCC-predictions: that there is a systematic downstream increase in the relative quantity of fine particulate organic matter relative to coarse organic material (e.g. leaves), due to the processing of material by invertebrates, and a concomitant decline of large shredders (e.g. trichopterans) [3]. Coarse organic material is often added to the stream along the entire course without a consequent, predictable change in the proportion of shredders. The proportion of coarse material is not systematically higher in forest streams than in open streams [5]. Shredders do not solely consume shredded terrestrial leaves, as they may also graze on live submerged plants and macro-algae, and occasionally even act as predators.

Despite the criticism of the RCC, it remains useful to consider streams as a continuum by tracking matter and processes as the water moves downstream. It requires, however, integration of local sources of organic matter and determinants of photosynthesis and decomposition in order to achieve an accurate overall picture.

0.13 m/s in streams smaller than 2 m to 0.26 m/s in streams wider than 6 m (Figure 3.2). This difference has consequences for the plants directly exposed to the free-flowing water. Flow conditions are different for micro-organisms, invertebrates and fish that live in close contact with the stream bed or the banks. Low flow velocities may prevail immediately above the stream bed at deep sites and in the shelter behind plant patches and behind bends close to the banks [2, 4].

Local flow conditions above the stream bed regulate erosion and sedimentation. Although intuitively we may believe that steep headwaters have coarse gravel substrata while large rivers have fine-grained mud, this does not apply to Danish lowland streams – neither in their original unregulated nor in their current, regulated state. In a nationwide study of 40,000 quadrate (25×25 cm) in 208 reaches in 45 streams, we did not observe systematic changes in the main substrata along the stream courses. Sand was the most common bottom substratum in both small and large streams.

We also determined substratum heterogeneity by calculating how often two neighbouring quadrates had dif-

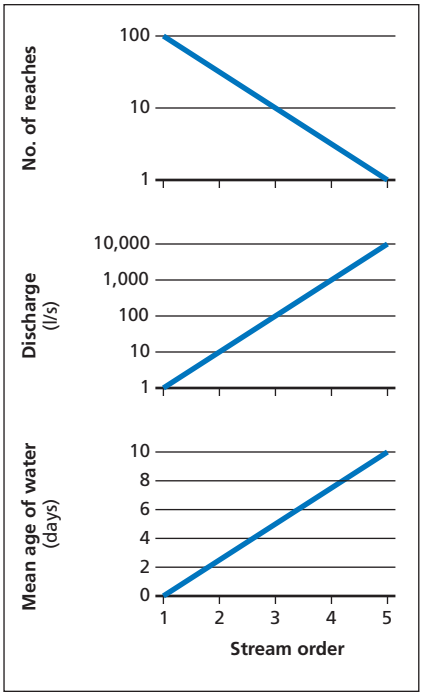


Figure 3.1 Three idealised graphs illustrating how large number of small headwater streams gradually merge into fewer streams of higher order (top), higher discharge (middle) and higher mean age of the transported water (bottom).

ferent substrata (Box 3.2). Substratum heterogeneity could be important for the diversity of plants and invertebrates because species differ in their substratum preferences. However, we observed only small and insignificant differences in mean values of substratum heterogeneity among different size categories of streams (Figure 3.3).

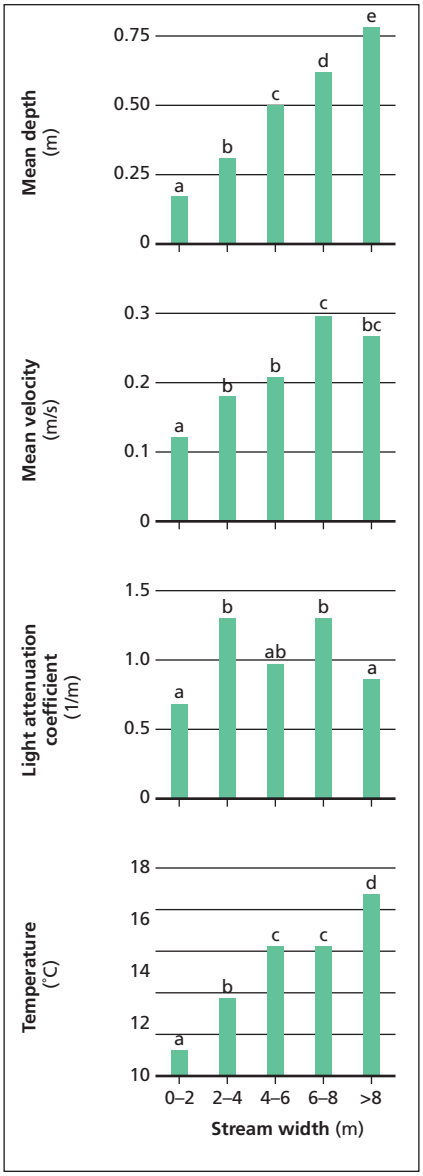


Figure 3.2 There are systematic changes in mean depth, velocity, light attenuation and temperature along the river continuum from source to outlet. Summer measurements in 208 Danish stream reaches illustrate the patterns. Columns sharing a common letter are not significantly different from each other. [Sand-Jensen and Riis, unpubl.].

Light

Light availability in streams is determined by solar radiation, bank shading, surface reflection and light attenuation through the water. In small narrow streams, the banks and terrestrial herbs can intercept most of the incident light. In wide rivers, however, large trees are needed to provide the same shading.

We can all recall the sight of grass-green water downstream of plankton-rich lakes and the sight of yellowish water rich in suspended particles during peak flow. Under these circumstances, light attenuation through the water column is so profound that plants and microscopic algae are unable to photosynthesise and grow at the stream bottom. These extreme conditions, however, are not representative of the general state of light conditions in streams, which are much better in most instances.

The survey of 208 Danish stream reaches found that during summer, light attenuation through the water of Danish streams was lower at small and large reaches than at reaches of intermediate size (Figure 3.2). These differences were mainly due to variation in the concentrations of mineral particles, which were lower in small streams receiving substantial proportions of particle-free groundwater and in larger streams where sedimentation exceeded re-suspension during low-flow periods.

The light attenuation coefficient (k) describes how rapidly light intensity decreases with water depth according to: $I_z = I_o \exp(-kz)$, where I_o is light intensity at the surface, I_z is light intensity at depth z, and exp is the exponential function. The mean exponential coefficient (k) ranged from 0.7 to 1.3/m among Danish streams of different

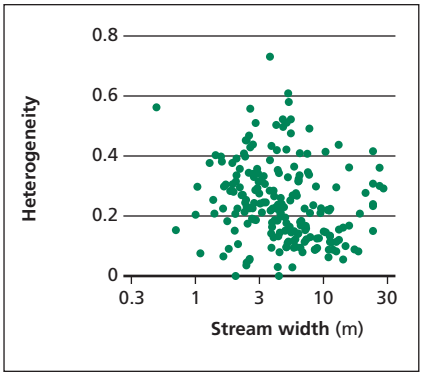


Figure 3.3 The heterogeneity of the stream bed (Box 3.2) is highly variable among reaches, but does not change systematically along the course of Danish streams [Sand-Jensen and Riis, unpubl.].

Box 3.2 The heterogeneity of the stream bed

The heterogeneity of the stream bed is calculated on the basis of the following expression

$$SH = 1 - \frac{\sum_{i=1}^{10}\sum_{j=2}^{n_i} I(x_{ij}, x_{ij-1})}{\sum_{i=1}^{10}\sum_{j=2}^{n_i} 1}$$

$$I(x,y) = \begin{cases} 1, \text{ if } x = y \\ 0, \text{ or} \end{cases}$$

where ***SH*** is the substratum heterogeneity, ***i*** is the transect and ***j*** is the quadrat. The value is a number between 0 and 1 and the closer the value is to I, the higher is the heterogeneity of the stream bed.

width (Figure 3.2). Consequently, an average of between 50% and 27% of the light intensity passing the water surface reaches a depth of 1 m [4]. Some groundwater-fed brooks had light attenuation coefficients of only 0.2–0.4/m, which is less than for most Danish clearwater lakes. The comparisons show that overall, streams have clearer water during summer than the mostly plankton-rich Danish lakes, which have attenuation coefficients of typically 0.4–4.0/m.

Temperature and CO_2

In the same survey, midday temperatures averaged about 11°C for the upper stream reaches and 17°C for the lower reaches during summer (Figure 3.2). There are two reasons for this difference. The small upper reaches are characterised by "young" water that has just recently been received from the cold groundwater aquifers. Headwater streams are also more shaded due to the narrow channel. Consequently, the water is colder, although shallow depths allow better heat exchange with the atmosphere than deep water. In the lower reaches, temperatures are higher and close to the mean air temperature because the water has been transported for a long time and has come close to equilibrium with the air. It is well known that water temperature is very important for the distribution and metabolism of invertebrates and fish [2, 7], but its influence on plants has been neglected so far (see later).

Temperature and CO_2 concentration tend to follow a parallel course in streams (Figure 3.4). Cold water is "young" water rich in CO_2 from soil respiration, while warm water is "old" water having lost part of the CO_2 supersaturation due to contact with the air and photosynthesis. Nonetheless, most streams maintain CO_2 supersaturation irrespective of stream type and location. Thus, 56 stream reaches in North Zealand had median CO_2 concentrations of 176 µmol/l in the morning and 90 µmol/l in the afternoon, corresponding to about an 11-fold and a 5.6-fold supersaturation relative to atmospheric equilibrium. Only reaches located immediately downstream of lakes were close to atmospheric equilibrium because of the long retention time and photosynthesis in the lakes. Studies of the long River Gudenå, which is interspersed with several lakes, demonstrated that there are distinct increases in temperature and phytoplankton biomass and decreases in CO_2 concentration downstream of the lakes (Figure 3.4).

Dispersal of stream organisms

There is a very good reason why the connectivity of the stream network is important for animals and vegetation. Streams are often exposed to considerable disturbances (e.g. peak flows) leading to a significant decline or eradication of populations at certain reaches, so immigration and recolonisation of new individuals are crucial in maintaining species richness. The protection of species against extinction in streams depends largely on the ability of a few

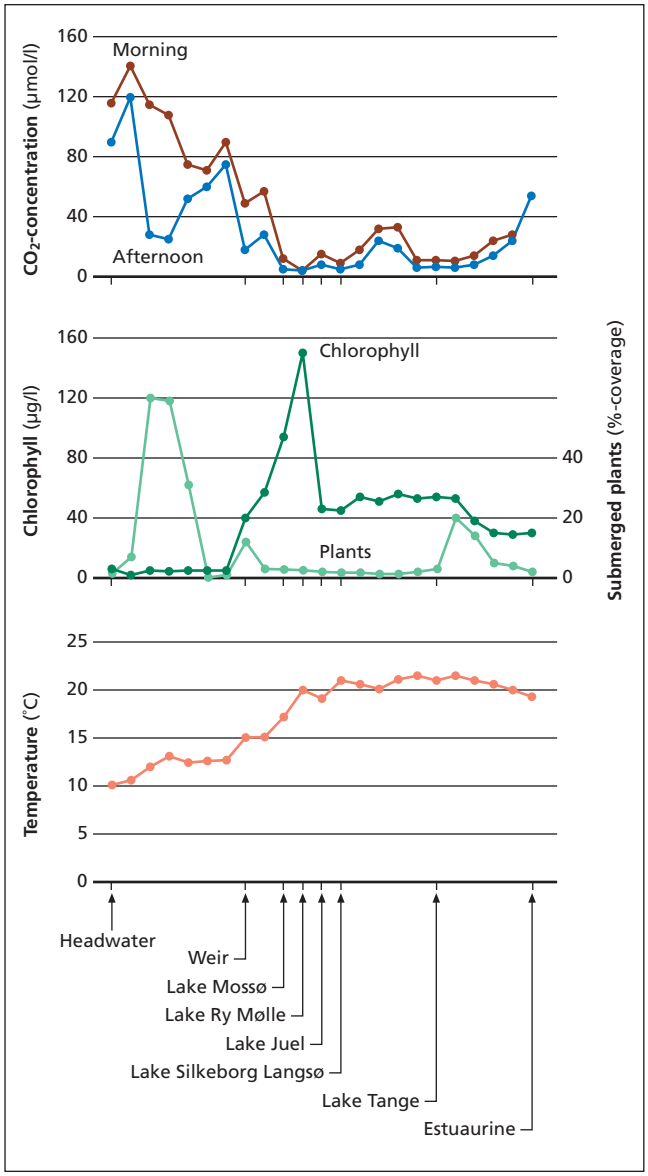


Figure 3.4 River Gudenå has many weirs and interspersed lakes. CO_2 concentrations and macrophyte cover decline downstream during summer, while there is an increase in phytoplankton biomass and temperature.

populations to survive, even following serious disturbances. From these refugia, species can disperse and re-colonise the entire stream network.

Hildrew and Townsend have described how invertebrates undergo a continuous redistribution in streams [8]. As a result, invertebrate populations are re-established relatively rapidly at reaches that have been subjected to catastrophic disturbance due to pollution or sediment erosion [3]. It is, therefore, surprising that the assumption of independent behaviour of populations of reaches is maintained in many biological studies.

Different species do not have equal ability to disperse upstream and downstream. The ability of the species to become established in new habitats or re-colonise former habitats depends on the location of the surviving populations and the biological characteristics of the species.

All organisms are able to disperse passively with the current and consequently the downstream dispersal capacity usually exceeds the upstream. Plants are able to deliver a continuous supply of seeds, detached shoots and some vegetative dispersal units (e.g. short shoots) to downstream reaches, thereby enhancing the chances of establishing new plant stands or maintaining old stands there.

Surprisingly few studies have attempted to quantify the transport of plant dispersal units. Moreover, the dispersal has rarely been evaluated on the basis of the actual distribution of plant species. In a study of *Ranunculus lingua* growing in wet soils, with most of the shoot exposed to air, shoots were tagged and later recovered at a considerable distance further downstream [9]. A lake, on the stream network, formed a trap for further downstream dispersal. Once lake populations have been established, however, not only do they ensure downstream dispersal, but they also enrich the downstream reaches with many individuals and species, provided that the lake populations are rich and abundant.

One hundred years ago, most Danish lakes had clear water and dense, submerged vegetation capable of enriching downstream reaches with species (Figure 3.5). Unrooted *Ceratophyllum demersum* (rigid hornwort), for example, was common in outlets from lakes while nowadays this species is no longer observed in streams [10]. Also *Myriophyllum spicatum* and *M. verticillatum* (spiked and whorled water-milfoil), *Ranunculus circinatus* (fan-leaved water-crowfoot) and several large species of *Potamogeton* (pondweeds) were previously more common. Due to eutrophication, lakes interspersed within streams have entirely lost their sub-

The quality of the lake water influences biological communities in the stream below.

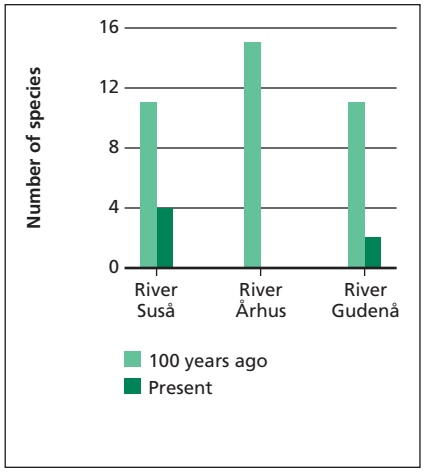


Figure 3.5 The number of submerged plant species has declined markedly at reaches downstream of lakes over the past century. The lakes have been enriched with nutrients that stimulate phytoplankton production and lead to loss of submerged rooted vegetation. The lakes now export turbid water and prevent plant dispersal. The figures are from the Suså Stream downstream of Lake Tystrup-Bavelse, the Århus Stream downstream of Lake Brabrand, and the River Gudenå downstream of Lake Silkeborg Langsø [10].

merged vegetation. They form a trap for the dispersal of species between upstream and downstream reaches and they export turbid plankton-rich lake water. As a result, there are few, if any submerged species downstream of the lakes (Figure 3.4 and 3.5). It has thereby become more difficult for submerged species to disperse between lakes and streams, and this has probably contributed to the development of greater differences between the submerged vegetation of lakes and streams today than there were 100 years ago [10].

There are numerous small brooks in the upper part of the stream network, which is richly branched throughout the landscape. The number of stream sections decline with increasing stream order [2]. Assuming, for example, an average 3-fold decrease of stream reaches per order, a fifth order stream system may include 81 small first order brooks and one fifth order river. The combination of the high number of brooks, their varied conditions and the downstream transport of water is likely to facilitate the enrichment of species along the downstream course of the river system.

Thus, if species richness rises as reaches increase in order and width downstream, it may not solely reflect the greater size and more varied environmental conditions [1]. Species enrichment may also result from the better supply of species and individuals from upper stream reaches.

The downstream dispersal is sometimes clearly reflected in the distribution of plant species. For example, observations may show that two upstream reaches have very different species compositions while the downstream reach has several species in common with the two upstream reaches after their confluence [11].

Plant distribution in stream systems

In a comprehensive study of plant distribution at 208 unshaded reaches of 45 Danish streams, we attempted to answer three important questions:

- How great is the plant cover?
- Which species and plant types dominate?
- How does species richness vary among the reaches?

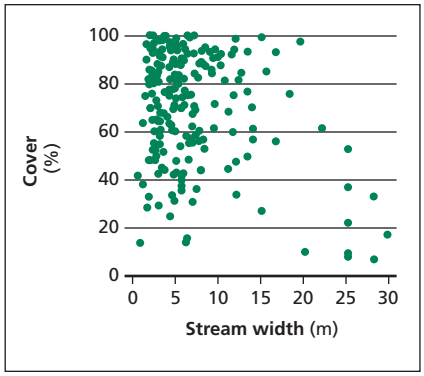


Figure 3.6 Mean plant cover in the middle-part of the stream bed declines along the stream course as plants receive insufficient light with increasing depth.

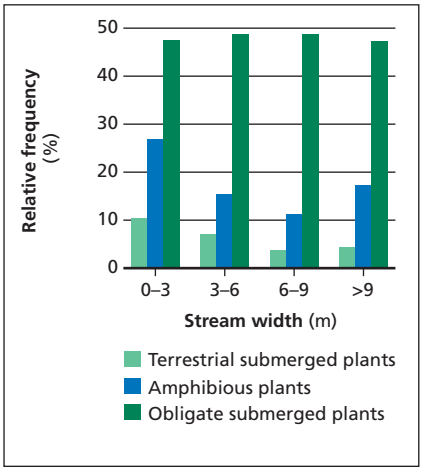


Figure 3.7 The mean relative abundance of three groups of plants (terrestrial, amphibious and obligate submerged plants) in the aquatic vegetation of 208 Danish stream reaches covering a range of widths. Abundance is based on the presence of plants in about 200 quadrats per reach. Note the gradual substitution of terrestrial and amphibious plants mainly associated with stream banks by obligate submerged plants, as the width and depth of the reaches increase. Terrestrial plants include species that may survive, but with poor growth, under water. Amphibious plants grow on land as well as under water, while obligate submerged plants are usually unable to survive in air.

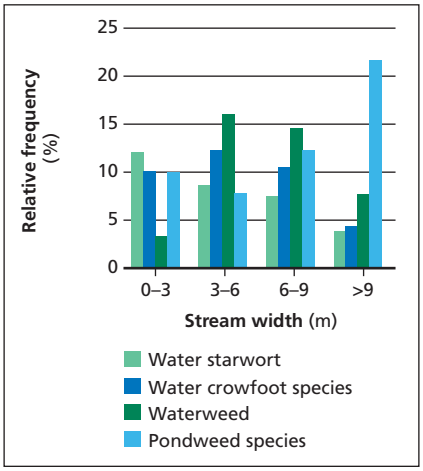


Figure 3.8 Among the obligate submerged plants there is a change in the relative abundance of species and species groups with increasing stream size. *Callitriche* species (water-starwort): mainly *C. cophocarpa* and *C. platycarpa*. *Ranunculus* species (water crowfoot): mainly *R. baudotii*, *R. aquatile* and *R. peltatus* and *Potamogeton* species (pondweeds): *P. pectinatus*, *P. crispus*, *P. perfoliatus*, *P. natans*, *P. praelongus*, *P. lucens*, *P. berchtoldii* and *P. frisii* in order of decreasing abundance.

The large species *Potamogeton praelongus* (long-stalked pondweed) is most common in large streams.

The first two questions are discussed below, while the third question is treated in the following section. The results showed that the vegetation often reached a very high cover in shallow Danish lowland streams during summer. Moreover, plant cover declined with increasing stream width (Figure 3.6) simply due to insufficient light in the deeper areas of the lower reaches. Not surprisingly, terrestrial plants, with sporadic aquatic occurrence, and amphibious plants constituted a decreasing proportion of the vegetation, as reaches become wider and deeper (Figure 3.7). Truly submerged plants, which always grow under water, were the most widely distributed and abundant at all reaches forming 45–50% of the cover.

The relative abundance of different permanently submerged species changed along the stream course (Figure 3.8). Species such as *Callitriche platycarpa* (various-leaved water-starwort) and *C. cophocarpa* were most abundant in small upper reaches not wider than 3 m. *Ranunculus* species such as *R. fluitans* (river water-crowfoot) and *R. peltatus* (pond water-crowfoot) were most abundant in streams smaller than 9 m. *Elodea canadensis* (Canadian waterweed) was most abundant in 3–9 m wide mid-section streams. Finally, the collection of large *Potamogeton* species, which includes *P. crispus*, *P. natans*, *P. pectinatus*, *P. perfoliatus* and *P. praelongus* (curled, broad-leaved, fennel, perfoliate and long-stalked pondweed), was most abundant in wide, lower reaches.

The distribution of plants is probably influenced by changes in temperature and water depth. Growth experiments in the laboratory have shown that the aforementioned species of *Callitriche* and *Ranunculus* are less sensitive to temperature variations than *Elodea* and *Potamogeton*. *Callitriche* often has the greatest abundance relative to the other submerged species during the winter. The peak abundance of *Ranunculus* is attained during the spring and early summer, while *Elodea* and *Potamogeton* peak during mid-summer, reflecting higher temperature require-

Unshaded lowland streams of medium size usually have very varied submerged vegetation.

A shaded forest stream without macrophyte growth.

ment [10]. Species of *Callitriche* are small and delicate and have a special ability to sprout and form emergent shoots on wet soils. Accordingly, they are considered close to the transition from amphibious to submerged plants. Like the amphibious species, most *Callitriche* species are totally dependent on CO_2, which is present at its highest concentration in cold headwaters. At the opposite extreme of the spectrum, in deep, warm, lower reaches, the large *Potamogeton* species benefit from the higher temperatures, their ability to use bicarbonate, their greater plant size and their ability to form a canopy close to the water surface [12].

Species richness of plants along streams

Total species richness in open Danish streams changes very little with location and width of the stream once it is wider than 3 m, where mean species richness is 12–13 per reach. However, mean species richness is consistently lower (10 species) in very narrow reaches not wider than 3 m.

There is a logical explanation for this pattern. In very narrow and shallow streams there is limited space and variability in water depth compared with the conditions in larger streams. Immigration of species from other reaches is also less likely to occur in the upper than in the lower reaches.

Species richness of animals in streams

While mean species richness of plants remains relatively constant along the course of Danish streams, the animals exhibit considerable differences. Wiberg-Larsen conducted an interesting study of species richness of caddisflies from a large number of Danish stream reaches [6]. Caddisflies increased markedly in species richness with increasing width of stream reaches. The increase was approximately linear when species richness was plotted as a function of stream width on logarithmic axes, although the rate of increase in species richness tended to decline in the widest reaches. Jacobsen and Friberg have also shown that species richness of all insects increases from upper to lower reaches with similar terrestrial surroundings and pollution level [5]. Other studies have shown that species richness of fish increases with the size of stream systems (Figure 3.9).

An important goal is to achieve a better understanding of the regulation of species richness among plants, invertebrates and fish. Differences and similarities among groups of organisms should reveal the importance of dispersal capability and environmental requirements for the distribution of the different species. Evaluations should be performed for individual reaches as well as entire stream systems. In individual reaches, evaluations must take into account their surface area, habitat heterogeneity, environmental conditions and location. Downstream reaches of the same length can support more species because water temperature, surface area, depth variation and the immigration of species are higher than in upstream reaches. This environmental complexity means that it is difficult or impossible to identify the mechanisms that are particularly important for the observed differences in species richness.

Relationships between species richness and surface area for lakes and terrestrial habitats usually follow an empirical power equation: $S = cA^z$ (i.e. $\log S = \log c + z \log A$). The increase rate (z) of local species richness with surface area is usually between 0.1 and 0.5 with a mean value of about 0.3. This value indicates that species richness in a local habitat doubles with a 10-fold increase in the surface area of the habitat. However, it is difficult to interpret the cause of different z-values, and it is particularly difficult to evaluate

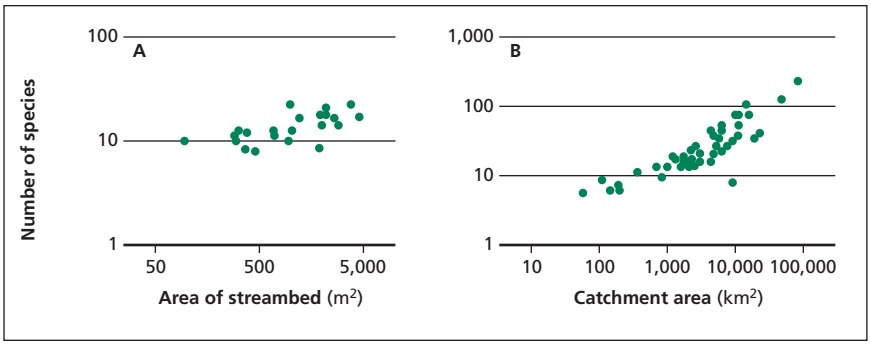
z-values for stream reaches within stream systems as species richness at individual reaches can hardly be considered as independent observations. Furthermore, the downstream increase in water temperature makes it problematic to compare the relationship between species richness and width in streams with the relationship between species richness (S) and surface area (A) as applied for lakes and terrestrial habitats [13].

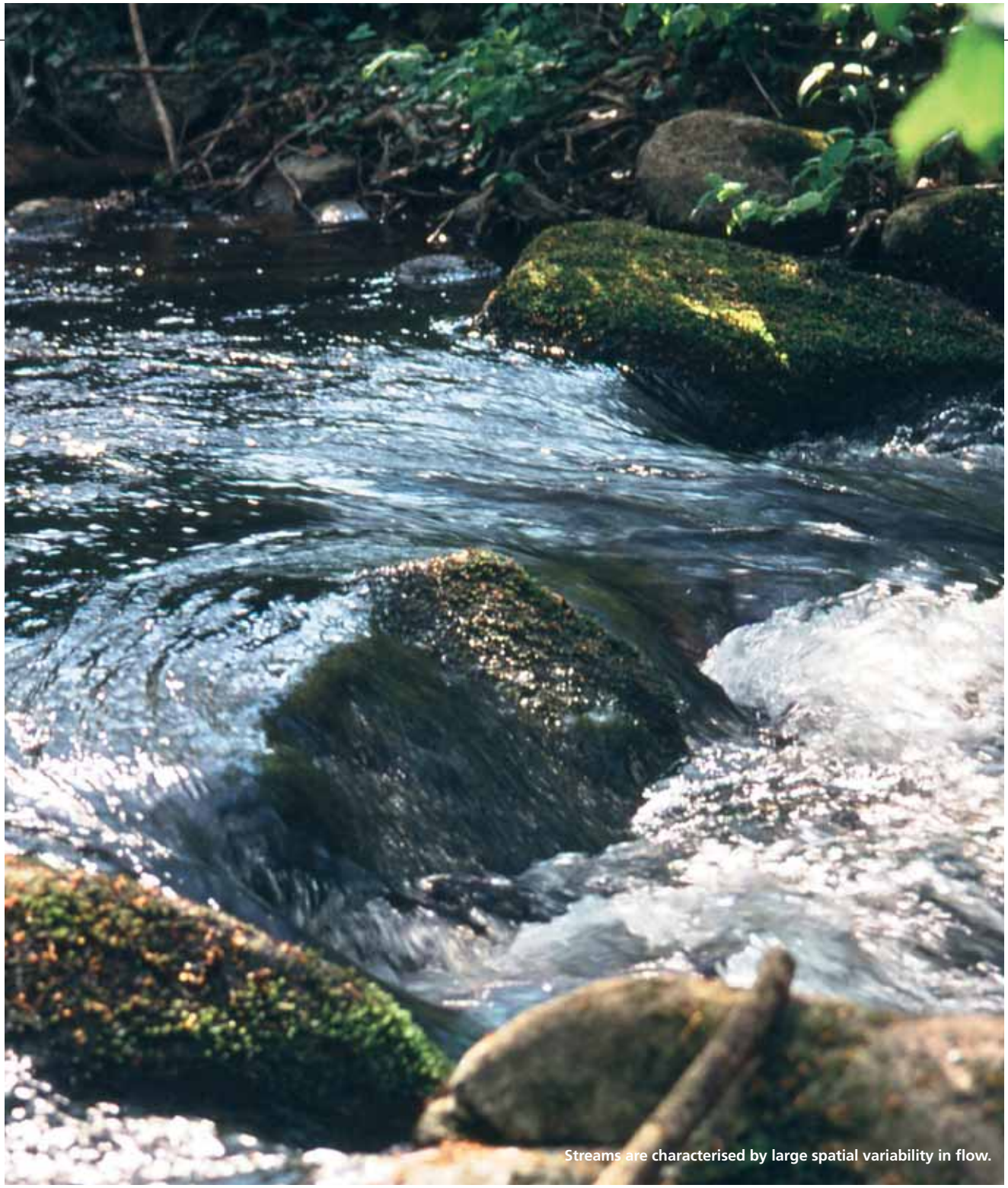
Some of these problems of interpretation do not occur when species richness of entire stream systems is evaluated as a function of their size. Size can be as expressed as either the entire surface area of the stream bottom, the water discharge at the outlet or the catchment surface area in regions with similar hydrology (Figure 3.9). Here, total species richness usually increases linearly with the size of the stream system when plotted on logarithmic axes [14, 15]. An increase in the surface area of stream systems has the important effect of increasing the number of individuals and thereby the number of different species. However, as habitat variability usually rises with system area, it remains difficult to determine to what extent an increase in the number of individuals and increased habitat variability are responsible for the increased species richness [13]. Time is another crucial determinant of species richness. Over thousands and millions of years, older stream systems will tend to have accumulated (via immigration) a greater number of species than younger systems. If large stream systems are also older than small stream systems, which is often the case, this connection between size and age will tend to strengthen the positive relationship between species richness and stream size.

In order to learn more about the regulation of species richness it is important to analyse why certain stream systems have more species, while others have fewer species, than would be expected from an average relationship, based on all of the stream systems examined. In other words, we need to test the reasons for positive and negative variations (residuals) from the main average pattern. If the historical influence of immigration can be discarded in a region with a common species pool for all stream systems, it is possible to evaluate the influence of stream size, habitat variability and water chemistry on species richness of the individual streams. In other cases it is possible to evaluate the influence of time and immigration history by comparing streams of similar size, habitat variability and water chemistry. It is important to remember, however, that history may have a strong impact on regional differences within one continent, and even within one country [2, 3]. In Denmark, for example, the species richness of caddisflies is lower on the main islands of Zealand, Funen and Bornholm than in Jutland (the peninsula connected to the European continent) [6]. As the local species richness derives from the regional species pool, there are fewer species in local streams when the regional species pool is low. There are also distinct differences in species composition of invertebrates and fish over distances of only a few km between the old streams (*c.* 150,000 years) in western Jutland, derived from the glaciers during the last glaciation, and the young streams (*c.* 10,000 years) in eastern Jutland, which were created when the glaciers retreated.

Over time there is no distinct upper limit for the size of the local and regional species pool. Given time, area and suitable environmental conditions then species richness will rise. Unfortunately, the profound reduction of the population size of many stream organisms during the last 100 years, together with the ever-rising human populations and the more intense use of land and water throughout the world, is likely to even further reduce species richness of the streams over the coming century.

Figure 3.9 Examples of increasing numbers of species with increasing scale of the stream systems. (A) Species richness of stream invertebrates on Bornholm Island. (B) Species richness of fish in larger stream systems.





Streams are characterised by large spatial variability in flow.

4 Water flow at all scales

Continuous water flow is a unique feature of streams and distinguishes them from all other ecosystems. The main flow is always downstream but it varies in time and space and can be difficult to measure and describe. The interest of hydrologists, geologists, biologists and farmers in water flow, and its physical impact, depends on whether the main focus is on the entire stream system, the adjacent fields, the individual reaches or the habitats of different species. It is important to learn how to manage flow at all scales, in order to understand the ecology of streams and the biology of their inhabitants.

Macroscale and overview

Flow conditions in stream reaches are often described by measurements of discharge, water velocity and water stage. If the downstream slope of the water surface, the cross section profile and the composition of the stream bed are also known, empirical equations can be used to estimate hydraulic resistance against the flow and shear stress on the sediment (Box 4.1). Moreover, water velocity and the characteristic linear dimension of water movement can be used to estimate the Reynolds number, distinguishing chaotic, turbulent flow from regular, laminar flow.

The Danish botanist Niels Thyssen has developed a simple empirical model to predict mean water velocity in small lowland streams (Box 4.1). The velocity increases with slope, which generates the downstream water movement due to gravity. The velocity also increases with higher water discharge because this is accompanied by an increase in width and depth (and hydraulic radius) so that the resistance to water flow is reduced during contact with the streambed and the banks. Finally, submerged plants resist water movement so that mean velocity declines with increasing plant biomass. Moving water encounters a greater resistance in a meandering stream, which reduces flow velocity compared with a straight channel. This is why channelisation has been used so extensively to drain water from the wet soils along the streams and thereby increase the cultivation of fields.

In all, the four parameters, slope, discharge, plant biomass and meandering, could account for 75% of the observed annual variation in mean velocity in eight lowland streams. The empirical equation is not always very precise in its predictions of the actual velocity, however, because of restrictions in its ability to account for other factors that also affect the hydraulic resistance e.g. channel morphology, substrate type and plant distribution.

Mean velocity is a simple and informative measure of macroflow. Danish lowland streams range from

Box 4.1 Macroflow in streams

Mean water velocity (**U**, m/s) can be used to characterise stream reaches. Other suitable descriptors are depth (**D**, m), width (**B**, m), cross section area (**A**, m^2), slope (**S**, m/m) and meandering (**I**, no dimension) which can be measured as the length of the main flow line (the thalweg) divided by the shortest distance.

In small Jutland streams, the Danish botanist Niels Thyssen [1] has found the best way to empirically predict the mean water velocity as:

$$U = 79.3\ Q^{0.47}\ B^{-0.058}\ S^{0.69}\ I^{-0.79}$$

where **Q** is water discharge (m^3/s), **B** is plant biomass (g dry mass/m^2), and **I** is an index for meandering: 1 at low, 2 at intermediate and 3 at high meandering.

The Reynolds number is the dimensionless ratio between inertial forces of moving water generating chaos and turbulence and viscous forces attracting water parcels to move in a laminar and orderly manner, in only one direction at constant speed [2, 3]. If the kinematic viscosity is **v** (approx. 1×10^{-6} m^2/s at 20°C), the Reynolds number (**Re**) of main flow in the stream channel is:

$$Re = U\ D\ /\ v$$

The flow is usually categorised as laminar at **Re** < 500, turbulent at **Re** > 1,000–10,000 and a mixture in between these. **Re** is already 5,000 at a velocity of 0.05 m/s and a depth of 0.10 m so the main flow in streams is almost always turbulent, although of variable intensity. In microhabitats, in sediments and within plant patches or close to the banks in still-flowing streams, laminar flow may be encountered.

Shear stress (η_o) at the sediment surface is important for the ability to erode particles or alternatively leave them in place. Shear stress can be estimated from shear velocity (U_*) derived from the logarithmic velocity profile (Box 4.2) or estimated from the equation [4, 5]:

$$U_* \sim 0.17\ U\ /\ \log\ (12\ D/k)$$

where **k** is sediment particle size or sediment roughness. Shear stress in uniform flow is given by [6]:

$$\eta_o = \rho\ U_*^2$$

where **ρ** is mass density of water (approx. 1.000 kg/m^3).

A direct way of measuring shear stress is to place calibrated metal hemisphere of the same size but variable weight on a small horizontal plate on the sediment surface and determine the lightest of the hemisphere set in motion [7].

Manning's equation is used to calculate the Manning number (**M**) or the roughness coefficient (**n** = 1/**M**) for water movement along a stream reach:

$$U = 1\ /\ n\ R^{0.67}\ S^{0.5}$$

Where **R** is the hydraulic radius (surface area divided by the length of contact between water and sediment in the cross section). The coefficients are not constants, but empirical averages of a large number of measurements. Thyssen's comprehensive studies showed a positive relationship of Manning's **n** to plant biomass, but the relationship varied substantially from one stream to another, preventing the construction of a general model.

reaches with rapid currents close to 1 m/s and a stream bed dominated by stones and gravel, to reaches with slow currents of less than 0.10 m/s and muddy substrata. Velocity is important for organisms freely exposed to the current, as drag forces increase steeply with the water velocity. In slow currents water masses pass slowly along the reaches, and turbulence and oxygen exchange with the atmosphere are restricted. As a consequence, oxygen concentrations in the water can change markedly between day and night in slow-flowing streams, while diel amplitudes are modest in fast-flowing streams, even if oxygen production and oxygen consumption on an area basis in the two stream types are identical.

Together, experts and the general public can share the fascination of a variable flow pattern along meandering reaches with alternating pools and riffle sections. Every angler, who

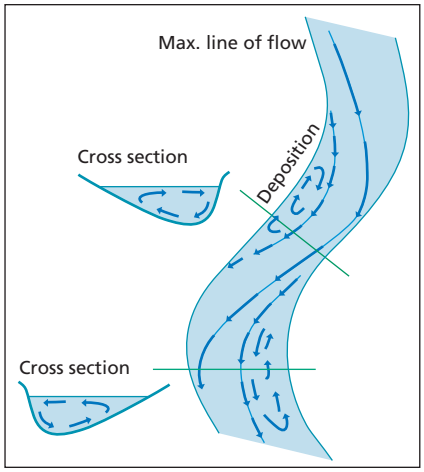


Figure 4.1 Main lines of flow at the surface of a meandering stream, as seen from above. The two cross sections show the weaker flow across the stream [8].

has tried his luck with a worm and float, knows that the current declines close to the banks, and that it can move upstream in the shelter behind meanders and plant patches. The angler uses his experience to attract fish in a territory chosen because of its favourable current and opportunities of shelter.

A meandering stream has a certain transversal flow in addition to the main downstream flow [8]. At the apex of meanders, maximum flow has moved close to the outer bank generating scour and bank recession. At the outer edge of the turn, where the flow hits the bank, the water level is slightly elevated generating a secondary flow towards the bottom and across the stream. At the inner edge of the turn, water depth is reduced and the current is diminished and directed towards the water surface leading to sedimentation of particles (Figure 4.1). This transversal, spiralling flow can even appear in straight channels [9]. The phenomenon influences erosion and sedimentation and is, therefore, important for the development of channel morphology and the distribution of bottom dwelling invertebrates.

Water stage is a practical parameter

Water stage (depth), width, discharge and discharge capacity are important stream parameters. Water depth and width set the limit for the existence of large fish and plants, and deep water increases the diversity of small invertebrates [10]. Water depth is also important for many physical processes. Greater water depth reduces the physical contact between the water volume and the atmosphere, thereby

Box 4.2 Velocity profiles

A regular velocity profile at depth is formed in large streams with a uniform slope and cross section and a fine-grained stream bed [8, 9]. The layer closest to the bed (the bed layer) is usually only a few millimetres thick. In slow flow over a smooth bed a viscous sublayer with laminar flow is formed, in which the microscopic water layers move orderly on top of each other with no vertical mixing and a linearly increasing velocity with increasing distance from the sediment (Figure 4.2). In the laminar sublayer, vertical transport is solely by diffusion. In a rough turbulent regime, a logarithmic layer is found further away from the sediment, in which water velocity (U_z) increases linearly with the logarithmic distance (z) from the sediment:

$$U_z = U_* / \kappa \log_e (z/z_o)$$

where U_* is shear velocity (Box 4.1), κ is von Kárman's constant (approx. 0.40) and z_o is roughness height which can be estimated iteratively by linear regression of U_z versus $\log_e z$. z_o can also be approximated as 1/30 of the particle size for sand and 1/15 for well-sorted gravel. When shear velocity is known, shear forces on particles and organisms on sediment or plant surfaces can be calculated (Box 4.1).

In deep streams there is a poorly defined outer layer above the logarithmic layer. The popular assumption that the mean velocity of the depth profile can be measured at 0.6 times of the depth requires that the logarithmic layer extends to the surface. This is often not the case. In small, plant-rich streams, the logarithmic layer is not developed because of frequent acceleration and deceleration of the flow due to the presence of large roughness elements (stones and plant patches) and a strong and variable bank roughness. In fast flow above an irregular sediment surface, the laminar sublayer is often absent, because roughness elements exceed the theoretical thickness of the laminar sublayer (δ) under ideal flow:

$$\delta = 11.5\, \nu / U_*$$

Like the logarithmic layer, the laminar sublayer is never well defined (e.g. the constant used can vary between 8 and 20). Overall, the hydraulic equations should be viewed as guide lines and not as physical laws.

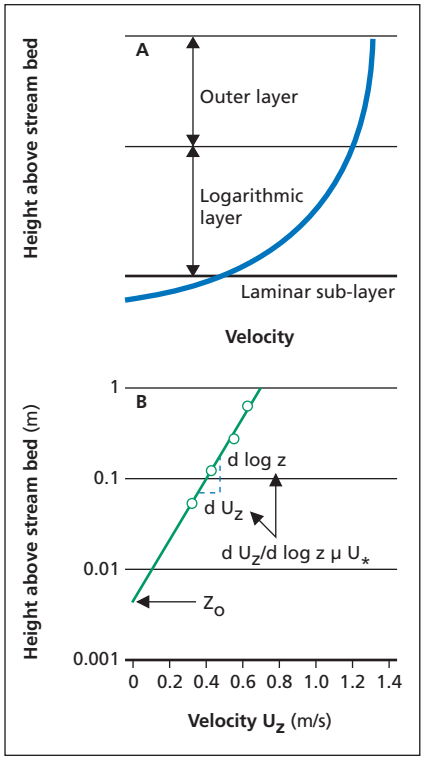


Figure 4.2 Vertical depth profile of ideal water velocity.
A: A thin viscous sub-layer with laminar flow is found above the stream bed (max. 2–3 mm), followed by a logarithmic layer and an outer layer with velocities approaching a constant level.
B: In the logarithmic layer, velocity increases linearly with the logarithm to distance from the sediment with a slope of κ/U_* (approx. 0.4/U_*). Redrawn from [9].

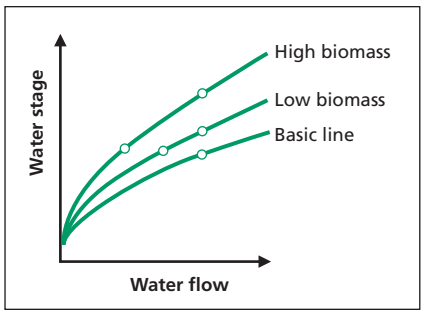


Figure 4.3 The water stage in streams increases with water discharge. When the discharge is the same/constant, water stage is lower in winter than in spring. Plants and fine sediments are usually washed out in winter, and the discharge-stage relationship follows the "basic curve". With the same discharge, the water stage is higher in summer because of flow retardation due to plants and accumulated sediments.

restricting the exchange of oxygen, carbon dioxide and heat. Greater water depth also reduces the contact between the water volume and the stream bed and thereby the frictional resistance to flow. Finally, water depth influences the velocity profile (Box 4.2, Figure 4.2) as greater depth combined with unchanged mean velocity reduces friction velocity and shear stress at the bottom permitting muddy bottoms to form, despite a relatively high mean velocity (Box 4.1).

Water stage has been measured continuously at numerous stations in Danish streams for more than 70 years. These measurements are often combined with monthly or biweekly measurements of water discharge defined as the water volume passing a given cross section per unit time (unit: m^3/s). The relationships between discharge (Q) and water stage (H) at a given site can be described by power functions of the type: $Q = a (H - H_o)^b$ which form straight lines by logarithmic transformation (i.e. $\log Q = \log a + b \log(H - H_o)$). H_o is the water stage at a discharge of zero, while "a" among other things reflects the resistance to flow, and "b" depends on channel morphology. Discharge capacity is of great interest to farmers. It is defined as the discharge that can pass the cross section at a given water stage, and is thus a measure of the water volume that can be drained per unit time from a given area without the water level reaching the mouth of the drain pipes or the upper level of the banks causing flooding of the fields.

Discharge capacity changes over the year. It is usually highest in late winter when plants are absent and fine-grained material has been transported away by high flows. In this situation the Q-H relationship follows a "basic curve" (Figure 4.3). During spring and summer there is a gradual curve shift of the relationship, concurrent with increasing plant biomass and the accumulation of bottom material. Discharge capacity can therefore be described by a set of curve variants based on actual measurements. It is possible to calculate a theoretical curve of water stage (showing "the reference stage") at a selected constant discharge (i.e. "the reference discharge"). Often the mean discharge for the summer or the entire year is used as the reference for evaluation. The reference water stage will reveal the influence of accumulated plant biomass and sediment during spring and summer and the later reductions in autumn and winter.

There are different ways of calculating the water stage at a selected discharge at a given time and plant biomass. The "proportionality method" assumes that water stage increases at the same percentage relative to the "basic curve" at all discharges [11]. This method is applicable in streams with few plants and within narrow ranges of water discharge. The "focal point method" assumes that all Q-H curve variants intersect in a common focal point at high discharge. The

assumption is that flow retardation caused by the plants is relatively more important at low water stage and declines at higher stages. The focal point method is commonly used and is the most realistic method for very variable discharges [12]. It may be less suitable when the vegetation consists predominantly of stiff species (e.g. amphibious and emergent species close to the banks), which do not bend over and become flooded at peak discharge in the same way as the flexible submerged plants.

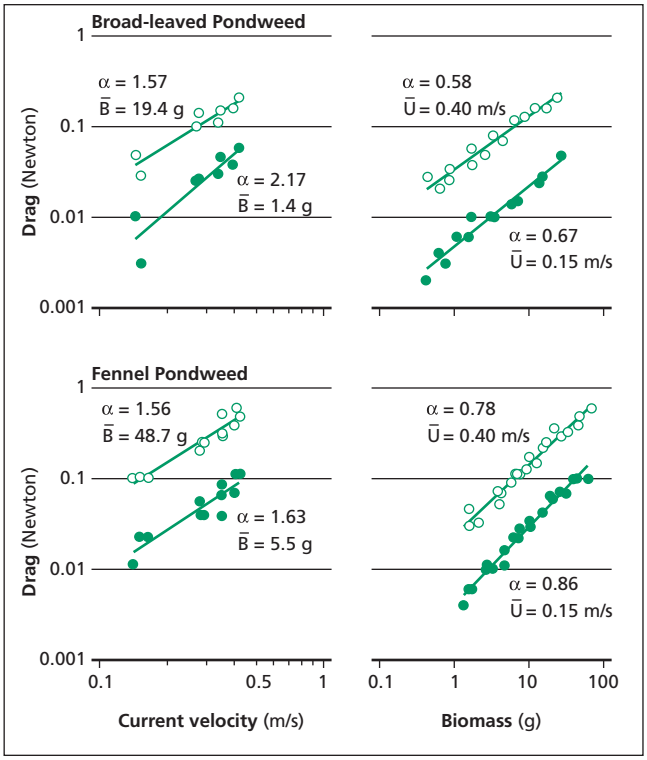


Figure 4.4 The drag on plants in flowing water increases with increasing current velocity and plant biomass. α: slope of the log-log relationship, U: mean velocity, B: mean biomass. • = 4 shoots, ∘ = 64 shoots.

Water level and plants

The influence of plants on water level has been evaluated in 65 Danish streams [11]. The presence of plants during summer meant an average increase of 7.5 cm in the water level, for a constant mean summer discharge, and in a few cases the increase was as high as 25–30 cm. The effect is most evident in mid-summer when the actual discharge is low. During high discharges and strong currents, the submerged plants bend over and are pressed towards the stream bed, and a large proportion of the water passes over the plants unimpeded. Amphibious and emergent plants in shallow water and on the banks are relatively stiff and remain resistant at increasing discharges and water levels.

The retardation of flow is highest along reaches with a dense plant cover and a modest downstream slope. No field measurements have addressed the effect of the different architectures of plant species and their spatial distribution on flow resistance. However, flume experiments and theoretical considerations lead to the suggestion that at a given biomass, submerged plants increase the water level most when they grow scattered across the stream bed and each shoot is freely exposed to the flow. When they are distributed in dense patches, mutual flow protection is possible among the shoots, and much of the water can pass unimpeded in the flow channels between the plant patches.

Plant species have a variable resistance to flow when they grow at low densities. Single shoots of stiff, ramifying species are more resistant to flow than flexible, streamlined species. These differences between species are less apparent at high shoot density within plant patches, because of mutual protection and shelter among the shoots. Stiff, ramifying shoots exposed to full-scale flow at the patch margin experience a substantial drag but these shoots also offer better shelter to downstream neighbours than flexible, streamlined shoots. As a consequence, the hydraulic resistance does not increase proportionally to the plant biomass as shoot density increases. Experiments in laboratory flumes show that flow resistance of the plants often increases 4 to 7 times as the biomass increases 10-fold (Figure 4.4). Moreover, the resistance of different species tends to converge towards a common value at high plant biomass and high water velocity. The plausible explanation for this behaviour is that species having a high flow resistance as single shoots exposed to low velocity will provide better shelter among neighbouring shoots when the biomass and velocity increase than species offering less resistance as single shoots.

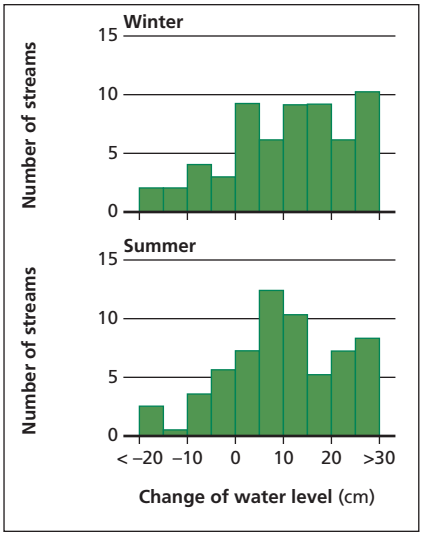


Figure 4.5 Directional change in mean water level during winter and summer in 65 Danish streams from 1976 to 1995. More streams have experienced an increase in water level than a decline [11].

Water stage and management

The introduction of more gentle management of large Danish streams, in the 1980s and 1990s, had the objective of reducing anthropogenic disturbance, diminishing cross section and increasing water level. In a study of 65 streams, 32 experienced a markedly higher water level for a given discharge, while 28 remained unchanged, and 5 experienced a marked decline in water level (Figure 4.5).

Streams developing a markedly higher water level have in several cases experienced a more gentle management regime. Increased water levels were for example observed in streams experiencing increased sedimentation and consolidation of the stream bed in the near-shore zone where the intensity of cutting and dredging had been reduced [13]. In several cases, however, it was difficult to establish unequivocally the reasons for an altered water level.

Plant patches

Stream plants commonly form a mosaic of individual plant patches across the stream bed. From year to year plant patches change position and different species may dominate. Plant patches diminish in size or disappear during the winter, after cutting or episodes of peak flow. They recover from surviving roots and rhizomes buried in the stream bed, or grow from seeds and drifting shoots being trapped by stones and other obstacles on the sediment surfaces [14]. A single shoot is capable of forming a patch of several square metres during the course of a few summer months. The daily linear expansion of patches is, for example, typically 0.3–2.0 cm for *Callitriche* (water starwort) and 0.5–4.0 cm for *Ranunculus* (water crow-foot) and *Sparganium* (bur-reed).

The disturbed environment together with the effective dispersal and the vegetative expansion of stream plants all contribute to forming the scattered mosaic of single-species patches. *Callitriche*, *Elodea canadensis* (Canadian waterweed) and *Ranunculus* form dense patches with a distinct margin, while *Sparganium* have long horizontal runners and form open patches. Reaches with unconsolidated sand sediments have a greater tendency to develop a patch mosaic than reaches with stable bottoms, the reason being that uprooting of new colonising shoots is more likely outside the established patches in reaches with unstable sediments. Plant patches stabilise the vegetated sediments underneath, while fast flow and erosion become concentrated in the flow channels between the patches.

Cushions of *Zannichellia palustris* (horned pondweed) in the Vindinge Stream.

Individual patches tend to behave as functional units. A single shoot often forms a large plant patch with a shape modulated by the current, while the patch generates its own characteristic flow and sedimentation pattern [15]. Studies of *Callitriche* have shown that patches become flatter and more streamlined with greater impact of the current. Viewed from above, the green canopy and the rooted area of exposed patches resemble an ellipse (Figure 4.6). A side-view shows the canopy as nicely rounded upstream and the height is often only 10–20% of the length in order to minimise form drag.

The elongated, streamlined shape is mainly observed in shallow (0.1–0.3 m) riffles where the flow is accelerated along the sides of the patches, and the shoots are pressed against the sedi-

Flowering bur-reed.

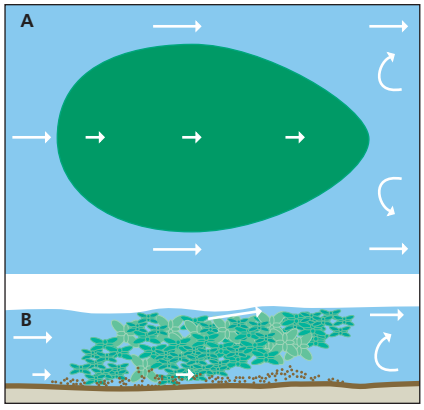


Figure 4.6 The most common shape of 50 plant patches of *Callitriche platycarpa* (various-leaved water starwort) found in small Jutland streams in the summer. The canopy is almost elliptical when viewed from above (A). From the side (B) the canopy appears flat and rounded upstream with a long unattached canopy trailing downstream. The green canopy covers a much larger area than the roots. Arrows indicate the direction and velocity of the flow [Sand-Jensen, original].

ment. The elongated shape is a result of daily growth rates of, for example, 1.5 cm in downstream direction in the shelter of mother shoots. Upstream growth rates against the flow are often close to zero and lateral daily growth rates from both sides may be 0.3 cm. With these growth rates a single shoot will form a 1.5-m long and 0.6-m wide patch in 100 days. In deeper reaches of slower velocity, flow can more easily pass above the patches which become higher and approach a circular shape because expansion can take place at the same rate in all directions.

Flow and drag in plant patches

The current generates drag in the green canopy of plant patches, while the roots keep these anchored. Shoots and roots must therefore develop a mutual balance between one another depending on the flow regime and the strength of anchoring.

There are three types of drag forces in streams (Box 4.3). Form drag is generated by pressure loss from the upstream exposed front of the canopy to the downstream part behind the canopy. Friction drag is due to friction between the moving water and plant surfaces. Lift is generated by the acceleration of water above the canopy surface. Form and friction drag act in the direction of flow, while lift acts upwards perpendicularly to the flow.

All three forces rise in proportion to the mass density of water and the square of velocity. Form drag increases in proportion to the frontal area facing the current, friction drag increases in proportion to the plant surface and lift to the projected area (Box 4.3). All these parameters are measurable and can be evaluated. Each force is influenced by an odd coefficient which depends on the shape of the canopy and the character of water movement around the entire patch margin and the individual shoot surfaces [2, 3].

The coefficient of friction drag (C_f in Box 4.3) declines with increasing velocity so that friction drag increases less rapidly than with the square of velocity; often in approximate direct proportion to the velocity. At increasing velocity the individual shoots and the entire canopy may become more compressed against the stream bed, thereby reducing the frontal area. Turbulence behind the plant patch may also change, but the width of the turbulent band and the pattern of turbulence (e.g. size and spatial distribution of vortices) are difficult to predict. The net result is that form drag increases at higher velocity with an exponent between 1.0 and 1.75 (i.e. a 10–56 times higher drag for a 10-fold higher velocity). In rare cases the exponent can exceed 2.0 (Figure 4.4). Because form drag is caused by pressure phenomena, while friction drag is the result of viscous forces, form drag will increase in importance relative to friction drag at increasing velocity and increasing size of organisms (i.e. at a higher Reynolds number). Because plants have a large surface area per plant biomass in order to absorb sunlight for photosynthesis, friction drag is never insignificant.

In very dense plant patches of *Callitriche*, much of the flowing water is diverted above and along the sides of the canopy, while the interior remains sheltered (Figure 4.7). As a result, form drag and lift are high for the entire canopy, but forces are concentrated at the exposed shoots at the canopy surface, while the shoots in the interior experience reduced forces. In contrast, the flow passes through the open cano-

Box 4.3 Drag forces

Flowing water generates three important dynamic forces: form drag (F_p), friction drag (F_f) and lift (F_L). The unit is Newton (kg m/s^2) and the equations are:

$F_p = 0.5\ \rho\ U^2\ A_f\ C_p$
$F_f = 0.5\ \rho\ U^2\ A_w\ C_f$
$F_L = 0.5\ \rho\ U^2\ A_p\ C_L$

where ρ is mass density of water, U is water velocity, A_f is frontal area of the object facing the current, A_w is the entire surface area of the object and A_p is projected area perpendicular to the flow. The three dimensionless coefficients are: C_p for form drag (1.0 for a flat plate facing the current, approx. 0.01 for the edge of the plate facing the current, and < 0.2 for streamlined objects), C_f for friction drag (declining at increasing water velocity and size of objects) and C_L for lift. Coefficients for certain geometric forms and organisms are found in [2, 3]. The coefficients should not be regarded as constants because they change with the character of the flow.

Form drag and friction drag act in the direction of the flow, while lift acts perpendicular to the flow. A fourth force, the acceleration force, is usually insignificant in streams because of small accelerations, while it is important for large objects on wave-swept shores in the sea and in lakes [2].

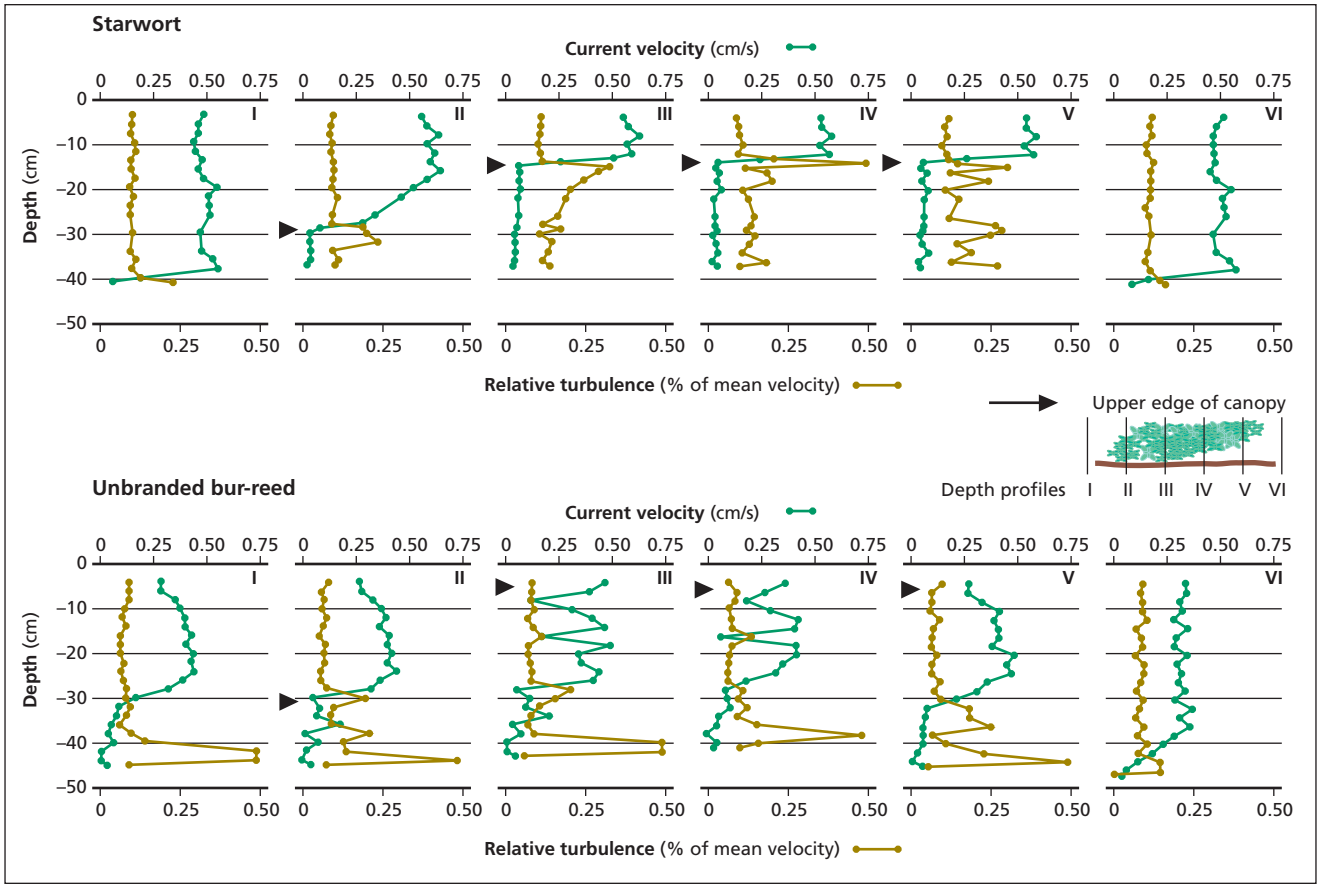
Small stream with localised patches of flowering *Ranunculus*.

pies of *Sparganium* at relatively high velocities (Figure 4.7) so that form drag and lift for the patch as a whole are low, while form drag is higher and more equally distributed among the individual shoots. It appears to be a suitable adaptation for *Callitriche* to have fragile, finely dissected shoots and streamlined canopies, and for *Sparganium* to have strap-formed, streamlined leaves and patches of a less streamlined shape.

As plant patches grow in size there is a parallel increase in the frontal area facing the current, the surface area viewed from above and the total surface area or volume. Studies on flow-exposed patches of *Callitriche* show that the sediment area covered by roots increases predictably with the size of canopy. On average, the frontal area increases sixfold and the total area 14-fold when the rooted area increases 10-fold (Figure 4.8). It is appropriate that the frontal area increases less than the rooted area, because larger patches tend to grow taller and are therefore exposed to higher velocities further away from the sediment than are small patches with shoots tightly compressed against the sediment. That the development of shoots and roots are in fact well adjusted appears from the fact that patches located in the shelter close to banks and behind turns develop more shoots as compared to roots than patches freely exposed to the current in the middle of the stream.

Flow and the individual

The influence of flow on individuals is two-sided. On the positive side, flow continuously supplies new, fresh water and reduces the laminar sublayer surrounding the surfaces of organisms and, thereby promoting the exchange of gases and solutes with the surrounding water [18]. At low concentration levels of dissolved nutrients, CO_2 and oxygen in the water, the biological uptake increases at gradually higher concentrations until saturation is achieved. This point of saturated uptake is reached at gradually lower external concentrations as the water velocity increases (Figure 4.9). The response is logical, because the biological uptake rate increases in proportion to the steepness of the gas and solute gradients across the laminar sublayer. Great differences in concentration between the free water and the surface of organisms and the thinner laminar sublayer will both lead to steeper gradients and promote the uptake. Thus the risk of suffocation of fish and invertebrates by oxygen depletion is highest when low oxygen concentrations and low water velocities coincide.



On the negative side, flow generates a physical disturbance, which can induce metabolic stress and a greater risk of being transported downstream with the current or being crushed or buried below moving sediment particles. The metabolic stress may be costly due to energy investment in greater basal respiration.

In order to balance the advantages and disadvantages of the flow, species have evolved adaptations that allow adjustment of their morphology, anatomy, habitat selection and behaviour. For example, when oxygen supply to invertebrates becomes critically low, the invertebrates can select the most elevated and exposed parts of the stream bed with the highest velocity. Some species can actively enhance ventilation by moving the gills or the abdomen or by moving legs and toes rapidly to push the body up and down [4].

The flapping movements of leaves and stems of submerged plants will enhance respiration. In response to these movements, the plants tend to grow more slowly, develop smaller cells with thicker walls, and form more robust shoots with shorter, denser and

Figure 4.7 Current velocity and relative turbulence in patches of *Callitriche cophocarpa* (starwort) and *Sparganium emersum* (unbranched bur-reed) were measured in depth profiles along the mid-axis from upstream (I) to downstream of the patches (VI). Arrows mark the upper edge of the canopy. Redrawn from [16, 17].

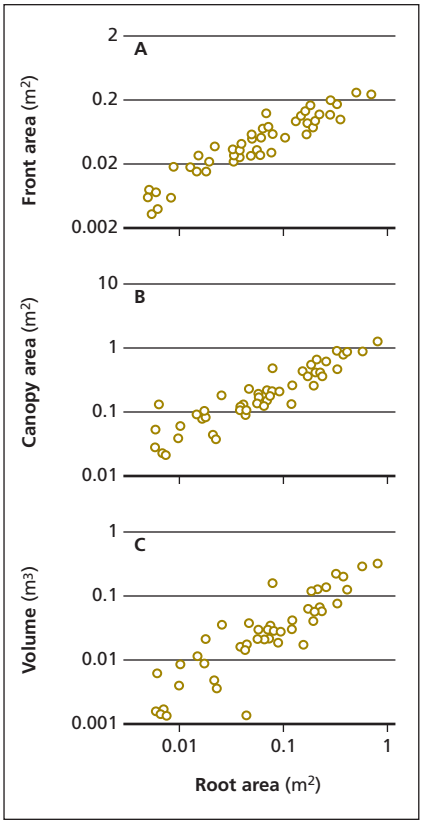


Figure 4.8 Relationship between size of the green canopy and the surface area of root anchoring of 50 patches of *Callitriche cophocarpa* in small Jutland streams during summer. Front area facing the current (A), canopy area as seen from above (B) and volume occupied by the canopy (C) [Sand-Jensen, original].

stiffer leaves. However, the most recent studies suggest that stream plants are capable of maintaining growth at relatively high velocities, probably because the flow is relatively predictable in both direction and velocity. If the plants are exposed to a very variable flow regime (e.g. a short daily peak velocity), growth is further inhibited.

Adaptation to rapid flow and disturbance

Plants and animals adapt to high velocity by reducing or resisting the impact. Common adaptations include: 1) streamlined shape, 2) small frontal area, 3) compression against the substratum, 4) large anchoring surface, and 5) high anchoring strength. Not just one, but several possible adaptations and combinations involving different advantages and disadvantages are observed.

In the case of the plants, a compact form and compression against the substratum reduce drag forces, but also the exposure to the surrounding water and to incoming light makes it harder to obtain the necessary resources for growth. If the canopy is instead freely exposed to the water and composed of thin tissue, it is easier to sequester the necessary resources, but the risk of excessive drag will require streamlining, efficient anchoring and resistance to breakage of the shoots. *Ranunculus*, for example, grow freely exposed to rapid currents which are tolerated because of streamlined, capillary leaf filaments, strong, flexible stems and long roots that wind around stones and cobbles. In shallow water with very rapid flow, the *Ranunculus* shoots become shorter to reduce drag, and the patches become anchored along most of their length.

Many stream invertebrates are flat and able to adhere closely to the substratum and they have strong legs and claws. Several species have characteristic positions or postures that reduce drag and ensure down force. Among some species of snails, the "foot" grows relatively large and the anchoring strength in rapid flow increases as compared with species living in

Beautifully sculptured patches of starwort.

streams with slow flow. Blackflies have exceptionally strong anchorage because they spin a net to the surface and attach to it by means of hooks on the base of their abdomen [4].

A traditional belief among stream biologists has been that the compressed body shape of invertebrates allowed these to live safely and sheltered within the laminar sublayer immediately above the substratum (Box 4.4). However, the animals are often much higher (2–5 mm) than the expected thickness of the laminar sublayer (e.g. 0.1–0.5 mm) and in rough turbulent flow the laminar sublayer does not exist at all and animals are exposed to high velocities and turbulence. The animals can cling to and press themselves against the substratum and thereby control and resist the form drag and lift caused by the current, but they cannot eliminate or avoid the forces at exposed solid surfaces.

Despite the adaptations, the organisms experience strong disturbances during peak flow. The risk of mortality is greatest when the stream bed is eroded and set in motion. The plant and animal life in streams therefore alternate between episodes of substantial loss and longer, calmer periods of recolonisation and reestablishment. The dynamic conditions for attached microalgae, whose biomass declines steeply during storm flow events and increases gradually during periods of low disturbance and suitable growth conditions, have been most extensively documented.

Documentation from New Zealand streams shows that species richness of benthic invertebrates depends on the frequency and extent of physical disturbance generated by peak flow [19]. The studies support the intermediate disturbance theory predicting that species richness is highest at intermediate disturbance. At very high disturbance only a few very robust species survive, and at low disturbance the competitively superior species have the sufficient time to out-compete the weaker species during the extended stable periods (Figure 4.10). The species richness of aquatic plants in English canals also appears to exhibit the maximum species richness at intermediate disturbance, although differences are relatively small between sites of low and intermediate disturbance [20].

Because intermediate water velocities are optimal for metabolism and intermediate disturbances are optimal for species richness, it appears that a compromise is the ideal situation here as it often is in nature and life in general.

Box 4.4 Turbulent or laminar flow

It was previously believed that benthic invertebrates always experienced laminar flow. This is probably the case when they live deeply buried in sediments or in non-ventilated burrows. Exposed at the sediment surface, however, they experience significant velocities and turbulence. Turbulent flow means that flow at a given point changes direction and velocity with time due to passage of vortices. Turbulence allows a greater supply rate of oxygen to animals, while the drawback is a greater physical impact and risk of drift with the current.

Flow was earlier believed to be laminar through plant patches. Water velocities within dense, free-standing plant patches often decline to 10–20% of the unrestricted velocity outside the patches [17]. The smallest velocities were about 2 cm/s within canopies of *Callitriche cophocarpa*. At a characteristic linear dimension of 1 cm for the flow within the canopy (e.g. the size of *Callitriche* leaves or the distance between the leaves), the estimated Reynolds number is 200. Nonetheless, the flow remained turbulent at an intensity of more than 0.2 cm/s (standard deviation of velocity). The intensity of turbulence increases linearly with mean velocity both in the free water and between the plants, but turbulence intensity relative to mean velocity was enhanced 1–4 cm above the sediment and canopy surfaces where flow is strongly retarded (Figure 4.7). Pressure differences and leaf movements are regarded as important for maintaining turbulence, despite low velocities in the cm-sized linear dimensions within canopies. It is likely that water velocity and turbulence are sufficiently reduced within dense plant patches to permit the development of laminar sublayers immediately above plant surfaces.

Figure 4.9 Metabolism of aquatic organisms commonly increases at higher external concentration and current velocity until saturation is reached. The ideal relationship applies to photosynthesis, growth and uptake of nutrients and inorganic carbon of plants and respiration of animals.

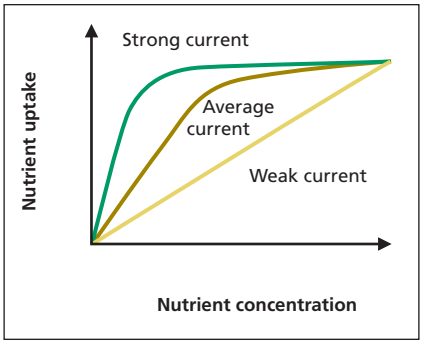
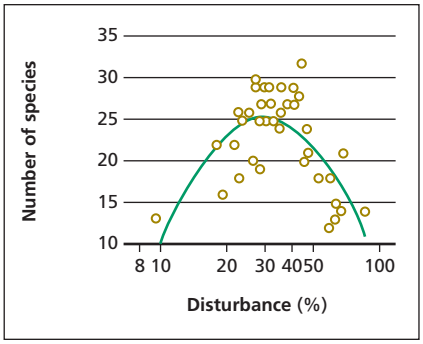
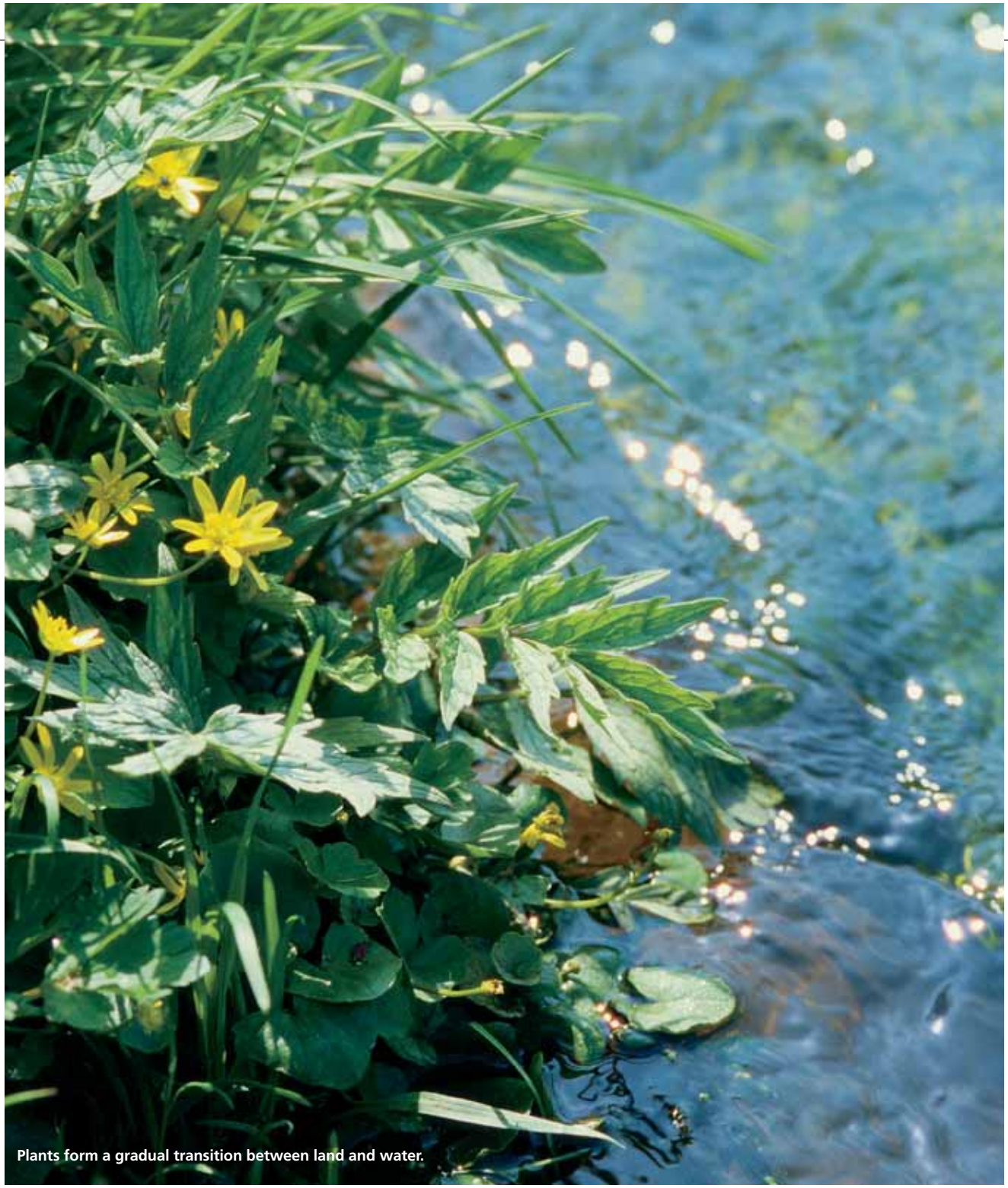


Figure 4.10 Species richness of invertebrates in New Zealand streams as a function of the proportional area of the stream bed set in motion at peak velocities. Maximum species diversity is observed at medium disturbance. Redrawn from [19].





Plants form a gradual transition between land and water.

5 Aquatic plants

Aquatic flowering plants form a relatively young plant group on an evolutionary timescale. The group has developed over the past 80 million years from terrestrial flowering plants that re-colonised the aquatic environment after 60–100 million years on land. The exchange of species between terrestrial and aquatic environments continues today and is very intensive along stream banks. In this chapter we describe the physical and chemical barriers to the exchange of plants between land and water.

Broad-scale patterns

Unique characteristics of streams and rivers are the unidirectional flow of water and the intimate contact with the surrounding terrestrial ecosystems. Assuming an average width of Danish streams of one metre, the riparian contact zone is an estimated 130,000 km or close to 3 km bank per km^2 of land. Across this transition zone between land and water is an intense flow of water with its content of dissolved and particulate inorganic and organic matter.

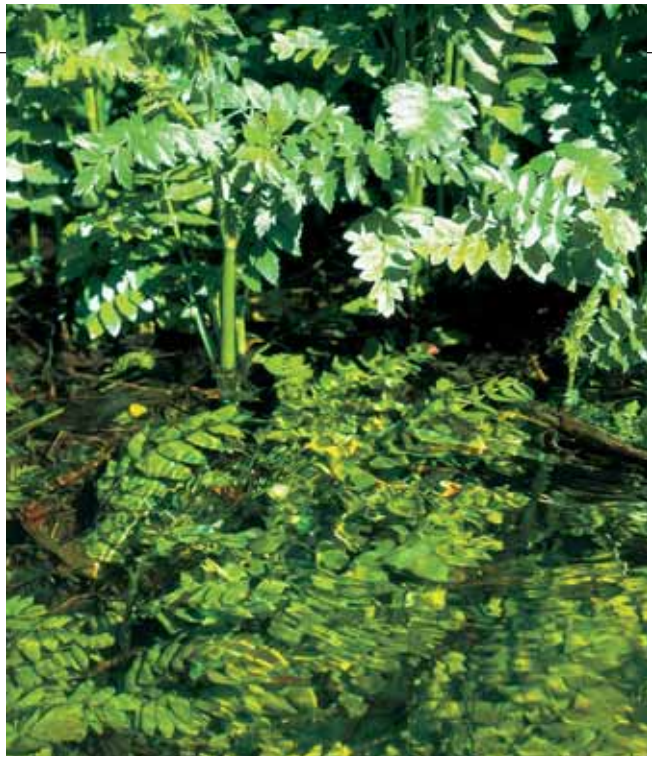
The dense animal and plant populations in the riparian zone allow an active exchange of species between the two environments. A well-known example is the dipper – a bird that forages on invertebrates under water, but otherwise lives on land. Many insects live in water during the juvenile stages, whereas the adults live on land, only to return to water to lay their eggs. Among plants, many terrestrial-aquatic transitions also exist. Some species live submerged, but raise their flower stalks up above the water surface during flowering and pollination. Other species have runners that grow from land to water to establish submerged populations. And yet others are essentially terrestrial plants that grow submerged when the water table is high.

The fact that plant species can move from one environment to another, in this case between land and water, makes it difficult to quantify the number of genuine water plants. The Danish flora contains about 1,265 species of flowering plants [1]. Of these, about 50 species are truly or obligate submerged plants with permanently submerged shoots, 55 species are amphibious species with the ability to grow submerged as well as emerged and 75 species are terrestrial plants that can survive submergence for shorter or longer periods (months), but can never form permanently submerged populations or develop distinct water forms (Table 5.1).

If we expand our time span and consider the aquatic flora from an evolutionary perspective, our impression of the riparian zone as an area with

	Number of species
Primary aquatic plants	51
Amphibious plants	55
Temporarily submerged terrestrial plants	75
Danish plants – in total	1,265

Table 5.1 Number of species of the various plant growth forms in the riparian and submerged zone of Danish streams.



***Berula erecta* is an amphibious plant that looks the same on land as under water.**

intense flow of plant species from one environment to the other is confirmed. Terrestrial plants are believed to have evolved from a group of freshwater green algae that colonised terrestrial habitats 300–400 million years ago and diversified under variable terrestrial conditions. One result of this diversification and evolutionary development was the flowering plants. During the past 80 million years several of these plants have recolonised aquatic habitats, and their descendants constitute the majority of the plant species currently inhabiting streams and lakes.

Irrespective of the time span, colonisation of aquatic habitats requires adaptation by the plants to the physical, chemical and biological conditions prevailing in the aquatic environment. In this respect, it is a general belief that water is an unfavourable environment for plant growth, and that this is the reason for the rather low species richness observed in freshwater habitats. We believe, however, that this view is unbalanced, as the plants will have both advantages and disadvantages from growing submerged, in the same way as they have advantages and disadvantages from growing on land. Thus, while some environmental factors might constitute a barrier to the colonisation of a new environment, other parameters may be more beneficial to plant growth. In line with this view, it should be noted that the

Aquatic *Ranunculus* species produce beautiful white flowers in air above the water where they are pollinated by insects.

Several terrestrial plants can sustain short periods of submersion.

species richness in freshwater habitats is not particularly low, considering that terrestrial habitats cover an area that is about 50 times larger than that of the aquatic habitats, and that only a small fraction of aquatic habitats is actually populated by plants.

We will consider the various factors to which plants have to adapt, and to assess the importance of barriers for the colonisation of aquatic habitats by terrestrial plants, that might be of importance. We define a barrier as a factor when it prevents plants from growing, unless they show specific traits that allows growth despite the negative impact of the specific factor.

There are two types of important factors affecting colonisation and plant growth in aquatic habitats. One type comprises the resources needed directly for growing, i.e. light, inorganic carbon, oxygen and minerals. The other type comprises factors that affect plant growth more indirectly by influencing plant metabolism without acting as resources. Among the indirect factors are temperature and other physical and chemical parameters (e.g. oxygen, pH, phytotoxins). For stream plants in particular, the moving water is of great importance for growth and distribution.

The force of the moving water can be vigorous and may up-root or prevent establishment of plants on the stream bottom. Establishment is prevented either because the plants are broken by the force of the water or because the rough substratum with gravel and stones, which is a result of a high flow velocity, is unsuitable for rooted plants. These aspects are discussed in more details in other chapters and will not be considered here. We will focus on resource limitation and acquisition.

Light and minerals

Light availability is restricted in aquatic habitats as compared to terrestrial systems due to reflection from the water surface and a high light attenuation by water with its content of dissolved and suspended material. Despite this loss, however, light is hardly a significant barrier to plant colonisation of aquatic habitats. First, aquatic plants grow close to the surface where irradiance is reduced by only a few percent (10–15%) relative to irradiance above the water. Growth is only prevented if the irradiance above the water is low, as in forests, or the light is restricted due to intense shading from the banks. Second, acclimation and adaptation to low irradiance is a common phenomenon among terrestrial plants and consequently among the predecessors of aquatic plants. A good example is the herb and understory vegetation in forests.

Terrestrial plants adapt to low irradiance by reducing biomass allocation to non-photosynthesising tissues, and thereby reducing respiratory costs. As a result, shade-adapted plants often have thin leaves, low root biomass, a low root:shoot biomass ratio, and less structural tissue in stem and leaves than sun-plants. These strategies can be fully exploited by aquatic plants. In fact, reduction in structural tissue may be more readily achievable for aquatic plants than terrestrial plants due to the high buoyancy in water.

Although light may not constitute a significant barrier to plant colonisation of aquatic habitats, light is still a very important factor that regulates plant growth and distribu-

Box 5.1 Nutrient supply to aquatic plants

For plants the main source of mineral nutrients is the sediment, while the incorporation of nutrients in organic matter often takes place in leaves and shoots. As a result, the nutrients need to be transported from the roots to the leaves. In terrestrial plants the nutrient are carried in the transpiration stream, which is a flow of water from root to shoot driven by evaporation from the leaf surfaces. Evaporation "sucks" water from the hydro-soil through roots and stem to the leaves and finally releases it to the atmosphere as water vapor.

Evaporation is not possible in submerged macrophytes. However, these plants still have a need for nutrient transport from roots to shoots. The transport can take place by diffusion from cell to cell in short plants, but for tall plants this process is much too slow. Research shows that aquatic plants are able to build up a root pressure sufficient to drive a significant flow of water up through the stem of the plants to the leaves. At the leaf rim the water is exuded through specialised pores called hydathodes.

It is technically difficult to measure the root pressure in aquatic plants. But preliminary measurements show that pressures above 0.3 kPa are attainable. Measured flow of water varies among species from 0.2 to 3.5 ml/g plant per day. These rates are sufficient to cover the need for nutrients under most natural conditions [2].

tion. Thus, in Danish streams no rooted plants are found at water depths above approx. 1.7 m due to lack of light.

With respect to nutrient acquisition it is likely that adaptation to nutrient-poor or nutrient-rich conditions evolved prior to the return of higher plants to the aquatic environment. And there is no reason to expect the availability of nutrients to differ significantly between aquatic and terrestrial environments. An assessment is difficult, however, and has to include not only a comparison of nutrient concentrations in the two environments, but also physiological and spatial aspects.

Terrestrial plants acquire nutrients through their roots and the nutrient ions are carried from roots to leaves by water transported in the vascular system driven by transpiration from the leaf surfaces.

In the aquatic environment the water flow driven by transpiration is blocked since transpiration is absent. However, there is still a significant transport of water driven by root pressure (Box 5.1). The flow rate is lower than flow driven by transpiration, but calculations have shown that the flow is sufficient to meet the nutrient requirements by the plants. In addition, submerged aquatic plants have the capability to acquire nutrients from the bulk water surrounding the leaf.

For rooted plants in Danish streams, studies conducted so far indicate that the availability of nutrients is sufficient to saturate growth. This conclusion is based on measurements of tissue concentrations of the most critical nutrients [3] and on field experiments where the availability of nutrients was enhanced by spiking water and sediment. The ample supply of nutrients in Danish streams results from high concentration in both water and sediment. Nutrient availability in the sediment is further enhanced by sedimentation of fine particles within the dense plant patches typical of most aquatic plants species growing in streams.

Oxygen and carbon dioxide

Light and nutrients do not appear to constitute significant barriers to plant colonisation of aquatic habitats. So the dogma that aquatic habitats are unfavourable to plant growth must rely on the availability of the metabolic gases oxygen and carbon dioxide.

Oxygen is essential in the breakdown of organic matter in respiration, and carbon dioxide is the substrate in photosynthesis and the carbon source used in synthesis of organic matter.

Carbon dioxide is easily dissolved in water and when air and water are in equilibrium, the concentration of carbon dioxide in air is almost equal to that in water (approx. 16 mmol/m^3 at 15°C). Oxygen is less soluble and the concentration in water is about 30 times lower than in air when in equilibrium (320 mmol/m^3 in water compared to 9,400 mmol/m^3 in air at 15°C).

The solubility of gases plays only a minor role in the regulation of plant metabolism, however, since all physiological and biochemical processes in the plants take place in solution in the cell sap. What is more important is the 10,000 times lower diffusion rate of gases in water compared to air. As a consequence, the diffusion of gases across the layer of stagnant air or water surrounding the leaf surfaces (the diffusive boundary layer) is substantially lower in water compared to air. The effect is greatest at low flow velocities,

Plants form dense stands in the riparian zone between land and water.

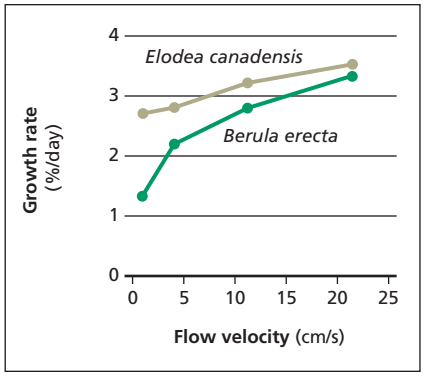


Figure 5.1 Flow velocity has a marked positive influence on the growth rate of submerged aquatic plants. ***Elodea canadensis*** (brown curve) and ***Berula erecta*** (green curve). [J. Bagger, unpubl.].

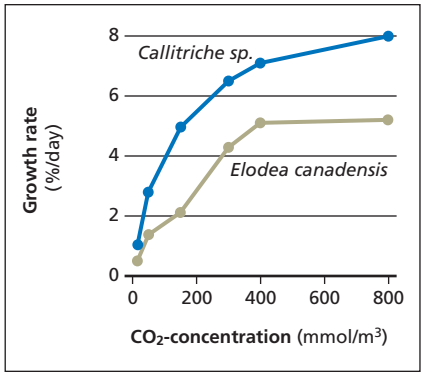


Figure 5.2 The growth rate of submerged aquatic plants is often limited by the availability of carbon dioxide in the water. Limitation is greater for ***Callitriche*** (only capable of using carbon dioxide) than for ***Elodea*** (able to use bicarbonate in addition to carbon dioxide). ***Elodea canadensis*** (brown curve) and submerged form of ***Callitriche sp.*** (blue curve) [T. Madsen, unpubl.].

where the thickness of the boundary layer is greater (Chapter 4). Thus, rates of photosynthesis measured in the laboratory on leaves or shoots of submerged water plants increase with increased flow velocity until a maximum is reached at velocities of 1–5 cm/s [4, 5]. At velocities above this range, the rate of photosynthesis once again declines, presumably due to the physical stress imposed by the fast-moving water. The optimal flow velocity for photosynthesis is comparable to flow rates measured in plant patches in streams (approx. 0.5–3.5 cm/s) [6].

Flow is expected to affect isolated leaves and shoots differently than plants growing in dense plant stands, where the complex architecture of the plants will modify flow conditions close to the leaves. As a consequence, laboratory experiments of the type described above cannot be extrapolated to field conditions without critical assessment. In line with this, growth experiments in the field using intact shoots have shown an increase in growth rate with flow velocities up to 20 cm/s (Figure 5.1). This result indicates that the supply of carbon dioxide to the leaves under natural growth conditions might be of great importance as a growth-regulating factor (Figure 5.2).

For plants in the riparian zone the low supply of carbon dioxide in water might constitute a barrier to colonisation of the aquatic environment. Therefore, species that can ameliorate the limitation by carbon dioxide will have a competitive advantage over species lacking this ability. Two acclimation strategies seem prevalent among aquatic plants. One strategy diminishes the importance of the boundary layer, and the other allows the plants to exploit other inorganic carbon sources in addition to carbon dioxide. The first strategy is discussed in more details below, the other in the next section.

The thickness of the boundary layer is dependent on the actual size of the leaf and increases with the length of the leaf, measured in the direction of the flow. No systematic studies of leaf sizes of aquatic and terrestrial plants have been performed. However, it is generally believed that submerged plant species have small or dissected leaves. It is also a general trait that the leaves of submerged plants are very

Rorippa amphibia **(Great Yellow-cress) is an amphibious plant that grows along the banks of slow-flowing streams and rivers.**

thin, often only two to six cell-layers thick (Figure 5.3). Leaf thickness has only a very limited effect on the thickness of the boundary layer, but the lower number of cells per unit leaf-surface area reduces the number of cells that have to be supplied with carbon dioxide through that surface.

The cuticle, a continuous waxy film on the external surface of the leaves, is thin and is expected to be highly permeable in aquatic plants. The cuticle protects terrestrial plants from water loss. This advantage might turn out to be a disadvantage to submerged plants, because the low permeability of the cuticle to water vapour probably also makes it less permeable to other gases like carbon dioxide. However, if the boundary layer is thick, the resistance to gas flow added by the cuticle might be of minor significance. On the other hand, in a situation with swift flow and thereby a thin boundary layer, the resistance imposed by the cuticle might be of importance. A thin and highly permeable cuticle is not necessarily an advantage to amphibious or temporarily submerged terrestrial plants. They will benefit, of course, when submerged, but will suffer when they become emerged during periods with a low water table. And since amphibious plants often grow close to the bank, it is most likely that they, in an unpredictable manner, are submerged during some periods and emerged in others. When the plants become emerged they will suffer from extensive water loss due to evaporation and risk dehydration and wilting if the cuticle is highly permeable to gases.

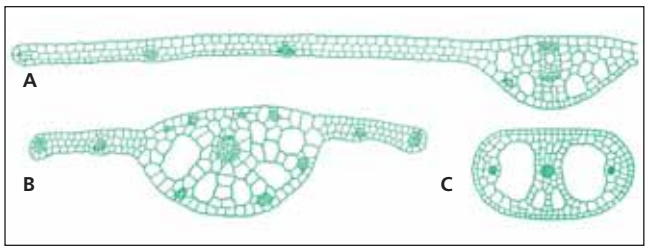


Figure 5.3 Most aquatic plants have submerged leaves that are only 2–6 cell layers thick. Cross sections of leaves of A: *Potamogeton pusillus*, B: *Potamogeton trichoides* and C: *Potamogeton pectinatus*. After [1].

Bicarbonate use

All obligate submerged plant species, with the exception of the bryophytes, have the ability to use bicarbonate in addition to carbon dioxide. The ability to use bicarbonate gives the plants access to an inorganic carbon pool that is up to 100 times larger than the carbon dioxide pool (Box 5.2). However, the physiological and ecological advantages are less than may be indicated by the quantitative difference in pool size, because the affinity for bicarbonate is 2–10 times lower than the affinity for carbon dioxide [7, 8]. Despite the obvious advantage of possessing the ability to use bicarbonate, no amphibious species able to use bicarbonate have been discovered yet.

Amphibious and terrestrial plants species are confined to carbon dioxide use when submerged. The affinity for carbon dioxide is rather low in these species and it appears that the success of these plant groups in colonising aquatic habitats is dependent on the often very high carbon dioxide concentrations in streams. When air and water are in equilibrium with respect to carbon dioxide, none of the

species are able to grow. If the concentration of carbon dioxide in the water increases 10-fold, which is comparable to the average concentration in Danish streams, the growth rate is high and comparable to the rate of obligate submerged species. Upstream and downstream variation in the concentration of carbon dioxide might, therefore, be a factor regulating the distribution of amphibious plant species.

Oxygen supply

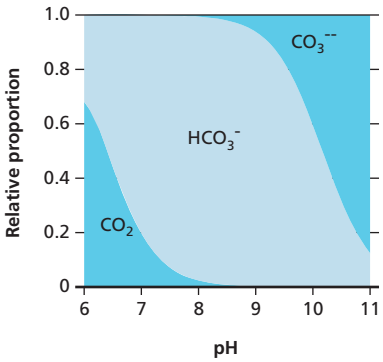
The transport mechanisms of oxygen in water and the restriction on supply rates are similar to those of carbon dioxide. However, the demand for oxygen by the plants is lower than the need for carbon dioxide. As a result, the supply of oxygen to leaves and stems of submerged macrophytes is generally sufficient to cover the demands.

The oxygen supply to roots of submerged plants is a quite different story. The characteristics of the soil change dramatically in the transient zone between land and water. On land a large number of the pore spaces in the soil are filled with air, and the supply of oxygen to roots of terrestrial plants is good. In contrast to this, the pores of stream sediment are filled with water and are usually anoxic – except from the uppermost few millimetres. As an adaptation to the lack of oxygen in the sediment, many submerged plants have a well-developed system of air-lacunae in shoots and roots that allow diffusion of oxygen from the shoot to the roots. If the supply of oxygen is insufficient the roots will die, and this will have a negative impact on the anchorage ability of the plants and thereby on the ability to develop persistent populations.

Box 5.2 Inorganic carbon in water

Inorganic carbon exists in water as: dissolved carbon dioxide (CO_2), bicarbonate (HCO_3^-), and carbonate (CO_3^{--}), in a series of equilibria that are controlled by pH (see figure). The total pool of inorganic carbon in water is the sum of the three forms. The concentration of inorganic carbon in water is mainly dependent on the geological conditions in the catchment area. High concentrations are found in areas with calcareous soils, and low concentrations are found in areas with sandy soils.

The pH of Danish streams varies between 6.5 and 8.5 and the predominant inorganic carbon form is bicarbonate (see figure).



Distribution of inorganic carbon species in water as a function of pH.

The low diffusion rate of gases in water presents the submerged plants with another problem not encountered by terrestrial plants. The low diffusion rate restricts the rate of gas exchange between the water and the air above. As a result, the oxygen released during photosynthesis might accumulate in the water to concentrations up to two times the concentration achieved when air and water are in equilibrium. High oxygen concentrations will have a negative impact on photosynthesis by partly impeding ribulose-bisphosphate-carboxylase-oxygenase, one of the key-enzymes in carbon dioxide fixation. As a result, rates of net photosynthesis might be severely restricted in streams developing oxygen supersaturation.

Conclusion

The most important barrier to the colonisation of aquatic habitats by plants is the low availability of carbon dioxide and oxygen in water compared to air.

The low availability of carbon dioxide, in particular, makes the aquatic environment unsuitable for plant growth unless the plants employ mechanisms that allow access to alternative carbon pools or they grow at sites with carbon dioxide concentrations well above air-equilibrium concentrations. Small lowland streams are an example of the latter. Thus, the active exchange of plant species across the transition zone between stream and land, over both short and long time spans, is probably more a result of particular physical and chemical characteristics of the aquatic habitats than a result of specific plant traits. When first colonised, a more general adaptation to the aquatic environment may then have developed. However, high carbon dioxide in the water is most likely a necessity for the existence of species growing in the transition zone between land and water.

The beautiful damselfly *Calopteryx virgo.*

6 The terrestrial life of stream-dwelling insects

Whereas the biology of the aquatic stages of lotic insects is well studied, detailed knowledge about the activities during their terrestrial life is scarce. These activities include feeding, mating, and ovipositioning. Adults disperse and may thereby colonise not only other parts of the natal stream, but also neighbouring or more distant streams. Together, all these activities are vital for the survival of populations and species. Moreover, adult aquatic insects play an important role in terrestrial food webs. Therefore, there are good reasons for focusing on the riparian zone and other parts of the terrestrial environment when attempting to restore the former quality of anthropogenically destroyed streams.

Life in two different environments

The insects probably developed 400 million years ago. The early ancestors were terrestrial, though aquatic groups appeared already 290 million years ago. Early mayflies (Ephemeroptera) are known from 286–245 million year-old fossil records, but aquatic groups as we know them did not appear until between 66 and 2 million years ago.

Thus, although the insects seem to have had plenty of time to adapt to and explore the aquatic environment, they have not totally given up adaptations to the former terrestrial life. Generally, they leave the aquatic environment in the adult stage of their life cycle. This is true even for elminthid and dytiscid beetles (Coleoptera) that pupate in moist soil along streams and lakes even though their larval and adult stages are truly aquatic. These beetles together with several aquatic bugs may occasionally disperse over land by flying in order to colonise suitable aquatic habitats.

Insects constitute a very important part of macroinvertebrate assemblages in Danish and other European streams. Especially rich in species are midges, flies (Diptera) and caddisflies (Trichoptera), but also mayflies, stoneflies (Plecoptera) and various beetles are relatively rich in species. Moreover, several species are widely distributed and high in abundance, often constituting a major part of the macroinvertebrate fauna. They are therefore well studied. We know a great deal about the immature stages, including life cycle, feeding mechanisms, growth, distribution, abundance and relations to other species or individuals of the same species. However, our knowledge about the life of aquatic insects outside the "wet" environment is quite limited.

Communication of adult insects

Stream-dwelling insects leave the aquatic environment in order to start the next generation. The sexes need to locate each other, to mate, and the

Box 6.1 Swarming in adult insects

The males of several adult aquatic insects (e.g. mayflies, caddisflies, midges) attract females by forming swarms. Swarming takes place at particular sites – markers – in the landscape or above the water surface. Markers may be bushes or trees, often located on a hilltop. Each species has its individual swarming pattern (e.g. lateral zigzag movements, vertical circles or ellipses, mixture of horizontal and vertical movements), here illustrated by different caddisflies (Leptoceridae and Hydropsychidae). One or a few males normally initiate swarming, whereupon they are joined by other individuals, sometimes forming dense clouds. In Hydropsychidae, males initiate swarming by excreting simple chemical substances. Illustration partly adapted from [1].

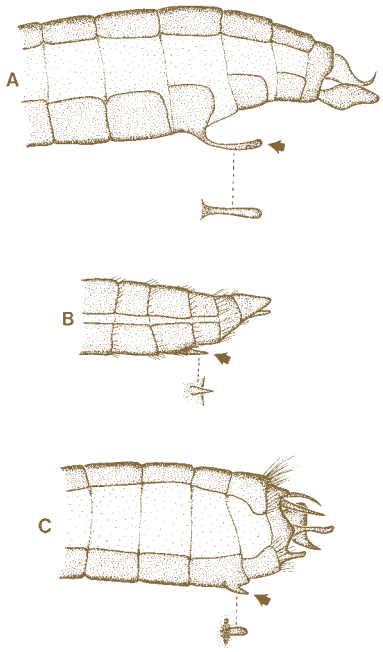
Many males of caddisflies perform a special flight – swarming – to attract females. Patterns and places of swarming are specific for each species.

females to oviposit at an appropriate site. The behaviour of each species during these processes varies considerably, implying that different species have different demands of the terrestrial environment.

Several communication methods are used in order to find the opposite sex. Particularly well known is the male swarming of mayflies, some families of caddisflies and dipterans (e.g., Chironomidae). Swarms of males attract females that fly into the swarms where they are seized by the males, and the couples then leave the swarm to mate (Box 6.1).

Several caddisflies use chemical communication. Females release species-specific pheromones to attract males. Such pheromones are found in the most species-rich group, Limnephilidae, and are apparently active over relatively long distances. Male limnephilids are more active than females in their search for the opposite sex, which may explain why significantly more males than females are usually caught in light traps.

Communication by sound signals is used in several groups of terrestrial insects (e.g. caterpillars, cicadas), but for decades it has also been recognised that male and female stoneflies communicate by tapping signals. These signals are typical for each species, and it even seems that there are "dialects" among populations. Just recently, the use of vibrational communication has been recognised in several families of caddisflies (e.g. Glossosomatidae, Hydroptilidae, Beraeidae) [2]. There are several different types of signals such as drumming, scraping, tapping, and knocking. The insects produce the sounds by moving the abdomen, with its sternal projections located on segments VI-VIII (Figure 6.1), against a selected substrate (stems, branches, twigs etc.). In some situations the sounds are produced by wing flapping or vibration of the entire body.



Adult stonefly (*Brachyptera risi*) feeding on algae and lichens on a tree trunk.

Figure 6.1 Abdomen of males of different adult caddisflies (lateral view). Sound signals are produced by beating the remarkable protuberances (see arrow and details in ventral view) against a suitable substrate. A: *Agapetus fuscipes*. B: *Ithytrichia lamellaris*. C: *Beraea pullata*.

The duration of the adult stage varies considerably among species, families and orders. Mayflies are especially short-lived and live for a few hours to a few days. The adults are unable to feed and are therefore completely dependent on energy reserves accumulated during the immature stages. This is also the case for short-lived members of other orders. Some species of caddisflies, alderflies (Megaloptera), and midges (Chironomidae) feed on nectar or honeydew excreted by aphids (Homoptera), which enables them to extend their lifespan, although the food is not necessary for the production of eggs. In contrast, female *Brachyptera risi* (Plecoptera) feed on algae, fungi etc. and increase their body weight about four-fold due to the production of eggs [3]. Also the blood-sucking behaviour of female blackflies (Simuliidae) is important for their egg production, although a smaller number of eggs may be produced in the absence of a proper vertebrate blood meal. Feeding thus extends the lifespan of adult insects, probably increasing their potential for dispersal, but also making them more dependent on suitable shelter against bad weather and predators. The prolonged lifespan of *B. risi* and the limnephilid *Micropterna sequax* enables these species to overcome the regular problem of streams drying up during summer, as they can colonise when these streams are flowing again in autumn. In *M. sequax* the lifespan is prolonged by the adults going into diapause during summer, e.g. hiding in crevices beneath the bark of trees.

Malaise traps (tents of black, finely meshed nylon net) are well suited for studies of lateral dispersal of adult aquatic insects. The insects are led to a capturing container placed in the upper corner of the trap.

Many stream insects do not choose the oviposition site by random. The females of some blackfly species are undoubtedly able to recognise a suitable spot. *Eusimulium vernum* only deposits its eggs in forest brooks, whereas *Odagmia ornata* prefers open reaches, even if these are just glades in a forest [4]. Safely arrived at a proper stream site, the female will often choose an especially suitable site to oviposit. Megaloptera and several caddisflies (especially limnephilids) place their egg masses on branches, twigs and other objects that overhang the water surface. Newly hatched larvae will then drop into the stream. Other females of certain mayflies and caddisflies may crawl or swim into the stream water to oviposit on dead wood, stones, and aquatic plants, while other females are rather unselective when they deposit their eggs on the water surface.

In forest regions close to streams the aquatic insects may represent a large proportion of the fauna. At sites located 5 and 150 m from a stream in a northern California forest, adult aquatic insects represented 37% and 15%, respectively, of the total arthropod number, and 25% and 11% of the biomass [5]. It is also well known that several terrestrial animals including bats, birds, spiders, and predatory insects eat adult stream insects. Thus, the mortality of the mayfly *Dolania americana* at a Pennsylvania forest stream increased with both increasing densities of a predatory ground beetle and with decreasing densities of alternative prey items [6]. Many aquatic insects die during their terrestrial life. It is estimated that only about 3% of adult stream insects survive to return to their native stream. In this way, aquatic insects may contribute significantly to terrestrial food webs, and thereby to the turnover of organic matter and nutrients in this environment.

Does an organised upstream flight take place?

In the mid-1950s, Karl Müller proposed the existence of a colonisation cycle among stream insects [7]. Females were supposed to actively fly upstream to deposit their eggs in order to compensate for the steady loss of their immature stages by drift with the flowing water that would otherwise lead to the eventual extinction of upstream populations. This idea is intriguing and has been promoted as a well-established fact, not least with the support of Danish studies of the behaviour of mayflies and stoneflies [8, 9]. However, there is evidence that organised upstream flight is far from universal among stream insects [10]. First of all, there are several rather contradictory studies indicating that the observed flight behaviour is considerably influenced by wind direction, light/shading, moisture, temperature and riparian vegetation. Apparently documented upstream flight may be an artefact due to specific local conditions. Calculations furthermore show that infrequent dispersal of randomly flying females coupled with improved ability of the immature stages in upper reaches to survive (density dependent) may explain why populations are able to persist there despite the losses due to drift [11].

Despite this "attack" on an apparently well-established fact and a popular theory with strong appeal to the public, stream insects actually do disperse upstream. We have observed this behaviour in several streams on Funen, Denmark's second largest

island, where mayflies and stoneflies have been able to extend their distributional range by approx. 5 km from one year to the next. However, this might just be a result of random dispersal (see next section of this chapter).

Is dispersal between stream systems random?

The ability of different stream organisms to disperse between isolated streams and whole stream systems deserves attention. This knowledge may help to explain the way that species are distributed nowadays, and to predict how quickly the organisms can recolonise restored streams. It may even have strong implications for conservation [12]. Differences among stream insects in their ability to disperse have been observed in several other studies. These differences appear even between closely related species, and may depend on, for example, morphological differences. Thus, short wings, and hence a reduced potential for dispersal, could be one of several factors explaining the rarity of Swedish mayflies and stoneflies [12].

Knowledge about the dispersal capacity of stream insects may be extracted from two types of field studies. First, insects may be caught in traps located at various distances from a stream. Depending on the distance and trapping device, such traps can be attractant (light traps) or non-attractant (malaise traps, window traps, pan traps). Second, the colonisation of newly made or restored existing streams can be studied by routine long-term monitoring of a fixed network of sites. The latter group of streams include streams that have been subjected to environmental disturbances resulting in the elimination of most original species, but where life conditions are again suitable for these species after a short period of time (e.g. heavy pollution with insecticides).

Studies using malaise traps (see photo on opposite page) in small Danish and English streams have shown that most adult stoneflies and caddisflies stay close to their native stream [13, 14, 15]. Thus, traps situated about 50 m from the stream captured 90 % of the plecopterans [13], whereas 95 % of trichopterans appeared in traps situated up to 15–20 m from the stream [14]. Small caddisfly species (*Agapetus fuscipes*, *Lype reducta*, *Silo pallipes*) dispersed even less, only 1% reaching traps located just 20 m from the stream. Dispersal was apparently random following an exponential decreasing function with distance from the stream (Figure 6.2A). Larger species of caddisflies (*Plectrocnemia conspersa* and *Potamophylax cingulatus*) behaved differently and were found more evenly distributed within a distance of 75 m from the stream [13, 14].

Mean lateral dispersal distance of Trichoptera (Hydropsychidae) was much greater (650–1,845 m) at a large river and lakeshore in Canada. Thus, 1 % of the populations dispersed more than 5 km from the water bodies [16], showing a much greater potential for dispersal and ability to colonise distant water bodies (Figure 6.2B). Light trapping studies carried out at various Danish localities have also shown that egg-bearing females of such different-sized caddisfly genera as *Hydroptila*, *Polycentropus*, and *Hydropsyche* were caught up to 8–9 km from the nearest suitable river habitat. Small brooks and streams are naturally abundant and situated relatively close to each other, whereas large streams and rivers are relatively fewer and more isolated. Consequently, insects inhabiting small streams only have to disperse a short distance in order to reach a similar neighbouring stream, whereas insect species restricted to larger streams have to travel much longer distances to colonise, or to exchange genes with other populations. Despite this, stoneflies and caddisflies dispersed just less than half of the mean distance between small neighbouring forest brooks in North America [17].

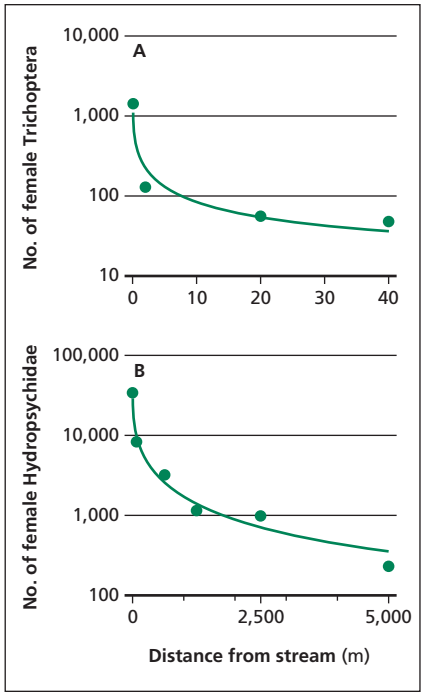


Figure 6.2 Lateral dispersal of adult caddisflies from two very different systems. A: Small forest brook on northern Funen, Denmark [14]. B: Detroit River and Lake St. Clair, Canada [16]. Note the difference in scale for individuals caught in traps, and the dispersal distance.

In the Canadian study [16], female Hydropsychidae seemed to disperse inland just after emergence. Here they mated with males that often formed swarms at distinct landscape markers (bushes, trees). Hereafter, females dispersed further away from the water body to find resting sites, where they might be relatively safe from predators. Then, when the eggs were mature and ready to be laid, females returned to their natal water body to oviposit. However, some females may accidentally – for example under specific wind conditions – reach another suitable water body instead. This could lead to successful colonisation as some species produce a large number of eggs. Thus, it seems that only a few successful females are required to establish new populations.

Such populations are found in our long-term studies of streams on Funen. Many of these streams were heavily impacted by organic pollution during the period 1960–1980. However, when the water quality improved due to extensive treatment of wastewater in the late 1980s, species of various groups of aquatic insects dispersed over land and successfully colonised "restored" habitats situated 4–18 km from the "inoculae" (i.e. the source of the colonising females) (Table 6.1). The dispersal ability of the species varies with *Leuctra fusca* (Plecoptera) and *Agapetus ochripes* (Trichoptera) dispersing significantly further than *Heptagenia sulphurea* (Ephemeroptera).

In a new man-made Swedish stream, blackflies were the quickest colonisers, soon followed by chironomids, certain mayflies and stoneflies, whereas beetles, dragonflies and caddisflies arrived much later [18]. Successful colonisation of new habitats is not only dependent on the distance to the nearest inocula. The number of possible inoculae and the size of their populations might be important too. This is well illustrated by the exponential spreading of *L. fusca* in streams on Funen (Figure 6.3). On the other hand, it seems most unlikely that ten insect species that were lost from the Odense Stream (the largest stream on Funen) in the 1950s would be able to recolonise this stream; the nearest potential inoculae in Jutland are few, widely scattered, and located more than 80–100 km from the Odense Stream. However, one of these species, the caddisfly *Brachycentrus subnubilus*, actually re-appeared in autumn 2000 after having been absent for 40 years.

Dispersal, colonisation, and recolonisation should of course be viewed in the perspective of time scales. There is evidence that many running water insects colonised streams from southern habitats soon after the latest deglaciation that started about 17,000 years ago. Thus, more than 20 species of lotic caddisflies – nowadays recorded in both Danish and Scandinavian streams – occurred in a large river in the Great Belt about 10,300 years ago when the climate was as warm as nowadays [19]. However, one cannot preclude the possibility that recent distribution of some aquatic insects is the result of an incomplete dispersal. *Anabolia nervosa* (Trichoptera) is very abundant and widely distributed in streams of both Jutland and Funen, but are not found at all on the island of Zealand which is separated from Funen by a currently 20 km-wide marine Great Belt. In the streams on Zealand, *A. nervosa* is substituted by *A. furcata* that also occurs in both Jutland and on Funen, but here

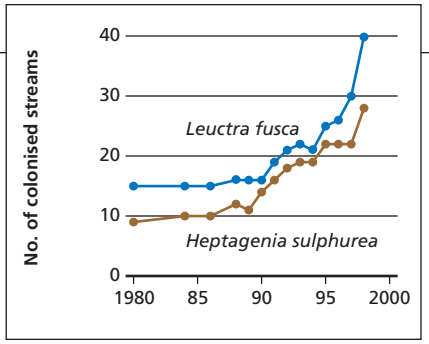


Figure 6.3 Recent colonisation by adult *Heptagenia sulphurea* and *Leuctra fusca* of environmentally suitable streams on Funen, Denmark, where these species had been absent for several decades. Note the almost exponential development in *L. fusca*, indicating that colonisation progresses concurrently with the number of "inoculae".

	Heptagenia sulphurea	*Leuctra fusca*	*Agapetus ochripes*
Dispersal distance (km)			
Median	3	5.5	7
Maximum	4	10	18
No. of observations	7	14	11

Table 6.1 Overland dispersal of adult aquatic insects in streams on Funen, Denmark. Median and maximum dispersal distances between isolated streams. Differences between *H. sulphurea* and the two other species are statistically significant (Mann Whitney U-test, P<0,01).

it exclusively inhabits small lakes and ponds. The fact that *A. nervosa* only dispersed a few metres from its home pond during a light trap study on Funen supports this hypothesis.

The terrestrial habitats of adult stream-dwelling insects

Studies of the lateral dispersal of adult stream insects indicate that the major part of the populations stay within a relatively small zone alongside the streams [20]. It is within this zone that mating, feeding, and maturation of the eggs take place. It is therefore important to obtain knowledge about the environmental demands of the insects in this so-called riparian zone.

Some caddisflies choose forests for shelter and rest [6, 21], and many stoneflies feed on algae and lichens on the branches and trunks in this habitat [3, 13]. The males of some groups (e.g. mayflies, alderflies, caddisflies, midges) use bushes and trees as swarming sites (see Box 6.1). It therefore makes quite a difference whether the riparian zone along Danish streams is vegetated by either a border of stinging-nettle (*Urtica dioeca*), low vegetation of herbs, crops, more or less scattered bushes and trees, or forest. Cropped areas, in particular, must be a harsh, inhospitable, and "toxic" site when the crops are sprayed with insecticides against pest insects.

The surroundings of a stream no doubt influence the dispersal of adult insects. Species that travel close to the ground may experience dense herbaceous vegetation as a barrier. Thus, the catch of caddisflies at a distance of 10 m from a Danish stream was greater in malaise traps placed in dense beech forest without herbaceous vegetation, than in traps located in an open alder swamp or in a fallow field, both having dense herbaceous vegetation [15]. This result could be interpreted in the way that the insects flew above the vegetation thereby escaping the traps. Thus, the density of vegetation may also influence long-distance dispersal, thereby probably explaining the relatively long distances travelled by the insects over cropped fields in the above-mentioned Canadian studies [16].

Apparently many factors influence the life of adult stream insects, and the relationship between these factors can be quite complicated. As knowledge in this field of research is rather limited, there is a great need for research that is both interesting, challenging, and not least, highly relevant for the survival of stream insects in the fragmented cultural landscapes around most of contemporary Europe. This knowledge is also important for evaluating the ability of the insects to recolonise restored streams and the near-stream surroundings.

Danish streams were forested until most of the woodland was cleared for cultivation.

Capnia bifrons stonefly nymph.

7 Macroinvertebrates and biotic interactions

Macroinvertebrates are extremely important in the evaluation of stream water quality. Macroinvertebrates are, however, much more than just bioindicators. They are an essential element for both structure and function of stream ecosystems. Macroinvertebrates are constantly interacting with each other as well as with other stream organisms such as plants and fish. These interactions are surprisingly complex and varied, and they have a high overall significance for streams as ecosystems.

What are biotic interactions?

Stream ecology was previously divided into two schools with separate conceptions of how important biotic interactions were for the structure and function of lotic systems. One school of scientists viewed streams as being completely dominated by physical processes with very limited possibilities for biotic interactions between species. The other school had the opposite view, namely that biotic interactions were a prominent feature of lotic systems and that they shaped stream communities in a way similar to what is known from other ecosystems such as lakes. However, these biological interactions had yet to be discovered and described.

Nowadays the view is more balanced: most scientists agree that the truth is somewhere between the two original conceptions. Streams are extremely dynamic with large spatial and temporal variability in physical features and biological elements. As a consequence, both types of processes are strongly dependent on when and where stream ecosystems are being investigated. This knowledge is the result of significant research efforts within the international scientific community. In Denmark, questions relating to biotic interactions have also been addressed within the last decade. This chapter provides examples of this research in which macroinvertebrates play a focal role. Before we look at the examples, however, it is necessary to define the term "biotic interactions".

Predation and competition are both concepts that relate to biotic interactions. Predation includes situations in which a predator eats a prey (carnivory) and a grazer eats a plant (herbivory). Competition for a resource, often food, can occur between individuals of the same species (intraspecific) or between different species (interspecific). With respect to streams, biotic interactions in the present context also include the effects of the organisms in the riparian zone on the in-stream biota. Examples can be found in the transitional zone between land and water, and between macrophytes and macroinvertebrates.

The land-water transitional zone

To understand the living conditions of stream macroinvertebrates, it is necessary to focus on the land-water transitional zone. Processes in the terrestrial ecosystem influence the amount of food available for the in-stream macroinvertebrate community. This is most pronounced in small streams that are very closely linked to the surrounding terrestrial ecosystem. The vegetation on land influences the amount of light that reaches the stream surface. Consequently, the riparian plant species regulate in-stream primary producers in small streams. In addition, in-stream quality and quantity of particulate organic matter (POM) will largely depend on inputs from the riparian zone. It is not possible for detritivorous macroinvertebrates to affect this donor-controlled contribution of POM, which constitutes the main energy source in small streams.

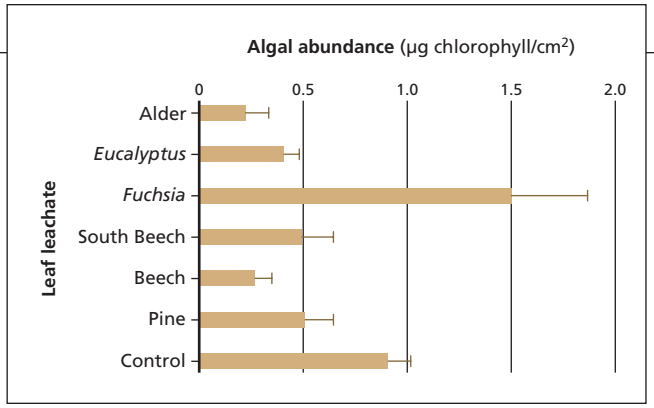
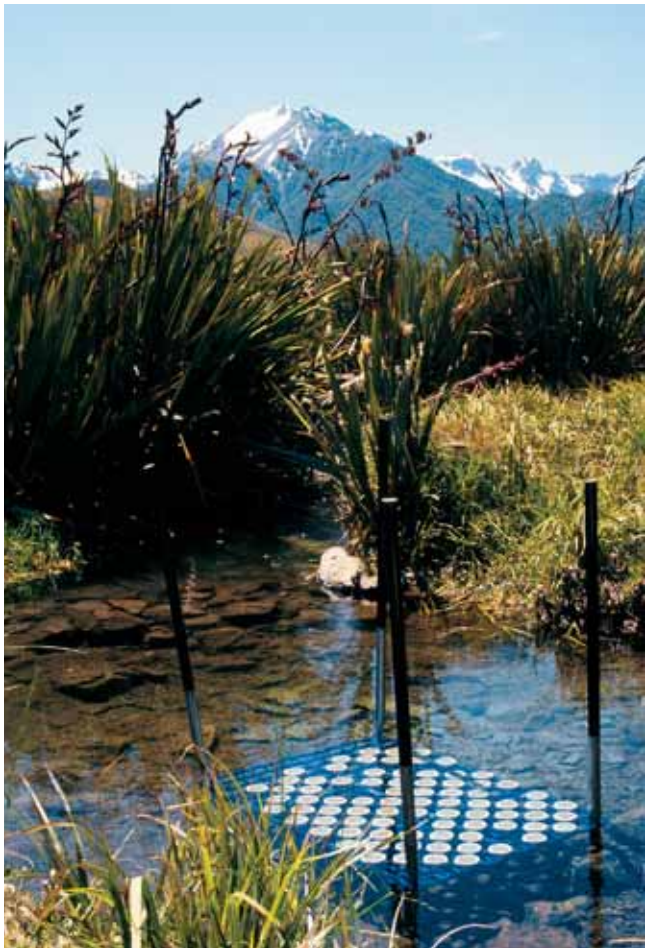


Figure 7.1 Leaf leachate from the majority of tree species investigated had an inhibitory effect on algal biomass, i.e. the biomass was lower when subject to leaf leachate than on artificial leaves without leachate (controls) [1].

The difference in colours was clearly evident in leaf leachates used.



Experiment with artificial leaves. Diffusion substrates with leaf leachates in a New Zealand spring.

Another example of interaction across the land-water transitional zone is the leaching of dissolved organic compounds from tree leaves and their effect on stream algae. When leaves from riparian trees enter the stream, various compounds are leached from the leaves into the stream water during the first week of submersion. The composition of the leachate depends on the tree species and has very variable effects on in-stream bacteria and algae. This aspect was investigated in an experiment using diffusion substrates with leachates from six riparian tree species as well as control substrates made from distilled water. Ten diffusion substrates for each species were made by dissolving the leachate in warm agar and subsequently transferring it to small plastic containers. They were subsequently placed in an unshaded spring area for two weeks. A piece of nylon netting was mounted on top of each container for the algae to colonise on. This design allowed continuous leaching of the compounds through the netting to the water. Only leachate

from one tree species stimulated algal growth, whereas the others showed inhibitory effects (Figure 7.1). Beech and alder, both common in the riparian zone of Danish streams, were most inhibitory. Compared to other regulatory factors (e.g. light) for stream algae, leaching of mainly inhibitory substances from leaves is probably of minor importance to the ecosystem function. However, it adds to the dependence of small streams on the terrestrial ecosystem and will potentially limit the energy available for higher trophic levels such as macroinvertebrates. Especially during autumn when incident light levels increase due to leaf fall, leaf leachates might prevent a secondary peak in algal biomass.

Macroinvertebrate grazing on in-stream primary producers

Many macroinvertebrates also feed on the streams' own production of algae and macrophytes, the most important food source being microscopic algae living on stones and plants. An important question in this context is whether macroinvertebrates can regulate algal biomass through their grazing.

Interactions between algae and grazers

In an investigation of Gelbæk, a small unshaded stream in mid-Jutland, all macroinvertebrate grazers were removed from stones in two experimental channels, while they were left undisturbed in two control channels [2]. Grazers were removed once a week by submersing stones into a weak insecticide solution. At the same time, stones from control channels were submersed into pure water to mimic the mechanical disturbance of the experimental treatment. The investigation ran for 44 days in spring when growth rates of benthic algae are highest and the experimental manipulation should have the greatest impact. At the end of the experiment, the grazer guild was dominated by the freshwater limpet *Ancylus fluviatilis* and non-biting midges belonging to the subfamily Orthocladiinae. Especially the occurrence of *Ancylus* varied significantly between treatments. Only 50 ind./m^2 were found in channels where grazers were actively removed using insecticide, whereas nearly 20 times as many *Ancylus* (approx. 900 ind./m^2) were found in control channels. The number of grazers was successfully reduced experimentally, but what about algal biomass? There was a significant lower algal biomass (measured as chlorophyll) on stones in control channels with normal grazer densities (Figure 7.2). Thus, ambient grazing rates in spring could reduce algal biomass on stones, while algal biomass increased twofold when grazer densities were reduced. This investigation shows that grazing macroinvertebrates can regulate the biomass of algae.

The opposite can also occur, namely that algae regulate the density of grazing macroinvertebrates. Investigations in six forest streams showed a positive relationship between algal biomass and grazer densities, i.e. the more algae, the higher density of grazers (Figure 7.3). It is difficult to determine which of these two interactions are more important: grazer regulation of algal biomass or algae regulation of grazer density. International investigations support the Danish results in that grazers can regulate algal biomass in open streams with good light conditions (and consequently algal growth), whereas the opposite occurs in shaded, forest streams with low algal biomasses [4]. Other factors such as disturbance of the streambed during high discharge events are also important for the interaction between macroinvertebrates and benthic algae. Frequent disturbances will reduce algal biomass and macroinvertebrate grazing will consequently lose its importance in determining algal biomasses.

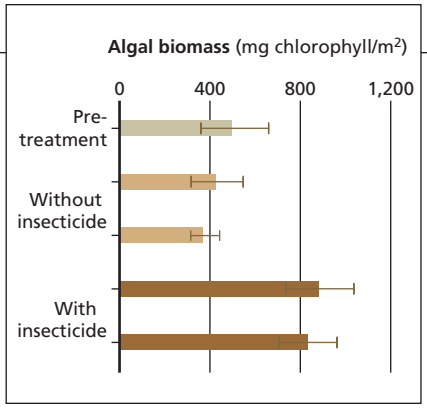


Figure 7.2 Algal biomass was greatest on stones treated with an insecticide solution. On stones where macroinvertebrates could graze freely, algal biomass was not different than at the beginning of the experiment [2].

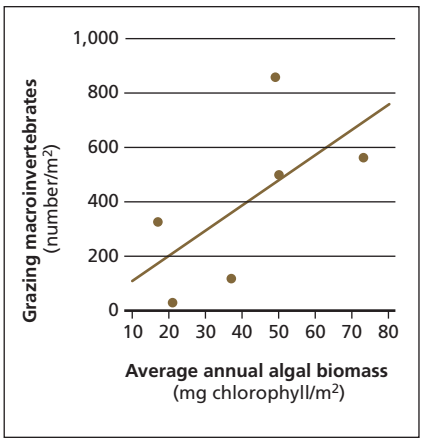


Figure 7.3 The more algae, the more macroinvertebrate grazers. Results for six shaded forest streams [3].

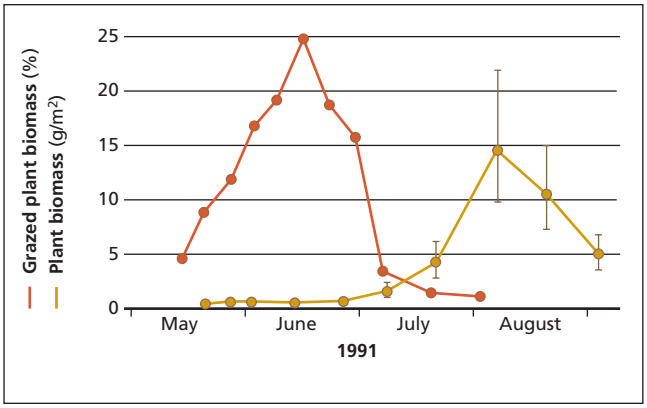


Figure 7.4 The caddis larvae *Anabolia nervosa* had a significant impact on the biomass of Perfoliate Pondweed in spring and early summer. Later in summer the impact of grazing was insignificant (from [5]).

Grazing of macrophytes

Grazing by stream macroinvertebrates on higher plants (macrophytes) was previously considered unimportant. However, several Danish investigations show that macrophytes can be an important food resource for macroinvertebrates. In an investigation in Mattrup Stream, the loss of leaves to grazing was estimated for Perfoliate Pondweed [5]. Clear effects of grazing were found in spring when macrophytes have their main growth period (Figure 7.4). Grazing removed almost 25% of the plant biomass and could delay the development of Perfoliate Pondweed. When plants have built up a large biomass in summer, grazing will be of minor importance and unable to regulate macrophyte biomass. Plants will gradually grow out of their problems with increasing biomass, as grazing will be distributed over a large number of leaves. The most important grazer in Mattrup Stream was the caddisfly *Anabolia nervosa*, which also during summer consumes dead organic matter deposited under the plants. Therefore, the macrophytes will indirectly remain important for *Anabolia*.

Plants create habitats for macroinvertebrates

The first thing that strikes you when looking at a Danish stream in summer, is the lush growth of macrophytes. Their direct importance as a food resource for macroinvertebrates is probably limited in most cases, but they are indirectly one of the most important elements for the ecology of Danish streams. This is clearly illustrated by an investigation from Suså Stream where 95% of all macroinvertebrates were found within the macrophyte vegetation [6]. Macroinvertebrate densities were enormous as more than 400,000 individuals per square meter of streambed were found when including those living on plants.

In addition to being a suitable habitat for macroinvertebrates, macrophytes also interact with the physical environment. By affecting current velocities and sedimentation rates, macrophytes indirectly create a range of habitats in which the macroinvertebrates can dwell. Despite the apparent importance of macrophytes for in-stream macroinvertebrate communities, only few investigations have addressed this interaction. However, a recent investigation in two reaches of Gelså Stream in southern Jutland indicated the importance of the interaction between macrophytes, physical features and macroinvertebrates. One reach had not been exposed to weed cutting for over 20 years whereas weed cutting took place twice a year in the other reach. Species composition and structural variation in the macrophyte community differed between the two reaches. The reach with frequent weed cutting was completely dominated by Unbranched Bur-reed, which covered approx. 50% of the streambed, while the different plant species were much more evenly distributed on the reach with no weed cutting for + 20 years. In this reach, the most frequently occurring species was Broad-leaved Pondweed covering approx. 25% of the streambed. In addition, in the reach without weed cutting, individual macrophyte stands contained more plant species than was the case in the reach with frequent weed cutting. These differences in the macrophyte community were also reflected in the macroinvertebrates: the species richness was higher in samples taken between the plants in the reach without weed cutting compared to the reach with frequent weed cutting (Figure 7.5). The same picture was seen in samples taken beneath the plants. In contrast, no clear differences in species richness were evident from macroinvertebrate samples taken on the plants even though several different macrophyte species were investigated, an exception being samples taken from the mixed macrophyte stands (3 macrophyte species) on the uncut reach. The mixed stands had higher macroinvertebrate species richness compared to single macrophyte species. When interpreting the results

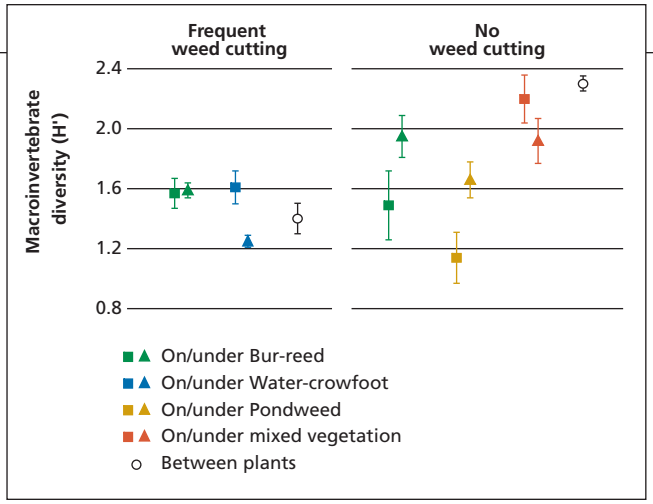


Figure 7.5 The greatest macroinvertebrate diversity was found on the reach where weed cutting had not been undertaken for more than 22 years – particularly large differences were found in samples taken between the macrophytes and in the mixed stands [Friberg, original].

Brown trout is one of the most important predators on macroinvertebrates in temperate streams.

from the study in Gelså Stream, the direct impact on weed cutting on the macroinvertebrate communities should also be taken into consideration. But weed cutting had not been undertaken several months prior to the study period and the direct impact can be considered as minimal. Therefore, the study demonstrates that macrophytes affect macroinvertebrate communities in streams and it seems to be mediated primarily through changes in the physical conditions.

Importance of fish

Brown trout (*Salmo trutta*) is the most important predator in the majority of Danish streams. It is also the primary game fish for anglers and has been quite extensively investigated. Brown trout affects its prey directly by consuming them and indirectly by inducing a behavioural change. Both mechanisms are important in Danish streams, e.g. in the predator-prey relationship between trout and the freshwater shrimp *Gammarus pulex*. *Gammarus* is found in the majority of Danish streams and it is probably the most important food source for trout.

That trout can have an impact on *Gammarus* populations has been shown in a study of previously fishless headwater streams in the forests Grib Skov and Rold Skov [7, 8]. In March, juvenile trout were released into an experimental reach of 100 m in two headwater streams in Grib Skov forest. A control reach, still without trout, was maintained upstream of the experimental reach in each stream. The released trout fed primarily on *Gammarus*, which constituted approx. 25% of their diet. In addition, the trout were size-selective in their feeding and consumed mainly the largest individuals of *Gammarus* in benthos as well as in drift (Figure 7.6 and Box 7.1). The preference for large prey is an advantage for the trout as they obtain most energy using this strategy as long as large *Gammarus* are abundant and hence easy to catch. Trout predation had a significant impact on *Gammarus* population development from March to June in the two experimental reaches. While there was a seven-fold increase in the number of *Gammarus* in the two control reaches without fish, there was only a two-fold increase in the experimental reaches with trout (Table 7.1). In addition to *Gammarus*, the caseless caddisfly *Plectrocnemia conspersa* (a macroinvertebrate predator) was heavily preyed upon by the released trout.

Indirect effects of trout on *Gammarus*

In the forest Rold Skov five spring brooks without fish were investigated. Due to the shallow depth and various barriers for migration, no trout were present in the brooks prior to the experiment. A small enclosure consisting of a cage with sides of iron netting was placed in each brook for three days. Then trout were released into the enclosures (four in each) in three of the brooks, while two brooks remained as controls with empty enclosures. The idea behind this design was to inves-

Box 7.1 Drift

Driftnet in use.

All macroinvertebrates in Danish streams dwell on the bottom or on plants. However, they are often found drifting downstream within the water column. The reasons for drift are several and can roughly be divided into three categories: behavioural drift, catastrophic drift and background drift. Behavioural drift occurs as a result of activity relating, for example, to the search for food, or predator avoidance. This type of drift is primarily governed by external stimuli (e.g. light) but also by endogenous rhythms controlling, for example, the time when the search for food commences. Catastrophic drift occurs when large numbers of macroinvertebrates enter drift simultaneously due to a substantial, external impact, such as a chemical pollutant or a sudden surge in discharge. Background drift is the drift that occurs when there is neither behavioural nor catastrophic drift. Background drift reflects accidental dislodgement of macroinvertebrates. Drift is measured by placing a net in the stream trapping macroinvertebrates that are transported with the current.

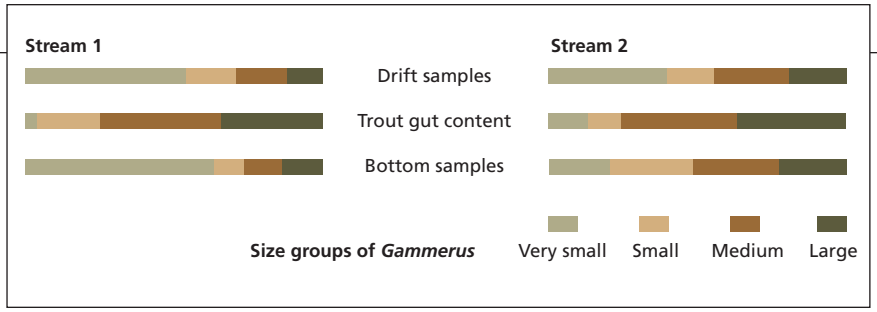


Figure 7.6 The proportion of large *Gammarus* was far greater in trout guts than in both drift and benthos samples. Results were similar for both streams studied [7].

	Relative increase in number of *Gammarus*
Stream 1	
Reach without fish	7.3
Reach with fish	3.0
Stream 2	
Reach without fish	8.7
Reatch with fish	2.3

Table 7.1 The increase in numbers of *Gammarus* was greatest in the two reaches that remained fishless [7].

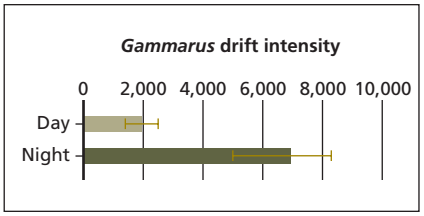


Figure 7.7 *Gammarus* exhibited a pronounced night drift pattern already prior to the introduction of trout [8].

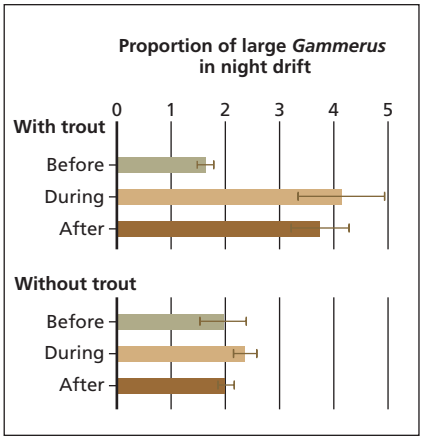
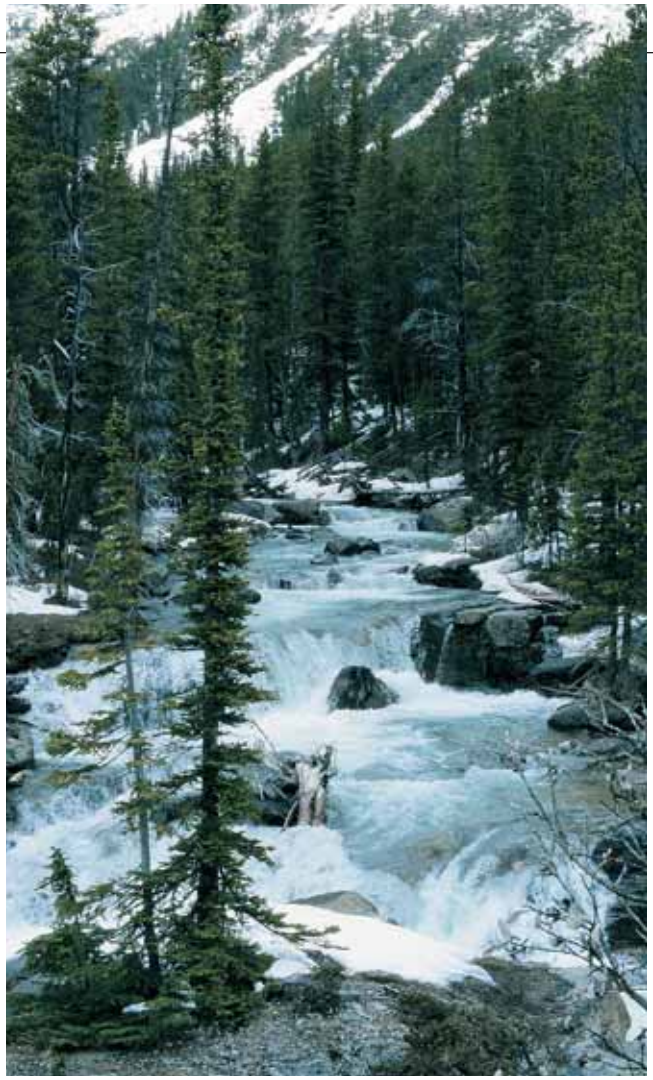


Figure 7.8 The proportion of large *Gammarus* in night drift increased after the introduction of trout in cages and remained high after the removal of trout. No changes were found in the two fishless spring brooks [8].

tigate indirect effects of trout on the macroinvertebrates as the enclosures prevented the trout from exerting a direct predation pressure on the prey community. Trout were kept in enclosures for three days and then removed, after which sampling was undertaken for another three-day period before the experiment ended. Indirect effects were measured as changes in macroinvertebrate drift by collecting drift samples approx. 20 m downstream of the enclosures. Already during the sampling period prior to the introduction of trout, *Gammarus* showed pronounced night drift behaviour (Figure 7.7). The significant higher drift at night compared to day drift reflects increased activity at night and is most probably an adaptation to avoid trout predation, trout being a visual predator and therefore more effective under good light conditions. It is interesting that this behaviour is sustained in streams without trout. After introducing trout into the enclosures, there was a significant increase in the proportion of large *Gammarus* in drift during night (Figure 7.8). They could change their behaviour by being less active during the day and more active at night when trout were present. As the large *Gammarus* had not been in direct contact with trout, they must have been capable of detecting chemical cues in the water released by the trout. This interpretation is consistent with findings in international studies on fish predation. Interestingly, the large *Gammarus* retained their changed behaviour in the third period after removal of the trout. These findings show that prey behaviour in streams can be affected by the presence of a predator. Less activity during day, as exhibited by large *Gammarus*, reduces the likelihood of being eaten. However, it also limits the time spent on food searching to mainly the night-time period and it therefore has energetic costs for *Gammarus*.

Interactions between trout and macroinvertebrates

Interactions between trout and macroinvertebrates are generally difficult to quantify, the main reason being that the majority of streams has, or have had, a trout population. Therefore, prey communities will already be adapted to the presence of a predator and *vice versa*. Another difficulty in assessing predator-prey interactions in streams is that the estimation of macroinvertebrate quantities (abundance and/or biomass) is probably not sufficiently precise. Hence, several studies over recent decades have found that fish eat more macroinvertebrates than are present in the stream, according to estimations of prey quantities from the samples taken!



Mountain streams are systems dominated by physical processes.

There is therefore still a lack of investigations that prove the overall importance of trout, and fish in general, in structuring macroinvertebrate communities in streams. This lack of knowledge comprises both the direct predatory impact and the indirect effects of behavioural changes. There is no reason to believe that fish are not important in this context, but multiple factors will affect biotic interactions in streams. Biotic interactions are summarised using a hypothetical food web in Box 7.2.

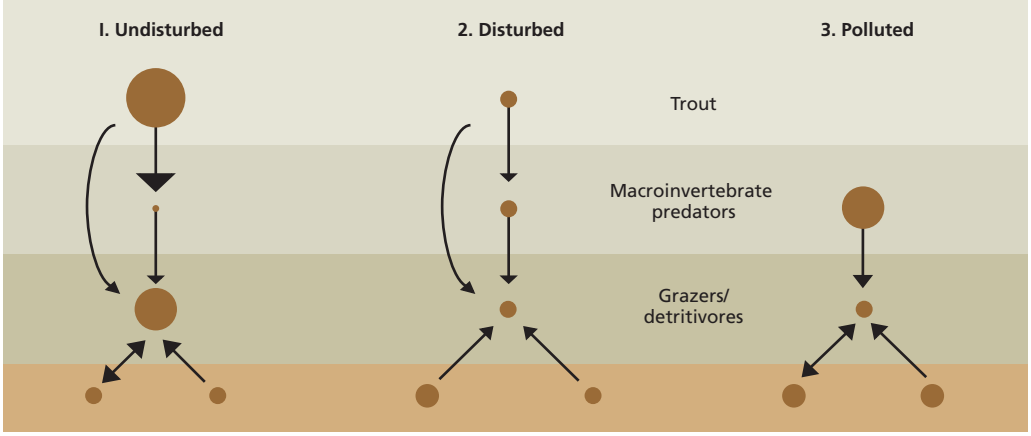
Biotic interactions and the future

The present chapter shows that several examples of biotic interactions have been found as part of Danish stream research in the past decade and these examples support findings on the international scientific arena. The main problem is how these findings, often obtained on very small spatio-temporal scales, can be linked and put into a common context enabling us to understand processes at the ecosystem level. What, for example, is the importance of macroinvertebrate grazing for the energy flow through entire stream ecosystems? – We do not know. Our ability to answer these questions is very limited, as the processes we want to understand are dependent on both spatial and temporal features that are way beyond the scales on which the experiments were conducted. It is a problem because all the major and interesting questions – and answers – are related to the whole ecosystem.

We are aiming at being able to assess the impact of various human impacts on the ecological quality of streams, e.g. in the context of the EU Water Framework Directive. Quality is currently almost solely assessed by use of chemical and biological indicators, which provide little or no information on ecosystem functioning. Understanding biotic interactions in streams is interesting from a pure scientific point of view, but it could be as important for the future management of streams in Denmark and elsewhere.

Studies on biotic interactions in Danish streams are relatively few, and most of the studies involving macroinvertebrates are actually cited in this chapter. There is an apparent lack of studies addressing the importance of competition in structuring macroinvertebrate communities in Danish streams. One reason for the limited number of studies on biotic interactions is probably that the experimental tradition in Danish stream research is relatively weak. In a global context, however, Danish streams are very stable and should be ideal for studying biotic interactions. Moreover, there are very significant scientific challenges in understanding the interactions between the riparian zone and the stream, and between macrophytes and the other biological components. Danish streams are both small and have a rich growth of macrophytes making them extremely suitable for this type of investigations. The scientific challenges and the natural setting exist– the question is only whether we seek the opportunity and raise our research effort to the level it deserves!

Box 7.2 What controls biotic interactions?



The size of the circles reflects the relative importance of each element. After [9].

Biotic interactions can be summarised by using a hypothetical food web from a small trout stream (**1.**). Streams have many omnivorous macroinvertebrates that feed on different food items. The bottom of the diagram shows the fundamental food resources consisting of algae (left) and dead organic matter (right). Detritivores and grazers, both primary consumers, use these food resources. A true interaction between grazers and algae occurs as indicated by the double arrow. Grazers feed on the algae and are therefore dependent on their productivity, but can, in certain cases, deplete the algal resource significantly, for example when grazers are very abundant and remove more of the algal biomass than can be replenished by the productivity of the algal community.

Both macroinvertebrate predators and trout prey upon primary consumers. In this example, trout has a strong regulatory effect (large arrow), especially on the large macroinvertebrate predators, which they preferred due to their large size. The caddisfly *Plectronemia* belongs to the group of large predatory macroinvertebrates. The trout population is often self-regulatory due to intraspecific competition for territories.

2. Shows the same food web, but in an unstable stream with a very fluctuating discharge pattern. The web is inter-connected as before, but the different trophic levels do not interact as strongly. This is illustrated by an increase in algal biomass due to reduced grazing pressure. Natural processes linked to physical features of the stream therefore define the borders within which the biotic interactions can take place. A stable stream is therefore much more likely to sustain complex biotic interactions than an unstable stream.

Human activities can also influence biotic interactions and fundamentally change the function of the ecosystem (**3.**). In the example, trout has become extinct due to some kind of pollutant and the predation pressure on the large macroinvertebrate predators has been released. As the large macroinvertebrate predators are more efficient predators on grazers and detritivores than trout, both algal biomass and standing stock of dead organic matter increase as compared to the unperturbed stream (**1.** and **3.**).

Brown trout (*Salmo trutta*) is a key species in Danish streams.

8 Stream fish and desirable fish stocks

Freshwater fish communities have always been valuable resources for society, particularly the species that migrate between freshwater and the sea. Historically, eel, salmon and trout were so abundant that good fishing luck could turn a capable fisherman into a wealthy person. Unfortunately, migrating fish became threatened by over-fishing quite early in human history. The more recent construction of dams and other habitat destruction associated with development of towns, industries and intensive agriculture have reduced populations further. The largest Danish river, the River Gudenå, illustrates this historical decline and also the difficulty of re-establishing healthy fish communities once the original populations have deteriorated or, in the case of salmon, become extinct. Efforts are currently needed to be made to effectively restore and manage fish communities in streams.

Historical use of stream fish

In the milder climate following the last Ice Age, new fish species immigrated to Denmark from the ice-free parts of Europe. The immigrants joined the species already living in the cold lakes and streams in SW-Jutland, which had remained free of ice during the glaciation and had received drainage water from the glaciers towards the north and east.

Over time almost 40 species of freshwater fish established populations in Denmark. Changes have been seen once again during the recent centuries as pollution and physical degradation have led to the loss of rare and sensitive species while intentional or fortuitous introductions have added even more new species. As a result, there are more fish species in Danish freshwaters today than at any other time since the end of the last glaciation.

Frisenvold weir was used for catching salmon in River Gudenå in the late 1800s.

Historically, eel has been the most important freshwater fish in Denmark.

Through the Middle Ages and up until the twentieth century, freshwater fish were consumed extensively by both rich and poor people. Fish were abundant and could be caught in all freshwater habitats: lakes, ponds, streams and ditches. The monks brought the most advanced fishing technology available in those days to Denmark from Germany and France. In many streams the monasteries installed fishing-weirs that caught the migrating fish with an unprecedented efficiency. When the monasteries were closed after conversion to the Reformed Lutheran Church, ownership of the fishing-weirs was transferred to the Royal House. This became the start of what has since been known as royal privileged fishing rights.

Different types of fishing weirs were used for catching salmon or eel. Salmon traps were wooden constructions placed on "flat" (i.e. undammed) currents to catch upstream migrating fish. They were made of woven willow twigs placed between solid oak poles, hammered down into the stream bed. Upstream migrating fish were led into consecutive small compartments, from which they were unable to leave. Eel weirs were often constructed in connection with mill dams. They consisted of horizontal wooden gratings filtering the falling water, whereupon the fish were led through a drain to the trap box, from where the catch could easily be retrieved. Whereas there are still about one hundred eel weirs in Danish streams, the last salmon traps disappeared in the early 1900s. The more practical fyke nets and pound nets, which are still in use, replaced the fixed salmon weirs.

Historically, freshwater fish remained an important commercial resource for a very long time. In regions with many streams such as in mid-Jutland, it was common practice until the 1920s to pay the rent of fishing privileges in natural products – for example a certain annual amount of roach. Not all fish species were equally sought after, however. A suitable size for a meal was an important criterion. Taste and catchability were other important criteria. All these qualities apply to eel, which was very popular. Large, predatory fish (piscivores) such as pike, salmon and trout were considered to be more delicious but were also less abundant than fish of lower trophic ranking. The abundance of coarse fish such as crucian carp, bream and roach made them particularly popular as measures against hunger. Hunger was a harsh reality in former days and this had taught the inhabitants to exploit the fish community in a relatively sustainable manner. The lesson was simple: in an intensive fishery there was a larger and lasting yield by catching the non-predatory fish rather than the predators themselves. Thus, the production of one kg of predatory fish requires in the order of 10 kg of prey fish.

It is possible to get some idea of the importance and popularity of different fish species in ancient history by scoring the frequency of place names associated with fish. As number one on this list, eel is part of more place names than roach (second place) and trout (third place) together. Peak levels in the abundance of eels must have been reached in the early Middle Age, when lakes, streams and wetlands had a surface area that was at least three times greater than today and when most watercourses offered an unhindered passage of glass eel (eel larvae) from the sea.

Value of stream fish

Over the last one hundred years the exploitation of freshwater fish has become more of a sport and leisure activity than a source of energy and protein. Nowadays, stream fish primarily serve as objects of recreational fisheries, but the most attractive species are still the same. Bream and roach have lost their importance in the freshwater fishery, as most Danes do not care to eat these species anymore. Instead the recreational fishery focuses on the catch of large fish, not serving as food, but merely offering a hard fight to the anglers before being released again. Most meals of eel, salmon and trout nowadays come from fish reared in aquaculture.

Commercial catches of Danish freshwater fish are small and are mainly exported to Germany, France and Italy. Only predatory fish and salmonids (i.e. eel, whitefish, perch, pike, trout, salmon, smelt and zander) are caught for consumption, while most non-predatory species have disappeared from the Danish menu. Even large specimens of bream, ide, roach, rudd

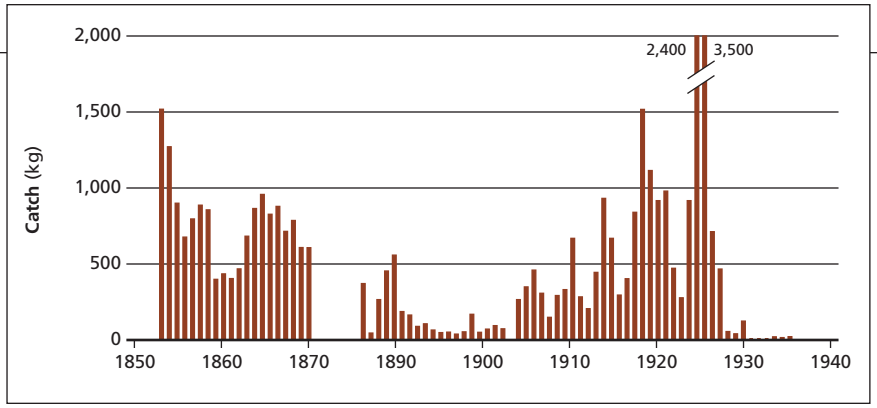


Figure 8.1 Annual catch of salmon in the salmon-weir at Frisenvold on the lower River Gudenå from 1853 to 1913 when the weir was finally abandoned. The remaining period shows the total annual catch from 1914 to 1934 when the salmon stock finally went extinct. Data compiled from [1] and [2].

and white bream are only caught to a limited extent by Danish anglers. On the other hand, many English, German, and Dutch anglers travel to Denmark to utilise the abundance of coarse fish. The largest of these, the carp, can grow to a size of 20 kg in Danish waters, and has also become increasingly popular with local specimen anglers.

One hundred years of fishery studies in River Gudenå

Fishery and fish biology have been studied for a long time in the River Gudenå, and important information on the development and decline of the fishery is available. For example, in 1664 more than 32 salmon traps were in operation, whereas this number had dropped to 14 in 1833. This decline continued and the last salmon trap at Frisenvold was commercially abandoned in 1907 [1]. The decline of salmon trapping matches the overall decline of the salmon stock (Figure 8.1). It is known that the original stock of spring salmon (i.e. multi sea-winter salmon that enter the river before summer) declined markedly after 1850. Over-fishing and sewage pollution were considered the main reasons for the decline during the 1800s [1], although straightening and dredging of the river channel most likely also contributed to impoverishing the salmon habitat, especially for spawning.

From 1898 to 1918 all weekly salmon catches at Frisenvold were registered by A.C. Johansen and J.C. Løfting [1]. Their study focused on salmon and trout and investigated size, age, migration and homing behaviour (the ability to return to the natal stream). Johansen and Løfting reported that, economically, eel was the most important species, but that roach was more important than eel in Randers Fjord – the estuary into which the River Gudenå flows. To attain an overview of the fish community in the downstream reaches of the River Gudenå, intensive studies were conducted with all suitable fishing gear in the lower 50 km of the stream channel and in all tributaries between the towns of Silkeborg and Randers. The same fish species were caught then as live there today, apart from salmon, which has become extinct, and zander, a recent introduction.

Hydroelectricity and dams in River Gudenå

In 1920 a 10-metre tall dam was established across the River Gudenå at Tange in order to produce electricity. Lake Tange, the reservoir that was created above the dam, submerged agricultural fields, farm houses and the main spawning grounds for salmon, under several metres of water. A fish ladder was built at the dam with the hope that it would allow the passage of migrating salmon and trout. Unfortunately, the ladder did not work and the salmon stock in the River Gudenå became extinct, while the trout stock was able to sustain itself by using suitable spawning grounds in small tributaries downstream of the dam.

In order to solve the problem a new fish ladder was built and about 500,000 trout fry were annually released into the river [2]. However, when E.M. Poulsen evaluated the situation in 1935 he recognised that neither the new fish ladder nor the restocking programme had been successful. Instead he recommended the implementation of a four-point-plan according to which:

1) the minimum legal catch size of salmon and trout should be raised from 37 to 45 cm.
2) restrictions on the use of pound nets should be imposed in the lower River Gudenå, and in the estuary of Randers Fjord from April to June,
3) the fish ladder was to be further improved
4) annual restocking of trout fry should be increased to 2 million individuals.

Following the dramatic extinction of salmon in the River Gudenå, the interest in the influence of dams and turbines on the populations of migrating fish also intensified. In addition to the hydropower station at Tange, five other hydropower dams had been constructed in the main channel of the River Gudenå. To evaluate the effects of these turbines on the survival of migrating fish, C.V. Otterstrøm conducted experiments with eel and trout that were forced to pass through the turbines. Several of the turbines were found to cause severe wounds in the downstream migrating fish, particularly the largest individuals [3]. The damage depended on the rotation rate and the number of lamellas and distance between these in the turbines. At one of the hydropower plants, 25% of the trout smolt were killed during passage through the turbines.

The fish ladder at Tange was reconstructed several times but only with very limited success [4]. Attempts were made to use electric current and lamps in order to direct the migrating fish towards the ladder. Independent evaluations in the 1980s and 1990s revealed, however, that only 5–10% of the upstream migrating trout actually passed through the ladder. In order to guide more fish to the ladder, a 50 metre wide metal fence was placed across the stream below the outlet of the turbines. Although the fence enhanced the traffic into the ladder, on one occasion it also worked as a gigantic fish trap. While the fence was lifted for cleaning, trout, salmon and zander moved in great numbers into the trailing water below the outlet from the turbines and when the fence was lowered again, the fish were trapped behind the fence. Thus, the obstructed fish passage at Tange has remained an unsolved problem for almost 90 years.

Currently the future of the salmon in the River Gudenå is uncertain; the potential solution is awaiting the decision of the Danish Parliament. A group of experts have recommended maintaining the Lake Tange reservoir because many recreational houses have been built on the banks. The proposed plan is to improve the river and the migration of fish by building a new by-pass channel alongside the lake, and by letting the majority, if not all, of the water of the River Gudenå through this reconstructed river channel. Several different models have been suggested. The by-pass channel will solve the passage problem, remove the high mortality risk in Lake Tange and give salmon and trout free access to the entire Gudenå system. Construction costs for some of the models have been estimated at amounts as high as 14 million EURO (in 2002 prices) or the equivalent of 4 km of motorway. A free river flow may turn out to be a good investment, improving recreational facilities for local people and for the tourist industry.

Electrofishing of spawning sea trout in a typical western Danish stream (Karup Stream).

Regulations on the fisheries

A heated debate on the extent of over-fishing of trout and salmon was raised in the mid-1980s [4, 5]. Comparisons of size and age data showed that the growth rate of sea-trout had declined markedly when compared with the 1930s. This was attributable to increased fish mortality. Investigations revealed that 4 out of every 10 smolt were caught in estuary pound nets [5]. Consequently, in the early 1990s the use of pound nets was banned in Randers Fjord during the main period of smolt migration, i.e. the last three weeks of May.

A few years later, in 1991, new investigations showed that the annual migration of trout smolt had more than doubled – probably due to an improved survival of trout at sea and thus greater spawning. The spawning population had almost doubled to 2,700 individuals [6]. A controversy

developed between the sea trout anglers and the commercial fishermen over the accidental by-catch of sea trout in the pound nets. In 1991, the commercial fishery in Randers Fjord took most of the sea trout catch (approx. 50%), with sport fishermen also taking a large toll (35%; Figure 8.2). When the sport fishermen realised that they caught a third of the sea trout and that the unintended catch of smolt in the pound nets could be reduced by 90% by lowering the nets so that they remained submerged at low tide, the debate on the fishing policy silenced [7]. The changes did not affect the much more important catch of eel in estuary pound nets, so the ban on pound nets could be lifted.

Salmon restocking programme in River Gudenå

In 1998, the municipalities in the town of Randers started a programme to stock one- and two-year old salmon. The aim was to try to restore the breeding stock of salmon in the River Gudenå. An aquaculture facility was built, and eyed eggs were imported from Ireland, Scotland and Sweden. Between 100,000 and 150,000 salmon smolts have been released every year since 1991. Initially, the salmon smolts were released in all parts of the river as well as at the mouth of the estuary in Randers Fjord. It was hoped that improvements of the fish ladder at Tange and the restoration of the breeding grounds in the upstream tributaries would provide suitable conditions for reproduction. Although more individuals did enter the river and several of these succeeded to pass the ladder at Tange, there was still no sign of natural reproduction. There were indications that the salmon smolts released in the upper parts of the river system experienced a very high mortality rate during downstream migration towards the sea. This was evaluated in 1995 by releasing large numbers of tagged individuals of trout and salmon in headwater streams. Calculations showed that for every 1,000 individuals released only 18 trout and 220 salmon would survive the 60-km long journey to Klostermølle where the river flows into the first large lake, Mossø. On the further 120-km long downstream course through lakes and river stretches, only 0.4 salmon smolts are estimated to survive and reach the river mouth at Randers. Thus 2,500 smolts would need to be released in the headwaters for just one individual to survive and be able to leave the river system [8].

The extensive mortality of smolts during downstream migration has been attributed to the numerous predators in the lakes of the lower River Gudenå, and the predator-naïve behaviour of the stocked smolts. In addition, the lakes reduce the migration velocity and thus prolong the risk of predation by fish and birds. Pike are believed to be the greatest mortality risk in the lakes while zander are the most important predators in the river channel [9].

Over the past 100 year fishery studies have revealed a complex picture regarding the causes for the decline of sea trout and the extinction of salmon in the River Gudenå. It is not possible to identify a single agent and disregard the rest; there are numerous factors, of which some may be interconnected. The low number of spawning fish cannot be explained solely as a result of over-fishing, migration obstacles or pollution. The extensive mortality of smolt arises from injuries when passing the turbines of the hydropower stations,

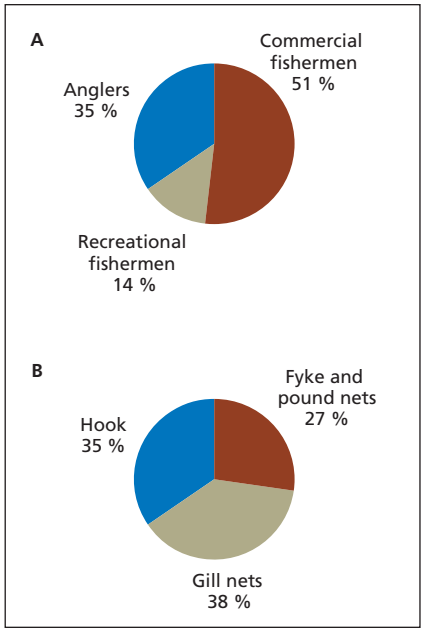
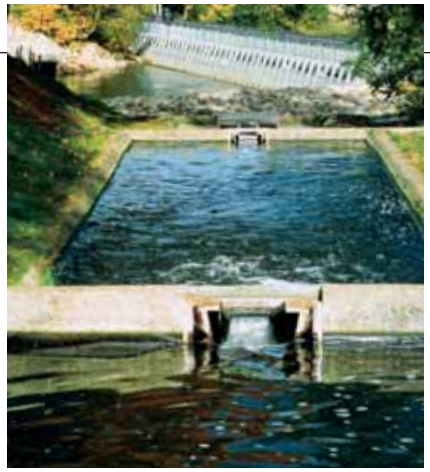


Figure 8.2 The catch of 2,750 sea trout in Randers Fjord in 1991 distributed in relation to type of fishermen (A) and fishing equipment (B) [6].

A non-migratory brook trout (above) and a migrating sea trout smolt (below).

predation by numerous piscivores in the lakes and unintentional by-catches in estuary pound nets. The poor survival of eggs and fry is not only due to poor water quality but also to unfavourable physical conditions and lack of breeding grounds. Thus, the recovery of prominent salmon and trout stocks will require many initiatives at different temporal and spatial scales.



A fish guidance fence and fish ladder at the Tange Hydropower Dam on the River Gudenå.

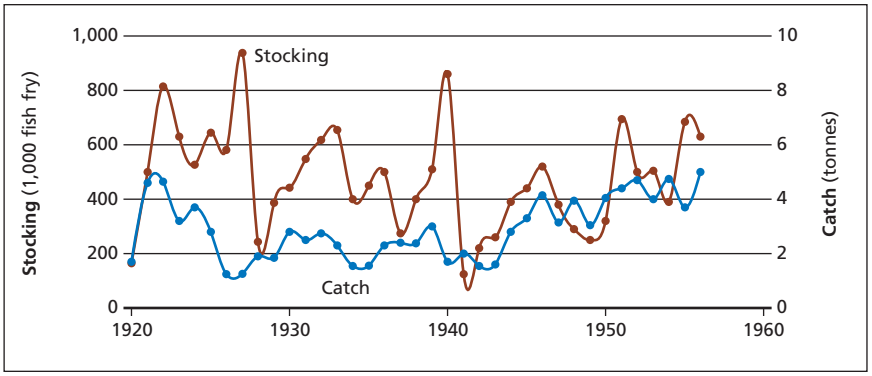


Figure 8.3 Improved trout fry stocking schemes since 1937 have generated a consistent relationship between numbers stocked and the annual catch of sea trout in tonnes. Data from the River Gudenå and Randers Fjord estuary [10].

National restocking plans and electrofishing surveys

From a Danish perspective, the River Gudenå was the first place where it was clearly recognised that fishery management was urgently needed in order to prevent further deterioration of the commercial fisheries. It is interesting to note that, at the start of the 20th century, the argument for improved management was based on the long-term interests of the fisheries, not on the endangered stocks themselves. Although useful as an example, the River Gudenå was not the only place where management schemes were about to incorporate the idea of "sowing before harvesting". According to Otterstrøm's "Rational Restocking Plan for Trout" implemented in the late 1930s, the fry should be distributed among all Danish streams according to ability of the watercourse to support the growth and production of trout. Because of this new practice a positive relationship between stocking and subsequent catch of trout emerged around 1940 (Figure 8.3).

Electrofishing was introduced in Denmark in the early 1950s.An electric potential is established in the water between a stationary cathode and an anode that is moved by the operator. All fish are briefly paralysed when they come into proximity with the anode and can then be removed with at pond net. The fish can be identified to species, sexed (where possible), counted, measured and weighed before being returned to the stream. Repeated electrofishing of the same reach allows estimation of population parameters such as density, mortality, age structure, biomass and production [10].

By combining visual evaluation of the stream habitat quality and the trout population density, a supplementary stocking programme can be devised, and in this way an efficient strategy to optimise the fish yield was attained during the 1970s. The continuous restocking of trout soon became an integral part of fishery management in most Danish streams. By 2004, restocking of trout has reached a standardised form that involves close collaboration with local angling clubs. Members participate in the practical work during electrofishing surveys, gather broodstock for artificial propagation in hatcheries, and release the reared fry.

Electrofishing also revealed that dams and other obstructions in the streams had blocked the access of diadromous fish to the headwaters with the result that many local populations had either declined or totally disappeared. Therefore, environmentalists and anglers demanded that fish passes be established at all obstacles to fish passage. A large number of fishways were built between 1965 and 1985, but their efficiency was seldom tested afterwards. Because of this uncritical construction, most fish ladders were not functional. Common errors were to feed the ladder with too little water relative to the river discharge, and inappropriate choices for the location of inlet and outlet of the ladders. If fish follow the main current, they easily get misled away from the fish ladders. Fish ladders are best placed as close as possible to the point where natural migration is impeded.

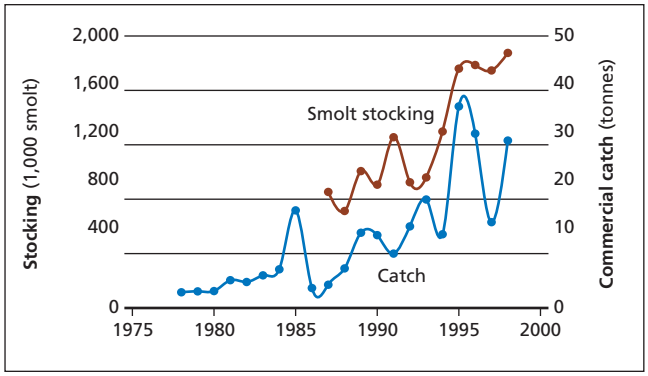


Figure 8.4 Annual stocking of smolt and the commercial catch of sea trout in Denmark correspond.

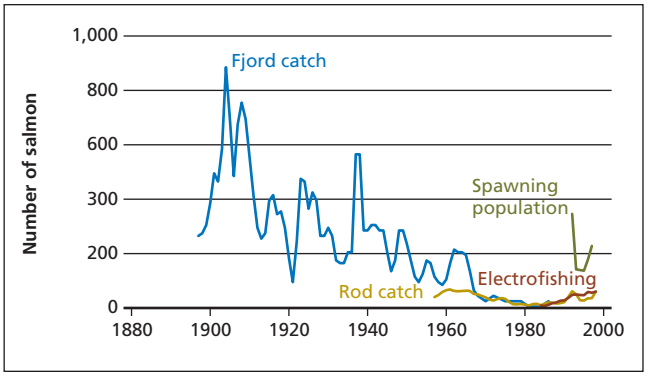


Figure 8.5 The twentieth century was catastrophic for salmon in the River Skjern. Commercial catches of salmon in the Ringkøbing Fjord and catches by anglers in the river are shown together with estimates of the total spawning population.

Attractive fish populations

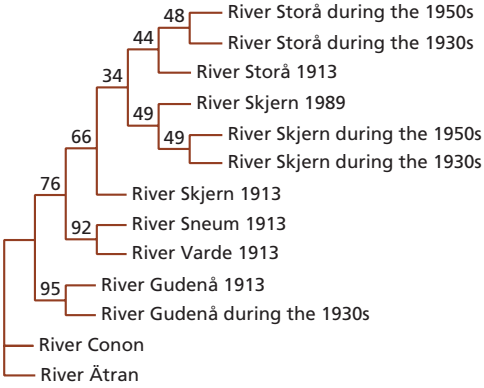
During the 1980s the cost of fish stocking was included in the Budget of the Danish Government. When the National Rod License – required for angling in freshwater – was passed in 1993 it was decided that the income should be used for stocking fish and for administration and research on fish management to improve the stocks. So far, resources have mainly been used for rehabilitation of sea trout and, to a smaller extent, on eel and salmon, reflecting the principle species of interest for the recreational fisheries in freshwater.

Trout

The widespread release of small trout over the past 30–40 years has increased the number and size of Danish trout populations, although it is difficult to separate this effect from that of habitat improvements and improved sewage treatment. Only a few watercourses are currently completely devoid of naturally reproducing trout. The impact of trout stocking can be seen in the landing of sea trout in the Danish harbours – omitting landings on the island of Bornholm in the Baltic Sea where most sea trout derive from Swedish rivers. The official statistics show that the commercial catch of trout has doubled along with the doubling of stocking intensity (Figure 8.4). This suggests that the commercial fishery has benefited from the stocking programme as well as from overall improvement of the environmental quality of the freshwaters.

New DNA-analyses have shown that there is a drawback to the massive stocking programme. Wild populations of resident and migrating trout face the risk of competition and hybridisation with hatchery trout bred in aquaculture facilities. DNA analyses have revealed that in some rivers the stock consists entirely of "pond trout" or their genes are mixed with the original wild stock. In several other rivers distributed throughout Denmark, however, the wild stocks are small, but still genetically intact and they are obviously much more efficient at reproducing than the introduced "pond trout". In the Karup Stream, for example, more than 300,000 hatchery-bred fish were released between1990 and 2000, but more than 90% of the fry were genetically identical to the wild stock. Among the sea trout virtually all were original wild fish, while the proportion of hatchery-bred fish was larger among the resident brown trout, which spend their entire life in the river. It appeared that while sexually mature dwarfs of hatchery-bred fish were capable of fertilising some of the eggs of spawning sea trout, they themselves were not able to migrate successfully to the sea.

Apparently hatchery fish are genetically deficient or poorly adapted to the complex and fine-tuned life cycle of sea trout which involves migration to the sea, growth in the sea for one to several years and return to the home river to reproduce. Therefore, if the objective is to ensure a native self-reproducing fish stock it is a bad idea to release foreign fish and fish from hatcheries. It is also bad business as the introduced fish generally have much higher mortality rate and are very inefficient at repro-



Genetic analysis was made on old salmin scales.

Figure 8.6 "Genetic distance" between salmon stocks in different Danish, Swedish (River Ätran) and Scottish (River Conon) rivers [11].

ducing compared to the well-adapted wild stock. Moreover, in certain circumstances released foreign fish can become strong competitors for the wild stock in the stream and severely reduce the survival of the fry and young of the wild stock. As a result, much fewer native fish develop and migrate to the sea, thereby diminishing both the commercial catch and the size of the reproductive population returning to the river for spawning.

Native salmon stocks

Since 1993 salmon have been released in streams that have been known historically to have supported natural salmon populations. The objective of the salmon rehabilitation plan was to re-establish self-sustaining stocks in the streams. However, only in the River Skjern has a natural, reproducing population of salmon survived with certainty. There are indications that the long-term decline of salmon in the River Skjern has now come to an end, as a combined result of efficient fishery regulations in the estuary Ringkøbing Fjord, greater water exchange through the sluice separating the North Sea and the estuary and improved passage of fish across the physical obstructions in the river (Figure 8.5). The other large rivers in Jutland offer the potential to support salmon stocks in the future. In the Varde Stream, Sneum Stream, Ribe Stream and Vidå Stream a comprehensive survey for surviving individuals of the native salmon stock has been conducted before stocking is continued. Captive breeding and release of fish of the native stock is preferred to that of foreign stocks.

DNA analyses of preserved salmon scales have shown that salmon caught in the River Skjern are derived from the native stock. The genetic composition of the living population closely resembles that found in analyses of DNA from scales of fish caught in 1913 and in the 1930s and 1950s [11]. Similar DNA analyses of salmon caught in other Danish rivers in the past, have also shown that the genetic distance between stocks from different rivers reflects the geographical distance between the rivers (Figure 8.6). It has therefore been recommended to search carefully for remnants of the native populations in the Danish rivers and, if they still exist, to use these in the breeding programme whenever possible. In two streams, namely Ribe Stream and Varde Stream, remnants of the original salmon stocks have recently been found.

When local stocks have become extinct, it is better to release fry from "neighbouring" stocks rather than use fish from more distant populations [12]. Fish from the native populations are adapted over many thousand years to the characteristic environmental (e.g. temperature regime and water chemistry) and biological (e.g. prey, competitors and predators) conditions at the local sites and they consequently perform better than foreign fish.

The decline of eel

Eel populations have experienced a dramatic decline during the 20th century (Figure 8.7). The collapse of the Danish eel fishery resembles that observed in the rest of Europe; catches have diminished and the numbers of glass eel reaching the European coast have declined year after year. Nonetheless, the intensive fishery has continued in Denmark. A study in the Sound between Denmark and Sweden revealed that the fishery is so efficient that of every five silver eel captured, tagged and released, one is recaptured within a few weeks. The eel fisheries industry has continued to show an

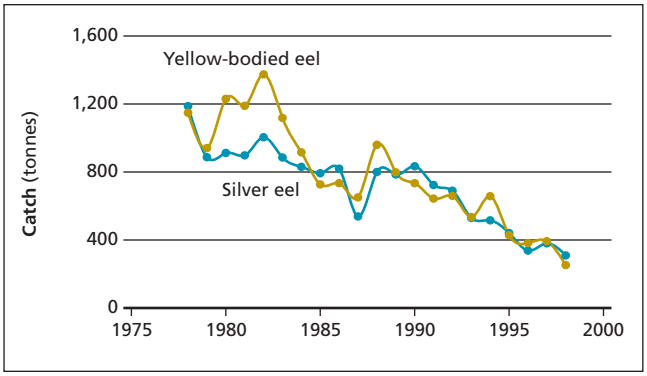


Figure 8.7 The number of eel is declining steeply, here shown in terms of the total commercial catch of yellow and silver eel in Denmark.

alarming lack of concern and responsibility for these issues: "As many silver eel as possible should be captured before they migrate out of the national coastal waters". The attitude is based on the belief that a sufficient number of silver eel will succeed to spawn and thus secure an unchanged recruitment of glass eels, independent of the fishing intensity. The data do not support this belief. On the contrary, the number of glass eel that reached Western Europe in 2000–2002 was only a few percent of the 1950–1980 numbers. Sustainability has never been on the agenda of the eel fisheries and the result has been severe over-fishing.

In Denmark, silver eel has no legal minimum size or a closed season. Fishing for silver eel is even permitted in river outlets, the transitory zones where all other fisheries are normally prohibited. Therefore, if the decline of European eel fisheries continues, a marked change in the attitude is needed. The seriousness of the situation has grown from being a question of preserving the size and health of the eel population, to preserving the future existence of the European eel as a species. Fishery biologists have recommended the enforcement of precautionary principles in the management of European eel, as they have not as yet been able to identify, with certainty, the key factors controlling the size of the eel stock. The overall recommendations are to maximise the growth of eel populations and minimise all controllable mortality factors. To attain a sensible management plan, however, an agreement is needed between all European eel-fishing countries. This agreement has not been reached and as yet no master plan has been implemented. There are several reasons for this lack of determined action. The most important reason is insufficient knowledge of the key factors regulating the population size of eel.

New threats

New threats to fish populations in streams will emerge in the future but are difficult to foresee. The growing use of genetically modified organisms for food may well transfer to the aquaculture industry. It is possible that genetically modified farmed fish could escape to the streams and influence wild populations through hybridisation. Also chemical pollutants, their degradation products, and hormone-like substances constitute a risk to the fertility of wild populations e.g. by causing inter-sex and disturbing sexual maturation. Currently there is a lack of knowledge of the long-term and wide-scale importance of these potential threats.

The immigration and introduction of foreign and native species of animals and plants can influence the composition of fish communities. One example is the establishment of predaceous mink populations in many Danish streams. Large numbers of this American mink have escaped from fur farms, and could be having a strong impact on stream fish communities. Also the quantitative influence on fish communities of the decline and recent recovery of fish-eating cormorants, grebes, egrets, seals and otters is unknown. Beaver has recently been re-introduced to one Danish stream system and their dam-building behaviour may have a strong impact on stream habitats, obstructing the free flow of water and forming wetlands and pools. A decline in the abundance of fish species preferring fast flow in the stream channel (e.g. trout, salmon and minnow) may be expected whereas species preferring sluggish flow in pools and backwaters (e.g. bream, roach, perch and pike) are likely to increase.

Ongoing urban expansion poses another threat to streams and their fish communities. Abstraction of groundwater reduces discharge in streams and increases the risk of small streams drying up temporarily. Conversely, efficient drainage of streets, buildings, car parks, etc. quickly returns precipitation over large areas to the streams. As a result, temporal discharge patterns become more erratic with associated extreme variations in current velocity, erosion/sedimentation, temperature and oxygen concentration in the

A sea trout smolt tagged with a radio transmitter placed in the abdominal cavity with the antenna sticking out through a small hole.

streams, generating greater physical and physiological stress on animal and plant life. For example, increased sediment input could reduce salmonid egg survival in spawning grounds. In low-gradient Danish streams, sediment deposition represents a common danger to the survival of fish eggs buried in the stream bed.

Fish stocking can also represent a threat to wild populations. Stocked fish are often raised in aquaculture facilities and as such are poorly adapted to wild conditions. When released, they can potentially inter-breed with wild populations, diluting the native genetic strains. Furthermore, fish mortality can be increased in wild populations due to greater fishing intensity on the artificially enhanced populations. In Denmark, the stocking of trout smolts at the mouth of streams and in the marine coastal waters has increased due to the pressure from sports fishermen wanting to catch more sea trout along the coast. The stocked smolts have never experienced the taste from "a home stream" unlike natural trout or smolt released in the streams. The spawning migration of such straying sea trout is thus probably less precise. The genetic consequence of straying on the native populations is not well known, but the risk of outbreeding is probably highest in small streams with vunerable populations.

New options

Several of the Danish plans initiated after the UN conference in Rio de Janeiro in 1992 also provided potential for improvements in stream habitat and biodiversity. Among these were initiatives to increase forest area, shift from conifers to a mixture of broad-leaved trees and change to a more extensive management of the forest to allow variations in landscape types and to encourage biodiversity. Currently, there are many physically homogenous streams in conifer plantations, these act essentially as drainage ditches and have low diversity because of their uniform morphology, acidic waters and tendancy to dry up during summer. One of the proposed plans is to bring water back to the forests and to aim towards a more natural hydrology, closing drainage tubes and ditches and allowing swamps, lakes, springs and streams to re-establish or improve. Forest streams have a major advantage because most are headwaters with little or no intensive management e.g. weed cutting and dredging. Therefore, forest streams may be ideal for attaining stable spawning grounds for salmonids.

There is also potential for the improvement of fish communities in streams in the open land if intensive agricultural practices along streams are abandoned and natural wetlands are given room to develop. This may result in a more natural abundance and diversity of the semi-aquatic flora and fauna. More terrestrial insects along the streams would serve as food for most fish species. Another goal is to use the potential of wetlands to reduce the dissolved and particulate nutrient loading of streams. Eutrophication, anoxia, and fish kills are regrettably still common in many Danish streams, lakes and coastal waters.

Fish research has been introduced to many new technical options. The possibility of examining the undisturbed behaviour of fish in their natural environment has improved considerably. By equipping individual fish with minute radio transmitters it has become possible to follow every movement, muscle contraction and heartbeat while the fish lives relatively undisturbed under field conditions. Small instruments can record the continuous changes in light, temperature, oxygen and current velocity in the environment. New automatic instruments can count the numbers, measure the size and take pictures of fish each time they pass obstructions during upstream or downstream migrations in the streams. The "fish counters" follow the principle that the fish intercept infrared light beams as they pass, and thereby they generate a silhouette which is used to determine the direction of the movement, the swimming velocity, the size and the identity of the species. Every picture can be saved electronically and a programme for pattern identification can discern plant debris and stream plants from the true fish counts. Such automatic fish-counters should greatly improve the control of fish passages and offer quantitative measures of the numbers of migrating fish.

A male salmon electrofished from the River Skjern to be used as broodstock for producing 1 and 2-year old salmon smolts for restocking.

Trends in recreational fishery

In 1995 the United Nations' Food and Agriculture Organisation, provided a code of conduct for responsible fisheries, declaring that: "States and users of living aquatic resources should conserve aquatic ecosystems. The right to fish carries with it the obligation to do so in a responsible manner so as to ensure effective conservation and management of the living aquatic resources".

So far, Germany is the only European nation requiring sport fishermen to follow a short course and pass an exam before they can receive a license to fish in natural waters. The applicant must show some basic knowledge on fishery biology, environmental conditions, handling of fish and fishery legislation. The objective of the course-exam-license system is to improve the management of aquatic ecosystems. In Germany the green movement has focussed on the well-being of animals and this has generated a push for improving the ecological knowledge and the proper behaviour of sport fishermen [13]. In France 500 schools have been established that offer courses in recreational fishery [13]. Both examples suggest that courses and insight into sport fishery will probably grow in Europe in the future and that education may stimulate interest in the sport.

A common practice in recreational fisheries is to release hatchery-bred salmonids as a basis for the fishery in small, often excavated, artificial lakes. Such put-and-take lakes have spread throughout Europe during the 1980s and are still growing in numbers. Most Danish put-and-take lakes are stocked with rainbow trout weighing from 0.5 to 3 kg. Apparently there is a strong demand for safe recreational fisheries for families with small children in friendly settings. In Denmark put-and-take fisheries do not take place in streams, but only in ponds or lakes where the fish are unable to escape.

Catch-and-release is another scheme that is expected to spread in the future. The idea is to release fish that are caught and to do it as gently as possible. The objective is to optimise the chance of an individual fish surviving several catches and to allow it to grow to an attractive size. Therefore, catch and release is adopted in closed waters and with non-migratory fish so that the same person or members of the same fishing club have a greater chance of catching trophy fish. Anglers fishing for carp mostly use catch-and-release, but the method has also been used in stream fisheries on brown trout. There are strong indications that this will be the only acceptable management strategy if fishing on threatened populations such as the salmon in the River Skjern is to be permitted. The North Atlantic Salmon Conservation Organisation has published a pamphlet describing how to treat a hooked salmon to ensure its survival upon release.

Fish management

The management of fish populations in Danish streams over the centuries illustrates an approach that tried to satisfy many conflicting interests at the one time. All severe impacts on streams and their fish communities have been accepted, including straightening, dredging, input of sewage and polluted drainage water, water abstraction for domestic use and for fish ponds, and hydro-electric power production. Dams and other obstructions have isolated many fish populations within small, restricted areas. Where migrating populations have gone extinct, obstructions have increased the vulnerability of non-migrating populations to pollution.

Even though Danish streams as a whole have more fish species today than in the past, local species richness is probably much lower because of the overall deterioration in the physical and chemical condition of stream habitats. In order to restore the species richness of stream communities it is essential to ensure the re-establishment of habitat heterogeneity, unhindered passage and relatively stable stream beds.

Fortunately, it is still possible to improve the relationships between environmental objectives and the practical management of streams and their fish populations. Richer and more robust fish populations can develop by means of well-founded, co-ordinated, and targeted efforts.

Dense vegetation of pondweed in lower River Gudenå.

9 Water plants past and present

How has the condition of the environment developed during the last 100 years? This is an important question because the conditions of the past influence those of the present, and knowledge about this development makes it possible to evaluate the causes of changes in species richness, species composition and environmental quality. Here we compare old and contemporary studies of the Danish stream flora.

Early studies of water plants

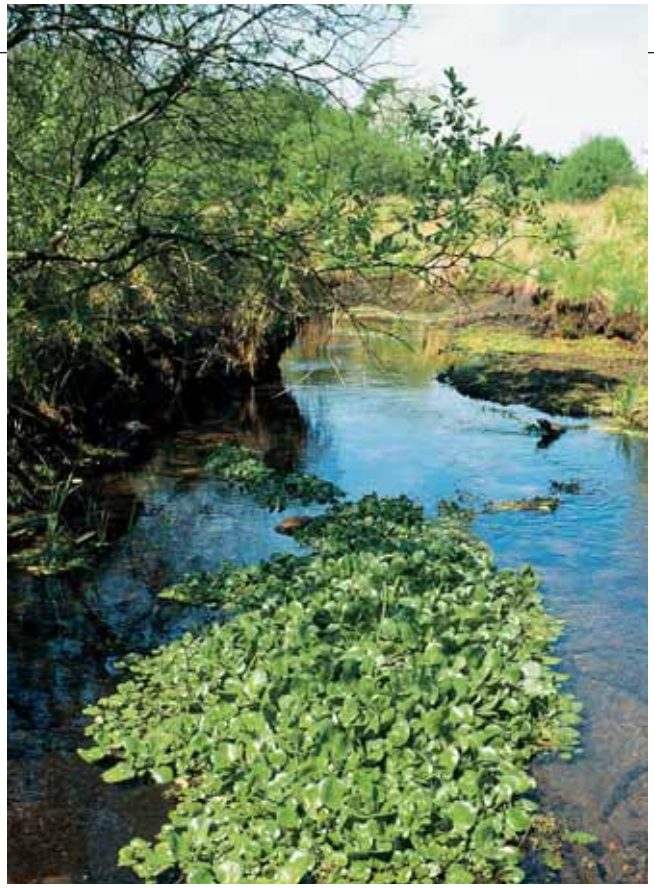
As early as the late 19th century there was a strong interest in natural history in many European countries. This interest resulted in several studies of the stream flora in Denmark [1, 2]. We have searched early publications and excursion reports from 1870 to 1920 for information on the Danish stream flora, and additionally included information from the main Danish herbarium at the Botanical Museum of Copenhagen. Based on this material we have compared old species lists from 27 streams distributed across the country with species lists obtained from our own study on the vegetation in 208 streams in Denmark carried out about 100 years later. In this comparison of old and recent studies, 13 reaches are identical and therefore directly comparable.

We consider the comparisons reliable because the species identification has been carefully undertaken and based on almost identical identification keys in the past and present studies. However, the botanists 100 years ago had a particular interest in pondweed species [1, 3], and therefore we will focus on the historical development within this group.

The stream environment 100 years ago

Maltreatment is probably the best word to describe the use and management of streams during the last 100 years. The biological and ecological value of the streams was completely ignored in the 19th and 20th century in favour of using the streams for drainage, land reclamation and diversion of wastewater. However, improved wastewater treatment and an increased focus on the ecological quality of the stream environment, during the past 10 to 25 years, has been a basis for improving the flora and fauna in streams.

What kind of maltreatment have Danish streams, along with other lowland streams around the world, suffered during the past century? The four most important impacts on streams



Today's streams receive more organic pollution and nutrients from towns, farms and cultivated areas compared to 100 years ago.

and their vegetation are: straightening of stream meanders, weed cutting, organic pollution and eutrophication.

More than 90% of the Danish streams have been channelised in order to drain wetlands, and the proportion is similarly high in other countries with high agricultural land usage. Most channel regulation was carried out during the period 1850–1965. The most severe regulation, using of heavy machinery, occurred towards the end of this period. Regulation meant that streams lost their meanders as well as the natural sequence of riffles and pools. At the same time many of the smallest creeks and streams were piped. Several thousand kilometres of streams have disappeared and the rest have lost much of their physical heterogeneity (see Chapter 1). The channelised streams quickly divert water from the catchment resulting in increased differences between winter and summer flow, and increased flow after heavy rainfall.

The loss of area and habitat heterogeneity in the streams would be expected to have lead to a reduction in the total number of species both in the entire stream and in some individual reaches. This prediction is based on the universal ecological concept that: species number and diversity increase with increased area and habitat diversity [4]. High-flow variation results in alternating erosion and sediment deposition zones on the stream bed. This reduces plant species richness because only a few disturbance-tolerant species with high recolonisation ability can tolerate such conditions [5]. We would expect a decrease in species specialised to live at permanently high water velocities or at consistently low velocities e.g. in backwaters. Several of the latter species are also common in lakes and were previously widely distributed in streams, but have now nearly disappeared.

Already in the late 19th century weed cutting was practised in some streams, but in most streams the practice was not introduced until after 1920. Weed cutting and dredging of the stream bed by use of machinery intensified between 1960 and 1990. Nowadays the vegetation is cut at least once a year in nearly all Danish streams, and the situation is similar in many other lowland areas in the world. In this highly disturbed environment we may expect the dominant species to be those that are able to quickly regrow and form new plant stands from individuals or fragments that have survived the cutting. It may also be species that are efficient dispersers and that quickly establish new populations on a bare stream bed that thrive under such management. Efficient dispersal and settlement capability, and high growth capacity are therefore necessary characteristics of plant species surviving a disturbed stream environment.

Species with high growth capacity have an advantage in a nutrient-rich stream environment. Lowland streams are often nutrient-rich because of the intimate contact with the surrounding land, from which nutrients are released continuously. The nutrient concentrations are especially high in streams surrounded by pastures or arable fields.

Water is only retained in the stream for a short time due to the continuous current, and only a small proportion of the nutrients are used in the stream. Most nutrients are transported to downstream lakes and coastal areas. Moreover, the streams receive much more organic pollution from urban and agricultural areas today than 100 years ago. At that time, the human population was lower, there was less sewage, and the use of fertiliser was minimal.

It is a well-known fact that most lowland freshwater systems in Europe have been subjected to extensive organic pollution over the last 100 years. In Denmark, the impact on streams was probably most severe between 1950 and 1970. Wastewater pollution has certainly impoverished the fauna in the streams, but the plants were also affected because species able to survive on unstable mud sediment facing periodic anoxic conditions were favoured while more susceptible species declined in abundance. However, the situation has improved with enhanced wastewater treatment starting in the late 1970s.

Eutrophication of Danish streams has been widespread and extensive both in terms of dissolved inorganic ions and total nitrogen and phosphorus. Nowadays, nitrate concentrations in streams are typically 1–4 mg N/l, probably 5–10 times higher than 100 years ago [6]. Typical concentrations of total phosphorus are also high (0.1–0.3 mg P/l [6]). The nutrient-rich conditions favour nutrient-demanding, eutrophic species, and restrict oligotrophic species, either because the latter cannot tolerate high nutrient concentrations or they are out-competed by eutrophic species.

***Callitriche* species (starwort) are common in Danish streams today.**

Prediction and testing of changes

The strategy that we adopted for analysing vegetation changes in Danish streams during the past century was based on known changes in physical and chemical characteristics of streams during the period, and established ecological rules. This allowed us to set up testable predictions of expected changes in the vegetation that could be rejected if they were not supported by the observed situation in present-day streams.

Stream conditions have changed towards smaller surface areas, reduced habitat variation, high disturbance and unfavourable stream bed characteristics. Therefore, we predict that: 1) species richness and diversity of the vegetation have been reduced, and 2) it has become more common for a few species to dominate plant communities. We also predict that: 3) eutrophic species, with high growth rates and high dispersal capacity have become more frequent compared to species with slow growth and poor dispersal capacity, due to high disturbance and eutrophication in streams. Species expected to have increased are those with an ecological ruderal strategy (*R*-strategists *sensu* Grime [7]). Species expected to have decreased in number during the period include species with low competitive ability that are only able to dominate under oligotrophic and stable conditions (*S*-strategists), large species with high competitive

Box 9.1 Ecological plant indices

Eutrophication indices

A morphology index assesses the architecture of pondweed species and thereby their ability to grow up through the water column and ramify at the surface to cope with turbid waters. Species are divided into three groups based on their height: 1 is species <0.5 m, 2 is species 0.5–1.0 m, 3 is species >1.0 m. The ability to ramify near the surface or develop floating leaves is scored as: 1 for species without ramification or floating leaves, 2 is intermediate, 3 for species that often ramify or easily develop floating leaves.

A trophic index describes the species distribution in streams according to their trophic level. The 16 pondweed species in Danish streams are ranked from 1, which is the species in the most oligotrophic streams, to 16, which is the species in the most eutrophic stream. It is not known conclusively whether this ranking accurately reflects the nutrient demands of the species.

Dispersal index

The ability to disperse at a regional scale, within and between stream systems, by means of stem fragments, specialised dispersal organs and seeds, is assessed on a three-level scale:1 describing low, 2 intermediate and 3 high dispersal ability. The ability to disperse on a more local scale, within a site, is assessed by the ability of the root system to disperse underground: 1 is species without a large root system; 2 is species with root systems <0.5 m in diameter; 3 is species with root systems >0.5 m in diameter. A collective dispersal index is the sum of the regional and the local dispersal indices.

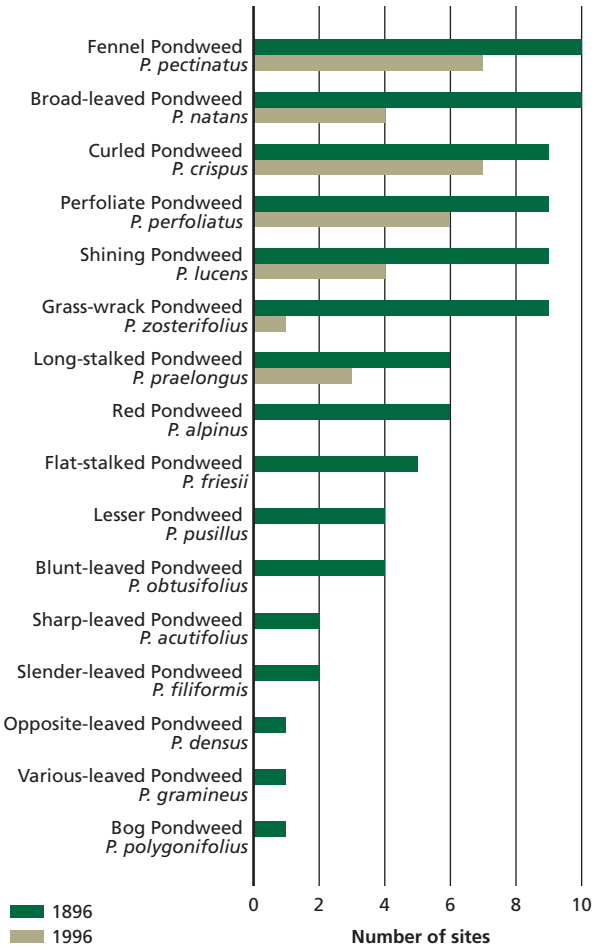


Figure 9.1 Frequency of 16 pondweed species at 13 sites surveyed in 1896 and 1996 [9].

ability and those demanding relatively high nutrient concentrations and low disturbance (*C*-strategist).

It is possible to determine the species richness and species composition in the stream vegetation today and 100 years ago and to test if any changes have taken place. It is more demanding, however, to examine if the species composition has changed towards a higher frequency of disturbance tolerant and eutrophic species with high dispersal ability. To do that, we need to express the ability of the different species to tolerate disturbance and eutrophication. Then we can compare the ecological strategies of species in previous and contemporary communities.

By means of the literature we have found three species traits among the pondweeds that may be described by numerical indices (Box 9.1). A trophic index developed for British streams ranks the species according to their occurrence in streams with low and high nutrient concentrations [8]. An index characterises the morphology

	Relative Freqency		
	1896	1996	
Sharp-leaved Pondweed	0.11	0	
Red Pondweed	0.41	0	*
Curled Pondweed	0.41	0.30	
Opposite-leaved Pondweed	0.07	0	
Slender-leaved Pondweed	0.15	0	
Flat-stalked Pondweed	0.33	0.02	*
Various-leaved Pondweed	0.15	0	
Shining Pondweed	0.52	0.03	*
Broad-leaved Pondweed	0.74	0.18	*
Blunt-leaved Pondweed	0.23	0	*
Fennel Pondweed	0.48	0.18	*
Perfoliate Pondweed	0.59	0.15	*
Bog Pondweed	0.04	0	
Long-stalked Pondweed	0.41	0.08	*
Lesser Pondweed	0.33	0.01	*
Grass-wrack Pondweed	0.56	0.01	*

Table 9.1 Relative frequency of 16 pondweed species in 1896 and 1996 at 27 and 208 sites, respectively. For species marked with * there is a low probability ($p<0.05$) that the decrease in occurrence from 1896 to 1996 is coincidental.

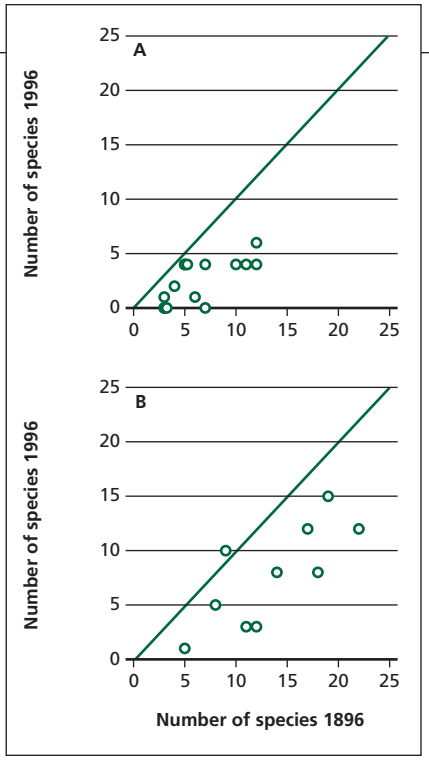


Figure 9.2 Number of pondweed species (A) and total number of submerged species per site (B) at 13 and 11 stream sites, respectively. The sites were surveyed in 1896 and 1996. The 1:1 line indicating no change in species occurence is shown.

of the plant species and their ability to grow up through the water column and ramify near the water surface in order to capture the maximum amount of light. Plant species more capable of withstanding the poor light conditions usually accompanying eutrophication, score higher. A dispersal index evaluates the dispersal ability of the species locally in their habitat and regionally over greater distances within the stream system. Because experimental work is lacking we were unable to assess the growth rate of the species and the direct tolerance for weed cutting.

Drastic decrease in pondweed vegetation

We found substantial differences in species richness and composition between the past and present pondweed vegetation. Pondweed species were very common in streams 100 years ago but most are rare today. At the 13 survey locations that are identical in both studies, there were 16 species in 1896, but only 7 species in 1996 (Figure 9.1). The number of pondweed species and the total number of submerged species per site have also decreased markedly over the period (Figure 9.2). If we include all the locations that were surveyed, 16 pondweed species were found across 27 sites in 1896, but only 9 species at 208 sites surveyed in 1996 (Table 9.1).

In summary, 7 out of the original 16 species were not even observed in 1996, 8 had decreased in abundance, and only one species (curled pondweed) has maintained the same abundance.

	Dispersal index	Morphological index	Trophic index	Ranking 1896	Ranking 1996
Common species in 1996	*	*			
Bog Pondweed	4	4	6	10	12
Fennel Pondweed	6	6	16	12.5	14.5
Perfoliate Pondweed	4	4	14	15	13
Curled Pondweed	6	4	15	10	16
Broad-leaved Pondweed	6	6	5	16	14.5
Rare species in 1996					
Bog Pondweed	4	4	1	1.5	4
Flat-stalked Pondweed	2	2	12	7.5	10
Blunt-leaved Pondweed	2	2	2	6	4
Grass-wrack Pondweed	2	3	10	14	8.5
Shining Pondweed	4	4	13	12.5	11
Various-leaved Pondweed	4	4	3	4.5	4
Lesser Pondweed	2	2	7	7.5	8.5
Red Pondweed	4	4	4	10	4
Sharp-leaved Pondweed	2	2	9	3	4
Slender-leaved Pondweed	5	2	11	4.5	4
Opposite-leaved Pondweed	6	2	8	1.5	4

Table 9.2 Indices describing dispersal ability, morphological ability to cope with turbid water, and trophic ranking of 16 pondweeds. The ranking of species in 1896 and 1996 ranges from 1 (most rare) to 16 (most common). In 1996, common species were found at 50% of the sites while rare species were found at less than 5% of the sites investigated. * indicates significant differences between the groups.

Greater tolerance for disturbance and eutrophication

We tested our third hypothesis, on trajectory changes in the stream vegetation during the past 100 years, using two methods. We compared the mean disturbance and eutrophication index values between frequently-occurring species in the past and contemporary surveys, and between rare species in the two surveys. Moreover, we studied the relationships between indices and the frequency of the species in the past and contemporary surveys.

The pondweed species occurring most frequently in the streams today have a higher dispersal index than the species, which have disappeared or decreased in abundance (Table 9.2). Today, the abundance of the pondweed species is in better accordance with their dispersal ability than 100 years ago (Table 9.3).

The pondweed species most abundant in the streams today have a higher morphology index than the species that have disappeared or become rare (Table 9.2). Remember that this morphology index describes the ability of the species to grow tall and ramify near the water surface as a response to bad light conditions. Species relative abundance is more strongly correlated with their trophic index today, than in the past, while the correlation with their morphology has not changed significantly (Table 9.3).

Species with high tolerance for disturbance and nutrient-rich conditions have become more common while nutrient-poor species and species susceptible to disturbance have decreased in frequency or disappeared completely. The group containing the nutrient demanding species with high dispersal ability (*R*-strategists) includes the four pondweed species: *Potamogeton pectinatus*, *P. perfoliatus*, *P. crispus* and *P. natans*. The nutrient-poor species (*S*-strategists) which have strongly decreased includes *Potamogeton praelongus*, *P. alpinus* and *P. filiformis*. The group of slow growing species that do not tolerate disturbance includes *Potamogeton polygonifolius*, *P. zosterifolius* and *P. lucens*. These large broad-leaved

	Ranking 1896	Ranking 1996
Dispersal index	0.15 (0.57)	0.37 (0.15)
Morphological index	0.58 (0.02)	0.49 (0.06)
Trophic index	0.43 (0.10)	0.62 (0.02)

Table 9.3 The frequency of pondweed species shows stronger relationships (the figures are correlation coefficients) between dispersal ability and nutrient demand in 1996 than in 1896. Small values in brackets indicate a low probability that the relationships are coincidental.

Water Mint

species were previously very common, but are now quite rare. For example, we only found *P. zosterifolius* at one of 208 stream localities examined in 1996 while it was present at 56% of the localities examined in 1896.

There are other observations that show the substantial influence of disturbance on the aquatic plant communities. Past surveys found that, not only were there many pondweed species in the streams, but that they also formed large continuous beds. Baagøe and Kølpin Ravn reported that the broad-leaved pondweed species in 1895 created macrophyte stands up to 60 m long in the two largest rivers in Denmark [2], but these were smaller where weed cutting had taken place. In contemporary streams with frequent weed cutting we never find such large stands of pondweeds. New studies confirm that stream vegetation is richer in species and forms a more complex canopy, where it has not been cut for over two decades compared to reaches that are cut once a year [10].

Current predominant stream plants

At present Danish stream vegetation is dominated by species that prefer nutrient-rich conditions and tolerate disturbance. Such species include *Potamogeton crispus* and *P. pectinatus*, which are ranked as number 9 and 11, respectively, on the list of the most frequently occurring plants in Danish streams (Table 9.4). *Sparganium emersum* (Unbranched Bur-reed) and *Elodea canadensis* (Canadian Waterweed) are the most common species and the predominant vegetation in about 50% of the Danish streams. *Callitriche* species (Starworts, mainly *C. cophocarpa* and *C. platycarpa*) and *Ranunculus peltatus* (Pond Water-crowfoot) are also placed higher on the list of abundance than the pondweed species. The most frequent stream plants all have high growth capacity and good dispersal ability. *Sparganium emersum* tolerates cutting well because it grows from the basal meristem, which usually survives cutting, or from the vigorous underground parts buried in the stream bed. *Elodea canadensis* disperses naturally by shedding stem fragments and this strategy is enhanced when the population is disturbed by cutting. The heavy fragments float with the current but easily sinks to the bottom to form roots and regrow at new sites downstream.

Detached stem fragments of species of *Callitriche* and *Ranunculus* also disperse efficiently with the current until caught by stones or other obstacles. They then develop adventitious roots from the stem and become established on the stream bed Moreover, *Callitriche* and *Ranunculus* can disperse by seeds. The importance of seed dispersal is only known from a few studies, but it is likely to be significant for dispersal over long distances and for establishment in new territories, while dispersal by stem fragments is more important to sustain the populations within the colonised stream.

Many rare stream plants

Among the 20 pondweed species growing in Danish streams only 4 species are still common. About 10 species have experienced a substantial decrease over the past 100 years. Many of these have also become rare in lakes due to eutrophication [11]. Among the rare pondweed species in Denmark, we can list 5 species as very rare, namely: *Potamogeton zosterifolius*, *P. rutilus*, *P. acutifolius*, *P. densus*, *P. coloratus*. Unfortunately, *P. polygonifolius*, *P. gramineus*, *P. alpinus* and *P. filiformis* now face a high risk of also being included among the very rare species.

Macrophyte species	Frequency (%)
Unbranched Bur-reed *Sparganium emersum* Rehman	75.1
Water-Starwort *Callitriche* sp.	69.7
Canadian waterweed *Elodea canadensis* L. C. Rich	60.6
Lesser Water-parsnip *Berula erecta* Hudson (Coville)	57.7
Water Forget-me-not *Mysotis palustris* L.	51.9
Branched Bur-reed *Sparganium erectum* L.	51.9
Water-crowfoot *Batrachium peltatum* (Schrank) Presl.	36.1
Blue Water Speedwell *Veronica anagallis-aquatica*	32.2
Curled Pondweed *Potamogeton crispus* L.	30.2
Floating Sweet-grass *Glyceria fluitans* (L.) R. Br.	29.3
Fennel Pondweed *Potamogeton pectinatus* L.	18.3
Broad-leaved Pondweed *Potamogeton natans* L.	17.8
Pond Water-crowfoot *Batrachium baudotti* (Godron) F. Schultz	17.8
Flowering-rush *Butomus umbellatus* L.	16.8
Perfoliate Pondweed *Potamogeton perfoliatus* L.	14.9
Common Water-crowfoot *Batrachium aquatile* (L.) Wimmer	13.5
Water Mint *Mentha aquatile* (L.) Wimmer	12.5
Watercress *Nasturtium* sp.	11.5
Water Horsetail *Equisetum fluviatile* L.	11.5
Fan-leaved Water-goosefoot *Batrachium circinatum* (Sibth.) Spach	11.1

Table 9.4 Relative frequency of submerged plants at 208 stream sites in 1996.

Species belonging to plant genera other than the pondweeds have also become more rare in streams. This is particularly true of species associated with still or slow-flowing water such as *Myriophyllum spicatum* (Spiked Water-milfoil), *M. verticillatum* (Whorled Water-milfoil), *Ranunculus circinatus* (Fan-leaved Water-crowfoot), *Ceratophyllum demersum* (Rigid Hornwort) and the submerged form of *Stratiotes aloides* (Water-soldier). These species were previously common in the lower parts of streams and in backwaters, and were favoured by their ability to disperse from lakes to streams. Now these backwaters have disappeared and the lower parts of the streams often have turbid water filled with phytoplankton from upstream lakes. Eutrophic lakes have lost their submerged vegetation and thereby their ability to enrich the lower stream parts with plant propagules such as stem fragments, short shoots and seeds.

A number of other species are threatened by extinction. This applies to *Luronium natans* (Floating Water-plantain), *Alisma gramineum* (Ribbon-leaved Water-plantain) and *Oenanthe fluviatilis* (River Water-dropwort). *Luronium natans* and *Oenanthe fluviatilis* receive great attention because they, along with *Potamogeton acutifolius*, only occur in Western Europe. These species have experienced a drastic decline that threatens their global survival.

Possibilities of re-establishment

What hope is there of recreating a more diverse aquatic plant community, once water quality has been improved and streams reaches remeandered, when so many species are now so rare? In fact no one has been able to answer this question, but we can make some

Stream vegetation is dominated by species that are tolerant to disturbance and nutrient-rich conditions.

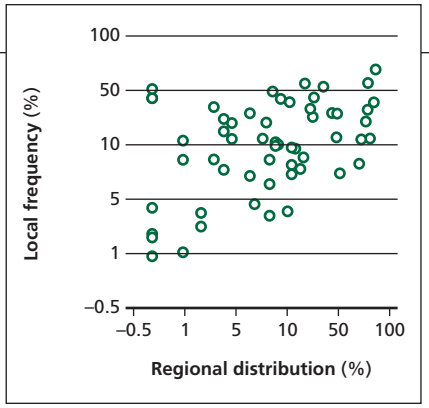


Figure 9.3 Relationship between the regional distribution of 57 stream species in Denmark in 1996, and the mean local frequency at the sites where the different species occur.

general reflections based on known theories and relationships.

First we have found a general positive relationship between the geographical distribution of stream plants across Denmark and their local abundance (Figure 9.3). The relationship means that species with a restricted geographical distribution also generally have a low abundance at the sites where they do occur. On the other hand, species with a widespread distribution among the streams usually have a high abundance at sites where they are present. The relationship can be explained by differences in their ecology. Species able to utilise commonly-occurring resources, or a broad range of resources, have widespread distributions, while species dependent on rare resources or a small range of resources have restricted distributions. An alternative explanation is proposed by the relationship between frequency and dispersal ability, which proposes that: "High local frequency provides opportunities for colonisation of many habitats, attaining a widespread distribution and thereby reducing the risk of disappearance from the already occupied habitats".

When the number of favourable habitats for water plants becomes limited in streams as well as in lakes, the local frequency of the species may also decrease in habitats not directly influenced, because immigration from suitable neighbouring localities is restricted. Thus, when the frequency of the species decreases in habitats because of environmental deterioration, the distribution of species may decrease in the entire country, and in the long term, over the entire distribution area. Essentially core areas of a species distribution, i.e. the areas where the species attain the highest abundance, can ensure the supply of individuals to remote satellite areas so that the species may also maintain a population there. The possibility of supplying the satellite areas with propagules will decline when the populations in the core areas decrease.

At present, many Danish water plants grow in so few habitats and in such small populations that statistically they have very little chance of reclaiming lost habitats, even if the environmental conditions were to improve. While physical and chemical conditions can be re-established by technical means, the re-establishment of biological diversity is much more difficult. The maltreatment of streams, lakes and wetlands has put many species in a marginal position that unfortunately may turn out to be permanent.

In this chapter we have shown that the composition of stream plant communities is not simply related to current environmental conditions but is also shaped by the legacy of historical development. Furthermore, the consequences of past abuses are seldom fully reversible. So yes: The past century has made a huge difference both to the present and future vegetation in streams.

The adult mayfly *Ephemera danica*.

10 Improvements ahead for macroinvertebrates?

During the 20th century, anthropogenic pressures, such as wastewater discharges, reduced the biodiversity of Danish streams. However, over the last 30 years, large sums of money have been invested in wastewater treatment and stream restoration in an attempt to improve the ecological quality of these streams. But what is the present state of the freshwater biology? Have we achieved improvements in environmental quality as a result of the investment? In this chapter, attention will focus on the macroinvertebrate fauna of Danish streams, and it is evaluated whether the ecological quality of the streams has improved in recent years. Finally, it is discussed how further changes are expected to affect the ecological condition of the streams.

Macroinvertebrate fauna in Danish reference streams – how was it before?

Currently, the majority of Danish streams are continuously exposed to one or more anthropogenic pressures (such as wastewater discharges, regulation, weed cutting, drainage, water abstractions, heavy metals and the use of pesticides). The crucial question is therefore, has the macroinvertebrate communities changed as a result of these impacts?

There is historical information on the macroinvertebrate communities of Danish streams dating from the beginning of the 20th century. During the period 1900–1950, collections were obtained from many streams. In 1916 and 1917, the zoologist, Wesenberg-Lund, initiated an investigation of a number of streams situated in different parts of the country [1]. The macroinvertebrate fauna was sampled by local professionals and amateurs; about 1,600 samples of mayflies, stoneflies and caddisflies were collected. These insects were preserved in alcohol and thereby kept for future study. In some watercourses, such as Funder Stream, Århus Stream and the lowermost parts of River Gudenå and River Skjern, there was particularly intensive sampling by the zoologists Esben Pedersen, J. Kr. Findal, Hj. Ussing and Carlo F. Jensen. In these streams we have particularly detailed information about the macroinvertebrate fauna before wastewater discharges, regulations in the stream channel and changes in catchment use occurred.

Therefore, it can be seen that we have some knowledge about the pre-disturbance state (or reference condition) of the macroinvertebrate fauna in Danish streams. A number of species are only known from the museum collections and have never been found since that time (Table 10.1), even though recent collections have

	Previous detections 1900–1960	Last detection	Present status 1990–1999
Mayflies			
Baetis digitatus [3]	Widespread (Zealand, Jutland)	1955	Extinct?
Baetis muticus [3]	Widespread (Zealand, Jutland)	1918	Extinct?
Heptagenia longicauda [4]	Hadsten, Lilleå Stream	1912	Extinct?
Siphlonurus lacustris [4]	Funder Stream	1918	Extinct?
Rhithrogena germanica [5, 6]	Grejs Stream, Jeksen Brook, River Gudenå, Bangsbo Stream, Varde Stream, Hansted Stream	-	Højen Brook
Baetis buceratus [3]	River Skjern	1956	River Storå (one induvidal in 2004)
Stoneflies			
Perlodes dispar [4]	River Gudenå	1955	Extinct?
Dinocras cephalotes [4]	Grejs Stream, Orten Brook near Varde	1949	Extinct?
Brachyptera braueri [4]	Grejs Stream	-	River Gudenå (one induvidal in 1991)
Siphonoperla burmeisteri [4, 7]	Widespread in Jutland (River Skjern, Varde Stream, Ribe Stream, River Gudenå, Kolding Stream)	-	Vidå Stream
Caddisflies			
Micrasema setiferum [8]	Funder Stream, River Gudenå	1917	Extinct?
Hydroptila forcipata [9]	Lellinge Stream	1907	Extinct?
Hydroptila occulta [9]	Lindenborg Stream, Gjern Stream	1948	Extinct?
Wormaldia subnigra [10]	Sæby Stream	-	Mattrup Stream, Øle Stream
Lasiocephala basalis [5, 10]	Århus Stream	-	Mattrup Stream, Åsbæk Brook
Odontocerum albicorne [10]	Occasionally	-	Rare

Table 10.1 Selected mayflies, stoneflies and caddisflies registered in the Red Data Book of threatened and rare plants and animals in Denmark [2]. Some species are now believed to be extinct. Other species are still present but were previously more widespread.

been much more comprehensive, both countrywide and at the previous sampling sites. Some rare species, now only found in a few streams, are present in the museum collections from a greater number of streams [3, 4, 10]. It is expected that these species were much more widely distributed and abundant than today.

A few Danish medium-sized and some larger streams have only been minimally impacted over the years. These streams give us another opportunity to obtain knowledge about the natural composition of macroinvertebrate communities.

Mattrup Stream, a tributary of the River Gudenå, is an example of a medium-sized stream with a macroinvertebrate community as it was 100 years ago. Here we still find some species of caddisflies, which are now rare in Denmark, but were previously found in the Funder Stream, the Århus Stream and other similar watercourses (Table 10.1). But generally, these species are no longer commonly found in Denmark.

It is important to protect these exceptional streams that have an undisturbed macroinvertebrate fauna because such streams are scarce not only in Denmark, but also in most other parts of the North European lowland. The continued existence of these undisturbed macroinvertebrate communities is also important as they act as a potential source of colonists for nearby streams as and when they are restored.

Most of the species that are now rare or have already disappeared from Denmark (Table 10.1) are associated with medium or large streams. These species represent a variety of different functional feeding groups and life strategies. However, for many of these species, Denmark represents the northern or north-western limit of their distribution in Europe. In contrast, some species, which are believed to be extinct in Denmark, can still be found in isolated populations north of Denmark.

The elimination of rare species from stream systems or even larger areas represents a loss of biological diversity at the local and the regional scale. Such losses are in many cases difficult or impossible to reverse because many

Osmylus fulvicephalus. **The larvae live under moss, bark and stones in the transitional area between water and air.**

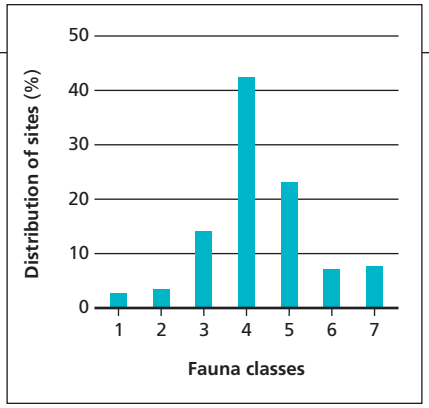


Figure 10.1 Moderate ecological quality (fauna class 4) characterised Danish streams in 2002 (1,051 stream sites investigated) [15].

macroinvertebrate species are unable to disperse over long distances.

Despite the changes in macroinvertebrate composition over the last century, the dominant species found in unimpacted streams a century ago are probably the same as are found in streams today. However, some of the most sensitive species of mayflies, stoneflies and caddisflies are no longer found in Denmark at all or they have survived in only a few streams.

Today's streams; how is the ecological quality?

For the last 20–25 years, the Danish regional authorities have assessed environmental stream quality using biological stream assessment based on macroinvertebrates. Since the mid-1980s, 10–15,000 assessments have been made every year. The same assessment methods have not been consistently used (Box 10.1) across all regions or over the 25-year period. As a consequence, it has been difficult to make countrywide and temporal comparisons of ecological quality.

The Danish Stream Fauna Index (DSFI) was therefore introduced in 1998 at 444 stream sites distributed throughout Denmark [14]. Since 1999 the number of stream sites has increased to 1,053 and the same method has been used annually at these stream sites. These surveys have found that the intermediate quality class, fauna class 4, indicating a moderately impacted site, is the most common in Danish streams (43%). Streams having a diverse fauna, with a number of sensitive species (fauna classes 5, 6 and 7), account for 37%, while heavily-impacted streams (fauna classes 1, 2 and 3) constitute about 20% (Figure 10.1).

More than 20,000 km of Danish streams are subjected to quality objectives, set by the regional authorities, based on the macroinvertebrate community. In 2000, about 45% of the Danish streams complied with their objectives [15]. Compliance typically requires an unimpacted or only slightly impacted macroinvertebrate community (fauna classes 5, 6 and 7). Unfortunately, some regional authorities accept fauna class 4 in slow-flowing streams with poor habitat quality. Overall, the ecological quality of Danish streams is far from the reference conditions associated with fauna classes 6 and 7.

The most important pressures on Danish streams

Why do most Danish streams not comply with the quality objectives?

The regional authorities responsible for performing the biological assessment of streams have concluded that nearly 12,000 km streams do not have acceptable macroinvertebrate communities. Furthermore, the regional authorities have evaluated the reasons for the unacceptable ecological quality in the streams (Figure 10.2). The main impact is believed to be wastewater from sewerage systems and scattered dwellings and it is estimated that the ecological condition of 6,000 km of Danish streams is unacceptable as a result. The discharge of wastewater to streams is reflected in the concentration of organic matter (BOD_5) in the stream water. Wastewater from about 99% of the wastewater treatment plants is biologically treated [16] and the BOD_5 content in the outlet of sewage treatment plants is typically 2–3 mg/l. However, diluted wastewater discharges during rainfall events are believed to result in many streams remaining in an unacceptable condition. The amount of oxygen-consuming organic matter from wastewater has been calculated since the Nationwide Monitoring Programme was initiated in 1989 [17]. The discharge of organic matter from wastewater treatment plants and industrial plants was reduced by 92% and 80%, respectively, during the period 1989–1999. The discharge of organic matter measured as BOD_5 from about 350 fish farms was reduced by more than 50% during the same period although, locally, biological conditions may still be unacceptable [17].

Currently, the most important wastewater problem is the discharge of mechanically treated wastewater

Box 10.1 Biological stream assessment in Denmark

Biological stream assessment
Four different assessment methods based on macroinvertebrates have been used in Denmark between 1970 and 2000. The basic principle is that many species of larvae of stoneflies, mayflies and caddisflies can only thrive under certain environmental conditions, e.g. fast flowing oxygen-saturated water, dense riparian vegetation cover. In contrast, some species of midge larvae and worms tolerate most pressures and can survive in polluted or physically disturbed streams. Based on the complete list of macroinvertebrates from a stream site an index value can be calculated (pollution degree or fauna class). This value expresses the ecological quality (see below).

Nymphs of the stonefly *Perlodes microcephalus* require clean water and a stony substrate.

Guidelines from the Ministry of Agriculture 1970
These guidelines were originally inspired by the Saprobic system [11] used mainly in central Europe since the beginning of the 20th century. The guidelines briefly describe the distinction between seven different pollution degrees (I, I-II, II, II-III, III, III-IV and IV). Today the Saprobic system is mainly used in Germany and Austria. The method requires laboratory sorting and identification to species level. The species list is used to calculate the **Saprobic value** by use of a special formula. In Denmark there has been a tradition for compiling a fauna list in the field, and then based on the findings, making a subjective judgement on which of the seven pollution degrees is appropriate for the site. Therefore, the guidelines from the Danish Ministry of Agriculture differ considerably from the more traditionally used Saprobic system. The weakness of the method recommended by the Ministry of Agriculture is that it is not reproducible. Different people can interpret a species list in different ways. And the same person can change his interpretation as more experience is gained. The guidelines made by the Ministry of Agriculture were the official method for biological stream assessment from 1970 to 1998.

Viborg Index
The Viborg Index also uses seven pollution degrees [12]. Sample collection is standardised. The sample sorting and identification is performed in the laboratory. The pollution degree is obtained by an objective procedure. For example, a species list can only give one single pollution degree and is therefore not subject to different interpretation by two or more persons. The Viborg Index is a biotic index where the combination of specific indicators are used together with the number of selected diversity groups to calculate the actual index value. Some county authorities have based their interpretation of the guidelines of the Ministry of Agriculture on the Viborg Index from the mid-1980s until 1992.

Danish Fauna Index (DFI)
Danish Fauna Index is a further development of the Viborg index [13]. The sensitivity of DFI has been adjusted in order to clarify the distinction between moderately and strongly polluted streams. The index values are named fauna classes instead of pollution degrees because the composition of the macroinvertebrate community is not only affected by the organic pollution, but also by the habitat quality, ochre compounds, hazardous substances and the water flow. Danish Fauna Index has been used as the official biological assessment method at 222 stream sites under the Nationwide Monitoring Programme from 1993 to 1997. The DFI has also been used by county authorities who previously used the Viborg index.

Danish Stream Fauna Index
Danish Stream Fauna Index (DSFI) is a further development of the DFI [14]. A minor change has improved the separation between fauna classes 4 and 3. The fauna classes in DSFI are denoted by numbers from 1 to 7; an index value of 1 corresponds with a strongly impacted stream, whereas an index value of 7 corresponds to unimpacted or slightly-impacted streams. In 1998, the Danish Stream Fauna Index was introduced as the new official method for biological stream assessment. In 1998 the method was used at 444 stream sites in the Danish Aquatic Monitoring and Assessment Programme. In 1999, the number of stream sites was increased to 1,053.

from scattered dwellings into small streams [15]. This is believed to be the main reason for unacceptable ecological quality in about 3,000 km of Danish streams (Figure 10.2). The wastewater discharged into small streams is inadequately diluted and therefore has a negative impact on the macroinvertebrate communities. Consequently, it is necessary to improve the treatment of wastewater from sparsely built-up areas. Initiatives have now been introduced, and most regional authorities have selected a number of small stream catchments where the implementation of improved treatment of wastewater from scattered dwellings will reduce the discharge of organic matter and thereby aim to improve the ecological quality of the streams. At the moment, this work is limited to these selected areas, and it is expected to take many years before the majority of stream catchments receive similar treatment programmes.

An additional problem in Danish streams is a general reduction in the habitat quality of some streams as compared to natural, unimpacted streams. Habitat quality can be reduced as a result of stream regulation, heavy-handed stream maintenance and the erosion of nearby agricultural areas leading to increased inputs of nutrients and sediment into the stream channel. As a result of these impacts on habitat quality, 3,000 km of streams do not comply with the quality objectives [15]. As mentioned above, the majority of Danish streams are more or less affected because of previous regulations and present stream maintenance methods. These pressures maintain the streams in an unstable condition. In many cases stone and gravel substrates have been removed or covered with fine-material. This is usually due to reductions in water velocity associated with the bank-to-bank dimensions of the streams, which have been increased as part of the stream maintenance. Weed cutting reduces the amount of vegetation periodically but it also changes the species composition of the macrophyte community [18]. As a result, the macroinvertebrate communities are reduced in abundance and the species composition is changed.

Revision of the Watercourse Act in 1982 resulted in the introduction of more environmentally-aware stream management methods. Maintenance was changed from a near-total removal of macrophytes and eventually a removal of the bottom sediments, to a more gentle maintenance with macrophytes being cut only in the main channel with a significant proportion of plant material being left untouched. Consequently, the fine sediments are typically no longer removed from the stream bottom [18]. This has resulted in an improvement in the macroinvertebrate communities and also trout abundance [19, 20]. However weed cutting is now more frequent and still maintains the macrophyte communities in a modified condition. A further reduction in weed cutting or, alternatively, a complete termination is a both desirable and feasible option that would improve the habitat quality and result in a higher number of more natural biological communities.

Other pressures leading to unacceptably poor ecological stream quality include draining of pyrite-rich soils leading to ochre pollution, and water abstraction leading to changed flow regimes and a general reduction in water velocities.

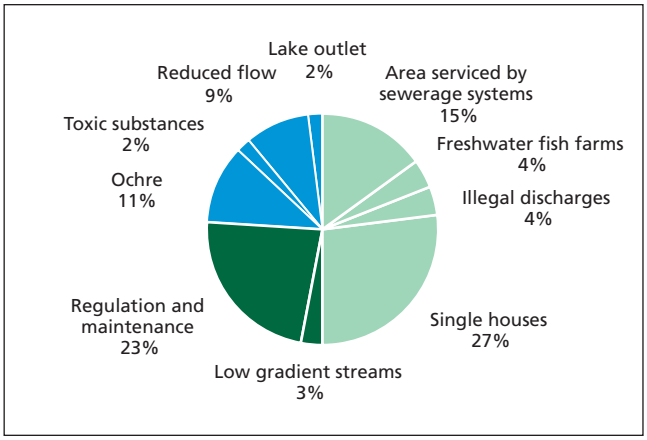


Figure 10.2 Reasons for non-compliance with quality objectives in 12,000 km Danish streams [16]. The three colours in the figure illustrate the pressures from organic pollution (light green), habitat degradation (dark green) and other pressures (blue).

Have the macroinvertebrates communities improved in recent years?

The answer can be found by comparing the general ecological quality in the streams 10 years ago with that of today. We know that the targeted effort of the counties and the municipalities has resulted in a significant reduction in polluting substances in streams. It is mainly the reduction in organic pollution that is responsible for the improved ecological quality. In the 1960s and 1970s new wastewater treatment plants were built or existing

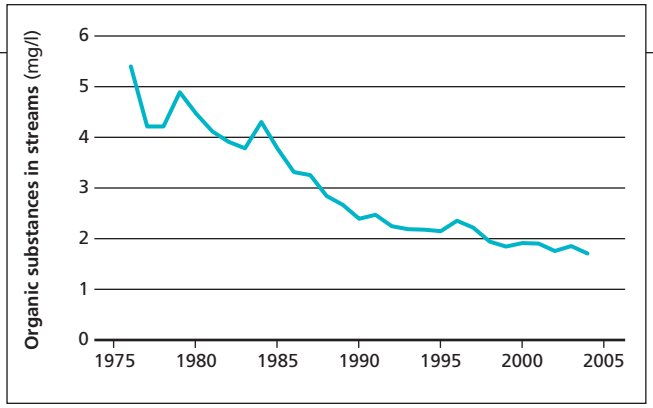


Figure 10.3 Mean BOD_5 content in streams has decreased from 1976 to 2004.

Adult female of the dragonfly *Calopteryx*.

plants were improved. Consequently, there has been a significant reduction in the most severe pollution from urban areas. Rationalisation and the shutdown of small dairies and slaughterhouses in small villages have also eliminated these sources of pollution for many streams. Furthermore, pollution from direct discharges of seepage water from manure etc. into the streams has now been stopped due to an active effort by the county and municipal authorities.

Unfortunately, there are no reliable national estimates of the extent of these reductions in pollution inputs. But it was during this period that the first major efforts were made to improve the environment. The only reliable values for the pollution loads from cities, industry, fish farms etc. are from after 1989 when the Nationwide Monitoring Programme under the Action Plan on the Aquatic Environment was initiated.

In the mid-1970s, two Danish counties started analysing the content of BOD_5 in a number of streams (Figure 10.3). The results show that the water quality has gradually improved up until the late 1980s and provides a clear documentation of the effect of the strong environmental measures introduced during the 1970s and 1980s. In many streams, the BOD_5 concentration has now stabilised at about 2 mg/l. This level is still higher than that found in unimpacted streams where the BOD_5 content is typically about or below 1 mg/l, but a BOD_5 level of 2 mg/l is not a limiting factor for the majority of macroinvertebrate species.

The interesting question is whether there are more pollution-sensitive macroinvertebrates in Danish streams now than 10–15 years ago? This question can be answered using information from 651 stream sites situated in the County of Southern Jutland. It would have been preferable to use results from various sites in all of Denmark, but the use of different assessment methods has, as previously mentioned, made it difficult to make both inter-regional and temporal comparisons.

Fauna lists from the County of Southern Jutland are here expressed as pollution degrees using the Viborg Index method [12] which resembles the method currently used, the Danish Stream Fauna Index [14]. Since 1986, the county has used the Viborg Index as an aid when estimating the level of pollution in accordance with the official guidelines provided by the Ministry of Agriculture (Box 10.1). The Viborg Index has been calculated using the macroinvertebrate fauna lists for the periods 1986–1987 and 1995–1997.

A Viborg Index of II-III (moderate ecological quality) is the most common for both periods. The most significant difference is that the proportion of heavily-impacted stream sites (III, III-IV and IV) has decreased from 28% to 18% with a corresponding increase in the proportion of un-impacted, weakly-impacted and moderately-impacted stream sites (Table 10.2). This general improvement in the ecological quality is found in both small (< 2 m wide) and larger streams (> 2 m wide). In the small streams there has been a significant reduction in the number of heavily-impacted streams and a corresponding increase in the number of moderately-impacted streams. In the larger streams, where generally, the ecological quality is better, there has mainly been a reduction in moderately-impacted streams corresponding with an increase in the number of weakly-impacted streams.

Several Danish counties have registered this general improvement in the ecological quality although different assessment methods have been used. The tendency is similar: the majority of streams previously classified as heavily impacted can now be classified as only moderately impacted. In the medium-sized and large streams, the improvements are also similar to those found

Viborg Index	1986	1995–1997
I (undisturbed)	12	18
I-II	21	26
II	121	146
II-III	313	347
III	79	69
III-IV	23	10
IV (seriously polluted)	82	35
All stations	**651**	**651**

Table 10.2 Water quality, as measured by the Viborg Index, for a number of investigated stream sites in the County of Southern Jutland in 1986 and 1995–1997. The comparison shows that the macroinvertebrate fauna has become less impacted in the 10-year period.

in the County of Southern Jutland with an increase in the number of slightly-impacted streams.

A change in the distribution of sensitive species is an alternative method of elucidating the general changes in the ecological quality. The County of Funen has previously documented improvements in the streams [20] using the general guidelines from the Ministry of Agriculture. These results have later been supported by following changes in distribution of the mayfly *Heptagenia sulphurea* and the stonefly *Leuctra fusca*. The range of these two species, both of which demand a relatively good water quality, has increased over the past 10 years [21]. A similar pattern for the genera *Heptagenia* and *Leuctra* (not identified to species) has been found in other Danish counties. Furthermore many species that were previously restricted to headwater areas; are now found further downstream. These species are also found in a number of neighbouring streams where migration has apparently occurred from one watershed to another.

In the River Storå, the largest stonefly in Denmark, *Perlodes microcephalus*, was for many years only found upstream of Holstebro, a town with 30,000 inhabitants. Due to improved methods of treating wastewater, *P. microcephalus* now also inhabits the 27 km stretch downstream of the town of Holstebro to the outlet in Nissum Fjord [22]. In 2000 and 2001, *P. microcephalus* was also recorded from two streams in another part of Jutland, where this stonefly had never previously been observed.

In conclusion, the ecological quality of Danish streams has generally improved and we have therefore achieved better environmental quality for the money invested. Many sensitive species are now so widespread that they were removed from the Danish Red Data Book when it was revised in 1997 [2]. In recent years investigations in the streams have been more comprehensive and with more detailed information of the distribution of individual species as a result. Therefore the improved conservation status of many species may not only reflect an improvement in ecological quality, but also a more comprehensive sampling regime and a consequent increased chance of finding sporadically occurring species.

The future ecological status

Can we achieve optimal conditions (fauna class 7) in all Danish streams? The answer is no. The prerequisite for reaching water and habitat of an acceptable quality is often not available. But there remains scope for improvement in most streams.

Previous initiatives have almost eliminated illegal contributions of farm wastes. Wastewater from cities is now more effectively treated, with a resulting improvement in water quality. However, the ecological quality is still unacceptable in about 50% of Danish streams. Further improvements must therefore be achieved by the use of other measures. First, the habitat quality must be improved, thereby creating more variable and diverse substrate conditions. This can be obtained by use of restoration measures and less intense stream maintenance. Second, the areas bordering the streams need to be managed as protective buffer zones against inputs of sand and other particulate material from surrounding fields. Third, an improved hydrological interplay between stream and stream valley allowing natural processes to occur and natural plant communities to develop is required e.g. by allowing streams to periodically flood their surroundings. Finally the improved treatment of wastewater from scattered dwellings and closure of storm water outfalls would also enhance the general ecological quality.

Such concerted efforts are expected to increase the proportion of streams where quality objectives are fulfilled from about 45% to 70–80%. Therefore, we anticipate that there will be better times for the macroinvertebrates in the future. We are on the way. The Danish counties and municipalities have performed a number of necessary measures, with more to follow. But it will take some years before wastewater from scattered dwellings is treated and before stream habitat quality is sufficiently improved. Therefore, we must arm ourselves with patience.

Brede Stream was re-meandered during the years 1991–1998.

11 A new development: Stream restoration

Streams have always been influenced by man. Thousands of kilometres of streams have been straightened – often to the detriment of animals and plants. Heavy-handed maintenance has further deteriorated the conditions. In the 1990s, Denmark started a new approach. More environment-friendly stream maintenance methods were introduced and streams were being restored. What are the future perspectives?

Streams destroyed

The many thousands of kilometres of streams in Denmark should be expected to sustain many diverse habitats with an animal and plant life rich in species. However, the variety of animal and plant species in the Danish streams has declined dramatically throughout the last century.

This decline is partly due to pollution of the streams with wastewater from agriculture, cities and industry. Streams were transformed into sewers and diversion canals and were thus prevented from sustaining any life. However, introduction of the first environmental plans in the 1980s has gradually solved the problem of wastewater, and the quality of stream water has been improved year by year. The stream water is once again so clean that it should be able to fulfil the goal of large and varied populations of animals and plants.

However, this goal will not be reached solely by stream water becoming clean. In addition, streams themselves also need to contain as much physical variation as possible. The more diverse the environmental conditions in streams, the more diverse animal and plant life they can support. If streams lack the natural variation created by the shift between riffles and pools, animals and plants will have fewer and less suitable habitats.

In 1864 Denmark had to surrender almost a quarter of its territory to Germany. This resulted in a shortage of cultivatable land forcing agriculture to include former unexploited natural land and introduce more effective farming methods. Government interventions and subsidies further accelerated this development between the 1930s and 1960s. Many thousands of hectares of wetlands were drained and thousands of kilometres of streams were straightened and deepened to quickly drain the water from the fields to the sea.

The streams lost their natural shape, and regular dredging and very heavy-handed maintenance further deteriorated the poor physical condition of the streams. Because of their uniform

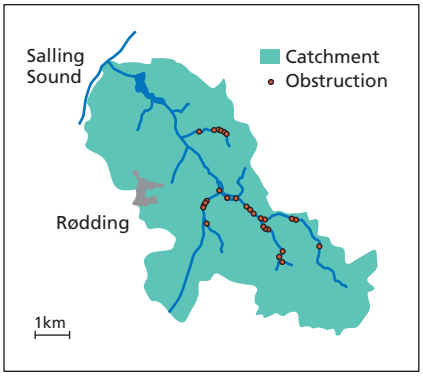


Figure 11.1 In 1992, there were 27 obstructions in the 38 km² catchment of Rødding Stream [1].

Following the construction of the Tangeværk hydroelectric power station in the upper reach of the River Gudenå between 1918 and 1920, salmon were unable to reach their spawning grounds. Only a few years later, salmon were extinct in this river.

nature, such straightened and deepened streams only provide very poor conditions for freshwater life.

The many dams and obstructions constructed in connection with the channelisation of the streams (see Chapter 1), cause additional problems for the animals living in the streams. The obstructions often hinder the free passage of animals up and down the streams with varying effects. Minor obstructions only have a moderate effect on the fish population, while larger obstructions prevent the migration of certain invertebrates and many fish. If the animals are thereby hindered from reaching their breeding grounds, they might face the risk of extinction. The most famous Danish example is the extinction of salmon in the River Gudenå following the construction of the Tangeværket, a hydropower station built between 1918 and 1920. The hydropower station totally prevented the salmon from reaching the upstream spawning grounds and it therefore became extinct within a few years.

In spite of concentrated efforts since the 1980s to remove the obstructions, many still remain – and even in small streams obstructions may still be found very close to each other (Figure 11.1).

Table 11.1 Reasons for non-compliance with the stream quality objectives in three municipalities in Vejle County in 1992 [2].

Cause of problem	Number of stations	%
Habitat degradation due to channelisation	101	38
Hard-handed maintenance	35	13
Sewage from rural areas	65	25
Sewage from wastewater plants	27	10
Low water discharge	17	7
Organic pollution from freshwater fish farms	10	4
Loading from agriculture	9	3
Total	**264**	**100**

Regulated streams and heavy-handed maintenance of streams contrast sharply with naturally meandering streams with great physical variation in discharge, depth, sediment, vegetation and stream banks. This physical variation offers many and very diverse habitats for plants and animals.

It is an enormous task to improve the physical conditions of degraded streams in such a way that the physical quality of the stream corresponds with the clean water now flowing in the streams. The poor physical variation is still the reason why so many streams do not continuously live up to the biological objectives set by the Danish counties. In three municipalities in the County of Vejle, 50% of the environmental problems in 1992 were attributable to poor physical conditions and heavy-handed maintenance (Table 11.1).

The road towards an improved physical environment

Improvement of physical stream diversity in compliance with the objectives set up by the Danish counties can be achieved by introducing more environment-friendly maintenance methods and by carrying out different types of stream restoration. On this basis, stream restoration as a means of improving the physical environment was introduced in the Danish Watercourse Act from 1982. Active restoration of streams is a quick and direct way of achieving the required

improvement of the streams, and, in some cases, stream restoration may be the only method for improvement.

Restored streams should preferably resemble the former natural conditions as much as possible and should only require a minimum of future maintenance. Take for example, the removal of all obstructions to re-establish the free passage of fauna upstream and downstream. Where this is not possible, free passage should be re-established by a constructed or restored riffle or a new bypass stream. Fish ladders, on the other hand, should preferably be avoided as they are selective; being often only passable to strong swimmers, such as salmonids, and hindering the passage of other fish and invertebrates. In contrast, all species of fish and stream invertebrates are able to pass a correctly constructed bypass stream. In addition, riffles and bypass streams can function as part of the natural stream.

It is primarily the counties that have carried out the restoration projects. Whilst many counties and municipalities have initiated restoration projects they have often received financial support from the National Forest and Nature Agency. The State, represented by the National Forest and Nature Agency, has also been responsible for a few projects – e.g. the River Skjern Project (see Box 11.1 on page 126–127).

In co-operation with the counties, the National Environmental Research Institute has gathered and compiled information on many restoration projects in a database [7]. Projects have been divided into three types (Figure 11.2); those where restoration has been carried out locally on short stretches of the stream (type 1), those where restoration re-establishes the continuity

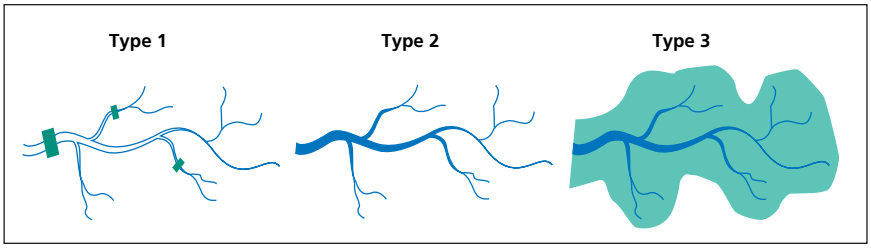
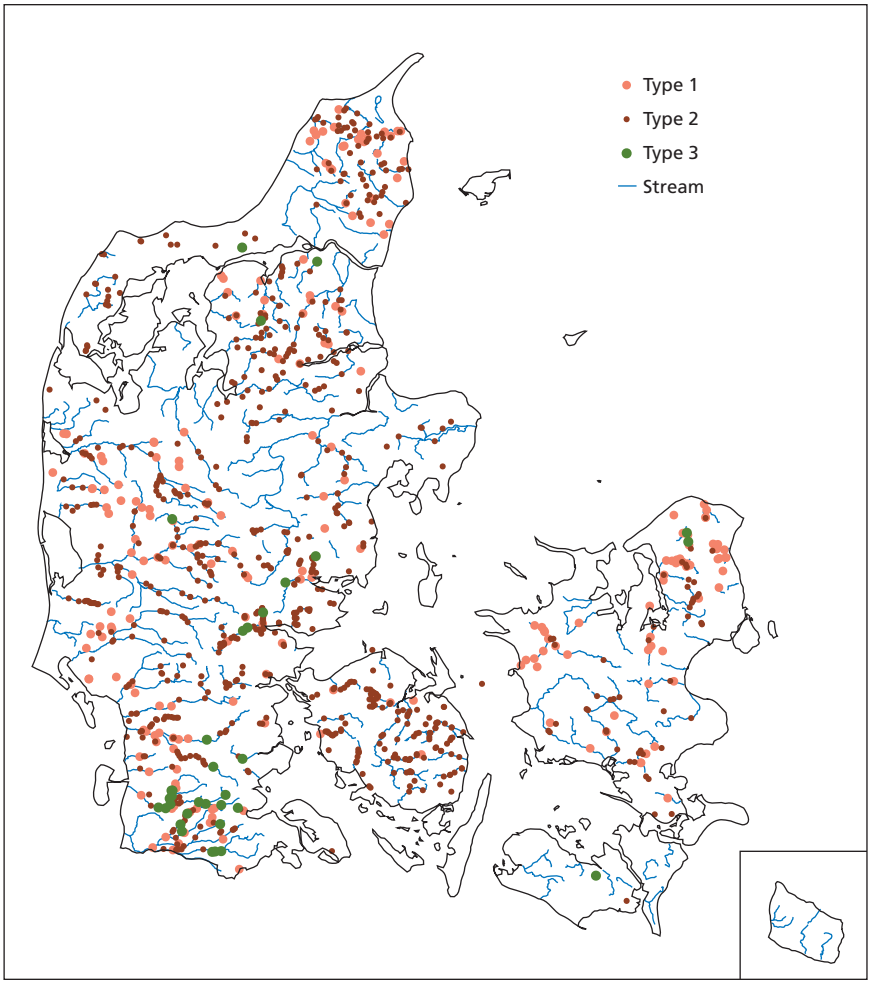


Figure 11.2 Schematic outline of the three types of restoration project. Each of the three project types is described in the text.

Figure 11.3 Map of Denmark indicating the location of the three types of restoration projects.



in the stream (type 2), and where the restoration includes both the stream and its adjacent areas in the stream valley (type 3).

Type-1 projects typically result in local improvement of stream and bank habitats. Type-2 projects restore free passage and continuity along the stream by reconnecting reaches and their nearest surroundings. Fauna are thereby enabled to migrate freely between different stream reaches and between the stream and its close surroundings. Type-3 projects involve both the stream and its valley. An example would be a project seeking to raise groundwater levels in floodplain meadows and thus encouraging the stream to flood at high water levels. Higher water level and more frequent flooding are desirable when one wants to reduce the transport of sediments or the concentration of nitrogen or ochre in the stream. Restoration methods are generally contrary to methods used in the past to drain the meadows.

By 1999, more than 1,000 restoration projects had been carried out by the Danish counties. These projects ranged from laying out spawning gravel to comprehensive projects re-meandering streams and improving connectivity between the stream and its valley (Figure 11.3).

The database informs about the division of the project types (Figure 11.4). Among other things, it gives a historic view of the development of stream restoration. The reconnection of continuity between stream reaches (type-2), for example, was given especially high priority during the 1990s, while type-3 projects involving both the stream and its valley have gradually received higher priority in recent years.

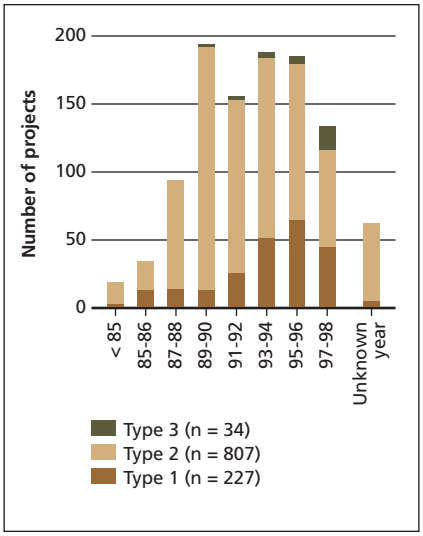


Figure 11.4 The number of implemented restoration projects between 1985 and 2000. Notice the shift over the years in the type of projects being implemented.

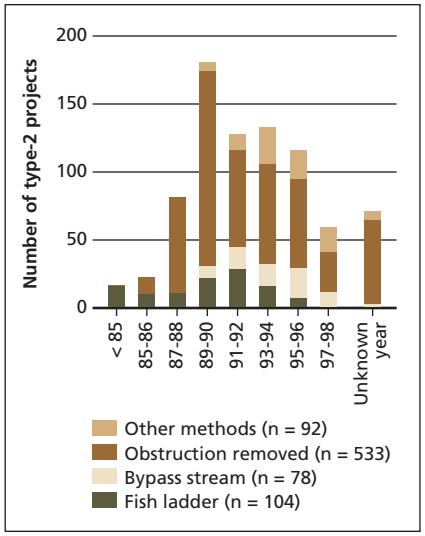


Figure 11.5 Type-2 projects (split into four groups) that reconnect the stream reaches and restore free passage and continuity of streams.

Restoration methods have changed over time (Figure 11.5). At the time when the restoration of continuity between stream reaches was initiated, the most frequent method was to set up or build fish ladders. Gradually it became obvious that fish ladders often only allow the passage of strong swimmers like trout and furthermore that they require intense maintenance. Consequently, bypass streams that go round obstructions, that cannot be removed entirely, are now preferred. These are much easier for fish and invertebrates to negotiate and do not require as much maintenance.

Restoration of the Brede Stream

It remains difficult to convince Danish landowners along streams to accept a restoration project. However, with steadily increasing experience of river restoration, the situation has improved. It has also become easier to award landowners one-off compensation in the form of either money or new agricultural land. An increasing number of landowners now accept restoration projects and many even warmly support the idea of restoring the dynamics and variation in streams as much as possible.

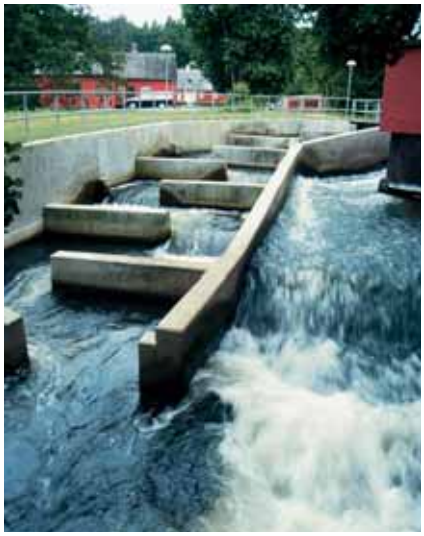
Re-meandering of the Brede Stream in the County of Southern Jutland proves the good intentions. This was the second largest Danish river restoration project, only surpassed by the River Skjern project. The Brede Stream was re-meandered during the years 1991–1998 and this involved almost 100 landowners. The once 19-km straight river was extended to a meandering river of 26 km (Figure 11.6). Some negotiation between the county and the first landowners involved was required to get the project running in 1991. But

as the years went by and the remaining landowners along the river saw the positive results of the re-meandering, and as the compensations in connection with the re-meandering became more attractive, it became easier for the county to obtain the landowners' acceptance. The restoration was carried out on a voluntary basis and all requests from landowners, regarding the course of the river, were taken into consideration.

When the re-meandering of the river was initiated in 1991 it was, as previously mentioned, one of the first projects of its kind to be carried out in Denmark. To estimate whether the project would meet the expectations of improved water quality, improved physical conditions and greater biodiversity, a comprehensive monitoring programme was carried out in connection with the second stage initiated in 1994.

Monitoring was initiated one year before the excavation and ran for the subsequent two years. Among other things, it showed that there were less nutrients and ochre in the water two years after the re-meandering. The same also partly applied to the transportation of sand. If gravel banks in the stream are infilled by sand they become unsuitable as spawning banks for fish and as habitats for invertebrates. The monitoring period proved too short for an unambiguous evaluation of the effects of the re-meandering on animals and plants. However, two years after the re-meandering the number of species and individuals was higher or at least at the same level as before re-meandering.

Scenically, the Brede Stream has become much more attractive than before and it is now a popular recreational area for both anglers and the local people.



Fish ladders (top picture) are often only passable for species that are strong swimmers. Bypass streams, on the other hand, extend the water drop over a longer reach and are therefore more often passable to all species of fish and invertebrates. The lower picture shows the 655 m-long bypass stream at the Holstebro hydroelectric power station on the River Storå.

The old straight run of the Brede Stream is being re-filled after the opening of a new meander.

Year	1991	1994	1995	1996	1997	1998	Total
Number of landowners	8	22	16	17	19	15	97
Length before (km)	2.7	2.8	3.6	4.0	3.4	2.8	19.3
Length after (km)	3.2	4.3	4.3	5.4	4.8	3.7	25.7
Earth excavated (m^3)	45,000	72,000	42,000	50,000	44,000	25,500	278,500
Area of the river valley (ha)	40	60	70	80	65	60	375
Costs excluding taxes (thousand EURO)	240	470	415	335	325	335	2,120

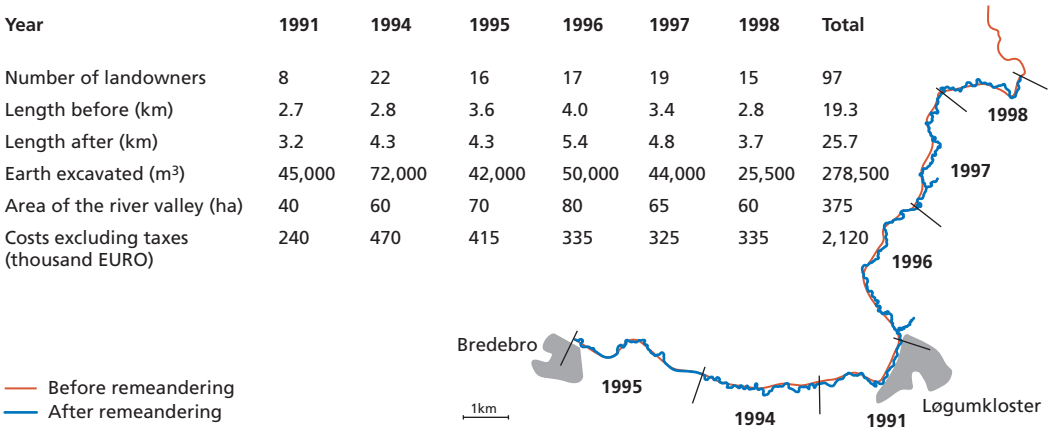


Figure 11.6 Brede Stream was previously a straight river of 19 km. After restoration between 1991 and 1998, it now meanders along a stretch of 26 km.

Maintenance as a tool for restoration

It is not only by restoration that we can change the physical conditions and the shape of streams. Beneficial changes can also be obtained if routine maintenance of streams is modified or totally stopped. Streams have traditionally been maintained in order to quickly drain water from the fields. This has been achieved by cutting all vegetation several times per year and by removing gravel and stones. In that way streams have been kept in their unnatural canal-like course to the detriment of animals and plants.

With limited or no maintenance, the physical conditions of streams will revert to a more natural state. Vegetation functions as a biological engineer in streams and may, if left undisturbed, change physical conditions [8]. In-stream and bankside vegetation will relatively quickly contribute to narrowing the profile of the stream, advance sediment deposition, and strabilise the stream bed [9]. In time, this will result in a more naturally meandering and elevated stream. A change in stream maintenance regime is a relatively cheap method and should therefore be used to a greater extent in connection with the rehabilitation of degraded streams and wetlands. In addition, if regular maintenance is stopped, the plant community in the streams will become richer and more diverse [10].

The areas adjacent to the stream will also be flooded more frequently, which, on one hand, may interfere with the agriculture, but on the other hand may have important benefits for society as a whole. To some extent, the public demand for reduced nitrogen discharges to fjords and the sea will be met by the natural stream valleys retaining nitrogen by means of more frequent flooding. The saved costs from not having to maintain streams several times a year to keep them in their present canalised and unstable state should also be considered in the overall evaluation.

However, changed maintenance methods do not attract the same public attention as restorations. With restorations, the public can see improvement in the stream from day to day. In contrast, the enhancements brought about by environment-friendly maintenance take place gradually over longer periods.

An excavator may dig new meanders. Piped streams may be re-opened, obstructions removed, and new gravel and stone bars established in previously sandy streams. However, it is usually necessary to use excavators to achieve an actual restoration, and they are expensive to run. An estimate of the total length of Danish streams improved during ten years of digging new meanders or re-opening piped stretches shows that it is less than 100 kilometres – and maybe only half of that. As a re-meandering project costs EURO 70,000–150,000 per kilometre of stream, it is totally unrealistic to have all streams re-meandered by active restoration. Changed maintenance methods, on the other hand, may improve the physical condition of thousands of kilometres of streams at a far lower cost. So, in spite of the longer time scale, it is the sympathetic maintenance that will promote good physical conditions in the majority of streams.

Weed cutting with a scythe is only possible in shallow streams. Although some vegetation is retained in the stream after cutting, the water does not necessarily flow slowly. Water crowfoot has the majority of its biomass at the water surface, which allows the free passage of water below the water surface.

What about the future?

Danish counties and the Ministry of Environment generally prioritise river restoration highly as demonstrated by the resources granted since the introduction of Danish river restoration. More than EURO 15 million has been spent on 550 of the more than 1,000 projects carried out so far by the counties. In spite of this, restoration projects are infrequently followed up by monitoring of the biological, physical and chemical effects on streams and their adjacent areas. If the effectiveness of a project is monitored, far too often the experiences and conclusions are not published for the benefit of others, but instead are prepared solely as internal reports. Consequently, in this chapter we are not able to take a closer look at the possible effects of the large restoration projects on the animal and plant life in streams. There is therefore a great need to examine the effects of different restoration approaches and the methods used. This could be achieved by setting aside a certain percentage of restoration grants for subsequent monitoring programmes, and by publishing all experiences, good as well as bad. Each project should include an element of monitoring, and adequate resources should be allocated for more comprehensive scientific monitoring programmes to investigate which stream restoration methods are the most efficient and cost-effective for achieving improved biodiversity.

It is also important to allocate some funds for the monitoring of the long-term effects of restorations. Too many of the monitoring programmes only describe conditions just before and after the project was completed. This applies, for example, to the monitoring of the Brede Stream. Short-term monitoring cannot contribute to a final evaluation of the biological, physical and chemical effects. As restoration projects often involve a pronounced interference in the stream, it is important to follow the long-term effects. This will generate invaluable knowledge on how future restoration projects should be carried out and how they may be prioritised to obtain rich and varied plant and animal communities in our streams.

Only small forested streams are today in a pristine state. All other Danish streams need to be restored to improve their quality.

Box 11.1 River Skjern – the most comprehensive Danish river restoration project

"But soon the areas will become a major attraction. As the dikes become covered with grass and the roads become passable, when it will be possible to wander along the river for hours, when the sand banks have gone and boats are able to sail from Borris to the fjord – well, then we will see crowds of tourists that will even surpass the number of 50,000 that each year visit the drained Fiil Lake. And it will become a publicly recognised nature experience."

Representative of the landowners, farm owner J. Smedegaard-Mortensen, at the beginning of the drainage in 1963 [3].

"The meanders and natural variation in water level will contribute to improving the general habitats for animals and plants, it will result in improved river quality for the River Skjern catchment and Ringkøbing Fjord. And the recreational and tourist value of the area will be many times multiplied."

Minister of Environment and Energy, Svend Auken, at the beginning of the restoration in 1999 [4].

The River Skjern is Denmark's largest river in terms of discharge. It has an average discharge of 35 m^3/s. Upstream of Borris town the river runs in its natural meandering bed for long stretches, while it has been totally regulated and dikes built along its length from Borris town to Ringkøbing Fjord.

For centuries, the River Skjern valley has played an important role for life and agriculture in the poor soils of Western Jutland. The river flooded its adjacent areas during winter and spring, thereby depositing '"fertiliser" as nutrients and organic matter. Consequently, the meadows were productive and large amounts of hay could be saved. However, the river was also unpredictable. Large flooding could occur at any time of the year and thereby destroy the haymaking – or the whole harvest of the year could disappear into Ringkøbing Fjord. For centuries the locals attempted to protect the meadows and control the river water by regulation. As early as 1901–02, the main channel of the River Skjern from Lønborg town to the fjord was partly regulated and secured with summer dikes. But even after this "the great river regulation", there were many wet and soft-bottomed areas where it was impossible to move about with horses and machinery during summer. And during winter the river continued to flood the area.

After World War II, a large number of drainage projects were carried out throughout Denmark with the support of the State and the public in order to obtain agricultural land for food production. Also the landowners in the River Skjern valley wanted new land for grain growing. Following numerous disputes the landowners finally obtained governmental support, and in 1962, Denmark's largest drainage project could begin. Over six years, 4,000 hectares of meadow and marshland were transformed into fields. The project involved the embankment of the downstream part of the river and its large tributaries. The groundwater level was lowered and flooding was hindered by drainage canals and pumping stations. The regulation was completed in 1968, but the first oat crop from the new fields was harvested as early as in 1966. The drainage project totalled DKK 30 million corresponding to DKK 220 million (or EURO 30 million) in 1999 prices. The State covered 70% of the expenses.

There is hardly any doubt that the drainage project proved to be a financial success for the farmers. On the other hand, the project undoubtedly also had negative consequences for nature and the environment of the river, its surroundings and Ringkøbing Fjord. Plant and animal habitats have deteriorated, and the increased load of nutrients and ochre have impoverished conditions for life in Ringkøbing Fjord. At the same time, 33 years of drainage and cultivation have caused the peaty soils to sink by up to one and a half metres. If the agricultural production was to continue, it would have required a new drainage project in the near future.

In the light of such environmental deterioration, a large majority in the Danish Parliament decided in 1987 that a nature

rehabilitation project should be carried out in the River Skjern valley. In 1990, the State started buying and re-allocating land. In 1997, the Danish Forest and Nature Agency published a detailed restoration proposal, and in 1998 the Parliament passed the project construction act. It included 2,200 hectares of the river valley from Borris to Ringkøbing Fjord and increased the river length from 19 km to 26 km. A 3 km regulated stretch of the Omme Stream, a major tributary to the River Skjern, was also included in the project and increased the river to 5 km of meandering river. The new meandering river course primarily followed the original meanders present before the initial comprehensive engineering of the early 1900s.

The purpose of nature rehabilitation was to re-create the extensive natural areas of former times and to improve the habitats for animals and plants. For the benefit of Ringkøbing Fjord, the project was also seeking to partly restore the self-purifying ability of the river valley to clean the water during the regular flooding.

In June 1999 the Minister of Environment initiated the largest river restoration project ever undertaken in Denmark. The project had three phases and was to be completely finished in autumn 2002. The first phase, from Highway 28 to the Fjord, was finished in October 2000, when the water was released into the new meandering course. The second phase, from the inlet of the Omme Stream to Highway 28, was finished one year later. Finally, the project was completed in autumn 2002, when the water was diverted into the final part of the restored course from the town of Borris to the Omme Stream in autumn 2002.

The total cost of the project is estimated at about DKK 250 million (about EURO 35 million). This is very similar to the cost of the drainage project when it was carried out in the 1960s, if calculated in prices of the time.

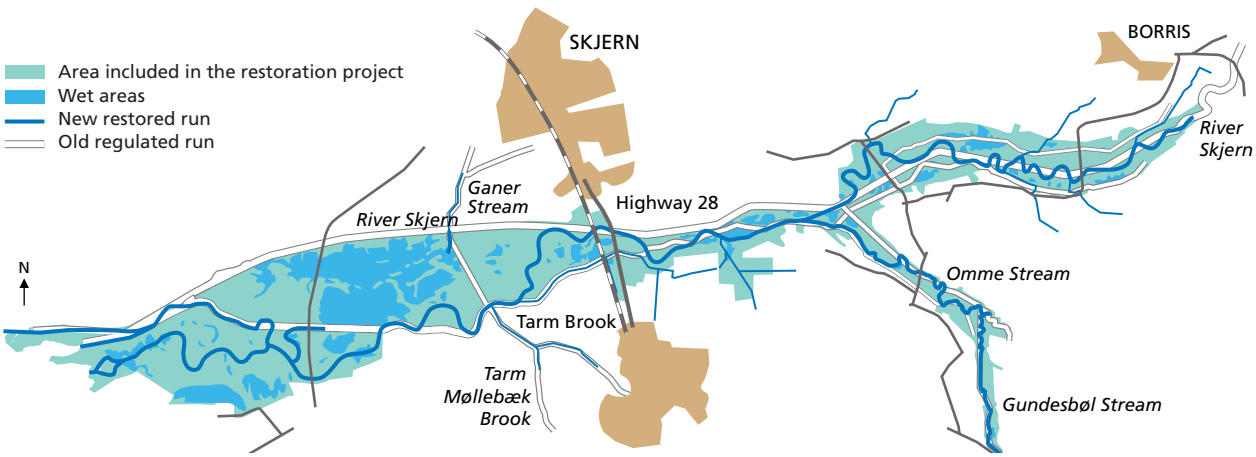
A total of EURO 1.2 million has been allocated for a project monitoring programme which will include the following main elements:

- Hydraulics, stream morphology, groundwater, and frequency and extent of flooding
- Water and material transportation, water quality and sedimentation
- Vegetation in the river and its adjacent areas
- Aquatic invertebrates
- Fish – especially the development of salmon
- Birds and otter.

Re-meandering of the river is expected to result in a more varied animal and plant life in the area. Especially plant species such as the rare River Crowfoot and Water Plantain, and animal species such as salmon and otter are expected to regain ideal habitats. The River Skjern valley is also expected to become a more attractive area for many nesting and resting birds.

The project is further described in [4] and [5].

Maps illustrating the downstream area of the former and future run of the River Skjern and the Omme Stream [6].



Danish streams are exposed to many different pressures.

12 Environmental state and research

Even though the environmental state of Danish streams has generally improved in recent years, for various reasons less than half of them meet their current environmental quality objective. The Water Framework Directive, recently adopted within the EU, will no doubt influence future management of Danish streams. This chapter summarises past developments in Danish stream research and describes the areas where our knowledge of the biological aspects needs to be enhanced in the coming years to ensure that the stream authorities have the necessary tools to improve the country's streams.

Streams in Denmark

There are more than 60,000 km of natural and man-made streams in Denmark, i.e. more than 1 km of stream per km^2 of land. Streams are therefore important elements in the Danish landscape and are of considerable importance to the biodiversity of flora and fauna.

At the same time, though, human population density is more than 100 persons per km^2 and about two thirds of Denmark's area is exploited for intensive agriculture. Streams are consequently one of the ecosystem types under greatest anthropogenic pressure. This imposes great demands on stream management.

One of the tenets of Danish nature and environment policy is that it must be firmly rooted in sound knowledge. The aim of this chapter is thus to identify some of the most urgent strategic research needs on the basis of an analysis of the environmental state of Danish streams. As the EU Water Framework Directive will unavoidably influence future Danish stream management, the Directive's intentions will be briefly reviewed.

The following account emphasises the ecological quality of the Danish streams, focusing on their biological state. However, the streams are also important with regards to input, transport and turnover of nutrients and hazardous substances derived from households, industry, aquaculture and agriculture. These processes are of great significance, not least for downstream lakes and marine waters. Our present knowledge of a number of these aspects is insufficient and concerted efforts are therefore needed to strengthen knowledge in these areas, in order, among other things, to be able to model the processes. For the sake of brevity these aspects will not be dealt with here, however.

Wastewater used to be the main cause of the unsatisfactory environmental state of Danish streams.

Environmental state of Danish streams

In Denmark, as in most of Europe, the environmental state of streams is traditionally assessed from the composition of the macroinvertebrate fauna. The method currently employed is the Danish Stream Fauna Index (DSFI, see page 118) [1] whereby an index value on a scale from 1 to 7 is calculated from the composition of the stream fauna. Pristine streams containing many sensitive species are assigned an index value of 7, while the most heavily disturbed streams are assigned an index value of 1. Due to the natural physical conditions pertaining, some of the streams will score less than 7 despite being completely unaffected by anthropogenic factors.

In 1997, the nationwide programme to monitor the aquatic environment encompassed 444 representative stream stations. An analysis of the results shows that the DSFI was 5–7 in 37% of the streams, 4 in 43% of the streams and even lower in the remaining 20% [2]. The environmental state is generally better in large (>2 m wide) streams than in the smaller streams. Due to the natural physical conditions pertaining, the environmental state of streams in Jutland is generally better than on the island part of Denmark.

Each county's Regional Plan stipulates environmental quality objectives for their streams. Three main categories of objectives are employed: stringent objectives, basic objectives and eased objectives. Streams with stringent objectives must be completely unaffected, whereas those with basic objectives may be slightly affected and those with eased objectives may be severely affected. In the period 1993–1996, quality objectives were only met in 45% of Danish streams [3]. More of the streams in Jutland (50%) fulfilled their objective than those on the island part of Denmark (30%).

Since the 1970s, biological assessment of streams has been undertaken many thousands of times in connection with routine stream supervision by the counties. There is little doubt that the environmental state of the Danish streams has generally improved. The distribution of a number of clean-water species has increased markedly on Funen and in Jutland, several species have been removed from the Danish Red List [4], and the trout population has increased considerably [5]. Since a sufficiently standardised procedure such as the DSFI was not previously used in stream supervision, it is not possible to quantify the improvement on the basis of the faunal class.

Pressures affecting stream environmental state

The counties have analysed why the quality objectives are not met in 11,600 km of stream [3]. Among the many different factors to which this is attributable, the most important is wastewater from sparsely built-up areas followed by stream regulation/maintenance.

The counties thus estimate that wastewater from sparsely built-up areas is the main reason for the unsatisfactory environmental state of 3,000 km out of the 11,600 km of stream. It is important to note, though, that concerted efforts to reduce wastewater discharges from sparsely built-up areas will not necessarily result in the quality objective subsequently being met in a further approx. 3,000 km of stream. While this measure is necessary, it is not necessarily sufficient – for example because of unsatisfactory physical conditions, discharges of pesticides and ochre, etc.

The EU Water Framework Directive

The overall objective of the Directive is to improve the environmental quality of European water bodies wherever they are, at present, unsatisfactory, as well as to prevent further deterioration. The objective is to be attained through the preparation of action plans for whole river basins and by documenting possible improvements through monitoring.

Ecological quality is one of the key phrases, and it is to be documented using physical, chemical and biological indicators. The emphasis is expected to be on the biological indicators. For streams these will include not only macroinvertebrates, but also macrophytes and fish. Indicators for the quality of the riparian areas will also be included due to the tight coupling

There is a tradition of stream ecology research in Denmark.

between streams and riparian areas. Another challenge in the Directive is to create a system able to ensure that good ecological quality in, for example, an Italian stream is comparable with good ecological quality in, for example, a Danish stream. Important tools for ensuring this will be methods for determining the baseline state, i.e. the ecological quality in a completely pristine stream, as well as methods to measure deviations from this state.

History of stream research in Denmark

Stream research has been conducted in Denmark for more than a century. For many years research was predominantly concerned with the flora, fauna or natural history of the streams. The main actors were scientists such as C. Wesenberg-Lund, P. Esben-Petersen, H. Ussing and C. V. Otterstrøm. The first major quantitative description of a Danish river system was the Suså Stream surveys carried out in the 1940s under the direction of Kaj Berg [6, 7].

As early as 1925, C. Wesenberg-Lund drew attention to the serious pollution of our lakes and streams [8]. However, as late as 1975, few pollution-related studies had still been conducted, [9–11]. In 1976, the Danish Environmental Protection Agency's Freshwater Laboratory (now part of the National Environmental Research Institute) was established in Silkeborg together with the Freshwater Fishery Laboratory (now the Danish Institute of Fisheries Research). This markedly strengthened research aimed at supporting the management of Danish streams.

Present structure of Danish stream research

Danish stream research is currently distributed among a number of universities and sector research institutes. The research among the universities is chiefly conducted at the University of Copenhagen Freshwater Biological Laboratory, while that among the sector research institutes is mainly carried out by the National Environmental Research Institute and the Danish Institute of Fisheries Research in Silkeborg.

In recent years some positive trends have been detectable in Danish stream research of both an organisational and a cognitive character:

- Enhanced cooperation between basic research at the universities and the strategic/applied research at the sector research institutes
- Enhanced cooperation between fisheries research and environmental research
- Enhanced recognition of the need to consider streams as an integral part of the landscape and focus on the interplay between streams and the riparian areas
- Enhanced international cooperation on the build-up of knowledge related to stream management

Research on the ecological interaction between the surroundings and the stream and the mutual interaction between plants, animals and fish has not previously been accorded high priority in either Denmark or at the European level. The Water Framework Directive is likely to help change this, however. Enhanced cooperation between Danish researchers and our European colleagues is a prerequisite if this is to succeed.

Perspectives for Danish stream research

In this section, we describe areas where there is a need for concerted efforts to support the future management of Danish and European streams, i.e. those pertaining to strategic and applied research.

Stream quality objectives

Implementation of the EU Water Framework Directive necessitates the establishment of comparable and quantifiable European-wide indicators of the ecological quality of streams and their riparian areas. The relevant indicators for Danish streams are macroinvertebrates, macrophytes and fish. While there is a century of experience with macroinvertebrates, considerable work is needed before operational macrophyte and fish-based indicators can be developed.

In order to be able to establish reasonable quality objectives, the natural state of the stream needs to be known, i.e. the biological communities that would be present under the natural physical and chemical conditions. Predictive modelling is a promising tool for predicting the probable composition of the flora and fauna and hence the ecological quality of streams on the basis of information on the physical and chemical conditions [12, 13]. Such a tool needs to be developed for macroinvertebrates, macrophytes and fish in order to be able to comply with the intentions of the Water Framework Directive. In Denmark too, a system is needed for establishing quality objectives on the basis of objective criteria, especially regarding the physical conditions. Such a system would ensure that stream quality objectives are established in a comparable manner throughout the country.

Stream maintenance and restoration

In order to ensure rapid drainage of agricultural land, the majority of Danish streams have been channelised. The spatial variation in current velocity and substratum conditions has consequently been reduced in the reaches in question, leading to deterioration in habitat conditions for plants and animals. Stream maintenance through weed clearance and sediment removal further reinforces the uniformity.

In Denmark, since the mid 1980s, stream maintenance practice has changed markedly in the direction of environmentally sound maintenance or no maintenance at all [3]. Moreover, more than 900 restoration projects have been carried out in large Danish streams in which the physical conditions have been improved, amongst other means, through the establishment of spawning grounds and habitats for fish. It is striking, though, that the environmental effects of the various measures are very poorly documented both nationally and internationally. At best the effects on the macroinvertebrates and/or fish have been recorded, while investigations of the plant communities and the long-term effects at the system level are virtually non-existent.

To improve this situation, the European Centre for River Restoration (ECRR) was established in 1994 founded by EU LIFE. The secretariat was at NERI until 2002, and then moved to RIZA, the Netherlands. Through conferences, a web site (www.ecrr.org) and other forms of networking the ECRR promotes river restoration as a cost efficient tool for improving river quality and stimulates river restoration research and dissemination of the findings.

Interaction between streams and their riparian areas

At both national and international levels, considerable research has been conducted on the interaction between forests and streams e.g. the input and biological processing of leaves and the structure and role of the macroinvertebrate community. However, as most Danish streams lie in open landscapes, it is likely that the structure of the riparian areas is of considerable significance for their biological communities. For example, the structure of riparian areas can influence the dynamics of the bank-side plant communities which in turn can influence the survival of adult insects and hence the possibilities for macroinvertebrate recruitment. Plant and animal diversity is particularly great in places where different types of ecosystems meet. Improved knowledge of the interaction between streams and riparian areas can help ensure the success of initiatives aimed at improving the quality of nature in general.

Fishery and aquaculture

Recreational fishing is a characteristic feature of Danish streams. Fisheries research in Danish rivers has chiefly focused on species such as trout and salmon and has often concerned optimisation of these populations through stocking. In recent years, genetic studies have been initiated to preserve the natural fish populations and genetic variation.

Fisheries research and environmental research have traditionally been separate disciplines. Cooperation has now been initiated to investigate the significance and dependence of fish in a broader ecosystem context. Some of the important themes are: the interactions between fish and the other biological communities, fish as indicators of ecological quality and methods for maintaining and restoring streams so as to ensure a rich and varied flora and fauna, including fish.

Aquaculture in the form of freshwater fish farms is a major reason for the failure of many streams in Jutland to meet their quality objective. In 1997, the 433 freshwater fish farms in operation together produced approx. 32,000 tonnes of rainbow trout [14], approx. 95% of which were exported, representing an annual turnover of DKK 482 million (65–70 million EURO) [15]. The fish farms affect streams through dams interrupting the streams' natural continuity, through the discharge of organic matter, nutrients, medicines and other ancillary substances often leading to "dead" stream reaches alongside the

fish farms [16]. If fish farming is to be sustainable, research and development work will be needed to ensure that production is compatible with fulfilment of the streams' quality objective. Cross-disciplinary research in this area has recently been initiated.

Laboratory identification of insects and extraction of chlorophyll.

Hazardous substances

An estimated 100,000 different products containing up to 20,000 different chemical substances are estimated to be on the market in Denmark. All these can potentially end up in the aquatic environment and hence affect its environmental state.

Little is presently known about the occurrence and distribution of hazardous substances in Danish streams. The Danish Aquatic Monitoring and Assessment Programme NOVA 2003 – and after 2004, NOVANA – has provided important information on approx. 300 substances, especially with regard to point sources. Pesticides are used in large amounts, and it is known that they are detectable in streams. In Funen County, pesticide contamination is purportedly the reason why 15% of the stream reaches fail to meet their quality objective. Little is known about the impacts of pesticides on the stream flora and fauna, though. These could involve direct toxic effects, although it is more likely that indirect effects are involved whereby the substances affect the interaction between the various organisms.

Some of the other substances discharged into streams from point sources undoubtedly have similar effects, but these are as yet unknown. In the coming years it is therefore necessary to develop experimental methods for investigating the effects of various chemical substances on the biological communities and their interaction and to further identify which substances affect the streams and how.

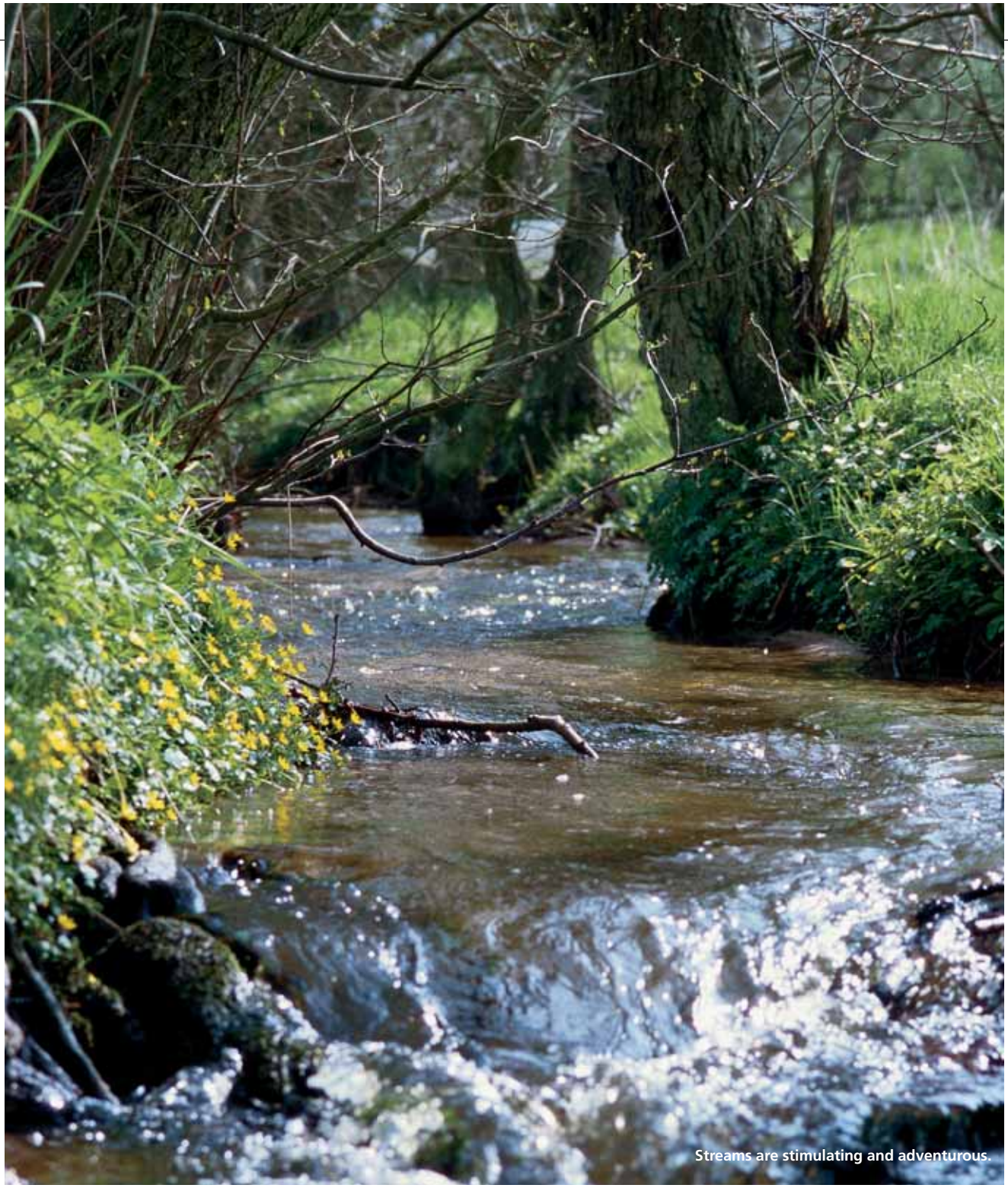
Research and the future

As is apparent from the above, Danish stream research faces many challenges. In the 1970s it was believed that, once treatment of urban wastewater was implemented, the quality objectives would be attained. When treatment of the wastewater had been implemented, however, it became obvious that poor physical conditions often hindered attainment of a satisfactory stream quality. We know that the future will also hold surprises in store, but not which ones.

Some of the areas where research is needed in order to be able to improve the environmental state of streams in the long term have been outlined above. Common to the majority of these is an enhanced understanding of the physical-chemical-biological interactions within streams and between streams and their riparian areas. Broad-based research in clearly defined areas is a prerequisite for procuring the knowledge and tools needed for stream management.

Interplay between research and county/municipal stream management is crucial if the research findings are to be utilised in practice. Fortunately, there is a strong tradition of close contact between researchers and environmental administrators in Denmark. This is fostered through scientific meetings aimed at keeping the administrators abreast of the latest research findings and the researchers abreast of the unsolved questions of importance to the county and municipal environmental administrators. It is the responsibility of the politicians to decide what the environmental state of Danish streams should be but it is a joint responsibility of the administrators and researchers to provide the politicians with a sound basis for decision making that is both relevant and founded on the latest knowledge.

It is impossible to stipulate stringent criteria for what is the most relevant research. Less than half of Danish streams meet the politically determined quality objectives and the reasons for this depressing figure are difficult to determine. If research efforts in the areas outlined above can help significantly enhance the number of streams meeting their quality objective, then the research will have been relevant.



Streams are stimulating and adventurous.

13 Streams and their future inhabitants

In this final chapter we look ahead and address four questions:

- *How do we improve stream management?*
- *What are the likely developments in the biological quality of streams?*
- *In which areas is knowledge on stream ecology insufficient?*
- *What can streams offer children of today and adults of tomorrow?*

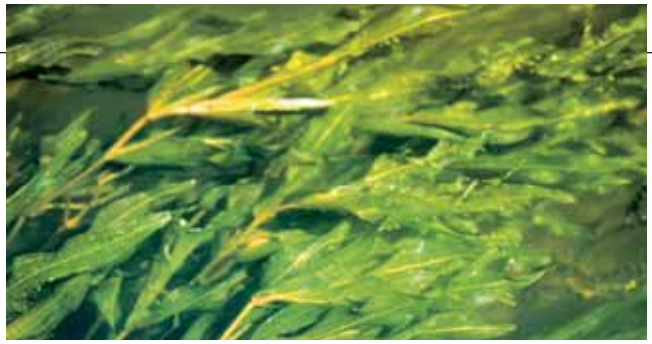
Improved management

When you are placed at a convenient distance from the legislators in the Danish Parliament and the local politicians, it is easy to wonder at the apparent lack of effectiveness in the management of streams, and the distribution of competence and power between the state, the counties and the municipalities. Let us take a look at two conspicuous conditions.

Consequent or realistic planning?

Thanks to heavy investments in biological and chemical purification of domestic wastewater, oxygen depletion and smothering of the stream bed is no longer found in most streams that were formerly heavily polluted. In consequence, the biological quality of streams based on the composition and richness of large invertebrate species has improved (page 121). Unfortunately, there has been an increase in the number of streams of intermediary quality, which are neither very clean nor very polluted. In many cases the small percentage of very clean streams have not been kept free from other polluting or disturbing impacts deriving from freshwater fish farms, agriculture, forestry, market gardens, sewage from scattered dwellings and water abstraction. There has been a lack in either political determination or sufficient administrative authority.

The required treatment of domestic sewage has been implemented throughout Denmark, while destructive dredging of the stream and washing down of ochre from the land drains have continued. In many forest springbrooks, where there are excellent opportunities of achieving a rich, almost unaffected fauna, this high quality status has not been reached because destructive impacts such as abstraction of water for freshwater fish farms and domestic water supply, or drainage for the enhancement of forestry production have been tolerated. In the vicinity of Copenhagen, the groundwater table has been drawn down by 5–13 m and numerous springs have dried up. In addition to the direct impacts on streams and their hydrology, the



There has been a serious decline in *Potamogeton praelongus* (long-stalked pondweed) in NW Europe.

terrestrial vegetation has undergone profound changes. Mixed deciduous forests have been replaced by planted monocultures of conifers along some of the most pristine streams. Because of the intimate coupling between land and water, such changes have had a severe negative effect on the flora and fauna of the stream, such as acidification, enhanced shading and a poorer nutrient quality of coniferous leaf litter for microbial decomposition and consumption by invertebrates.

Zig-Zag course in management

The municipalities are responsible for the management of small local and privately owned streams, and they keep control on the sources of pollution (e.g. agriculture and market gardens). The municipalities are usually small administrative units with limited professional expertise. Environmental issues are often treated with a rather mixed degree of attention and understanding. Some municipalities make a great effort to secure the biological quality of streams, often encouraged by strong environmental awareness of the public. The municipalities may even undertake restoration projects such as remeandering of streams and re-establishment of stone and gravel beds that have been lost during decades of intensive dredging.

In other municipalities with strong agricultural interests, however, the attitude and administrative practice may be quite the contrary. Small streams with very clean water are physically destroyed by severe dredging. Huge machinery is used to excavate the streams to a greater width and depth than strictly necessary to transport the water. Stones are left on the banks and the entire operation resembles a development that usually requires special permits. It is a paradox that the high physical and biological quality of streams restored by means of goodwill and the large investments of some municipalities is actively destroyed in other areas by contrasting actions of people with different priorities.

Development of plants, invertebrates and fish

Stream plants and animals are generally tolerant of sporadic disturbances and are able to re-establish former communities [1]. Following a pollution incident which kills most invertebrates and fish along a stream reach, or after extensive weed cutting and dredging, the communities usually become re-established within a relatively short period. Depending on the circumstances and the type of organism, the recovery may take a few weeks, months or 1–2 years [1]. There are several reasons for this overall robustness. Streams are naturally exposed to substantial fluctuations in discharge and flow velocity leading to erosion of the stream bed and a catastrophic loss of organisms. Stream species have therefore evolved the ability to cope with disturbances either by avoiding them, taking shelter, or resisting the disturbances by strong anchoring and reduction of drag forces by changes in shape and orientation. Streams are connected systems allowing all organisms to disperse passively with the current from populations that have survived the disturbance. Fish can swim actively to all reaches in the stream system, and insects can disperse both along and between the streams as flying adults. Moreover, plants and animals produce numerous offspring that may disperse with the current and large animal vectors (i.e. fish, birds and humans), giving the organisms the potential for rapid colonisation of depleted reaches.

It is an essential prerequisite for rapid re-establishment of lost populations that invertebrates and fish must have survived in parts of the stream system, and preferably in close proximity to the affected sections (page 80). Re-establishment of plants is most successful when populations still grow upstream of the affected reaches (page 49).

Where species have not survived in refuges in the stream systems, recolonisation will be slow even though the environmental conditions may become suitable. Within a few years or decades species can recolonise from neighbouring stream systems, but successful re-establishment becomes more and more difficult as the distance to neighbouring populations increases and stronger barriers have to be passed. The likelihood of recolonisation is reduced even further if the potential donor populations are few and small.

Will rare plants return?

Within the large plant genus *Potamogeton* several species which were widespread and locally abundant are now restricted to very few localities and have small populations (page 109). In general most aquatic plants are widely distributed regionally as well as globally. This widespread distribution can be explained by the high probability of propagule establishment because open space frequently becomes available on the stream bed. Dispersal depends, nevertheless, on the existence of viable populations. In that respect the premise of readily available propagules has changed dramatically in Denmark during the past 100 years.

Many pondweed species such as *Potamogeton acutifolius*, *P. densus*, *P. filiformis*, *P. frisii*, *P. gramineus*, *P. pusillus*, *P. rutilus* and *P. zosterifolius* are in a very vulnerable position. The populations in Denmark and most other parts of NW Europe are few and small (page 109). River drop-wort (*Oenanthe fluviatilis*) and water-plantain (*Elisma natans*) are even more threatened. It is probably unlikely that these species will become more widespread and abundant in Danish streams just by natural means of dispersal, and we are uncertain as to whether this can happen at all. Fortunately, analysis of a recent national mapping of the distribution of stream species will reveal future needs.

Will rare insects return?

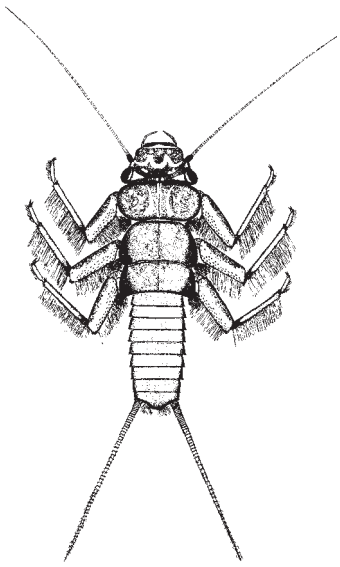
In Denmark, several species of caddisfly, damselfly, mayfly and stonefly have become rare over the past 100 years and some species are now extinct (Table 13.1). Among the 42 species of mayfly recorded from Denmark, five species have become extinct, and fifteen species are currently threatened [2] . Among the 25 known species of stonefly, the two large, impressive species *Perlodes dispar* and *Dinocras cephalotes* have disappeared from Denmark.

From 1980 to 2000, several species have become more widespread and abundant (page 121). Among mayflies this expansion includes *Ephemera danica*, *Heptagenia fuscogrisea*, *H. sulphurea* and *Paraleptophlebia submarginata* which are no longer considered as threatened species. Among stoneflies, *Isoptena serricornis* has virtually disappeared in Europe, but the species have become more abundant in some Danish rivers (the Varde Stream, Karup Stream and River Skjern). Also *Perlodes microcephalus* has become more common [3].

It is apparent that many insects are capable of dispersing and recolonising if the environmental conditions improve. However, the disappearance of some species could prove irreversible, once the species have disappeared from the entire country or some of the main islands (Funen and Zealand). Peter Wiberg-Larsen and colleagues have shown that rare species have recolonised new reaches in streams on Funen [4]. They have also emphasised that species that are extinct on Funen are unlikely to arrive from distant populations in Jutland by travelling many kilometres over open terrain and crossing the Little Belt to reach the former habitats in the Odense Stream. The journey is simply too long and dangerous (page 80).

	Extinct species	Threatened/ rare species	All species
Damselflies	4	17	50
Mayflies	5	15	42
Stoneflies	2	8	25
Caddisflies	10	44	167
Blackflies	0	7	24

Table 13.1 Many species of Danish freshwater insects are threatened or have become extinct.



The large stonefly *Dinocras cephalotes* is extinct in Denmark.

North Sea houting is an endemic species in the rivers of SW Jutland.

Future development of North Sea houting and salmon

The Danish fauna includes 38 species of native freshwater fish and nine introduced or escaped species [5]. Among the stream species, Denmark has an international obligation to protect the habitats of rare species, such as brook and river lamprey, salmon and North Sea houting. Special conservation and rehabilitation initiatives have been undertaken in the case of salmon (*Salmo salar*, page 100) and North Sea houting (*Coregonus lavaretus*) [6].

North Sea houting was previously distributed throughout the Wadden Sea area of the North Sea from the Netherlands to Southern Denmark where it spawned in large and medium-sized river systems. Due to pollution, river regulation and establishment of impassable weirs, the populations became extinct, except for a small population in the Vidå Stream. Genetic studies have suggested a recent common origin of all whitefish populations (*Coregonus* sp.) in Denmark, including the North Sea houting, via the postglacial River Elben [7]. While the Danish whitefish populations differ in morphology and physiology, they exhibit very close genetic relationships as detected by molecular markers, and appear to have evolved within a very short evolutionary timescale. Nonetheless, the North Sea houting is still to be considered unique because of the distinctive number of gill rakers, the elongated upper jaw, the anadromous life cycle and the ability to withstand high salinities. The North Sea houting has been hatched artificially and introduced in substantial numbers in the Vidå Stream and adjacent rivers entering the Wadden Sea. The populations have increased, and the species is no longer endangered.

Salmon used to be common in several rivers in West Jutland (e.g. Ribe, Skjern, Sneum, Varde og Vid) and in the River Gudenå in eastern Jutland. DNA-analysis of dried, old salmon scales has shown that populations differed genetically among the rivers in SW-Jutland, but they were more alike than populations from the River Gudenå and foreign populations from Scotland and Sweden [8]. The populations in the three rivers, Skjern, Varde and Ribe are probably the only native surviving salmon populations in Denmark. Restoration of native Danish salmon stocks aims at ensuring an optimal chemical and physical stream environment, unrestricted passage of migrating fish and spawning grounds. These initiatives have been combined with the introduction of offspring reared from wild fish in farms. Fishery authorities have become very reluctant to approve the introduction of foreign salmon or offspring from other Danish salmon stocks into rivers where native stocks have (or may have) survived. Such native salmon stocks probably hold essential adaptations to the local stream temperature, water chemistry and food supply.

The recent increase in the size of salmon stocks in the River Skjern has been positive. The catch reached 1,000 individuals in 2000, which is the largest numbers since the 1940s. Prospects for the future are promising, particularly because of the ongoing large-scale restoration of the River Skjern (page 30). Magnificent progress in salmon population recovery would be possible if major parts of the river system, which are not accessible at the moment due to trout farms, were opened. Freshwater fish farms could be abandoned or moved from headwaters to downstream sites or coastal waters. Although salmon is still present in the Danish fauna, the species is nevertheless rare and the genetic diversity low, as many ancient, local stocks have become extinct during the past 100–200 years. The native stocks of small stream, lake and sea trout (*Salmo trutta*) have experienced the same restriction of local genetic diversity.

Extensive help or left undisturbed

There are clear differences in the way plants, insects and fish in streams are managed. Plants and insects are mostly left undisturbed and they recolonise restored streams solely by natural immigration from neighbouring populations. In contrast, fish populations are manipulated to a very great extent. In most Danish streams, trout fry are introduced at intervals of 1–4-years and their potential competitors or top predators are managed. For the North Sea houting and salmon, costly conservation and rehabilitation programmes have been implemented. The interest in other rare fish species e.g. bullhead (*Cottus poecilopus*), however, is aston-

ishingly limited because they do not provide an attractive catch [5].

We feel that future stream and river management should include more general and comprehensive evaluations including their interactions with the catchment, the surrounding valley and the interdependence between plants, invertebrates and fish (page 12 and 82). It is unacceptable that a narrow focus on fishery interests can become a threat to the well-being of plants and invertebrates – or vice versa. We also propose a closer evaluation of whether many years of severe physical regulation, pollution and inappropriate management of the streams in NW Europe have brought some plant and invertebrate species to such a threatened position that they are unlikely to recover and return to improved and restored habitats, where they used to live in large populations only 50–100 years ago.

There are situations where it may be beneficial to reintroduce plants or insects to streams. This is especially the case where species have disappeared from a region and hence are unable to naturally recolonise sites where they are known to have previously been. Such management could counteract the situation we have at present, where the same group of robust plant and insect species, with a high dispersal capacity, tend to dominate all streams, irrespective of the present environmental conditions.

It is important, however, that the reintroduction of rare or extinct plants and insects is performed under strict official control to avoid circumstances where rare species are introduced arbitrarily to generate local publicity. Most botanists and entomologists are against planned re-introductions of native species, but accept accidental introductions of alien species and large-scale dispersal among stream systems by weed cutting companies, anglers, biologists and canoeists.

Trout is regarded as the most important Danish stream species. Nonetheless, it is surprising just how much this species has dominated the discussion and management policy of streams. In most cases, the population density of trout has been the main (or only) criteria for judging the success of management policy and stream restoration. Continuous stocking of trout has a selective impact on the biology of streams and it is surprising that intensive stocking has continued even in streams where a self-reproducing population has been established. The discovery of small native populations of salmon or trout in several Danish rivers has recently led to reluctance among fishery authorities to introduce foreign fish. There have also been increased efforts to stimulate native populations which otherwise could be lost to fierce competition and hybridisation with introduced fish. Anglers often want to continue the tradition of stocking artificially reared trout fry, even when the density of fry surpasses the stream carrying capacity by several orders of magnitude, leading to enhanced density-dependent mortality.

Brown trout in Danish streams is the most important catch for anglers.

New research themes

Several authors of preceding chapters in this book recommend a holistic view of the stream and the catchment from the spring source to the river mouth (page 12, 26, 45, 66 and 74). Others recommend a stronger focus on the interactions between the organisms and the physico-chemical environment as well as the mutual interactions between the organisms (page 54 and 82).

These contributors recommend a stronger focus on the environment and the biota rather than the biology of particular species or types of organisms. Even the well-being of a single species such as salmon depends on a holistic

Comparative studies of streams in different habitats and geographical regions can be used for drawing general conclusions on biological regulation in streams.

attitude towards environmental exploitation and fishery in the sea as well as water quality, food availability, spawning areas and impassable weirs in the streams (page 92).

Holistic studies have two main advantages. They can be transformed into real environmental policy and management and they are also easily absorbed and appreciated by public and administrative circles outside the "world of the stream ecologist".

Because streams form the network for transport of water and nutrients between the terrestrial and aquatic environments, it is important to establish the principles for this transport and exchange. This attitude raises questions such as: 1) How does stream morphology depend on soil, topography, vegetation and hydrology?, 2) What are the risks of floods or prolonged low water flows for streams, and 3) What are the patterns and trends of erosion, retention and transport of mineral particles, organic matter and nutrients along the streams? (page 26). In Denmark there is an urgent question concerning how much of the nutrient loading, which leads to extensive eutrophication from agricultural activity, could be reduced by re-establishment of meadows and wetlands along the streams.

The riparian zone is an integral part of the scenic beauty of streams in the landscape. On closer inspection, the riparian zone may also be important for the biological dynamics, as numerous organisms cross back and forth between land and water during their lifetime. The close interactions suggest that the physical features and vegetation in the riparian zone may be as important for the variety and quality of stream biota as the physico-chemical conditions within the streams (page 81). We still need to qualify and quantify the importance of the riparian zone.

Broad-scale ecological research also needs to address the importance of terrestrial and stream vegetation as a source of organic matter that ends up being consumed and degraded by animals, fungi and bacteria in streams. By analysing the proportions of natural isotopes of carbon (C^{13}) and nitrogen (N^{15}) in animals and plants it is possible to distinguish between the sources of organic matter from land and water. Thus the import, export and biological conversion of organic matter through the food webs can be traced. This approach is likely to reveal exciting differences between streams in forests and more open landscapes and between streams of different climates. For example, the food webs in forest streams can rely entirely on organic matter supplied from the trees e.g. leaves, twigs. In unshaded streams, internal production of microalgae and plants is more important for the biological transformations. In tropical streams several fish species live on seeds and fruits falling from the trees, while fish species in temperate regions mainly

live on invertebrates and other fish. Interactions between invertebrates and fish in tropical and temperate streams may, therefore be markedly different.

In recent years we have learned much more about the importance of the physical environment for the biology of stream organisms and the role of aquatic plants for the flow, sediment properties and shelter of invertebrates and fish (page 54). However, there is scope for more studies of the effects of water flow and the physical forces experienced by stream organisms, as more advanced instruments and methods become available. Moreover, stream biologists have not traditionally dwelled on bio-physical questions and have instead concentrated on the chemical aspects in biology. As a consequence, we know very little about the influence of flow and oxygen concentrations on the respiration and survival of invertebrates on and within the stream bed. Likewise, although we are aware that flow and turbulence must be accounted for when plant photosynthesis and growth are evaluated as a function of carbon dioxide concentrations (page 66), we still need to establish the relationships under field conditions.

Biological interactions

While the focus has been on the importance of the chemical environment for the organisms and less on the physical environment, the biological interactions and the ability of organisms to influence the environment have received very little attention.

Fishery biologists have traditionally focused on the distribution and abundance of economically important fish species, while the role of fish in the control of prey populations, food web structure or overall ecosystem function has been of less interest. Also in the management of streams the main focus has been on species composition and relative abundance of fish and invertebrates and less on overall ecosystem function. We believe that more emphasis will be placed on broad-scale issues of ecosystem function in the future as the natural landscape becomes more fragmented and human populations in most countries continue to rise.

We recommend a comprehensive review of the control of food webs looking at both quantity and quality of basic food sources ("bottom up control") and the predators ("top down control") exploiting the basic food sources. We recommend a broader consideration of the structure of food webs, and the conversion of energy through these, to be used, rather than focusing on a few selected interacting species in prey-predator and competitor-competitor associations. The wider extrapolation of such latter studies is limited and important compensatory responses of other species will be difficult to include within the time frame commonly used. Under any circumstances spatio-temporal variations in the abundance of plants and animals are fundamentally controlled by available resources and boundaries set by physical forces. We also recommend that testable hypotheses are formulated a priori to avoid the unfortunate tendency of making post hoc explanations to support a preferred concept.

There are reasons to be sceptical about the relevance and interpretation of food web interactions based on small-scale manipulations in enclosed stream reaches because it is difficult to ensure the natural dynamics and compensatory behaviour when organisms are prevented from moving freely along the stream. As previously emphasised it is important for the animal communities that streams work as networks so that communities at any one site depend on and influence the composition at neighbouring sites through immigration and emigration. Enclosed reaches lose the essential feature of streams and increase the risk of developing "exaggerated responses" because animals are unable to leave if intolerable conditions develop. Biased conclusions for entire stream systems can, therefore, be reached based on manipulation of enclosed reaches.

In what way are streams a benefit to the community?

For many years the biological, ecological and aesthetic quality of natural habitats has not been sufficiently appreciated and valued. There was little concern about the consequences for the public when ecosystems lost their natural functions. However, the public, is paying for the loss of ecological services in the streams and their terrestrial surroundings by enhanced risks of erosion and flooding, decimation of valuable fish stocks and pollution of groundwater and coastal waters [9, 10].

Catastrophic flooding, with grave economic consequences and loss of life, has taken place all over the world because of channelisation, clear-felling of forests and reclamation of land for intensive agriculture and industrial or urban development in the river valley. Loss of wetlands has reduced the retention of nutrients during transport of water from the land to the sea. It is possible to estimate the value of reduced nutrient loss, for example, by estimating the costs of a similar nutrient reduction in the sewage plants. It

Streams and stream valleys are essential elements of the scenic beauty of open landscapes.

is also possible to estimate the price required for buying land and thereby putting an end to cultivation of the river valley. Finally, it is possible to estimate the costs of increased pollution of groundwater and drinking water following intensive cultivation of fields along the streams. Scientists have evaluated these ecological services provided by wetlands and streams/lakes at $14,800 and $8,500/ha per year in 1997 prices [11]. The main areas of expenditure involve prevention of erosion and flooding, and the introduction of measures to secure the water supply and counteract eutrophication. On a national scale, Danish society will probably pay a high price for a nonchalant attitude towards groundwater quality as it becomes increasingly difficult and expensive to offer drinking water free of pesticides and with nitrate concentrations below the limits recommended by the World Health Organisation.

Future EU policies for the conservation and, if possible, improvement of natural resources and environmental quality will be based on the EU Water Framework Directive and the EU Habitats Directive. These directives should ensure a more sustainable use of the river valley and the survival of rare and threatened species. Overall, effective nature management must secure the availability of natural habitats for plants, invertebrates and fish whilst the serious eutrophication of streams, lakes and coastal waters should be reduced. In future, the public should be able to enjoy the landscape and the various recreational activities associated with inland waters and should also be provided with drinking water of high quality.

Because virtually all European lowland streams have been extensively impacted by human activity, it will be especially important to select entire stream systems to serve as future references for relatively unregulated and unpolluted natural streams. Such stream systems could stimulate new research, ecological understanding and offer exiting opportunities for recreational activities if the streams are selected and protected at a sufficiently large scale. Denmark should be able to promote a few small, species-rich lowland streams of high quality.

Adventure, understanding and excitement

Streams and adjacent areas offer possibilities of excitement and pleasure, in addition to their ecological and economical value. Most people find it stimulating to look at a varied landscape and a meandering stream rather than a straight channel lined by monotonous fields. This experience is further enhanced if the river valley includes a variety of landscape types, such as bogs, fields, meadows and wetlands. Some appreciate the

sharp contour of streams lined with tall vegetation of shrubs and trees, and wet meadows generate special experiences because of their exceptional diversity of flowering herbs.

The rich animal life in streams offers adventure and enlightenment to every interested person. By sweeping a kitchen sieve (or pondnet) over the surface of the stream bed or through the vegetation, a myriad of animal species appear. In clean streams it is possible to collect more than 50 different species within a short time. This collection will include representatives from most larger invertebrate groups that have developed during the course of evolution. There will be sponges, flatworms, roundworms, annelids, leeches, snails, clams and crustaceans. And most insect groups, including beetles, caddisflies, damselflies, true flies, water bugs, mayflies, stoneflies and even species of moth will be represented.

People who are more interested in the adaptation of species, will find animal species that are adapted to fast currents with robust and strong legs, claws and suckers that permit secure attachment to the exposed surface of stones. Also present will be species with large moveable gills that assist respiration in slow currents close to the banks or in the vegetation. The tube-living species in the sediments are capable of ventilating the tubes and tolerating periods of oxygen shortage during resting. Species will have different food sources and preferences encompassing capture of particles by silk meshes, rasping of microalgae on stone surfaces, consumption of dead or living leaf fragments, consumption of fine organic particles on the mud surface and the capture of animal prey. Although the collection of 50 species within a very short time may seem a high number, taxonomic experts have been able to identify about 1,000 animal species in a small, unpolluted temperate stream (Table 13.2). If microscopic algae and animals are included, the experts could probably add an extra 400 species to the list.

It is an important point to recognise that high biological diversity and the living exhibition of the evolutionary development can be observed by everybody and is easily accessible within small brooks that flow through the forest or across the meadow in the vicinity of residential areas. Equipped with a kitchen sieve mounted on a stick and a jar, a white tray and a few inexpensive guide books on freshwater life, children can safely go in search of adventure [13].

People who prefer larger animals can target a wriggling fish on the line and into the frying pan. The excitement accompanying the first fish caught can easily match the thrill of a ride on the roller-coaster in an amusement park, and this excitement of fishing persists in adulthood. Anglers are often the largest interest group working actively in favour of improvement of the environment and the fish populations in streams. Fishing in Danish streams is often overlooked although the chance of a successful catch is better here due to the much higher density of trout present than in the more famous rivers of Iceland, Norway and northern Sweden. These latter rivers, however, attract more tourists due to the possibility of catching a salmon.

Fish stocks in Danish rivers could be improved even further if a number of harmful impacts are reduced or eliminated. By removing the presently impassable weirs there would be excellent opportunities for sea trout fishing in most Danish streams and attractive opportunities for salmon fishing in the River Gudenå and the large rivers in western Jutland. A potential role model is the Mørum Stream in southern Sweden. This river is an angler's paradise for trout and salmon fishing and provides an important income for the local community, who are therefore actively involved in the prevention of acidification, organic pollution and harmful exploitation of the river system.

Streams and rivers have much to offer children of today and adults of tomorrow in terms of adventures, knowledge and positive attitudes towards nature. Streams can also become an important source of income for local communities. There is always a stream passing close to your home – and it is up to you, us and everybody to work for its ecological qualities.

	Number of species
Insects	627
Flies and mosquitoes	476
Beetles	60
Caddisflies	57
Stoneflies	18
Mayflies	16
Roundworms	125
Annelids and leeches	56
Flatworms	50
Crustaceans	24
Water mites	22
Total	**904**

Table 13.2 Number of macroinvertebrate species within the most common groups in a small German stream [12].

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Running Waters is about the ecology of Danish streams. It exemplifies Danish stream research and monitoring over past decades. It is a tale of wasted opportunities and long-term abuse of Danish lowland streams from about 1850 to 1990: Channelisation, intensive management and pollution have in this period deteriorated ecological quality significantly. However, it is also the recent story of improvements accompanying physical restoration of the streams and large-scale water purification.

The state of the environment in Denmark, as in other densely populated countries in Europe, is mostly determined by cultural factors. This is a constraint but also an opportunity. If political willingness and courage exist, streams can recover their physical variability and develop a high diversity of plants, animals and fish. We demonstrate that the potential is certainly there.

With many illustrations and a direct language, Danish stream ecologists describe the knowledge we have gained and the excitement of experiencing the varied landscape along meandering streams with their diverse life and potentially rich catch of trout.

Professor Kaj Sand-Jensen, University of Copenhagen, Dr Nikolai Friberg, National Environmental Research Institute, Denmark, and Dr John Murphy, Centre for Ecology and Hydrology, U.K., have edited the book.

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