Physical habitat structure in lowland streams and effects of disturbance

PhD thesis

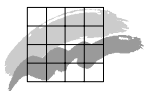*Morten Lauge Pedersen*

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National Environmental Research Institute
Ministry of the Environment · Denmark

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Data sheet

Abstract:	The first overall objective of the PhD-study was to study variations in physical habitats and macroinvertebrates across multiple scales in Danish lowland streams. The second objective was to study the effects of anthropogenic and natural disturbances on physical habitats and biota. The thesis is comprised of an introduction and 5 accompanying papers which all deals with different aspects habitats and biota in lowland streams. Discharge, near bed currently velocities were found to influence stream substratum patterns in general and the coverage mud substratum in particular. Physical habitats varied in a consistent way through the upper part of the lowland river systems in Denmark. Habitats and biota were influenced by a number of variables acting and interacting on multiple scales within the stream ecosystem. Human influence on the habitats and biota was analysed using weed-cutting as a disturbance. Biotic communities were significantly less varied in weed cut streams than in streams without weed cutting. Stream channelization influenced habitat variability, esspecially in riffle habitats where depth and current velocity was lower and less varied in disturbed and channelized streams than in near-natural streams. Danish lowland streams have been heavily modified over the past 200 years causing a significant degradation in biotic communities.

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Foreword

This Ph.D. thesis is the result of a 2½-year study undertaken at the Department of Freshwater Ecology, National Environmental Research Institute, Silkeborg, Denmark and the Freshwater Biological Laboratory, University of Copenhagen. The funding for the study has been provided jointly by the Danish Research Agency and the National Environmental Research Institute.

Danish lowland streams have been heavily modified over the past 200 years leaving less than 5% in a natural condition. The study of natural physical variations in Danish streams is therefore a challenging task due to the many different constraints imposed on the streams by human activities. The scarcity of natural undisturbed habitats in the Danish landscape makes the joy of working in a natural stream even greater.

The work concentrated on small lowland streams (< 6m wide) which make up approximately 75% of the entire stream length in Denmark. The work has been based on data collected during the Ph.D.-study and data collected prior to the initiation of the study as well as data collected as part of the National Monitoring Programme (NOVA).

My overall objective was to address physical habitat structure in small lowland streams in relation to the in-stream biota and to study effects of disturbances on physical habitats and in-stream biota. I have primarily focused on the interactions between physical stream morphology and macroinvertebrates but have also included other biota such as fish and macrophytes.

The thesis is comprised of an introduction and five accompanying papers, which have all been submitted to international scientific journals. The introduction introduces the reader to the subject of physical structure in streams in relation to natural and anthropogenic disturbance and interactions with in-stream biota. In the introduction I present current scientific concepts and place my own findings in perspective to these concepts as well as to the work of other researchers. The papers are listed in order of completion and are numbered by the Roman numerals I – V. Three further papers in Danish are included as Appendix A, B and C, and a supplementary English poster in Appendix D.

The four appendices (A-D) are included because they were prepared during the course of the Ph.D. study and they deal with related subjects. They are not part of the Ph.D. study and should therefore not be considered in the evaluation of the Ph.D.-thesis.

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Introduction

This introduction outlines the background of my Ph.D. study of physical habitat structure in lowland streams. I present important results from the project and place these in relation to work performed by other researchers and to the overall scientific challenges in the studies of physical aspects of stream ecology. Five scientific papers follow the introduction. In the introduction I will refer to these with Roman numerals in parentheses.

The introduction deals with different aspects. The importance of scale in stream morphology and ecology is introduced first because all subsequent discussions of results rely on scale considerations. The scale issues are illustrated with examples drawn from my own studies as well as work of other researchers. This part is relatively long because I find scale to be of major importance to the understanding of the physical habitat structure in streams. Part two is a description of Danish landscape development and the stream habitat structure in regions and along the continuum of small streams in Danish catchments. The third part describes biotic utilisation of the in-stream habitat at different scales. Special reference is given to macroinvertebrates and macrophytes. The fourth part concentrates on describing the effects of physical disturbance (anthropogenic and natural) on habitats and biota. The final part of the introduction concludes on the results and puts these into perspective in an applied context. Suggestions for future research are also outlined.

Background

Morphologic units in the stream ecosystem such as riffles and pools are essential to the generation of the in-stream habitats. Large-scale phenomena such as hydrology and sediment transport govern the dynamic nature of riffles and pools. Overall, however, geomorphological classification of distinct morphological flow units has developed somewhat independently of the analyses of habitat utilisation by the stream biota (Padmore, 1997; Kemp et al., 2000). Therefore, there is a need for cross-scale studies that integrate stream ecology and geomorphologic processes at multiple scales (Lane & Richards, 1997; Poole, 2002).

The physical habitats in stream ecosystem form the level at which biotic interactions occur. The physical environment thus plays an extremely important role for the functioning of the stream ecosystems by determining the environment and the habitat characteristics used by stream organisms (Southwood, 1977). The habitat template creates consistent changes in community structure and functions along with loading of organic matter, transport and utilisation along the river continuum. These continuous changes in biotic and physical structure form the River Continuum Concept (RCC) (Vannote et al., 1980). The unidirectional flow creates a unique aquatic environment in which fluvial processes form the habitat template with respect to temporal and spatial variations in the flow. These variations in flow and the physical habitats play an extremely important role for the distribution of organisms and community structure in streams. In contrast to other aquatic environments such as lakes and the oceans, the ecosystem structure and functioning in streams are heavily influenced by the physical environment at all scales (Hildrew & Giller, 1994; Townsend & Hildrew, 1994).

Macroinvertebrate distribution and habitat utilisation are influenced by flow variables such as velocity and shear stress (Statzner et al., 1988; Barmuta, 1990). Substratum characteristics such as particle size (e.g. Pennak & Van Gerben, 1947), stability (Stanford & Ward, 1983), texture (Harman, 1972; Lamberti & Resh, 1979; Erman & Erman, 1984) and heterogeneity (Hynes, 1970; Tolkamp, 1980) influence macroinvertebrate distribution and colonisation. Combinations of variables (the habitat structure) have been shown to explain a greater proportion of the variation in habitat analyses than single-parameter models (Statzner et al., 1988). Distribution of biota not only responds to the physical environment but also to biotic interactions (e.g. Lancaster, 1990; Dudley et al., 1990), water chemistry (Minshall & Minshall, 1978), temperature (Sweeney & Vannote, 1981) and food resources (e.g. Cummins, 1973; Minshall & Minshall, 1977).

The habitat template is hierarchically organised at gradually lower temporal and spatial scales and is therefore formed by interactions of physical parameters acting at a number of spatial and temporal scales (Frissell et al., 1986; Hildrew & Giller, 1994). Habitats and biota have therefore been studied at a range of different scales. The microhabitat scale - the immediate environment surrounding the organism - has been studied in relation to the significance of the substratum (Minshall, 1984) and the flow conditions (Statzner & Holm, 1982). The meso-habitat scale (defined her as a patch of uniform substratum) has also received attention (Armitage et al., 1995; Downes, 2000; Kemp et al., 2000). Overall differences in macroinvertebrate communities on the larger scale such as riffles and pool unit are well-documented

(Scarsbrook & Townsend, 1993), but detailed physical habitat descriptions of these morphological units have been limited. Reach-scale studies have been performed and the influence of the surrounding landscape has also been analysed in relation to biological communities (e.g. Allan & Johnson, 1997; Bojsen & Barriga, 2002).

Macrophytes play a key-role in stream ecosystems and also play a dual role by being a part of the in-stream biota and at the same being a moderator of the physical conditions. Current velocity, depth (light attenuation) and substratum are the primary physical parameters affecting macrophyte growth, abundance and community structure (Haslam, 1971). Furthermore, macrophytes offer important habitats for several macroinvertebrate taxa. Macroinvertebrates are more abundant in macrophyte-rich streams than in streams without macrophytes (e.g. Percival & Whitehead, 1929; Mortensen, 1977; Kaenel et al., 1998). Macroinvertebrates associated with macrophytes benefit from increased shelter and food. Thus, grazers utilise the high epiphyte biomass on macrophytes (Cattaneo & Kalff, 1980), while shredders feed directly on the macrophytes (Jacobsen, 1993). Detritivores feed on the accumulated fine particulate organic matter trapped within the macrophyte stands (Mann, 1988). The fish fauna benefits from the increased abundance of macroinvertebrates in macrophyte-rich streams because they provide sheltered areas and nursing habitats (Iversen et al., 1985). Macrophytes increase the in-stream physical complexity by reducing current velocity within macrophyte stands and by accelerating the current velocity around the stands (e.g. Sand-Jensen & Mebus, 1996; Sand-Jensen, 1998).

Streams are subjected to natural disturbances due to the temporal variations in discharge and current velocity. High-flow events help structure the large-scale stream morphology (Leopold et al., 1964; Richards, 1982) and redistribute macroinvertebrates among physical habitats (Hildrew & Townsend, 1987; Poff & Ward, 1989; Poff & Ward1990). In highly unstable streams physical disturbance can control macroinverte-brate community structure (Scarsbrook & Townsend, 1993). In winter, high stream flow scours the stream bed and coarse grained substrata are exposed as fine sediments are eroded. In summer, low-flow conditions and high coverage of macrophytes potentially reduce the current velocity and fine sediments are deposited (e.g. Sand-Jensen et al., 1989; Sand-Jensen, 1998). Both high and low-flow events can be considered natural disturbances since both flow regimes alter the physical stream environment by either deposition or erosion of sediment (Clausen &

Biggs, 1997; Wood & Armitage, 1997; Miyake & Nakano, 2001). The biota responds to disturbances by using refuge habitats from where they recolonise less stable habitat patches after a disturbance (Lancaster & Hildrew, 1993; Robertson et al., 1995; Lancaster & Beleya, 1997).

The physical stream environment is also susceptible to disturbance by human impact. Freshwater has been used by man at all times and in all regions of the world, either for drinking purposes, transportation, removal of waste or for irrigation of agricultural areas. Streams have been damned in order to reduce the risk of flooding and to generate dams for hydropower plants or fish farms (Haslam, 1991). In lowland areas such as Denmark, the main human interference affecting stream ecosystems today are draining and channelization, which have been carried out to enhance the productivity of agricultural areas and to use the riparian areas for agricultural purposes. Stream channels have been dredged to reduce flooding of the riparian areas (Iversen et al., 1993). As a consequence, Danish streams have lost their natural longitudinal profiles due to multiple dams created for hydropower, water mills or fish farming. Disturbance of the stream ecosystem is widespread in Denmark and approximately 95% of all streams have lost their natural physical structure over the past 200 years (Brookes, 1987). The majority of Danish streams have a marked seasonal growth of submerged macrophytes and are therefore often subjected to stream maintenance and weed cutting (Sand-Jensen et al., 1989; Iversen et al., 1993). The intensified agricultural production during the twentieth century has led to a general eutrophication of freshwaters due to increased use of fertilisers. The combined effects of stream regulation, maintenance and eutrophication have affected natural physical processes and stream morphology and have caused significant habitat degradation resulting in decreased biological stream quality in the Danish streams (Ward & Stanford, 1979; Hansen, 1996).

Objectives

The overall objective of this project was to study variations in physical habitats and macroinvertebrates across multiple scales in lowland Danish streams. Another overall objective was to study the effects of anthropogenic and natural disturbance on in-stream physical conditions and habitats. These two overall objectives have been divided into several specific objectives:

- To describe regional and seasonal differences in physical habitats in small lowland streams (Article I, IV and V).
- To study variations in physical habitat structure and variability in physical parameters and physical stability at different scales and the effects of these properties on macroinvertebrate community structure (Article I, III, IV and V).
- To study the effects of anthropogenic disturbance (channelization and weed cutting) on physical habitats and in-stream biota (Article I, II, IV and V).
- To study the variations in physical habitat structure of small Danish streams along the upper continuum (Article I and V).
- To analyse physical parameter relations in small lowland streams and gain insight into the parameters controlling physical habitat structure (Article I, III, IV and V).

Small lowland streams in Denmark – physical structure and regional variations

The Danish landscape – geomorphologic and geologic overview

The landscape comprises the geomorphologic and geologic setting and forms the basis on which the streams develop their characteristics. The present Danish landscape has been formed during the last two glacial periods (Weichsel ending approx. 10,000 years BC and Saarle ending approx. 250,000 years BC). Denmark was located at the line of maximum ice progression during the last glacial period, which has created a varied landscape with regional differences in topography and soil types (Fig. 1). Here I will distinguish between four main regions in Denmark. The western part of Jutland (Zone 1) was ice free during the last glacial period (Krüger, 1989) and therefore consists of two landscape elements; the moraine hills from the Saarle Ice Age and the glacial melt plains from the Weichselean Ice Age (Fig. 1). The eastern part of Jutland (Zone 2) was located close to the glacier front and the landscape is dominated by high topography, which is the result of sub glacial rivers transporting water towards the glacier front (Sugden & John, 1976; Nørrevang & Lundø, 1980). The soil pattern is very heterogeneous but consists primarily of loamy deposits. The northern part of Jutland (Zone 3) was also covered by ice during the Weichsel Ice Age. Following the recession of the ice sheet the land has experienced upheaval (Nørrevang & Lundø, 1980) and the geomorphology and geology therefore include two distinct features, namely the moraine landscape in the central part of the area and the surrounding sandy raised seabed (Fig. 1). The eastern part of

Denmark (Zone 4) was ice covered during the last glaciation and is dominated by loamy soils deposited from the glacier base and moderate topography. Areas of sandy soils and high-gradient topography are scattered in the landscape as a result of sub-glacial processes (Krüger, 1989).
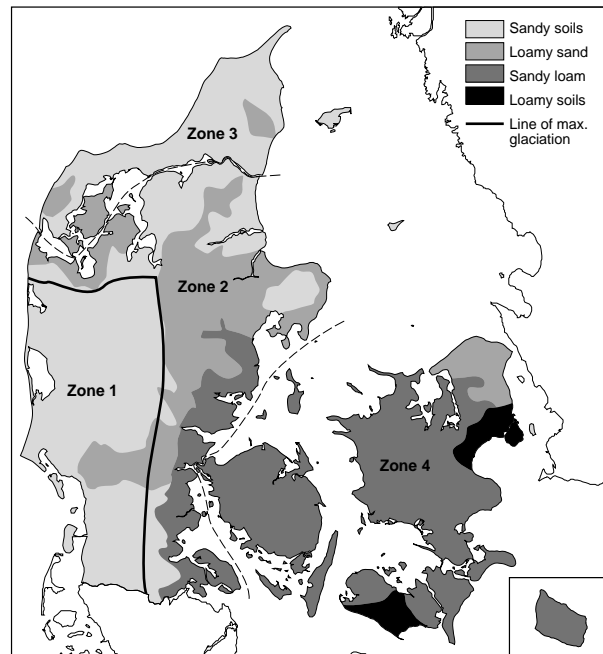
Figure 1. Soil types and landscape types in Denmark

Following the last glaciation Denmark became almost completely covered by forests (Nørrevang & Lundø, 1980). However, human activity changed the landscape and today agricultural land use represents approx. 65% of the total area. The landscape is drained by a dense network of natural small streams and artificial canals. There are approximately 65,000 km streams in Denmark and 36,000 km of these are of natural origin (Markmann, 1990). Riparian zones are often narrow and strongly modified by agricultural activities (Rebsdorf et al., 1994).

Danish catchments are generally small. 70% of the country's area is drained by rivers with catchment areas of less than 500 km^2 and only two rivers are longer than 100 km. The majority (75%) of Danish streams are less than 2.5 m wide. The natural drainage density in Denmark is 0.9 km km^{-2} of which 98% is physically modified. This modification intensity is 15 times higher than in England and Wales (Brookes et al., 1983) and 300 times higher than in the USA (Brookes, 1988).

Danish streams – habitat structure and regional variations

Regional and seasonal variations in the physical habitat structure were studied in 40 small streams located in three different river systems in Denmark; the Storå system in zone 1, the Gudenå system in

zone 2 and the Susà system in zone 4 (Fig. 1). The streams in the Gudenà and Storà system had similar habitat structure, whereas the streams in the Susà system differed significantly. Sand dominated the substratum in winter and mud dominated in summer across all three regions. The mud coverage remained high in the Susà streams during winter, but decreased significantly in the Gudenà and Storà system. The enhanced mud cover decreased macroinvertebrate diversity (Article I). Similar results have been found in other groundwater-dominated streams with substantial mud deposition during low flow (Wood & Armitage, 1997; Wood *et al.*, 2001; Miyake & Nakano, 2002). Coverage of coarse substrata was significantly higher in the Gudenà and Storà river systems than in the Susà system (Article I). Discharge played a major role in determining physical habitat structure. Stream slopes increased near bed current velocities, which also influenced substratum characteristics. The hydrological conditions differed significantly among the three systems, which resulted in higher discharge in the Storà and Gudenà system than in the Susà system. The higher discharges in the two first mentioned areas were thus capable of removing mud during winter and exposing coarse substrata, whereas lower discharge and stream slopes made it difficult to remove the deposited mud in the Susà streams. These results demonstrate that large-scale parameters such as discharge (climate) and stream slope (topography) are essential to the development of the stream habitats (Article I).

Studies of changes in physical habitat structure along river systems have primarily focused on downstream fining of stream bed sediments (e.g. Brierly & Hickin, 1985; Ichim & Radoane, 1990; Ferguson & Asworth, 1991; Petts *et al.*, 2000). An empirical concept of downstream changes in physical structure has been developed from measurements in large river systems (Fig. 2). The concept describes changes in stream slope, discharge, sediment transport and sediment grain size along the river continuum (e.g. Leopold *et al.*, 1964; Schumm, 1977; Church, 1996). The majority of

Danish streams are located in the upper part of this continuum. Therefore, I wanted to study variations in reach-scale habitat structure along the upper part of this continuum in Danish streams. I analysed data from 143 small streams in order to see how small lowland streams concurred with this general geomorphologic concept.

The physical structure in the small streams that I studied, agreed with the overall geomorphologic concept with respect to discharge, stream slope, catchment area, mean current velocity and channel dimensions (Fig. 2). These finding are in agreement with the findings of Riis *et al.* (2000) and Riis *et al.* (2001) obtained from relations between stream plants and environmental factors in Danish streams. The substratum characteristics showed a significant deviation from the continuous concept, however. Coarse substrata and mud coverage (stones and gravel) were high and showed little variation along the upper continuum, so the exponential decline in stream bed material size proposed by the concept (Church, 1996) was not valid for Danish streams (Article V). Sand and mud coverage varied significantly between summer and winter/spring in small open streams. We included data from larger streams in the survey and found that high coarse substrata coverage persisted in streams up to approx. 11 m wide and mud cover declined markedly when streams reached a width of 4.3 m (Table 1). In studies of downstream fining of stream sediment and general gemorphological concepts, the environmental gradient is normally relatively broad ranging from bedrock-dominated mountain streams to large lowland rivers (e.g. Petts *et al.*, 2000). Variations in coarse substrata coverage along the lowland Danish streams may be naturally limited by homogeneous geologic conditions. The combination of low-power streams and these uniform large-scale geologic features may govern a more evenly distribution of the substrata along the continuum. The substitution of coarse substrata with fine substrata along the river continuum may thus be true for large streams covering a range of geological conditions, but not necessarily for relatively small groundwater fed lowland streams.

Table 1. Substratum characteristics in Danish streams located at different distances from the source and with different catchment areas. Values for forested and small upland streams are mean values based on the number of observations indicated.

	Forest streams N=33	Small streams N=110	Mattrup stream	Tange stream	River Gelså	River Skjernå
Catchment area (km^2)	1	14	45	70	311	2500
Distance to source (km)	1.3	4.6	9.9	16.7	41.0	97.5
Width	0.8	1.9	4.3	6.5	11.0	30.0
Stone	15	10	2	1	5	0
Gravel	15	17	20	21	25	8
Sand	40	43	60	42	62	88
Mud	25	25	18	2	6	4
Clay/peat	5	5	0	4	2	0

The concepts are based on natural levels of disturbance and environmental heterogeneity in large river systems. These conditions may be far from the natural conditions in Danish lowland streams and catchments. Furthermore, the studied Danish stream systems were all small and impacted by human disturbance, which can have caused homogenisation of the stream habitats and substratum (Brookes, 1987; Iversen et al., 1993). The results indicate that the Danish lowland stream systems are perhaps not real continua, but systems where a number of physical thresholds determine morphological characteristics such as substratum characteristics. This threshold system is in agreement with other concepts describing the river system as a mosaic of patches (e.g. Townsend, 1996; Poole, 2002). As discussed later, these thresholds may be natural or anthropogenic or a combination hereof due to the widespread disturbance of Danish streams.
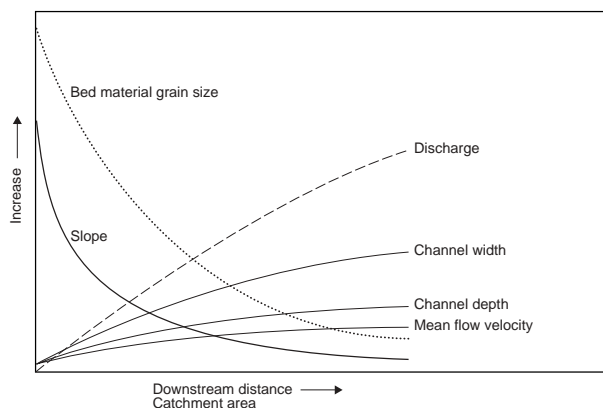

Figure 2. The geomorphological continuum concept of variations in physical conditions along the river continuum (Modified from Church, 1996).

Scale issues in the stream environment

In order to understand the physical habitat structure in streams, it is necessary to identify the dynamic processes on different scales and understand their interconnection. The scale- issue is further complicated because river system research has traditionally been divided between ecology and geomorphology that have developed along different lines. Physical surveys have always played a major role in studies of stream biota on multiple scales (e.g. Statzner et al., 1988). However, actual integration of processes and patterns in stream ecology and geomorphology across multiple scales has been limited (Poole, 2002) due to the lack of concepts and testable models integrating the disciplines. However, in recent years concepts have been developed that link physical structure and processes and community ecology under the name of fluvial stream ecology (e.g. Poole, 2002).

Frissell et al. (1986), Minshall (1988) and Townsend (1996) and others have described the function and organisation of the different scales in the stream ecosystem (Table 2). Stream ecosystems are hierarchically organised and incorporate a number of levels nested at successively smaller spatio-temporal scales. The system is hierarchical because the higher scale processes and features impose constraints on features and processes on the lower scales. Developmental fluvial processes govern progressive changes to features within each level in the hierarchy, while at the same time determining the creation or destruction of features at lower levels in the hierarchy (Hildrew & Giller, 1994). Thus, we see a number of fluvial processes at different spatio-temporal scales acting together to create the channel habitats. Within the system we can identify a number of levels each governed by different processes, disturbance regimes and persistence times (Table 2; Ward, 1989). The hierarchical structure has also been described as a patch hierarchy in which patches at one level can be amalgamated to form a distinct patch on a higher scale in the hierarchy (e.g. Naiman et al., 1988; Turner, 1989). Beisel et al. (2000) showed that macroinvertebrate colonisation of different substrata depended not only on the substratum type that was sampled, but also on the surrounding patch complexity and substratum structure. The nature of each patch within a unit thus affects the structure of neighbouring patches as well as the higher-scale unit structure (Naiman et al., 1988; Townsend, 1996; Poole, 2002). Macroinvertebrate communities have been studied in relation to physical habitat structure on a number of scales ranging from the reach/catchment scale to individual particles (Statzner & Holm, 1982; Scarsbrook & Townsend, 1993; Downes, 2000).

Geomorphologists have traditionally analysed large-scale patterns in stream morphology, which have generated valuable knowledge of the large-scale morphological processes and structure of streams. However, this work has primarily focused on describing the spatial and temporal organisation of the large-scale morphological structure and distinct morphological units such as riffles and pools (Church, 1996). Trans-scale processes (processes that span and operate on multiple scales) have been recognised to operate in the fluvial geomorphology (e.g. Schumm, 1977) but have typically been assessed as a top-down control of features on lower scales, i.e. sediment transport controlling the structure of the morphological units at a lower scale. Recent trends towards finer scale studies in geomorphology have initiated a shift from describing the dynamic nature of the morphological units towards an understanding of

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Table 2. A short description of the hierarchical patch structure in streams (modified after Frissell *et al.* 1986; Ward, 1989; Poole 2002). Spatial scales are indicated for Danish catchments.

Hierarchical element	Spatial scale	Persistence time or disturbance frequency	Description	Destructive processes	Developmental processes
Region			Incorporates climatic conditions and large-scale geology. Region and catchment is often referred to the same level in the hierarchy	Tectonic disturbance Glaciation Climate change	
River system	10^3 m	$10^5 - 10^6$ years	The river system is viewed in the context of the catchment.	Tectonic disturbance Glaciation	Denudation
Segment	10^2 m	$10^3 - 10^4$ years	Channel segments are determined from changes on morphology and geology. The channel and the floodplain are seen as an integrated ecotone	Major landslides	Channel system developments
Reach	10^2 m	$10^1 - 10^2$ years	The ecosystem is divided into distinct feature such as the river and the floodplain. Channel characteristics (slope) may vary between reaches	Channel shifts Meander cutoffs	Sediment transport Deposition / erosion
Unit (riffles, pools)	10^1 m	$10^0 - 10^1$ years	The reach is divided into distinct morphological units with different flow conditions	Deposition / erosion Sediment transport	Small scale bed movement Velocity changes Seasonal variation
Mesohabitat	10^0 m	$10^{-1} - 10^0$ years	Differences in substratum and small-scale morphology determine the division into meso-habitats.	Small scale bed movement Velocity changes Seasonal variation	Periphyton and macrophyte growth
Microhabitat	10^{-1} m	$10^{-2} - 10^0$ years	Within meso-habitats small-scale differences in flow and substratum may lead to further subdivision. This is also referred to as the point-scale	Small scale bed movement Velocity changes Seasonal variation	

the dynamics creating the different units (e.g. Lane & Richards, 1997), and this has highlighted the importance of bottom-up control of morphological units (bottom-up control is exerted when small-scale differences in hydraulics, morphology and sediment transport control the structure of the unit). The dynamic nature of the stream hierarchy thus requires knowledge of both bottom-up and top-down trans-scale processes because these influence the physical conditions at all scales (Poole, 2002).

Geomorphologists have traditionally described the large-scale morphological features of the stream in relation to disturbance, grouping streams as being stable or unstable based on information of sediment transport, discharge and available energy in the systems (Schumm, 1977; Church, 1996). It has also been suggested that different physical features have different stability thresholds depending on their position in the hierarchy, i.e. small-scale habitat features are less stable and more persistent than the large-scale morphological units (Ward, 1989; Werritty, 1997). Recent studies on the meso-scale suggest that different morphological units have distinct hydraulic conditions and substrata (e.g. Padmore, 1997; Sear, 1995) whereas within-unit variations are less well understood. Studies of deposition of spawning gravel beds have quantified deposition in relation to discharge and sediment transport, thereby recognising trans-scale interactions (Acornley & Sear, 1999). Ecologists have taken the scale dependence of disturbance and stability a bit

further, recognising that morphological units such as riffles and pools have different responses to disturbance (Scarsbrook & Townsend, 1993). Other studies have identified differences in stability between small patches and have differentiated between areas prone to disturbance by spates and stable refuge areas that can be used by macroinvertebrates during high-flow events (Lancaster & Hildrew, 1993; Robertson *et al.*, 1995; Lancaster & Beleya, 1997).

We analysed different aspects of scale in relation to the stability of physical habitats and macroinvertebrate communities in Danish streams. In the regional study of 40 streams we found that streams with high discharge had low mud cover (Fig. 3). Thus, larger scale hydrological differences (discharge) influenced the substratum composition at the reach-scale (Article I). Discharge also controlled the difference in riffle habitats in 14 streams. A multivariate measure (PCA) of habitat structure was calculated from physical variables, and the Euclidean distance between the PCA co-ordinates of two adjacent riffles was used as a measure of riffle habitat difference (Article IV). The results indicate the possible control of lower-scale features, such as habitat conditions in the riffle and mud coverage on the reach, by parameters on higher scales, such as discharge (Frissell *et al.*, 1986).
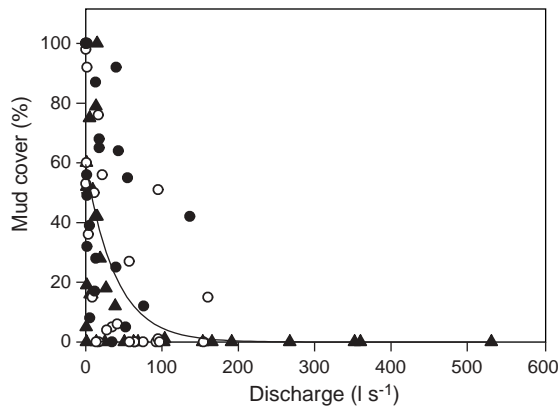
Figure 3. Mud cover as a function of discharge in 40 small Danish lowland streams. Different symbols are used to differentiate between the sites: (○) Storå, (▲); Gudenå and (●) Suså.

Results from an intensive study on the riffle habitat structure on two adjacent riffles showed how important small-scale features and processes could be for the structure at larger scales (Article III). The adjacent riffles were located at similar points in the stream and had identical mean depth, current velocity and mean particle size. Macroinvertebrate abundance was, however, significantly different, indicating a difference in either food resources or habitat conditions. Our results showed that differences in the physical structure of the two lowland riffles could be explained by small-scale variations in flow, depth and substratum characteristics. These results raised a central question of how stable these units are and what processes that determine the stability? The stable riffle had the most compact substratum structure, which was the result of small-scale variations in flow, depth and substratum characteristics (Article III). Structure at one scale (compactness of substratum) interacted with flow and depth in a complex pattern to create the observed physical structures. We could identify the processes and parameters controlling the physical structure on the riffles, but it was impossible to exactly determine cause and effect though.

Biotic utilisation of stream habitats

Macroinvertebrates
Macroinvertebrate communities and diversity were studied as a function of reach-scale physical structure and catchment parameters (Article I). Macroinvertebrates diversity was also studied in two stream types - disturbed and undisturbed by weed cutting (Article II). The variation in macroinvertebrate community and diversity between two neighbouring riffles in Tange stream was studied in order to relate community structure and species composition and diversity to small-

scale physical variations in the physical riffle structure (Article III).

We found significant regional differences in macroinvertebrate community structure (Article I). Streams in the Suså river system had consistently lower diversity, species richness and EPT (Ephemeroptera, Plecoptera and Trichoptera) abundance than river Gudenå and river Storå. In contrast, total macroinvertebrate abundance was highest in the Suså streams. Macroinvertebrate community structure and diversity were influenced by a number of interrelated physical variables acting on several spatial scales (Table 3). Fisher's α-diversity and EPT abundance were highest in streams where pristine land use and sandy soils dominated. The macroinvertebrate abundance decreased in catchments with sandy soils, whereas richness increased in streams with a percentage of pristine land use. Differences in macroinvertebrate communities were thus influenced by a complex combination of variables acting on a regional, catchment and habitat scale. The result of these parameter interactions was that extensive mud coverage probably affected the macroinvertebrate community and diversity in the streams. The discharge and topography were lower in the Suså streams and pristine land use and sandy soils dominated in river Gudenå and river Storå. But Suså streams in catchments with pristine land use and sandy soils were similar to streams in the other regions. The presence of coarse substrata and near-bed current velocity was also positively correlated to community diversity and EPT abundance (Article I). Mud coverage was negatively correlated to EPT abundance, species richness and diversity (Fig. 4) and positively correlated to macroinvertebrate abundance. These results indicated a possible influence of substratum on macroinvertebrate community structure.

Table 3. Spearman rank correlation between physical variables at different scales and macroinvertebrate variables in 40 catchments in the Storå, Gudenå and Suså systems.

	No. of individuals	Species	EPT	Fisher's α
Pristine land use		0.264	0.511	0.295
Sandy soils	-0.245		0.387	0.312
Slope			0.331	
Coarse substrate			0.380	0.302
Mud substrate	0.288	-0.245	-0.535	-0.468
Substrate heterogeneity				
$V_{nearbed}$			0.435	0.295

Enhanced mud deposition and low coverage of coarse substrata probably affected EPT abundance and EPT species richness negatively in streams disturbed by frequent weed cutting (Article II). EPT species occurred in lower numbers in disturbed streams, whereas deposit feeders such

as *Micropsectra* spp., *Potamopyrgus antipodarium* (Smith) and macroinvertebrates preferring low current velocity such as *Pisidium* spp. were more abundant. These results indicate that mud deposition is probably central to the habitat structure and macroinvertebrate communities in small lowland streams. Mud coverage is high even in small forested streams and remains high in all the upper parts of the Danish streams (Article V). In larger streams the significance of the mud coverage decreased as mentioned above. Mud deposition increased as discharge decreased in the regional study. This indicates that enhanced mud deposition due to low-flow conditions in small Danish streams could potentially affect habitats. Similar results indicating significant effects of mud deposition have been obtained from other groundwater-dominated streams in other parts of the world (Wood & Armitage, 1997; Wood *et al.*, 1999; Miyake & Nakano, 2002).
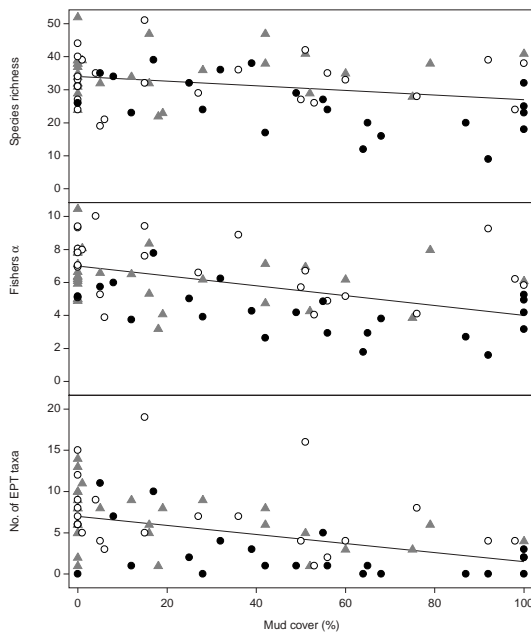

Figure 4. Relationships between the mud cover and species richness ($R^2 = 0.25$, $P = 0.030$), Fisher' α diversity ($R^2 = 0.22$, $P < 0.001$) and number of EPT taxa ($R^2 = -0.30$, $P < 0.001$). Different symbols are used to differentiate between the three river systems: (o) Storà system, (▲); Gudenà system and (•) Susà system.

Riffles are normally perceived as relatively homogeneous habitat units and are believed to host macroinvertebrate communities different from those found in pools (Scarsbrook & Townsend, 1993). We studied macroinvertebrate communities on two adjacent riffle in Tange stream and found significant differences in macroinvertebrate abundance (4137 m^{-2} vs. 1698 m^{-2}). Large-scale habitat structure and hydraulic conditions did not differ between the riffles. The small-scale habitat environment,

however, differed significantly between the two riffles and the riffle with lowest macroinvertebrate abundance had a more compact substratum structure than the other riffle. The large-scale stability of the unconsolidated riffles was also lower than the compact riffle, which had the highest surface coverage of coarse substrata. Mean particle size did not differ between the riffles. On the unconsolidated riffle, macroinvertebrate abundance and EPT abundance increased with increasing median particle size (Fig. 5). In contrast, this relationship was not established on the compact riffle, indicating reduced colonisation (Minshall, 1984). EPT abundance was not significantly different between riffles, indicating that species associated with coarse substrata probably had identical habitat conditions on the two riffles. Burrowing species were, however, significantly less abundant on the compact riffle. The results clearly indicate that bottom-up physical processes and difference in consolidation created significant different microenvironments on the two riffles, leading to differences in stability and consolidation. Therefore, these riffles probably supported significantly different macro-invertebrate communities (Article III).

This comparative study of stream riffle structure raises the geomorphological question whether the stability of lowland streams has been overestimated by considering stability mainly from a large-scale point of view (Church, 1996). Our results show that on the large scale, meandering stream riffles had significant differences in stability and that stability appeared to affect the macroinvertebrate community structure.

Macrophytes
We studied macrophytes as part of the physical habitat structure along the upper continuum in Danish streams (Article V) and studied the use of macrophyte species as environmental variables in relation to macroinvertebrate distribution in undisturbed streams (Article II). Plant species were used along with current velocity and coarse substrata as environmental variables in a CCA analysis (Article II).

Macrophyte coverage increased with distance to source in the 143 streams. Coverage ranged from 1% in the forested streams to 63% in larger streams. The open streams with macrophyte coverage of approx. 40% had the highest variations in substratum between summer and winter/spring. In the larger streams, seasonal differences became less apparent. Macrophytes may influence the substratum variations and thus help to stabilise the stream bed and reduce the seasonal variability (Article V). The large coverage of sand in all streams along the upper continuum
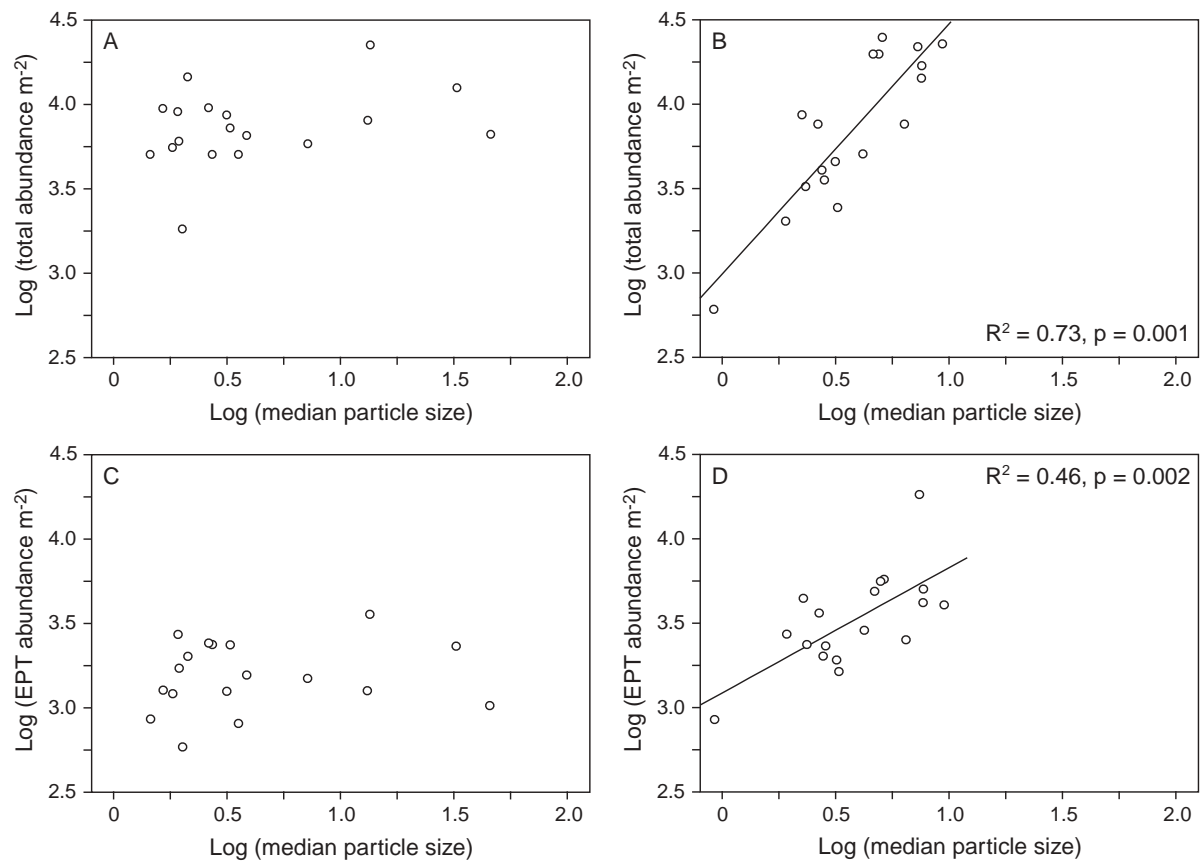
Figure 5. Relationship between median particle size and total macroinvertebrate abundance and between median particle size and EPT taxa abundance on the compact riffle (A, C) and the unconsolidated riffle (B, D).

enhances the likelihood of macrophyte growth even in streams with relatively high current velocity. Macrophyte species were generally good predictors of the EPT macroinvertebrate species assemblages in the undisturbed streams. The results showed that species normally associated with dense vegetation were located along the *Batrachium* spp. vector (e.g. *Ephemerella ignita* (Poda)). Species requiring fast currents or erosional habitats (many Trichoptera taxa) were associated with coarse substrata and high current velocity. Species found along a wide substratum gradient were associated with the *Potamogeton* spp. vector. The results indicated that macrophytes in combination with physical variables could be used as habitat indicators. Data directly linking macroinvertebrate species and macrophyte species have to be collected in order to confirm these preliminary results. The results indicate that, potentially, many EPT live in association with macrophytes, and weed cutting is therefore likely to affect the EPT abundance directly when the substrata on which they live are removed.

Effects of disturbance in streams
Stream ecosystems are frequently disturbed by naturally occurring processes, primarily resulting from changes in discharge and sediment load. In lowland streams, large-scale disturbance primarily originates from human activities such as weed cutting and channelization. We analysed physical habitat structure with the main emphasis on anthropogenic disturbances (Article I, III, IV, and V). Disturbances by natural phenomena were also included (Article I and III).

Anthropogenic disturbance of stream habitats and biota
We studied several aspects of anthropogenic disturbance. The effects of stream regulation and dredging on the physical structure were studied in riffles and pools (Article IV). We used changes in the naturalness of the cross sections and riparian land use to separate disturbed and undisturbed streams. Long-term effects of continuous disturbance (weed cutting) on the in-stream physical habitats and biotic communities were studied in 17 disturbed and 16 undisturbed streams (Article II).

Many short-term studies have identified and quantified initial changes in physical habitat structure following plant removal (e.g. Kaenel & Uhrlinger, 1998). The effects include higher current velocities, increased hydraulic stress, increased sediment transport and subsequent deposition of sand. We did not find a significant long-term

increased current velocity on disturbed sites as is normally seen from vegetation clearance in streams. In the studied streams, weed cutting was carried out in early summer and the physical habitat study was carried out after the vegetation re-growth had occurred in late summer. The results showed that increased current velocity is not necessarily a long-term effect. In contrast, our results suggested that one effect of disturbance is that a larger in-stream area experiences low-flow and enhanced mud deposition in late summer when macrophytes are re-established. This is probably due to the formation of a dense plant community consisting of species that are better at obstructing flow and raising water levels, thereby enhancing deposition of fine sediment. Similar results have been demonstrated in a study of plant community structure on regulated and unregulated streams in Denmark (Baattrup-Pedersen & Riis, 1999). In contrast to these results, we did not find any significant differences in substratum heterogeneity and coverage of coarse substrata between disturbed and undisturbed streams, despite the fact that both were highest in undisturbed streams. Variation in stream width declined in disturbed streams and was the only significant physical difference between the two stream types, which indicates that natural variations in physical habitats of the near-bank zone are lost. The mud deposits are maintained in disturbed streams throughout the year. Being located in the sheltered areas along the stream margin, these deposits become stable compared to a sandy substratum located in the free flow in the middle of the stream. This development is similar to that observed in canalised streams that loose their natural morphological structure and develop less variable edge habitats (Brookes, 1988; Garner *et al.*, 1996) (Article II).

Depth and current velocity in riffles and pools varied significantly and independently of disturbance. Despite overall differences in disturbance, natural channel morphology prevailed and created a substantial physical variation between riffles and pools. The differences in current velocity and depth between riffles and pools were significantly higher in undisturbed streams than in disturbed streams. Thus, stream regulation homogenised the depth and current velocity distribution between riffles and pools, which supports results from other studies (Brookes, 1988). Frequency distributions of current velocity and depth were altered most radically on the riffles, which demonstrate their greater sensitivity to disturbance. Channelization generally involves dredging of the streams, which mainly affects the riffles. Dredging increases depth and levels the streambed, thereby shifting the stream to a uniform channel with greater mean depth. As a consequence, riffles are more strongly affected than pools. Levelling of the stream bed is most effectively carried out by removing coarse gravel beds forming the riffles and this operation destroys the natural riffle structure (Brookes, 1987). Destruction of riffle-pools sequences have also been reported in other streams impacted by stream regulation (Brookes, 1988) (Article IV).

The species richness, diversity and patch complexity of macrophytes were markedly higher in undisturbed than in disturbed streams, which indicates a significant long-term effect of disturbance. Riis & Sand-Jensen (2001) found that macrophyte species with high dispersal ability were more abundant in disturbed streams than the less dispersed species. They concluded that this shift in community structure was a consequence of frequent disturbance. The impact of disturbance should be that species with a high colonisation potential profit relative to susceptible, less weedy, species. Dominance patterns should therefore change towards a community of species characterised by rapid growth, fast dispersal and/or a high reproductive output in weed-cut streams (Grime, 1979; Henry & Amoros, 1996; Barrat-Segretain *et al.*, 1998). However, we did not find any difference in dominance patterns of macrophyte species between stream types. This result may reflect a predominance of amphibious and terrestrial species in both stream types, which may render the macrophyte community less vulnerable to frequent cutting, which may blur any effects of disturbance. It may be more important, however, that the studied stream systems consist of a complex matrix of reaches with and without weed cutting. As a consequence, no entire stream is entirely undisturbed or disturbed along its whole length. When comparing sites located in this mixture of disturbance regimes where colonisation from upstream areas is possible, differences in species richness and diversity will be less marked compared to the differences expected if entirely undisturbed and entirely disturbed streams systems had been available for comparison (Turner, 1998) (Article II).

Alterations to the macrophyte community structure were cascaded through the stream ecosystem, affecting macroinvertebrates and trout (*Salmo trutta*). Macroinvertebrates normally associated with stable habitats, such as EPT taxa, declined. Nursery and feeding habitats for trout were degraded as a consequence of weed cutting and potential food resources were removed, leading to lower trout density in disturbed streams (Article II).

Studies of weed cutting disturbance on macroinvertebrate communities have either focused on short-term effects or recovery following weed cutting (e.g. Kern-Hansen, 1978; Pearson &

Jones, 1978; Dawson *et al.*, 1991; Kaenel *et al.*, 1998). The main results of these studies demonstrate a significant decrease in macroinvertebrate abundance and diversity. In our study, macro-invertebrate communities in disturbed and un-disturbed streams did not differ with respect to species diversity, species richness and abundance (Article II). As for the macrophytes, a possible explanation for this similarity in macroinvertebrate communities between stream types is that no streams are solely weed-cut or undisturbed; all systems are mixed. Undisturbed and disturbed sites are located in a network of stream reaches witg different weed cutting practices. Macro-invertebrate drift from upstream-undisturbed sites is thus capable of supplying species to downstream weed cut sites and *vice versa*, thereby maintaining species diversity and richness at comparable levels in the two stream types despite marked differences in disturbance regimes and physical habitats (Williams & Hynes, 1976; Turner, 1998).

Macroinvertebrate species composition in disturbed and undisturbed streams was, however, different. This was probably caused by a substitution of species in the disturbed streams due to a possible long-term change in physical habitats. High coverage of mud substrata and low current velocity in disturbed streams are likely to affect macroinvertebrate communities and our results indicated that this may have increased the abundance of detritus feeders. Relatively abundant taxa were *Micropsectra* spp., *Potamopyrgus antipodarium* (Smith) and *Pisidium* sp. in the disturbed streams, whereas EPT taxa were more abundant in undisturbed streams. Generally, species living on muddy substrata grow faster and have a shorter life cycle compared to EPT species (Merritt & Cummins, 1996). Very few EPT taxa are capable of living and feeding in the mud substratum and their abundance was low in disturbed streams (Ward, 1992). The lower EPT species richness in disturbed streams indicates a possible vulnerability to frequent habitat disturbance (Merritt & Cummins, 1996). We found a total of 35 EPT species, which, with a few exceptions, are all associated with stable substrata such as stones, gravel and macrophytes. These substrata are removed during dredging and weed cutting or become covered by the increased sediment load following the disturbance. Drift from upstream areas cannot compensate for this loss because habitats are degraded or lost and the EPT taxa will be unable to colonise the disturbed sites (Article II).

Gammarus pulex L. has been shown to migrate following disturbance by weed cutting (Kern-Hansen, 1978). The species uses sheltered areas and macrophytes as refuge and is likely to be affected by weed cutting. We found a reduced abundance of *G. pulex* on disturbed sites, which indicates that *G. pulex* has been unable to recover after 2-3 months, despite being known to be abundant in drift and a good coloniser (Elliott, 2002). Therefore, the low abundance in the disturbed streams is probably a long-term result of habitat loss here (Fig. 6; Article II). Macroinverte-brate densities can control trout growth and may therefore be affected by reduced macroinvertebrate abundances (Andersen *et al.*, 1992). Abundance of simulids was 90% lower on disturbed sites, probably due to removal of macrophytes, which is a stronger effect than the decrease of 22% found by Dawson *et al.* (1991), when macrophytes were removed in an English chalk stream. Species of *Baetis* are found in association with either coarse substrata or macrophytes and moderate flow. They feed on attached microalgae on macrophyte surfaces and coarse substrata (Wiberg-Larsen, 1984). Abundance of *Baetis* decreased in weed-cut streams, probably as a consequence of habitat loss (macrophytes) and habitat degradation following weed cutting (Article II). Limniphilids are vulnerable to deposition of fine sediments (Wood & Armitage, 1997; Wood *et al.*, 2001). *Ecclisopteryx dalecarlica* Kolenati, *Chaetopteryx villosa* (Fabricius), *Potamophylax latipennis* (Curtis) and *Anabolia nervosa* (Curtis) were abundant in undisturbed streams where habitats were characterized by stable substrata and moderate to high current velocities preferred by these species (Article II) (Merritt & Cummins, 1996).

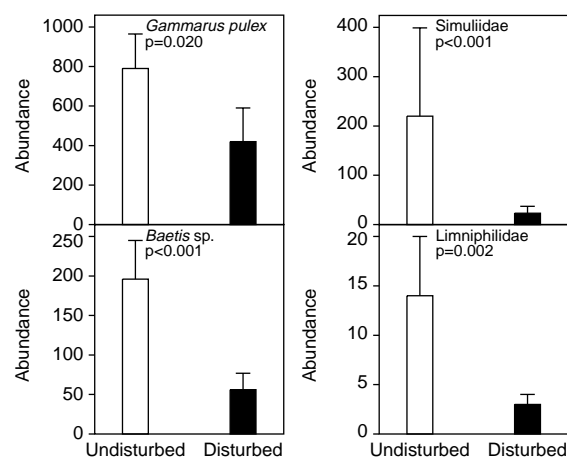**Figure 6.** Abundance of macroinvertebrates associated with stream vegetation in weed cut streams and streams without weed cutting.

Natural disturbance in streams
Natural disturbance in streams has traditionally been studied in upland streams where it is associated with movement of gravel or stones during high-discharge events (Death & Winterbourn, 1994; Downes *et al.*, 1997; Matthaei *et*

al., 1999). Less attention has been given to low-flow disturbance in groundwater fed streams where deposition of fine-grained sediment prevails (Wood and Armitage, 1997; Miyake and Nakano, 2002). The use of refuge by macroinvertebrate during spates is, however, well documented (e.g. Lancaster & Hildrew, 1993).

Very little is known about disturbance and stability in Danish lowland streams. Ituitively, they are normally considered to be relatively stable on a large-scale due to the relatively low energy available because of the topography and the relatively low runoff (approx. 10 l s^{-1} km^{-2}). In countries with high-energy streams, such as New Zealand, disturbance is well documented (e.g. Scarsbrook & Townsend, 1993; Death & Winterbourn, 1995). The natural disturbance in low-energy streams has a different character from that of the high-energy streams. The entire stream bed is seldom set in motion in lowland meandering streams. However, small-scale disturbances, where limited areas within the streams are disturbed, occur to a large extent in lowland streams. The seasonal variation in discharge in groundwater dominated streams may cause low-flow disturbance during summer when discharge is low (Wood & Petts, 1994).

We analysed natural disturbance on the reach scale in 40 small Danish streams by comparing the shear stress on the stream bed with the substratum characteristics (Article I). Natural variations in stability and disturbance were studied in relation to macroinvertebrates on two similar riffles in Tange stream (Article III; see above).

Despite regional differences in substratum characteristics, a general pattern emerged from the 40 streams (Article I). Sand dominated the stream bed in winter and mud dominated in summer. Coarse substrata generally varied little between seasons. However, more than 60% of the stream bed shifted substratum category between seasons, indicating that a substantial part of the stream bed underwent changes irrespective of the size distribution of the substrata. The streams in which the smallest part of the stream bed changed substratum also had a heterogeneous substratum composition. The heterogeneous environment in these streams was probably better at dissipating the flow energy and thereby prohibiting substratum movement, compared to homogeneous sites where all energy is directed into a uniform sediment matrix (Minshall, 1984). Substratum stability was assessed by means of reach-scale shear stress. The shear stress at the study sites ranged from 0.5 N m^{-2} to 20 N m^{-2}, which is approximately a factor 5-10 below the values that Death & Winterbourn (1994) reported from streams in New Zealand. Shear stress in the order of 1-10 N m^{-2} generally corresponds to initiation of movement of particles with a diameter of less than 2 mm (Mangelsdorf *et al.*, 1990). Mud coverage decreased with increasing shear stress. In summer, more than 50% of all streams had a shear stress lower than 1-2 N m^{-2}, which indicates deposition of fine sediments. In winter, only three streams could transport gravel. Based on the relatively low shear stress, we therefore conclude that erosion of coarse sediment is of secondary importance to the stability of Danish lowland streams as compared to fine sediment deposition, which took place extensively in most streams in summer. Macroinvertebrate species richness and diversity decreased as mud coverage increased. The EPT species also decreased as the coverage of mud increased. The results suggest that extensive deposition may have significant effects on the macroinvertebrate community and the effects of deposition can act as a natural disturbance in lowland streams (Article I).

Conclusions

The coverage and deposition of mud in the stream ecosystem are very important for both habitat structure and distribution of macroinvertebrates. Mud dominates the substratum on the stream bed in summer, whereas sand dominates in winter. High shear stress at high discharge and fast near-bed current velocity erode fine sediments and mud during winter. Mud persisted in streams with low shear stress and probably affected macroinvertebrate communities. High mud coverage correlated negatively to species richness, diversity and EPT abundance. These results indicate that deposition of mud may act as a disturbance at low flow in small lowland streams. Mud covers a substantial part of the stream bed along the upper continuum in summer. Our results indicate that the mud coverage is a significant habitat variable in the headwaters. Extensive mud coverage is also associated with weed cutting. In weed cut streams the mud cover is increased and this probably decreases limited the number of potential EPT species habitats. This may potentially influence the EPT species richness in disturbed streams negatively.

Local variations in hydrology, land use and catchment topography influenced the habitat structure in Danish streams rather than large-scale regional differences. However, theses catchment features were unevenly distributed in the regions, and streams therefore grouped along a regional gradient too. The habitat structure in streams in the Susà catchment differed from that in the streams in the Gudenà and Storà catchments. The highest mud coverage was found in the Susà streams. Substrata were highly dynamic in the

streams in the Gudenå, Storå and Suså catchments, causing 60% of all observed points in the streams to change substratum type between seasons. This indicates a high seasonal variability in stream bed structure in small lowland streams.

Anthropogenic disturbance significantly affected the physical habitat structure in small Danish streams. Channelization affected the distribution of depth and current velocity more strongly in riffles than in pools. Riffles in channelized streams had a smaller range in depth and current velocity and experienced lower current velocities and were deeper. Weed cutting primarily affected the overall morphology and reduced the variations in width in disturbed streams. Results also showed a tendency towards higher mud coverage on weed cut sites in summer. The macrophyte communities were directly affected by the ongoing disturbance, and species richness and diversity declined in disturbed streams. The patch complexity (the number of species occupying a plot) also decreased in disturbed streams. These effects cascaded through the ecosystem and affected macroinvertebrates and fish. Macroinvertebrate species (EPT species, *Gammarus pulex*, simulids) associated with macrophytes declined significantly in disturbed streams. Fish densities also declined in response to reduced prey densities and loss of sheltered habitat.

The physical habitat structure is the complex outcome of multiple interactions of physical and biological parameters at many different scales. Stream discharge affected variations in riffle structure in the streams. High discharge created high variations in habitats on the riffles, thus reflecting the function of the nested hierarchical stream system, whereby variation in a habitat on a certain scale is controlled by a higher-scale variable. The results from the detailed study of the physical habitat conditions in two riffles showed that small-scale hydraulic processes also controlled the physical structure of the riffles. These processes affected consolidation, stability and macroinvertebrate colonisation. Small-scale hydraulic differences thereby caused bottom-up control of the large-scale physical structure of the riffles. This resulted in a significant relationship between sediment particle size, macroinvertebrate abundance and EPT abundance on the uncon-solidated riffles, whereas these relationships did not exist on the compact riffle.

The physical structure in streams along the upper continuum in Denmark generally follows the geomorphological concept with respect to discharge, stream slope, channel dimensions and current velocity. Substratum characteristics deviate significantly in small Danish streams, however. Generally, the coverage of coarse substrata remains constant along a substantial part of the streams. The proportion of coarse substrata is only low in the largest streams. High coverage of coarse substrata is thus a distinct characteristic of a substantial proportion of Danish streams. Mud cover is also high in small Danish streams, but it is generally affected by weed cutting, naturalness of cross sections and riparian land use. The substratum distribution in Danish streams is apparently not continuous but is governed by physical thresholds in the system, creating a more discontinuous distribution along the continuum.

Perspectives

As outlined many times in this thesis, the physical environment plays an important role in stream ecology. However, we have relatively little knowledge of the physical habitats despite their significance. The Water Framework Directive calls for action in order to describe the quality of the hydromorphological elements in the streams. In other words, we need some tools that indicate the features of good physical quality and the features of disturbed conditions. The reference condition also needs to be established for all European stream types and the WFD requires information on which parameters that cause various types of disturbance. Therefore, much effort is put into describing the physical habitat quality. This work is also progressing in Denmark (Appendix A). However, as demonstrated by the papers in this thesis, there are still many gaps in our understanding of the physical processes affecting the habitats in lowland streams.

Scale issues are important for understanding and analysing the physical aspects of stream ecology. Models that help integrate processes across spatial scales therefore need to be developed along with routines for identifying these processes and patterns at different scales. Future studies need to incorporate scale aspects and data have to be collected in such a way that both small-scale and large-scale patterns can be identified. Instead of settling for a manageable level of habitat surveys, we need to expand our knowledge on the widest number of scales so that both bottom-up and top-down controls of physical habitat structure can be analysed in relation to the in-stream biota.

Future research needs

A comprehensive set of data has not previously been used to study the physical habitat structure in small Danish lowland streams, and aspects of disturbance and stability of habitats have only received limited attention. The present project raised four important questions about the physical stream environment in lowland streams in general, and Danish streams in particular:

Are lowland streams unstable?
I briefly touched the subject of stability in lowland streams. But in order to understand the biotic responses to natural disturbances in lowland streams, we need to quantify the level of disturbance and its spatial and temporal distribution of the disturbance. We also need to analyse what units or habitats within the streams that are prone to disturbance.

What causes instability in lowland streams, bottom-up or top-down controls?
Understanding the physical processes and development of the habitat units within the stream channel requires a link of processes and patterns across spatial scales. This understanding is needed to identify the processes that cause instability and to determine at which scale these can be assessed (Lane & Richards, 1997; Poole, 2002).

What is the variation in physical habitat features along the entire continuum in Danish stream systems?
Very little is still known about the spatial variations in morphological features, associated biotic communities and parameters relations along the river continuum. Therefore, integrated surveys along the river continuum are needed to couple the physical environment and biota in order to identify the relationships between the geomorphological units (or habitats) and the biota.

What is the ecological significance of the extensive deposition of fine sediments and organic matter in small streams?
I have identified the deposition of mud as a significant feature in small lowland streams. But further knowledge is required to understand the dynamics of the mud patches and how and why they develop. Are they caused by disturbance? And how widespread are these patches in natural pristine streams?

Acknowledgements

References

Acornley RM & Sear DA (1999): Sediment transport and siltation of brown trout (salmo trutta l.) spawning gravels in chalk streams. *Hydrological Processes*, **13**, 447-458.

Allan JD & Johnson LB (1997): Catchment-scale analysis of aquatic ecosystems. *Freshwater Biology*, **37**, 107-111.

Andersen TH, Hansen HO, Iversen TM, Jacobsen D, Krøjgaard L & Poulsen N (1992): Growth and feeding of 0+ brown trout (*Salmo trutta* L.) introduced to two small Danish streams. *Archiv für Hydrobiologie*, **125**, 339-346.

Armitage PD, Pardo I & Brown A (1995): Temporal constancy of faunal assemblages in mesohabitats - application to management. *Archiv für Hydrobiologie*, **133**, 367-387.

Baattrup-Pedersen A & Riis T (1999): Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology*, **42**, 375-385.

Barmuta LA (1990): Interaction between the effects of substratum, velocity and location on stream benthos – an experiment. *Australian Journal of Marine and Freshwater Research*, **41**, 557-573.

Beisel JN, Usseglio-Polatera P & Moreteau JC (2000): The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia*, **422**, 163-171.

Barrat-Segretain MH, Bornette G & Hering-Vilas-Bôas A (1998): Comparative abilities of vegetative generation among aquatic plant fragments in relation to the disturbance frequency of their habitats. *Archiv für Hydrobiologie*, **145**, 111-127.

Bojsen BH & Barriga R (2002): Effects of deforestation on fish community structure in Ecuadorian Amazon streams. *Freshwater Biology*, **47**, 2246-2260.

Brierly GJ & Hickin EJ (1985): The downstream gradation of particle size in the Squamish River, British Columbia. *Earth Surface Processes and Landforms*, **10**, 597-606.

Brookes A (1987): The distribution and management of channelized streams in Denmark. *Regulated Rivers: Research and Management,* **1**, 3-16.

Brookes A (1988): *Channelized rivers – perspectives for environmental management.* John Wiley and Sons, Chichester.

Brookes A, Gregory KJ & Dawson FH (1983): An assessment of river channelization in England and Wales. *Science of the Total Environment*, **27**, 97-112.

Cattaneo A & Kalff J (1980): The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography,* **25**, 280-289.

Clausen B & Biggs BJF (1997): Relationships between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology*, **38**, 327-342.

Church M (1996): Channel morphology and typology. In: *River flows and channel forms* (Eds. GE Petts & P Calow), pp. 185-202. Blackwell Scientific Publications, Oxford.

Cummins KW (1973): Trophic relations of aquatic insects. *Annual Review of Entomology*, **18**, 183-206.

Dawson FH, Clinton EMF & Ladle M (1991): Invertebrates on cut weed removed during weed-cutting operations along an English river, the river Frome. *Aquaculture and Fisheries Management*, **22**, 113-121.

Death RG & Winterbourn MJ (1994): Environmental stability and community persistence - a multivariate perspective. *Journal of the North American Benthological Society*, **13**, 125-139.

Death RG & Winterbourn MJ (1995): Diversity patterns in stream benthic invertebrate communities - the influence of habitat stability. *Ecology,* **76**, 1446-1460.

Downes BJ (2000): Patch dynamics and mobility of fauna in streams and other habitats. *Oikos,* **59**, 411-413.

Downes BJ, Glaister A & Lake PS (1997): Spatial variation in the force to initiate rock movement in 4 upland streams: implications for estimating disturbance frequencies. *Journal of the North American Benthological Society,* **16**, 203-220.

Dudley TL, D'Antonio CM & Cooper SD (1990): Mechanisms and consequences of interspecific competition between two stream insects. *Journal of Animal Ecology*, **59**, 849-866.

Elliott JM (2002): A continuous study of the total drift of freshwater shrimps, *Gammarus pulex*, in a small stony stream in the English Lake District. *Freshwater Biology*, **47**, 75-86.

Erman DC & Erman NA (1984): The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia*, **108**, 75-82.

Ferguson R & Asworth P (1991): Slope-induced changes in channel character along a gravel-bed stream: the Allt Dubhaig. Scotland. *Earth Surface Processes and Landforms*, **16**, 65-82.

Frissell CA, Liss WJ, Warren CE & Hurley MD (1986): A hierarchical framework for stream habitat classification - viewing streams in a watershed context. *Environmental Management*, **10**, 199-214.

Garner P, Bass JAB & Collett GD (1996): The effects of weed cutting upon the biota of a large regulated river. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **6**, 21-29.

Grime JP (1979): *Plant strategies and ecological processes.* John Wiley and Sons, Chichester.

Hansen HO (ed.) (1996): *River restoration – Danish experiences and examples.* National Environmental Research Institute, Silkeborg, Denmark.

Harman WN (1972): Benthic substrates - their effect on freshwater mollusca. *Ecology*, **53**, 271-276.

Haslam SM (1971): *Physical factors and some river weeds.* Proceedings of the European Weed Research Council. Lattague 3rd International Symposium of Aquatic Weeds, Oxford, pp. 29-39.

Haslam SM (1991): *The historic river: Rovers and cultures down the ages.* Cobden of Cambridge Press, Cambridge.

Henry CP & Amoros C (1996): Are the banks a source of recolonization after disturbance: an experiment on aquatic vegetation in a former channel of the Rhône River. *Hydrobiologia*, **330**, 151-162.

Hildrew AG & Giller PS (1994): Patchiness, species interactions and disturbance in the stream benthos. In: *Aquatic ecology - scale, pattern and process. The 34th Symposium of the British Ecological Society University College, Cork* (Eds. PS Giller, AG Hildrew & DG Raffaelli), pp. 21-62. Blackwell Scientific Publications, Oxford.

Hildrew AG & Townsend CR (1987): Organization in freshwater benthic communities. In: *Organization of communities: Past and present* (Eds. JHR Gee & PS Giller), pp. 347-371. Blackwell Scientific Publications, Oxford.

Hynes HBN (1970): *The ecology of running waters.* University of Toronto Press, Toronto.

Ichim I & Radoane M (1990): Channel sediment variability along a river: a case study of the Siret River (Romania). *Earth Surface Processes and Landforms*, **15**, 211-225.

Iversen TM, Thorup J, Hansen T, Lodal L & Olsen J (1985): Quantitative estimates and community structure of invertebrates in macrophyte rich stream. *Archiv für Hydrobiologie*, **102**, 291-301.

Iversen TM, Kronvang B, Madsen BL, Markmann P & Nielsen MB (1993): Reestablishment of Danish streams - restoration and maintenance measures. *Aquatic Conservation: Marine and Freshwater Ecosystems, 3*, 73-92.

Jacobsen D (1993): *Herbivori af invertebrater på submerse makrofyter i ferskvand* (In Danish). Ph.D.-Thesis. Freshwater Biological Laboratory, University of Copenhagen.

Kaenel BR & Uehlinger U (1998): Effects of plant cutting dredging on habitat conditions in streams. *Archiv für Hydrobiologie, 143*, 257-273.

Kaenel BR, Matthaei CD & Uehlinger U (1998): Disturbance by aquatic plant management in streams: Effects on benthic invertebrates. *Regulated Rivers: Research and Management, 14*, 341-356.

Kemp JL, Harper DM & Crosa GA (2000): The habitat-scale ecohydraulics of rivers. *Ecological Engineering*, **16**, 17-29.

Kern-Hansen U (1978): Drift of *Gammarus pulex* L. in relation to macrophyte cutting in four small Danish lowland streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie, 20*, 1440-1445.

Krüger J (1989): *Gletcheren og landskabet i nutid og istid* (In Danish). Gyldendal, Copenhagen.

Lamberti GA & Resh VH (1979): Substrate relationships, spatial-distribution patterns, and sampling variability in a stream caddisfly population. *Environmental Entomology*, **8**, 561-567.

Lancaster J (1990): Predation and drift of lotic macroinvertebrates during colonization. *Oecologia*, **85**, 457-463.

Lancaster J & Hildrew AG (1993): Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society*, **12**, 385-393.

Lancaster J & Belyea LR (1997): Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society, 16*, 221-238.

Lane SN & Richards KS (1997): Linking river channel form and process: time space and causality revisited. *Earth Surface Processes and Landforms*, **22**, 249-260.

Leopold LB, Wolman MG & Miller JP (1964): *Fluvial processes in geomorphology*. W. H. Freeman and Co., San Francisco.

Mangelsdorf J, Scheurmann K & Weiss FH (1990): *River morphology. A guide for geoscientists and engineers*. Springer-Verlag, Berlin.

Mann KH (1988): Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnology and Oceanography, 33*, 910-930.

Markmann PN (1990): 65.000 km vandløb (In Danish). *Miljø Danmark*, **4**, 12-13.

Matthaei CD, Arbuckle CJ & Townsend CR (1999): Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society, 19*, 82-93.

Merritt RW & Cummins KW (Eds.) (1996): *An introduction to the aquatic insects of North America 3rd edition*. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Minshall GW (1984): Aquatic insect-substratum relationships. In*: The ecology of aquatic insects* (eds. VH Resh & DM Rosenberg), pp. 358-400. Praeger Scientific, New York.

Minshall GW (1988): Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society, 7*, 263-288.

Minshall GW & Minshall LN (1977): Microdistribution of benthic invertebrates in a Rocky Mountain (USA) stream. *Hydrobiologia*, **55**, 231-249.

Minshall GW & Minshall LN (1978): Further evidence on the role of chemical factors in determining the distribution of benthic invertebrates in the River Duddon. *Archiv für Hydrobiologie*, **83**, 324-355.

Miyake Y & Nakano S (2002): Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. *Freshwater Biology*, **47**, 219-230.

Mortensen E (1977): Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to management of small streams. *Journal of Fish Biology, 11*, 613-617.

Naiman RJ, Décamps H, Pastor J & Johnston C (1988): The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society*, **7**, 289-306.

Nørrevang A & Lundø J (1980): *Danmarks Natur Bind 1 – Landskabernes opståen* (3 udgave) (in Danish). Politikens Forlag, Copenhagen.

Padmore CL (1997): Biotopes and their hydraulics. A method for defining the physical component of freshwater quality. In: *Freshwater quality: defining the indefinable* (eds. PJ Boon & DL Howell), pp. 251-257. Edinburgh, Scottish Natural Heritage.

Pearson RG & Jones NV (1978): The effects of weed-cutting on the macroinvertebrate fauna of a canalised section of the river Hull, a northern English chalk stream. *Journal of Environmental Management*, **7**, 91-97.

Pennak RW & Van Gerpen ED (1947): Bottom fauna production and physical nature of the substrate in a northern Colorado trout stream. *Ecology*, **28**, 42-48.

Percival E & Whitehead H (1929): A quantitative study of the fauna of some types of stream-bed. *Journal of Ecology,* **17**, 282-314.

Petts GE, Gurnell AM, Gerrard AJ, Hannah DM, Hansford B, Morrissey I, Edwards PJ, Kollmann J, Ward JV, Tockner K & Smith BPG (2000): Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **10**, 249-266.

Poff NL & Ward JV (1989): Implications of streamflow variability and predictability for lotic community structure – a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences,* **46**, 1805-1818.

Poff N L & Ward JV (1990): Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management,* **14**, 629-645.

Poole GC (2002): Fluvial landscape ecology: addressing uniqueness within the river continuum. *Freshwater Biology,* **47**, 641-660.

Rebsdorf A, Friberg N, Hoffmann CC & Kronvang B (1994): *Ånære arealers samspil med vandløb* (In Danish). Environmental project no. 275, Ministry of Environment and Energy, Danish Environmental Protection Agency, Copenhagen.

Richards KS (1982): *Rivers: Form and process in alluvial channels.* Methuen, London.

Riis T & Sand-Jensen K (2001): Historical changes in species composition and richness accompanying pertubation and eutrophication of Danish lowland streams over 100 years. *Freshwater Biology,* **46**, 269-280.

Riis T, Sand-Jensen K & Vestergaard O (2000): Plant communities in lowland Danish streams: species composition and environmental factors. *Aquatic Botany,* **66**, 255-272.

Riis T, Sand-Jensen K & Larsen SE (2001): Plant distribution and abundance in relation to physical conditions and location within Danish stream systems. *Hydrobiologia,* **448**, 217-228.

Robertson AL, Lancaster J & Hildrew AG (1995): Stream hydraulics and the distribution of microcrustacea - a role for refugia. *Freshwater Biology,* **33**, 469-484.

Sand-Jensen K (1998): Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology,* **39**, 663-679.

Sand-Jensen K & Mebus JR (1996): Fine-scale patterns of water velocity within macrophyte patches in streams. *Oikos,* **76**, 169-180.

Sand-Jensen K, Jeppesen E, Van Der Bijl L, Nielsen K, Wiggers-Nielsen L & Iversen TM (1989): Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology,* **22**, 15-32.

Scarsbrook MR & Townsend CR (1993): Stream community structure in relation to spatial and temporal variation - a habitat templet study of 2 contrasting New Zealand streams. *Freshwater Biology,* **29**, 395-410.

Schumm SA (1977): *The fluvial system.* John Wiley and Sons, New York.

Sear DA (1995): Morphological and sedimentological changes in a gravel-bed river following 12 years of flow regulation for hydropower. *Regulated Rivers: Research and Management,* **10**, 247-264.

Southwood TRE (1977): Habitat, the template for ecological strategies? *Journal of Animal Ecology,* **46**, 337-365.

Stanford JA & Ward JV (1983): Insect species diversity as a function of environmental variability and disturbance in stream systems. In: *Stream ecology: application and testing of general ecological theory* (Eds. JR Barnes & GW Minshall), pp. 265-278. Plenum Press, New York.

Statzner B & Holm TF (1982): Morphological adaptations of benthic invertebrates to stream flow – an old question studied by means of a new technique (Laser Doppler Anemometry). *Oecologia,* **53**, 290-292.

Statzner B, Gore JA & Resh VH (1988): Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society,* **7**, 307-360.

Sugden DE & John BS (1976): *Glaciers and landscape.* Edward Arnold, London.

Sweeney BW & Vannote RL (1981): *Ephemerella* mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. *Ecology,* **62**, 1353-1369.

Tolkamp HH (1980): *Organism-substrate relationships in lowland streams.* Agricultural Research Report 907, Agricultural University, Wageningen, The Netherlands.

Townsend CR (1996): Concepts in river ecology: pattern and process in the catchment hierarchy. *Archiv für Hydrobiologie Supplement,* **113**, 3-21.

Townsend CR & Hildrew AG (1994): Species traits in relation to a habitat template for streams: a patch dynamics approach. *Freshwater Biology,* **31**, 265-275.

Turner MG (1989): Landscape ecology: the effect of pattern and process. *Annual Review of Ecology and Systematics,* **20**, 171-197.

Tuner MG (1998): Landscape ecology – living in a mosaic. In: *Ecology* (Ed. SI Dodson), pp. 77-122. Oxford University Press, New York.

Vannote RL, Minshall GW, Cummins KW, Sedell JR & Cushing CE (1980): The river continuum

concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.

Ward JV (1989): The 4-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, **8**, 2-8.

Ward JV (1992): *Aquatic insect ecology.* 1. Biology and habitat. John Wiley and Sons, New York.

Ward & Stanford (eds.) (1979): *The ecology of regulated rivers.* Proceeding of the first symposium on regulated rivers, Erie, Pennsylvania.

Werritty A (1997): Short-term changes in channel stability. In: *Applied fluvial geomorphology for river engineering and management* (Eds. CR Thorne, RD Hey & MD Newson), pp. 47-65. John Wiley and Sons, Chichester.

Wiberg-Larsen P (1984) *Plecoptera and Ephemeroptera – keys and ecological notes* (In Danish). National Environmental Protection Agency, Copenhagen.

Williams DD & Hynes HBN (1976): The recolonization mechanisms of stream benthos. *Oikos*, **27**, 265-272.

Wood PJ & Petts GE (1994): Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management*, **9**, 303-316.

Wood PJ, Vann AR & Wanless PJ (2001): The response of *Melampophylax mucoreus* (Hagen) (Trichoptera: Limniphilidae) to rapid sedimentation. *Hydrobiologia,* **455**, 183-188.

Wood PJ & Armitage PD (1997): Biological effects of fine sediment in the lotic environment. *Environmental Management,* **21**, 203-217.

Wood PJ, Armitage PD, Cannan CE & Petts GE (1999): Instream mesohabitat biodiversity in three goundwater streams under baseflow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **9**, 265-278.

Physical habitat structure in Danish lowland streams

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Abstract

Dredging or channelization has physically modified the majority (90%) of the 64 000 km of Danish stream network with substantial habitat degradation as a result. Analyses of physical habitat structure in streams, biota, catchment features and regional differences in hydrology, topography and geology have never been carried out in Denmark. Therefore, there is little knowledge of processes, interactions and patterns across the different scales. Physical habitats, catchment parameters and macroinvertebrates were sampled at 39 sites in three major river systems during summer and winter 1993.

In-stream physical conditions and catchment attributes affect the physical habitat structure in Danish lowland streams. Local differences in hydrology, land use, catchment topography and soil types correlated to the in-stream physical habitat parameters. Local differences in hydrology and topography resulted in a separation of the Susà streams with respect to physical habitats. Mud deposition was pronounced at sites with low discharge and low near bed current velocity. Low mud cover was primarily associated with streams with high discharge located in pristine catchments. Stability in the streams was therefore closely linked to in-stream deposition of fine sediment. Generally, macroinvertebrate community diversity increased as discharge increased. Mud cover negatively affected macroinvertebrate diversity and EPT taxon richness.

Regional physical habitat structure and macroinvertebrate community structure were primarily associated with local variations in hydrology, geology and topography. Low-energy streams were primarily located in the Susà river system and the high-energy streams in the Gudenà and Storà river systems, leading to extensive deposition of mud during summer. Streams in the Susà river system generally had lower diversity and species richness compared to the streams in the Gudenà and Storà river systems.

Hydraulic conditions and substratum dynamics in streams are important when managing lowland streams. This study therefore analysed interactions and parameter correlations between physical habitats, stream stability and catchment attributes as well as macroinvertebrate community structure across multiple scales.

Keywords

Lowland streams, physical habitats, stability, macroinvertebrates, catchments, regional differences

Introduction

Regional variations in geology and hydrology are important for the prediction of catchment water balances and stream flow regimes (Shaw, 1994). Thus, large-scale spatial variations in flow regimes should result in regional differences in ecosystem structure and function (Poff and Ward, 1989). Increasing emphasis has been placed on characterising stream flow regimes across geographical regions to make inferences about the functioning of the stream ecosystem (Resh *et al.,* 1988; Poff, 1996).

Rivers are hierarchically organised and consist of different levels nested at progressively smaller spatio-temporal scales, from river systems to single substratum elements. Due to this hierarchical structure, different processes act at different scales and impose constraints at lower levels of the hierarchy (Frissel *et al.,* 1986; Minshall, 1988). Rivers interact with the surrounding landscape at all scales creating a complex pattern of interactions with the terrestrial environment and between scales within the river system hierarchy (Hildrew and Giller, 1994). These interactions have been used to study the physical habitat structure and macroinvertebrate community at the reach scale in relation to higher-level features, such as catchments, regions, geology and hydrology (Poff, 1996; Wright *et al.,* 2000).

Stream flow influences many processes and is recognised as an important part of the habitat template that influences the composition and dynamics of biological communities in streams. Stream flow regimes are characterised by periods of stable flow conditions separated by

discrete high-flow events often referred to as disturbances (Hildrew and Giller, 1994). These disturbance events result in stream bed erosion and low environmental stability (Death and Winterbourn, 1995). Natural disturbances are important features of all environments (Sousa, 1984) and the magnitude and timing of these disturbance events are important for the development of stream biota (Jowett and Duncan, 1990). Disturbances influence species composition and interactions in biotic communities in stream ecosystems by opening up habitat niches (Hildrew and Giller, 1994). Less attention has been given to the effects of low-flow disturbances on the ecosystem stability (Miyake and Nakano, 2002) and habitats (Wood and Armitage, 1997). In groundwater-fed streams, the prolonged periods of low-flow during summer influence deposition and substrate movements in the streams and introduce important seasonal differences in the environmental stability (Wood and Armitage, 1997; Miyake and Nakano, 2002). Anthropogenic disturbance associated with channelization, dredging and continuous weed cutting has resulted in numerous lowland streams in cultivated areas becoming physically degraded and unstable and has reduced the availability of coarse substrata and heterogeneous in-stream habitats (Crisp and Gledhill, 1970; Brookes, 1988).

More than 90% of all Danish streams have been severely modified over the past 150 years by drainage of the riparian wetlands and channelization and dredging of the stream channel. The majority of the Danish streams have thereby lost their natural dynamic physical structure (Brookes, 1987). The majority (75%) of Danish streams are small (<2.5 m wide) and are characterised by low-gradient environments with low current velocity, fine sediments and marked seasonal growth of submerged macrophytes often subject to weed cutting (Sand-Jensen et al., 1989; Sand-Jensen, 1998). So far, studies of variations in Danish stream flow regimes have focused on large-scale relations between climate, geology and hydrology (Ovesen et al., 2000). The present study aimed at characterising the physical habitat structure in lowland streams along local and regional gradients in hydrology, geology and stability. Specifically, the importance of local differences in geology, hydrology, catchment attributes and channel stability for the physical habitats was analysed. Because Danish lowland streams have undergone significant habitat degradation, an analysis was performed in order to clarify whether the resulting instability was more pronounced in streams with low stream power than in streams with high stream power. As the biological communities are expected to be highly dependent on the physical habitats, it was also tested whether the quality and stability of the physical habitats influenced the composition of the biological communities.

Materials and methods

Study sites

The study was carried out in 39 small streams in three river systems in Denmark: river Storå, river Gudenå and river Suså (Fig. 1). These represent three distinct regions in Denmark with respect to geology and hydrology. The majority of the Storå river system in the western part of Jutland is situated on a pro-glacial washout plain formed during the Weischelean Ice Age (20,000 years ago). Sandy soils are dominant here and sandy loam soils dominate on the moraine hills in the northern part of the region. Low-gradient topography predominates on the sandy soils, whereas moderate-gradient topography dominates on the sandy loam soils (Nørrevang and Lundø, 1980). The average annual rainfall is 760 mm year^{-1} compared to an average precipitation of 710 mm year^{-1} in Denmark (Frich et al., 1997).

The Gudenå river system is located in the eastern part of Jutland and is dominated by sub-glacial loamy sand moraine till deposits. During the Weischelean Ice Age large sub-glacial rivers created a high-gradient landscape in this region. Patches of low-gradient landscape and sandy soils are also present (Nørrevang and Lundø, 1980). The average annual rainfall is 650 mm year^{-1} (Frich et al., 1997).

The Suså river system is located on Zealand, which was covered with ice during the majority of the last glaciation. The river system has
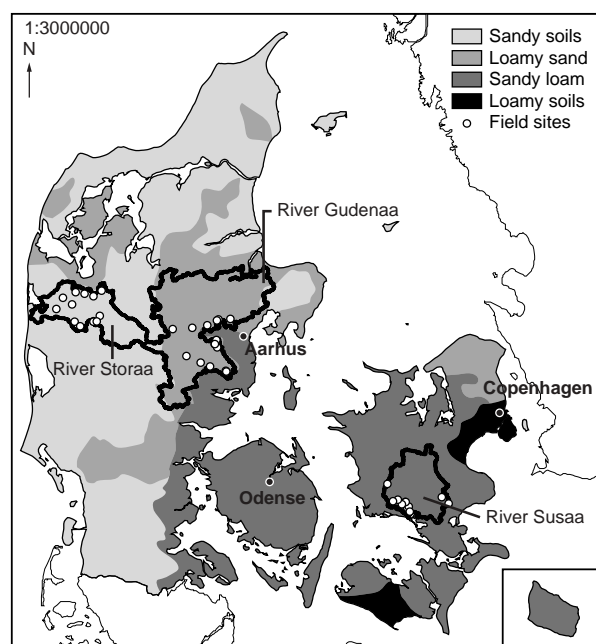

Figure 1. Location of the 3 river systems, 39 field sites and distribution of dominating soil types in Denmark.

moderate-gradient topography and is dominated by sandy loam soils (Nørrevang and Lundø, 1980). The average annual rainfall is 580 mm year^{-1} (Frich *et al.*, 1997).

Reworking of the deposited sediments during the retreat of the Weischelean ice and the variable sub-glacial and pro-glacial environments have created a very heterogeneous soil pattern in the studied river systems. Agricultural land use prevails in the majority of the catchments, but forest and pristine land use dominate some catchments. The 39 streams are 1st and 2nd order streams in the river systems. A total of 15 streams were selected in the Gudenà river system, 13 streams in the Storà river system and 11 in the Susà river system. Channelization and dredging has disrupted natural channel morphology in the investigated streams.

Catchment data

Catchment areas were digitised using the Arc-Info software package. These digital catchment areas were used to extract catchment parameters, such as soil type, land use and topography from the Danish Area Information System (Nielsen *et al.*, 2000). Land use was recorded as pristine, agriculture, mixed coniferous and deciduous forest (semi-natural), heaths and wetlands. Heath, forests, pristine areas and wetlands were subsequently grouped together as pristine land use. The topographic index (TI) was calculated as the difference in elevation between the highest and lowest point in the catchment.

Field survey

All field sites were visited twice, once in June and again in December 1993, using an identical field protocol. At each stream site a 20 m representative reach was selected covering approximately 1-2 riffle-pool sequences. Cross sections were established every 5 meters along the reach. The cross-sections were levelled by use of a laser levelling equipment (ZEISS, REC-ELTA-5). This enabled the slope (I) of the stream bed and the exact water surface width (w) to be calculated in each cross section. The water surface depth (D) was measured at 10 points across each of the 5 cross-sections. Mean depth and width were calculated separately for the summer and winter measurements for each stream.

Discharge and current velocity

The discharge (Q) was measured using the mid-section method (Shaw, 1994) based on 10 vertical profiles and measurements in up to five depths using an inductive current meter (OTT: Nautilus C2000). The near-bed current velocity ($v_{near\ bed}$) was measured for 30 seconds 5 cm above the stream bed at 12 points at each reach (4 points evenly distributed across the wetted width in the cross sections at 0, 10 and 20 m) using an inductive current meter (OTT: Nautilus C2000). Mean near-bed current velocity was calculated.

Stream bed substrata

The stream bed sediments (substrata) were divided into five classes depending on particle diameter, colour and structure. The particle size classes approximated the Wentworth-scale (Wentworth, 1922): Cobble (> 64mm), pebble / gravel (64-2 mm), sand (2-0.1 mm), silt/clay (<0.1mm, inorganic particle, usually with compact structure) and mud (<0.1 mm a mixture of organic debris (FPOM) and inorganic particles, typically brown or black colour and loosely structured). In each cross-section, the coverage of each sub-stratum was measured in 10 plots. Mean cover of the substrata was calculated for each stream. The substratum heterogeneity expresses how often two neighbouring plots differ with respect to sub-stratum type and was calculated as:

$$SH = 1 - \frac{\sum_{i=1}^{n}\sum_{j=2}^{n_i} I(x_{i,j-1}, x_{i,j})}{\sum_{i=1}^{n}\sum_{j=2}^{n_i} 1} \quad where: I(x,y) = \begin{cases} 1, x=y \\ 0, x \neq y \end{cases}$$

where *i* is a cross-section and *j* is a point in the cross-section.

The value is a number between 0 and 1. The closer the value is to 1, the higher the substratum heterogeneity.

Substratum stability and movement

The critical shear stress needed to move a non-cohesive particle is proportional to the diameter of the particle and can be used as a measure of substratum stability. To estimate seasonal variations in stream bed stability, shear stress (τ, N m^{-2}) was calculated both in summer and winter (Newbury, 1984):

$$\tau = D \cdot I \cdot g \cdot \rho_w$$

where: *D* is depth (m), *I* is stream slope (m m^{-1}), *g* is the gravitational acceleration (9.82 m s^{-2}) and ρ_w is the density of the water (1000 kg m^{-3}).

Stream bed stability was also evaluated by considering near bed current velocity in relation to the velocity needed to initiate transport of sediment particles (Mangelsdorf *et al.*, 1990). Stream bed substratum was surveyed and categorised in 40 plots as described above both in summer and winter. By recording the number of substratum changes between the seasons out of a

possible 40, a measure of stream bed substratum stability was calculated.

The stream bed stability and movement and deposition of sediment on the stream bed are closely linked to the discharge regime. Continuous records of daily discharge were available from three gauging stations in small streams in each of the major river systems. The data are held in a nation-wide database at the National Environmental Research Institute in Denmark (Ovesen *et al.*, 2000). Data were available from 1 January 1989 to 31 December 2001 for all nine stations. Clausen and Biggs (1997) identified peak flows of three times the median discharge (Q_{50}) as ecologically useful. For each of the nine continuos records the median discharge (Q_{50}) was calculated along with the number of flood events per year with a peak discharge three times higher than Q_{50} (FRE_3). To include information on severity of the events mean magnitude ($PEAK_3$) and duration (DUR_3) of the events were also calculated (Clausen and Biggs, 1997). The discharge regime parameters were calculated as the mean value from the three gauging stations in each major river system. The normal runoff for the period 1989-2001 for each gauging station was calculated from the continuos discharge records. Information on normal precipitation for a period of six months prior to each sampling occasion for each river system was also obtained from the national climate records (Scharling, 1999).

Macroinvertebrates

Macroinvertebrates were sampled in both June and December using kick sampling (200 μm mesh size) at the 12 points where current velocity was measured. Samples were preserved in 70% ethanol and identified to species level, if possible.

Macroinvertebrate community structure and diversity were expressed as the total number of individuals, EPT (the total number of Ephemeroptera, Trichoptera and Plecoptera taxa at each site), species richness and Fisher's α (diversity) calculated as:

$$\alpha = \frac{N \cdot (1-x)}{x}$$, x is iteratively calculated from:

$$\frac{S}{N} = \left[\frac{(1-x)}{x} \right] \cdot \left[-\ln(1-x) \right]$$

where: N is the total number of individuals and S is species richness (Washington, 1984).

Data analyses

Differences in the physical habitat and catchment parameters between regions and seasons were analysed using 2-factor ANOVA F-tests. Differences in mean values between two regions were analysed using paired Student t-tests (Snedecor and Cochran, 1989). In all 2-factor tests, the interaction between the region and season was also tested. In case of no interaction, the interaction part of the model was left out of the statistical test. Seasonal differences in physical habitat variables within regions were analysed using paired t-tests. Substratum coverage, discharge, land use and soil type parameters were arcsine transformed in order to normalise data and to ensure variance homogeneity between groups (Snedecor and Cochran, 1989). All other data were normally distributed and had equal variances, and transformation was therefore not applied. Correlations between variables were calculated using Spearman rank correlation due to the non-linearity of correlations (Snedecor and Cochran, 1989). Regression analyses were performed using least squares regression. All statistical tests were carried out in SAS/STAT version 8.2 (SAS Institute, 2000).

Results

Hydrological characteristics of sampling periods
The hydrologic conditions varied among the three river systems. The total precipitation for 1993 was approximately equal to the normal in the Storå system, whereas it was 130 and 110 mm above normal in the Gudenå and Suså systems, respectively (Table 1). In the first six months of 1993 (January – June) the precipitation was lower than normal and in the last six months of 1993 (July-December) it was significantly higher than normal (Table 1). This resulted in lower runoff in summer compared to the normal in all three systems. Only the Suså system had higher than normal winter runoff. The temporal runoff pattern in 1993 varied in concordance with the normal runoff, however (Table 1).

The period prior to sampling in June was characterised by decreasing discharge pattern in all three systems. Sampling was carried out under hydrologic conditions similar to mean summer discharge. In the three months prior to sampling in December, five high flow events of approximately similar magnitude and duration took place in all three river systems. Sampling was carried out under discharge conditions corresponding to mean annual discharge.

Catchment characteristics

The alkalinity varied in concordance with the soil types. The lowest alkalinity and pH were found in streams in the upper river Storå, whereas the highest alkalinity and pH were found in streams on the clayey soils in river Suså (Table 1). The soil type distribution varied between the river systems.

Table 1. Overall characteristics of the three river systems. Soil types are expressed as percent cover. Mean values are shown in bold typeface and the coefficient in italic. Lowercase letters indicate groups of significantly different mean values (Pair wise t-test, $P < 0.05$). The runoff is based on continuous discharge records from three stations in each system. Normal discharge is based on the nine continuous discharge records from 1989 to 2001. Summer runoff is the mean of daily discharge during May to August and winter runoff is the mean daily discharge during September to April. Precipitation data is from the nearest 40x40km grid in the national climate grid database (Scharling, 1999).

	Storå (N = 13)			Gudenå (N = 15)			Suså (N = 11)		
	Mean	Range	CV	Mean	Range	CV	Mean	Range	CV
Catchment parameters									
Catchment area (km^2)	6.5	(0.5-10.4)	50	8.7	(0.3-18.9)	62	7.3	(2.3-20.5)	81
Topographic Index (m)	30^a	(6-47)	43	44^b	(25-75)	40	20^a	(2-56)	83
Soil types									
Sandy (%)	72^a	(0-100)	59	8^b	(0-95)	281	0^b	(-)	-
Loamy Sand (%)	27^a	(0-96)	145	81^b	(0-100)	40	85^b	(0-100)	18
Sandy Loam (%)	1^a	(0-69)	255	11^b	(0-95)	245	15^b	(0-100)	103
Water chemistry									
Alkalinity (mmol l^{-1})	984^a	(290-3710)	38	1328^a	(21-3700)	87	5805^b	(4100-7328)	19
pH	7.6^a	(6.4-9.0)	4	7.5^a	(4.5-9.1)	7	8.1^b	(7.0-9.0)	4
Hydrology									
Summer runoff (l s^{-1} km^{-2})	5.0	(0.7-8.6)	79	1.6	(0.7-2.2)	27	0.6	(0.4-0.7)	37
Winter runoff (l s^{-1} km^{-2})	9.9	(8.0-12.2)	22	8.4	(6.7-11.0)	51	15.6	(10.5-19.9)	51
Normal summer runoff (l s^{-1} km^{-2})	5.6	(1.5-8.6)	65	2.3	(1.6-3.1)	34	1.4	(1.3-1.7)	12
Normal winter runoff (l s^{-1} km^{-2})	10.6	(7.6-12.3)	25	9.3	(7.0-12.8)	33	10.8	(9.0-11.9)	14
Precipitation (Jan-Jun) (mm)	235	-	-	229	-	-	160	-	-
Precipitation (Jul-Dec) (mm)	515	-	-	572	-	-	535	-	-

Soil types also varied substantially within the systems as indicated by the ranges and coefficients of variance (Table 1). In the Storå river system, sandy soils dominated (72%), whereas loamy sand dominated in the Gudenå river system (81%) and the Suså systems (86%).

Agriculture was the dominant land use in most catchments, but land use varied considerably among catchments within all three river systems (Table 1). The catchments in the Gudenå river system generally had the highest gradients as indicated by the topographic index values (Table 1). The parameter ranges and CVs indicate significant variation within the river systems in catchment topography.

Correlations between catchment parameters were generally weak. Pristine land use was significantly negatively correlated to the catchment area ($r = -0.29$, $P = 0.009$) indicating a higher percentage of pristine land use (primarily forests) in the smaller catchments.

Physical habitats
Variations in the physical habitat structure across all the surveyed streams were analysed by generating a PCA biplot from the in-stream variables (substratum, depth, discharge and current velocity) and channel dimension variables (slope and width) (Fig. 2). With respect the to the river system, the streams grouped along PCA axis 2 (Fig 2; ANOVA, F-test, $P < 0.001$). In contrast, streams showed little
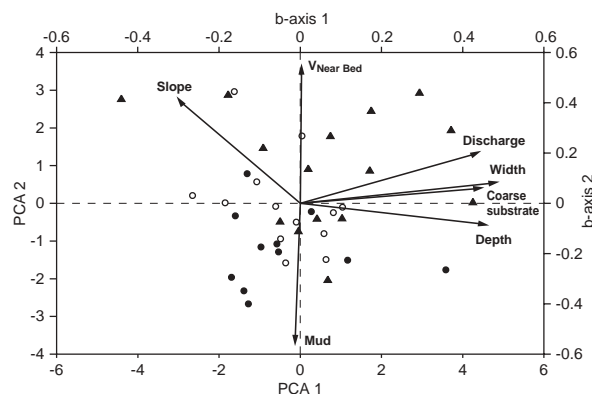
Figure 2. Principal Components Analysis (PCA) bi-plot of the physical habitat-structure in the 39 streams. Points show the location of the individual sites on the PCA axes. The different symbols indicate the major catchments: (o) Storå, (▲); Gudenå and (•) Suså. The length and position of the vectors on the b-axes indicate the significance of the physical parameter. The eigenvalues of the first two axes were 3.06 and 2.42 respectively and together they explained 60% of the variation in the data set.

differentiation between the river systems along PCA axis 1. This result implies that local variables relating to topography and in-stream environment influence the habitat structure and that similarities exist between streams within the river systems, reflecting the regional variations in hydrologic regime. The influential variables on PCA axis 1 were discharge and stream dimensions whereas the

near-bed velocity, stream slope and the mud coverage dominated on PCA axis 2 (Fig. 2).

Discharge directly influences the physical habitat structure in streams by providing the necessary force to open up habitat niches. In all streams, winter discharge was significantly higher than summer discharge (Table 2; Paired t-test, P < 0.001). The average discharge varied between 12 l s^{-1} in summer and 163 l s^{-1} in winter in the streams in the upper river Gudenå. In the Storå river system, the average discharge varied from 14 l s^{-1} in summer to 79 l s^{-1} in winter, whereas discharge ranged from 6 l s^{-1} in summer to 45 l s^{-1} in winter in the Suså streams. Mean summer discharge was not significantly different among the three systems, however (Table 2; ANOVA, F-test, P = 0.268). Average winter discharge was higher in the Gudenå streams than in the Suså streams (Table 2; t-test, P = 0.023). The depth and wetted stream width varied significantly between seasons in concordance with the variations in the discharge in all three river systems (Table 2; Paired t-tests, P < 0.050).

The near-bed current velocities were significantly higher in winter as compared to summer in the Storå and Gudenå streams (Paired t-tests, P < 0.050). Despite a seasonal difference in discharge in the Suså streams, near-bed current velocity varied little between seasons (Paired t-test, P = 0.091). Across all sites, the substrate heterogeneity varied significantly between summer (0.11) and winter (0.17), while no regional differentiation was present (Table 2; ANOVA, F-test, P$_{season}$ = 0.002, P$_{region}$ = 0.890).

In summer, mud substratum dominated the stream bed in all streams. Mean coverage was significantly higher in the Suså streams (69%) compared to the Storå streams (45%) and Gudenå streams (35%). Differences among the river systems remained during winter, but the mud percentage on
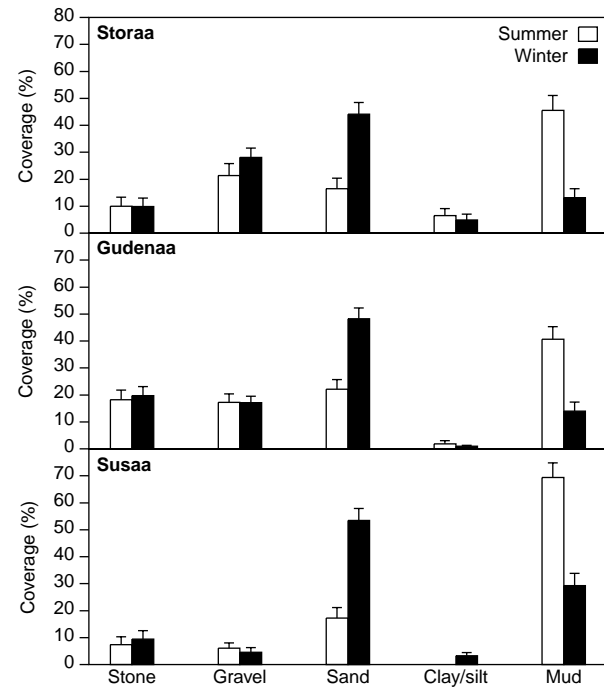
Figure 3. Mean substratum distributions for the streams in the three river systems from the summer and winter field surveys (■: Summer; : Winter). The whiskers on the bars indicate the standard error (SE) on the substratum cover.

the stream bed was significantly lower than in summer (Fig. 3; ANOVA, F-test, P$_{region}$ < 0.001, P$_{season}$ < 0.001). Sand dominated the stream bed in all three regions in winter averaging at 44-53%, which was significantly higher than in summer where the sand coverage ranged between 16% and 22% (Fig. 3; ANOVA, F-test, P$_{season}$ < 0.001; P$_{region}$ = 0.311). Compact silt and clay covered a very small proportion of the stream bed (~ 3%) in all streams. Cobble coverage was constant between seasons, but varied from 8% in river Suså to 19% in river Gudenå (Fig. 3; ANOVA, F-test, P$_{season}$ = 0.573, P$_{region}$ = 0.091).

Table 2. Physical habitat structure in the streams in the three river systems in summer and winter. Mean values are shown in bold. Parameter ranges are given in bracket below the mean value and the coefficient of variation is also presented in italic typeface. Lowercase letters indicate groups of significantly different mean values among the system (Pair wise t-test, P < 0.05).

		Storå		Gudenå		Suså	
		Summer	Winter	Summer	Winter	Summer	Winter
Width (cm)	Mean	111[a]	146[b]	125[a]	191[b]	107[a]	135[b]
	Range	(50-190)	(52-215)	(37-203)	(44-343)	(51-273)	(85-280)
	CV	38	29	42	41	67	44
Depth (cm)	Mean	10[a]	21[b]	8[a]	24[b]	8[a]	16[b]
	Range	(2-28)	(8-36)	(2-16)	(4-51)	(2-22)	(8-25)
	CV	64	38	57	48	75	34
Discharge (l s^{-1})	Mean	14[a]	79[bc]	12[a]	163[c]	6[a]	45[b]
	Range	(0-57)	(14-160)	(0-39)	(1-532)	(0-40)	(12-137)
	CV	118	56	90	98	191	80
$v_{near\ bed}$ (cm s^{-1})	Mean	10[a]	15[b]	12[a]	19[b]	6[a]	11[ab]
	Range	(1-24)	(8-30)	(0-34)	(3-34)	(0-16)	(4-17)
	CV	81	58	72	58	96	32
Substrate heterogeneity	Mean	0.11[a]	0.19[b]	0.13[a]	0.16[b]	0.10[a]	0.18[b]
	Range	(0-0.22)	(0-0.33)	(0-0.27)	(0-0.27)	(0-0.29)	(0.04-0.23)
	CV	68	58	69	58	94	51

Likewise, coverage of pebble / gravel varied little between seasons and was highest in the Storå river system (19%) while it was significantly lower in the Suså river system (4%) (Fig. 3; ANOVA, F-test, $P_{season} = 0.650$, $P_{region} = 0.002$).

The results document a seasonal shift in substratum composition. Generally, the coverage of coarse substrata (cobble + pebble / gravel) remained constant over time, but sand and mud varied significantly between seasons. Looking at variations in substratum at the plot-scale, 62% of all sampled plots differed in substratum type between summer and winter. Thus, the stream bed in the majority of the streams was very dynamic, undergoing erosion and deposition between seasons. Coverage of coarse substrata varied little at the river system scale. However, variations at the stream scale were significant. Approximately 50% of all plots with coarse substrata also shifted substratum type between seasons, indicating significant variations in stream bed stability. Streams with high coverage of coarse substrata had the highest substratum heterogeneity (Table 3).

The stream slope varied between the river systems. The majority of the streams in the Suså river system had slopes of less than 5 m km^{-1} (5‰), whereas the majority of the Storå- and Gudenå streams had slopes larger than 5‰. Near-bed current velocity was positively correlated to the slope and the discharge (Table 3 and Fig. 4). The results indicate that both discharge and slope positively increased near-bed current velocities, thereby reducing mud coverage and enhancing coverage of coarse substrata (Table 3 and Fig. 4). Substratum composition changed from mud-dominated to a domination of coarse substrata as the stream size increased (Table 3). Stream bed heterogeneity also increased with increasing discharges (Table 3). Low mud cover on the stream bed was found in catchments with a high percentage of pristine land use (r = -0.23, P = 0.046) and high gradient topography (r = -0.36, P = 0.001). The near-bed current velocity was highest in streams in catchments dominated by pristine land use (r = 0.31, P = 0.006), indicating a cross-scale link between in-stream habitats and catchment land use.

Stream bed stability

The regional variations in discharge and stream slopes suggested a regional difference in stream bed stability. Summer shear stress was highest in the streams in the upper river Gudenå and river Storå, 6 N m^{-2} and 5 N m^{-2}, respectively. The shear stress was significantly lower in the Suså streams 2 N m^{-2} (ANOVA, F-test, P = 0.021).
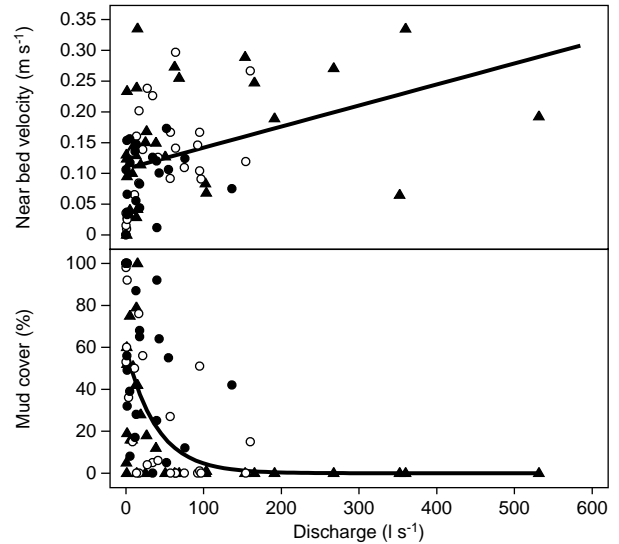
Figure 4. Regression scatter plots of (A) the discharge versus the near bed current velocity (Linear; R^2 = 0. 14, P = 0.001) and (B) the discharge versus the mud cover (First order exponential decay; R^2 = 0.35, P < 0.001). Different symbols are used to differentiate between the three river systems: (o) Storå system, (▲); Gudenå system and (•) Suså system.

Variations in the shear stress determine in-stream zones of erosion and deposition of substrata and are governed by many factors mainly driven by changes in discharge. During summer, only 31% of the sites had shear stresses above 5 N m^{-2}, which corresponds to the threshold of sand transport (Mangelsdorf et al., 1990). During winter, this increased to 62%. Approximately 50% of the streams experienced shear stresses of 1-2 N m^{-2} or lower during summer, which probably caused extensive deposition of mud.

Table 3. Spearman rank correlations between physical habitat variables. Only significant correlations are shown. Asterisks indicates significance level (*0.05; **0.01; ***0.001). The number of observations is 78 for all parameters. The coverage of mud substratum and coarse substrata is in percent of the stream bed. SH is substratum heterogeneity.

	Q_{mean}	$V_{near-bed}$	Width	Depth	SH	Coarse substratum	Mud substratum
$V_{near-bed}$	0.472***						
Width	0.733***	0.230*					
Depth	0.874***		0.707***				
SH	0.430***	0.507***	0.294**				
Coarse substratum	0.270**	0.457***	0.235**		0.423***		
Mud substratum	-0.595***	-0.651***	-0.325**	-0.400***	-0.376***	0.455***	
Slope		0.357**				0.333**	-0.295**

The near-bed current velocities on the sampling days ranged from 0 to 17 cm s^{-1} in the Suså streams. This interval corresponds to transport of fine sand (less than 0.4 mm in diameter). In the other two river systems, near-bed current velocity ranged from 0 to 34 cm s^{-1} which corresponds to transport of a slightly larger particle size, approx. 2 mm (Mangelsdorf *et al.*, 1990).

High summer discharge is thus important for maintaining a relatively high shear stress and near-bed current velocity, thus creating a substantial area of exposed coarse substrata. During winter, most sites were dominated by high discharges and the streams were thus capable of eroding fine substrata (mud and sand) leaving the coarse substrata exposed.

The discharge regime in the Suså system was dominated by flood events that were generally more extreme and lasted for longer periods. In the Storå and Gudenå system the duration and magnitude were generally lower than in the Suså system. Flood events occurred most frequently in the Gudenå system, however (Table 4).

Table 4. Flood event parameters in the three river systems. Parameters are mean values based on continuos discharge records from three stations within each river system. All three parameters are calculated on the basis of flood with a magnitude 3 times the median discharge during the period 1989-2001.

	Parameter name	Storå	Gudenå	Suså
Frequency (year^{-1})	FREQ$_3$	3.4	8.8	5.8
Duration (days)	DUR$_3$	7.3	5.3	19.0
Magnitude	PEAK$_3$	7.6	6.8	10.6

When the results from the analysis of shear stress, near-bed current velocities and discharge regimes were combined, an interesting result emerged with respect to stream bed stability. Despite higher flood magnitude and generally longer flood duration over the year in the Suså streams, the slightly lower discharge in both summer and winter resulted in lower near-bed current velocity and shear stress. This led to higher mud coverage in the Suså streams. In contrast, high discharge resulted in low mud coverage in the streams in the Storå and Gudenå systems.

Macroinvertebrate communities

The macroinvertebrate communities in the Gudenå and Storå river systems resembled each other with respect to the number of individuals, species richness diversity and the number of EPT taxa. The streams in the Suså system generally experienced a lower number of EPT taxa, diversity and species richness (Table 5). The ranges in the biotic variables, however, indicate that some of the streams in the Suså system have values of the same magnitude as the two other river systems. In order to ensure that differences in regional species pools did not affect the results, taxa not occurring in the Suså river system were removed from the calculations and all invertebrate community variables were re-calculated. In total, 6 taxa present in the Gudenå and Storå river systems were not present in the Suså catchment. Correcting for the lower EPT taxon richness had, however, no effect on the results.

The importance of the different physical habitat variables and catchment characteristics for the invertebrate community was analysed by Spearman rank correlation analysis (Table 6). The coverage of mud correlated negatively to diversity (Fisher's α), species richness and EPT taxa, whereas the number of individuals increased as mud cover increased. The streams in the Suså catchment had the highest mud coverage and the lowest macro-invertebrate community scores, whereas the Gudenå and Storå river systems had lower mud coverage and a tendency towards higher macro-invertebrate community scores. The near-bed current velocity, shear stress and the presence of coarse substrate are all positively correlated to the Fishers α and the number of EPT taxa. Correlations between depth, width and substratum hetero-geneity and biotic variables were low. The slope was positively correlated to the number of EPT taxa, while discharge correlated negatively to the number of individuals and positively to macroinvertebrate diversity and number of EPT taxa (Table 6). The correlations between the physical habitat variables and the biotic indices were significant, but no clear regional separation emerged when the correlation between mud coverage and macroinvertebrate community variables was plotted (Fig. 5). When the mud coverage on all sites was plotted against macroinvertebrate species richness, diversity and number of EPT taxa, a general negative effect of increased mud coverage emerged. Sites only separated slightly with respect to region (Fig. 5).

Table 5. Mean macroinvertebrate community characteristic in the three river systems. Variables include species richness the number of individuals, Fisher's α diversity and the number of EPT taxa. Lowercase letters indicate groups of systems with significantly different mean values (Pair wise t-test, P < 0.05).

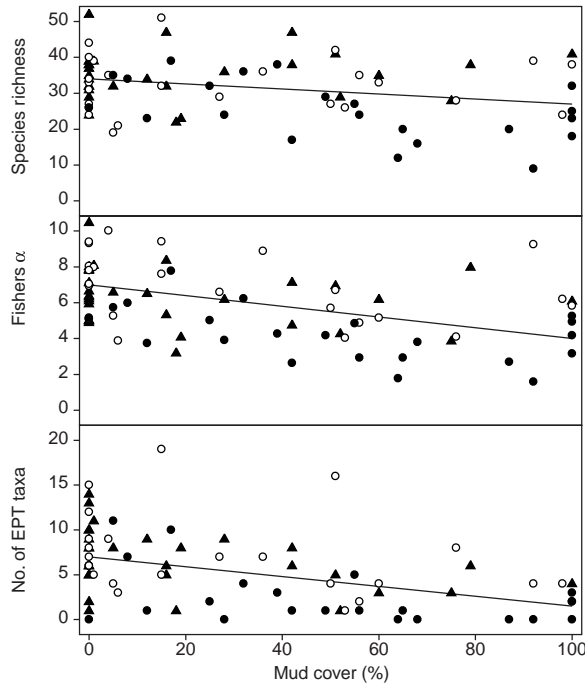|	No. of individuals		Species richness		EPT taxa		Fisher's α	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Storå	1531[a]	(189-6506)	32.5[a]	(19-51)	7[a]	(1-19)	6.3[a]	(3.9-10.0)
Gudenå	2567[a]	(626-14844)	35.3[a]	(22-52)	7[a]	(1-14)	6.8[a]	(3.2-10.5)
Suså	4561[b]	(253-47409)	25.4[b]	(9-39)	2[b]	(0-11)	4.2[b]	(1.6-7.8)

Figure 5. Relationships between the mud cover and species richness ($R^2 = 0.25$, $P = 0.030$), Fisher' α diversity ($R^2 = 0.22$, $P < 0.001$) and number of EPT taxa ($R^2 = -0.30$, $P < 0.001$). Different symbols are used to differentiate between the three river systems: (o) Storå system, (▲); Gudenå system and (•) Suså system.

Larger-scale catchment parameters correlated to the macroinvertebrate community variables (Table 6). High values of the number of EPT taxa, species richness and species diversity were found in streams where the catchments had pristine land use, sandy soils.

Table 6. Spearman rank correlations between physical variables and macroinvertebrate indices across all the catchments. Only significant correlations are included in the table. Asterisks indicate significance level (*0.05; **0.01; ***0.001). The number of observations is 78 for all parameters. Soil types, land use and substratum parameters were arcsine transformed prior to analysis (Snedecor and Cochran, 1989).

	No. of individuals	Species	EPT	Fisher's α
Catchment parameters				
Pristine land use (%)		0.264**	0.511***	0.295**
Sandy soils (%)	-0.245**		0.387**	0.312**
Topographic index (m)		0.310**	0.366**	
Channel parameters				
Slope (‰)			0.331**	
Discharge (l s^{-1})	-0.236**		0.304**	0.295**
Physical habitat parameters				
Coarse substrata (%)			0.380**	0.302**
Mud substratum (%)	0.288**	-0.245**	-0.535***	-0.468***
$V_{nearbed}$ (cm s^{-1})			0.435***	0.295**
Depth (cm)	-0.231*			0.234**
Width (cm)				

Discussion

Physical habitat structure

The aim of the present study was to investigate physical habitat structures and macroinvertebrate communities in Danish streams in relation to local and regional variations in hydrology and geology. Our results suggest that there is no simple relation between the physical habitat structure, catchment characteristics, hydrology, geology and macro-invertebrates in lowland Danish streams. The habitat structure in the streams is believed to be a complex combination of factors acting at different scales (point, reach and catchment scale) (Frissell *et al.,* 1986).

Transport and subsequent deposition of fine sediment and mud characterise lowland streams (Brookes, 1987). In this study, enhanced mud deposition occurred in streams that experienced low discharge and low current velocities. A similar occurrence has also been reported from other Danish streams (Svendsen 1992; Sand-Jensen, 1998). Discharge varied among the river systems. Streams in the Storå and Gudenå systems generally experienced higher summer and winter discharge compared to the streams in the Suså system where summer discharge was low and winter discharge moderate. These differences in discharge and flood regimes affected the shear stress, near bed current velocities and subsequently the stream bed substratum. During winter, mud was eroded from the streams, but the streams with highest summer deposition also had the highest coverage of mud during winter. The highest coverage of mud substratum was found in the Suså streams during both summer and winter. During winter, moderate discharges in the Suså system led to low near-bed current velocities that reduced the stream transport capacity and thereby also the removal of mud substratum (Newbury, 1984). High groundwater input and moderate to high gradient topography probably caused higher near-bed current velocities in the Gudenå and Storå streams throughout the year, leading to higher coverage of coarse substrata and lower coverage of mud (Ovesen *et al.,* 2000). The hydrology and habitat structure resembles that of other lowland areas where the streams are dominated by groundwater runoff (Sand-Jensen *et al.,* 1989; Svendsen, 1992; Wood *et al.,* 1999; Miyake and Nakano, 2002). Generally, high discharge and near-bed current velocities dominated in streams located on sandy soils and dominated by pristine land use. These are equivalent to areas in landscapes with low potential for agricultural land use. These correlations probably reflect a less intense destruction of natural habitats in these streams.

Stream stability in lowland streams

Traditionally, disturbance in streams has been studied in upland streams where it is associated with movement of coarse substrata during high discharge events (Death and Winterbourn, 1994; Downes *et al.,* 1997; Matthaei *et al.,* 1999a) while stability issues associated with low-flow conditions and deposition of finely grained sediment in groundwater-fed streams have attracted less attention (Wood and Armitage, 1997; Miyake and Nakano, 2002).

On average, more than 60% of the substratum plots shifted substratum between seasons indicating that a substantial part of the stream bed in small Danish streams undergoes changes irrespective of the substratum composition. Streams with high coverage of coarse substrata also had a more heterogeneous substratum composition. The variable environment at these sites is probably better at dissipating the flow energy and thereby prohibits substrate movement, compared to homogeneous sites where all energy is directed into moving fine substrate (Brookes, 1988).

Stream bed stability was analysed using several measures, shear stress, near bed current velocities and discharge regimes within the major river systems. Shear stress values ranged from 0.5 N m^{-2} to 20 N m^{-2}. This is approximately a factor 5-10 below the values reported by Death and Winterbourn (1994) from New Zealand streams. The values in the present study correspond approximately to the movement of particles less than 2 mm in diameter (Mangelsdorf *et al.,* 1990). The correlation between discharge, near-bed current velocity and substratum composition indicates that the most stable streams have high coarse substratum coverage and that the ecological stability is closely linked to deposition of fine sediments. The response in the macroinvertebrate parameters also indicates the detrimental effects of high mud coverage. The Suså streams generally had higher mud coverage despite higher peak flows and longer duration of the floods. The effects of these high-flow events are well-documented (Clausen and Biggs, 1997). However, the absolute magnitude of the summer and winter discharge seems to be more important. The results indicate that low discharge has primary control on the substratum composition and that the effects of the floods are of secondary importance in small lowland streams. Substantial flood effects are, however, to be expected also in lowland streams as in other stream types (Clausen and Biggs, 1997). It was, however, not possible to document the effects of the floods in the present study. The discharge and subsequent deposition of fine-grained substrata such as mud is therefore likely to play a key-role in the ecology of small lowland streams.

In many lowland streams, weed cutting and dredging of streams channels have caused bank erosion and stream bed instability, leading to enhanced input of sediments to the streams (Brookes, 1988). The combination of high discharge, shear stress and excess inputs of sediment may cause enhanced deposition. In many streams, the transport threshold is exceeded by the erosion input, leading to deposition despite natural flood events (Laubel *et al.,* 1999). This indicates that high discharge can increase or decrease habitat quality, depending on sediment transport and input to the stream.

Macroinvertebrates and physical habitats

Stream bed deposition and erosion have been identified as important factors in determining macroinvertebrate distribution patterns in streams (Matthaei *et al.,* 1999b; Miyake and Nakano, 2002). In this study, analyses revealed significant correlations between macroinvertebrate species richness and diversity (expressed as Fisher's α) and the discharge, slope, current velocity and presence of coarse substrata. Negative correlation between species richness and diversity and the coverage of mud, and positive correlations between flow variables and mud coverage indicate the importance of high summer flows for the physical habitat quality. The results indicate that the highest macroinvertebrate diversity, species richness and presence of EPT taxa are found in streams with low mud cover and high discharges, which corresponds to the findings of Wood *et al.* (1999). This study revealed that in a low-gradient environment discharge, an active channel area and fine sediment deposition are determining factors with regard to the macroinvertebrate community composition (Wood *et al.,* 1999).

Catchment characteristics, such as pristine land use, sandy soils and topography correlate well with species diversity and richness and the presence of EPT taxa. The correlation between physical habitat variables, such as substratum composition, pristine catchment land use and topography indicates that extensive mud cover is likely to increase in catchments at low elevations and with little pristine land use. In a major habitat survey in Great Britain, Jeffers (1998) found that catchment attributes, such as source height, distance from source, catchment area and geological variables, influenced reach-scale habitat characteristics. This suggests a cross-scale coupling of the physical habitats, macroinvertebrates and the catchment parameters. Our results suggest that the regional differences in macroinvertebrate communities, species richness and diversity are a result of the local differences in in-stream habitats as well as local catchment characteristics and large-scale differences in hydrology. The regional

differences in physical habitat structure also imply a regional difference in physical habitat structure dictated primarily by local differences in hydrology and topography. The correlation between physical habitats and catchment characteristics is, however, not strong. This suggests that the macroinvertebrate community may be influenced by physical processes acting at the reach scale, but also by processes acting at the higher catchment scale (Richards *et al.,* 1996).

In lowland streams, instability is caused by 1) natural variations in flow and 2) anthropogenic interference with the natural dynamics in the stream ecosystem, such as channelization, dredging and weed cutting (Brookes, 1987). The anthropogenic impacts are super-imposed on catchment features and natural physical variations and disturbance is thus enhanced in streams with low energy. The primary physical impact in Danish lowland streams comes from agricultural land use (dredging and weed cutting for drainage purposes). As indicated by our results, agricultural land use dominates in low-gradient landscapes on loamy soils. Small streams in this environment also have the lowest discharge, near-bed current velocity and shear stress and subsequent high deposition of mud substratum. These low gradient environments are the most susceptible to natural disturbance due to the dominance of fine sediments. The homogeneous environment is less capable of dissipating the power from high discharge events, which makes it sensitive to enhanced erosion and deposition from disturbances. These streams with low stream power will also have a low potential for regaining their original physical and biological structure when first degraded by dredging, channelization or weed cutting.

Conclusions and perspectives

Large-scale differences in in-stream variables and catchment features affect the physical habitat structure in Danish lowland streams. The discharge in general and the summer discharge in particular are essential for maintaining high physical habitat quality. Local differences in hydrology, soil types, land use and catchment topography and large-scale differences in the parameters are the primary cause of regional differences in the physical habitat structure. Generally, streams with low discharge and subsequent low near-bed current velocity and shear stress were located in catchments with loamy soils in low topography catchments (primarily the Susà river system) and streams with high discharge were located in pristine catchments in the Gudenà and Storà river systems.

Discharge, near-bed current velocity, stream slope and shear stress are important for the quality of the in-stream habitats by reducing the mud cover, which affects the macroinvertebrate community. High discharge and current velocities, as well as high shear stress erode fine sediment from the stream bed thereby exposing coarse substrata. Low discharge resulted in low current velocities, and shear stress values not capable of moving coarse substrata dominate the in-stream environment in summer and winter. Therefore, it is most likely that the stability of small Danish streams is linked to deposition of fine sediment rather than erosion of coarse substrata.

Macroinvertebrate community diversity and quality increased as discharge and shear stress increased. Mud cover affected macroinvertebrates negatively by reducing the diversity. The Susà streams generally had low diversity and species richness, but a higher number of individuals as compared to the Gudenà and Storà streams, reflecting differences in the physical habitat structure and substratum characteristics caused by differences in hydrology and catchment attributes.

In the management and restoration of lowland streams it is vital to take into account the ability of the streams to regain their natural dynamics. As our results show, the key issues when working with lowland streams are discharge and stream power. Alterations to the stream ecosystem, such as dredging, channelization and weed cutting that affect overall stream morphology and sediment dynamics are likely to result in increased erosion and deposition of fine sediments. When the hydrology is dominated by pronounced periods of low flow and moderate high-flow periods as in Denmark, this feature becomes increasingly important. The deposition of mud and fine sediments in Danish streams is controlled by both natural variations in hydrology, geology and geomorphology, and by anthropogenic disturbance. The deposition of mud was highest in the streams located in the Susà system where low summer discharge prevails and channelization is most widespread. This clearly shows that a further reduction of the discharge in this region by water abstraction can severely affect the habitats and biota.

Reduction of the mud deposition by means of active restoration of the natural stream morphology may be an option in streams with low power. Reduction of the mud deposition has so far not been a main aim of the restoration projects carried out in Denmark (Iversen *et al.,* 1993). Restoration projects have primarily been carried out in relatively large streams (River Brede and River Gels) with high summer discharge where extensive deposition of mud substratum is of secondary importance (Friberg *et al.,* 1998; Holmes

and Nielsen, 1998). The results presented here have identified some of the environmental problems in small lowland streams that make up 75% of the entire stream length in Denmark. By focusing on discharge during low-flow periods and deposition of mud substratum, it is possible to set the goals for future restoration projects in small lowland streams. Moreover, the results from the present study will help identify the streams that require restoration in order to meet the quality objectives of the EU Water Framework Directive.

Acknowledgements

References

Brookes A. 1987. The distribution and management of channelized streams in Denmark. *Regulated Rivers: Research and Management* **1**: 3-16.

Brookes A. 1988. *Channelized rivers – perspectives for environmental management.* Wiley & Sons: Chichester. 326 pp.

Clausen B, Biggs BJF. 1997. Relationships between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology* **38**: 327-342.

Crisp DT, Gledhill T. 1970. A quantitative description of the recovery of the bottom fauna in a muddy reach of a Mill Stream in southern England after draining and dredging. *Archiv für Hydrobiologie* **67**: 502-541.

Death RG, Winterbourn MJ. 1994. Environmental stability and community persistence – a multivariate perspective. *Journal of the North American Benthological Society* **13**: 433-455.

Death RG, Winterbourn MJ. 1995. Diversity patterns in stream benthic invertebrate communities - the influence of habitat stability. *Ecology* **76**: 1446-1460.

Downes BJ, Glaister A, Lake PS. 1997. Spatial variation in the force to initiate rock movement in 4 upland streams: implications for estimating disturbance frequencies. *Journal of the North American Benthological Society* **16**: 203-220.

Friberg N, Kronvang B, Hansen HO, Svendsen LM. 1998. Long-term, habitat-specific response of a maroinvertebrate community to river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 87-99.

Frich P, Rosenørn S, Madsen H, Jensen JJ. 1997. *Observed precipitation in Denmark, 1961-90* (In Danish). Technical Report 97-8. Danish Meteorological Institute, Copenhagen. 38 pp.

Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification – viewing streams in a watershed context. *Environmental Management* **10**: 199-214.

Hildrew AG, Giller PS. 1994. Patchiness, species interactions and disturbance in the stream benthos. In *Aquatic ecology – scale, pattern and process*, Giller PS, Hildrew AG, Raffaelli DG (eds). Blackwell Scientific Publications: Oxford: 21-62.

Holmes NTH, Nielsen MB. 1998. Restoration of the rivers Brede, Cole and Skerne: a joint Danish and English EU-LIFE demonstration project, I – Setting up and delivery of the project. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 185-196.

Iversen TM, Kronvang B, Madsen BL, Markmann P & Nielsen MB. 1993. Reestablishment of Danish streams - restoration and maintenance measures. *Aquatic Conservation: Marine and Freshwater Ecosystems* **3**: 73-92.

Jeffers JNR. 1998. Characterization of river habitats and prediction of habitat features using ordination techniques. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 529-540.

Jowett IG, Duncan MJ. 1990. Flow variability in New-Zealand rivers and its relationship to in-stream habitat and biota. *New Zealand Journal of Marine and Freshwater Research* **24**: 305-317

Laubel A, Svendsen LM, Kronvang B, Larsen, SE. 1999. Bank erosion in a Danish lowland stream system. *Hydrobiologia* **410**: 279-285.

Mangelsdorf J, Scheurmann K, Weiss FH. 1990. *River morphology: a guide for geoscientists and engineers.* Springer-Verlag: Berlin. 245pp.

Matthaei CD, Arbuckle CJ, Townsend CR. 1999a. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society* **19**: 82-93.

Matthaei CD, Peacock KA, Townsend CR. 1999b. Scour and fill patterns in a New Zealand stream and potential implications for invertebrate refugia. *Freshwater Biology* **42**: 41-57.

Minshall GW. 1988. Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* **7**: 263-288.

Miyake Y, Nakano S. 2002. Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. *Freshwater Biology* **47**: 219-230.

Newbury RW. 1984. Hydrologic Determinants of Aquatic Insect Habitats. In *The Ecology of Aquatic Insects,* Resh VH, Rosenberg DM (eds.). Praeger Publishers: New York: 323-357.

Nielsen K, Stjernholm M, Olsen BØ, Müller-Wohlfeil DI, Madsen I, Kjeldgaard A, Groom G, Hasen HS, Rolev AM, Hermansen B, Skov-Petersen H, Johansen VK, Hvidberg M, Jensen JE, Bacher V, Larsen H. 2000. *Area Information System - AIS* (In Danish). Danmarks Miljøundersøgelser: Silkeborg. 110 pp.

Nørrevang A, Lundø J. 1980. *Danmarks Natur Bind 1 – Landskabernes opståen* (3 ed.) (In Danish). Politikens Forlag, Copenhagen. 448 pp.

Ovesen NB, Iversen HL, Larsen SE, Müller-Wohlfeil DI, Svendsen LM, Blicher AS, Jensen PM. 2000. *Hydrologic regimes in Danish streams* (In Danish). Faglig Rapport fra DMU nr. 340: Silkeborg. 238 pp.

Poff NL. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* **36**: 71-91.

Poff NL, Ward JV. 1989. Implications of streamflow variability and predictability for lotic community structure – a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1805-1818.

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* **7**: 433-455.

Richards C, Johnson LB, Host GE. 1996. Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 295-311.

Sand-Jensen K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology* **39**: 663-679.

Sand-Jensen K, Jeppesen E, Van Der Bijl L, Nielsen K, Wiggers-Nielsen L, Iversen TM. 1989. Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology* **22**: 15-32.

SAS Institute. 2000. *The SAS System Version 8.2.* SAS Institute: Cary.

Scharling M. 1999. *KLIMAGRID – Denmark. Precipitation, temperature and potemtial evapotranspiration (20*20 and 40*40 km)* (In Danish). Technical Report 99-12. Danish Meteorological Institute, Copenhagen. 48 pp.

Shaw EM. 1994. *Hydrology in Practice 3. ed.* Chapman & Hall: London. 539 pp.

Snedecor GW & Cochran WG (1989): *Statistical Methods.* Iowa State College Press. Ames, Iowa. 503 pp.

Sousa WP. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **14**: 353-391.

Svendsen LM. 1992. *Dynamics of phosphorus, organic nitrogen and organic matter in watercourses.* PhD-Thesis. National Environmental Research Institute, Silkeborg. 260pp.

Washington HG. 1984. Diversity, biotic and similarity indices. *Water Research* **18**: 653-694.

Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* **30**: 377-392.

Wright JF, Sutcliffe DW, Furse M (eds). 2000. *Assessing the biological quality of freshwaters – RIVPACS and other techniques.* Freshwater Biological Association: Ambleside. 373 pp.

Wood PJ, Armitage PD. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**: 203-217.

Wood PJ, Armitage PD, Cannan CE, Petts GE. 1999. Instream mesohabitat biodiversity in three groundwater streams under baseflow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**: 265-278.

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Physical habitats and diversity of biological communities in Danish lowland streams with contrasting disturbance

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Summary

1. We used the difference in weed cutting as an experimental tool to study long-term effects of disturbance on physical habitat structure and density and diversity of macrophytes, macroinvertebrates and fish in 33 lowland streams in Denmark.

2. Macrophyte communities suffered from the long-term disturbance. Average species richness and diversity was significantly lower in disturbed than undisturbed streams. Cumulative species richness was 146 in the 16 undisturbed streams and 107 in the 17 disturbed streams. More complex growth forms, expressed as niche overlap between plant species, were encountered in undisturbed streams.

3. Physical habitat structure in disturbed stream was characterised by lower current velocity and higher coverage of mud than in undisturbed streams where coarse substrata, high slopes and high current velocities prevailed. Disturbed streams were morphologically less variable and sinuosity and variations in stream width were the most significantly different features.

4. Macroinvertebrate species adapted to lower current velocities and fine substrata habitats were more abundant in disturbed streams subjected to continuous weed cutting. The total number of Ephemeroptera, Plecoptera and Trichoptera species (EPT) was significantly lower in disturbed streams (3.6) than in undisturbed streams (7.7). Macrophyte dwellers such as simulids, *Gammarus pulex* and *Baetis* spp. was directly influenced by weed cutting and their abundance was reduced by 50-90% on disturbed sites. In undisturbed streams specific macrophytes supported distinct macroinvertebrate assemblages.

5. Density of trout (*Salmo trutta* L.) was markedly lower in disturbed streams (22 100m^{-2}) than in undisturbed streams (108 100m^{-2}) due to degradation of in-stream physical habitats and lower food resources following weed cutting.

6. The present study documents that anthropogenic disturbance of the macrophyte communities has profound cascading effects in lotic ecosystems and underline the key-role of macrophytes in lowland streams.

Keywords

Streams, habitat-disturbance, macrophytes, macroinvertebrates, trout

Introduction

The physical structure of lowland streams is very closely linked to the growth of aquatic macrophytes. The seasonal variation in biomass of submerged macrophytes has a significant impact on the in-stream flow regime and physical habitats, by reducing mean velocity and raising water levels (Sand-Jensen *et al.*, 1989; Hearne & Armitage, 1993). Macrophytes alter in-stream flow patterns and create a range of current velocities, varying from static flow environments within stands to high velocities outside stands where flow is accelerated and gains sufficient energy to expose coarse grained-substrata (Watson, 1987; Sand-Jensen & Mebus, 1996).

Aquatic macrophytes are known to influence the structure and spatial distribution of benthic invertebrates (Ward, 1992). The macrophyte surfaces offer additional habitat area within the water column, thus enhancing in-stream habitat diversity (Hearne & Armitage, 1993). This increased habitat area increases invertebrate abundance and diversity compared to streams without aquatic macrophytes (Percival & Whitehead, 1929; Rooke, 1984). Macrophytes provide a flow refuge, a stable substratum and oviposition sites for benthic invertebrates (Harrod, 1964; Cattaneo & Kalff, 1980). Fish communities are also affected by the presence of macrophytes. Macrophytes provide shelter as well as refuge during high flow events, and are typically areas of high food densities (Garner, Bass & Collett, 1996). Macrophyte stands are also important nursery habitats for juvenile fish (Copp, 1990).

Macrophytes play a key-role in the trophic relationships of lowland streams. Shredders may feed directly on the macrophytes (Sand-Jensen & Madsen, 1989; Jacobsen & Sand-Jensen, 1994) or on decaying autochthonous plant tissue (Smock & Harlowe, 1983). Grazers feed on epiphytic algae and other micro-organisms attached to macro_phyte surfaces (Cattaneo & Kalff, 1980), and detritivores utilise the fine particulate organic matter that accumulates within the macrophyte stands (Mann, 1988; Sand-Jensen, 1998).

More than 90% of the Danish streams have been canalised, widened and deepened over the past 100 years. The majority of these changes have taken place between 1920 and 1970 (Brookes, 1988). Dredging of stream sediments and weed cutting were initiated during the 1920's and has since been intensified as drainage and cultivation of the riparian meadows increased. Today weed cutting is still applied in the majority of Danish streams in varying degrees. As a combined result of canalisation, dredging and weed cutting, the spatial physical variability has declined in Danish lowland streams (Iversen *et al.*, 1993).

The long-term physical stream management and eutrophication of surface waters have caused significant changes in species composition and a decline in species richness of aquatic macrophytes (Riis & Sand-Jensen, 2001). Macrophyte communities have changed towards a dominance of fast-growing species adapted to frequent weed cutting and more homogenous habitats (Baattrup-Pedersen, Larsen & Riis, 2002).

Macrophyte cutting has an immediate impact on the physical structure and macroinvertebrate communities of the stream ecosystems (Kaenel & Uehlinger, 1998). The short-term (days to months) effects of plant removal have been reported to lead to increased macroinvertebrate drift (Kern-Hansen, 1978) and a decline in the abundance of macroinvertebrates (Dawson, Clinton & Ladle, 1991; Monahan & Caffrey, 1996; Kaenel, Matthaei & Uehlinger, 1998). However, limited attention has been devoted to studying the more important long-term effects (years to decades) of weed cutting as a recurring management practice in most lowland streams. The few studies that have been performed have primarily focused on direct effects on the distribution and abundance of macrophyte species (Riis, Sand-Jensen & Larsen, 2001). Studies of the long-term influence of weed cutting on physical habitat structure and macroinvertebrate communities are few.

In this study we address the central question of how strong impact on the macrophytes may influence physical and biotic features in lowland streams. Our main hypothesis is that macrophytes play a key-role for the structure and function of unshaded lowland streams. As a consequence, we predict that major changes within the macrophyte community will alter environmental conditions and have cascading effects on higher trophic levels composed of macroinvertebrates and fish. We also predict that the lotic ecosystem will change both due to direct and indirect effects. Direct effects include removal of macrophytes as habitats and subsequent removal of invertebrates as potential food resources. Indirect effects primarily comprise changes in abundance and suitability of the habitats. By comparing a large number of streams which have been disturbed by weed cutting for a least eight years with undisturbed streams where no weed cutting has taken place, effects on macrophytes, physical habitats, macroinvertebrates and fish communities can be evaluated. Weed cutting provide a large-scale experiment suitable for investigating the role of macrophytes in lowland streams. These results can be used to evaluate the effects of long-term disturbance on in-stream habitats and biotic communities.

Methods

Study sites
The 33 study sites were located throughout Denmark in major river systems (>100 km^2) thus representing different hydrological and environmental conditions. All sites had substantial in-stream vegetation and limited cover from riparian vegetation. Stream slopes varied from 0.7 to 13.7 m km^{-1} and channel sinuosity varied from 1.00 to 1.33. Catchment land use was dominated by agriculture at all sites (Table 1). The selected sites were representative of 75% of the entire stream length in Denmark as streams are generally small, unshaded and drain agricultural catchments.

We used weed cutting to study the effects of a large-scale experimental disturbance. Information on weed cutting practice from the period 1993-2000 was obtained from local water authorities. On 16 sites no weed cutting or dredging had been applied throughout the entire 8-year period. The other 17 sites were cut twice a year, whereby all stream plants and a substantial part of the bank vegetation were removed.

Water chemistry was measured 6 times per year in 1998 and 2000. The chemical characteristics of the two stream groups are outlined in Table 1. Water chemistry, land use and soil types were generally the same in the two groups. Typical total phosphorus concentrations were 20-400 mg P m^{-3} and total nitrogen concentrations were 1-14 g N m^{-3}. Thus, both substances were found in concentrations in excess of plant requirements (Kern-Hansen & Dawson, 1978), reflecting intensive agriculture in the catchments (Table 1).

Table 1. Characteristics of catchments, water chemistry and overall stream morphology in undisturbed and disturbed stream types.

	Undisturbed (n=16)	Disturbed (n=17)
Catchment area (km^2) (mean and range)	14.9 (0.9-46.5)	12.9 (1.1-41.9)
Distance to source (km) (mean and range)	5.5 (0.4-12.0)	3.9 (0.3-11.9)
Catchment land use (%) (agriculture/forest/pristine/urban)	75 / 10 / 9 / 6	77 / 9 / 9 / 5
Soil types (%) (sand/clay/organic)	64 / 33 / 3	63 / 33 / 4
Oxygen demand (BOD_5;mg l^{-1}) (mean ± SE)	1.35 ± 0.16	1.60 ± 0.13
Alkalinity (meq l^{-1}) (mean ± SE)	2.06 ± 0.39	3.27 ± 0.29
Total iron (mg l^{-1}) (mean ± SE)	0.59 ± 0.03	0.94 ± 0.03
NH_4-N (mg l^{-1}) (mean ± SE)	0.07 ± 0.01	0.19 ± 0.05
PO_4-P (mg l^{-1}) (mean ± SE)	0.06 ± 0.01	0.12 ± 0.04
Stream slope (‰) (mean and range)	5.9 (1.7-12.8)	3.5 (0.7-13.7)
Sinuosity (mean and range)	1.09 (1.00-1.33)	1.02 (1.00-1.10)

Field survey

Vegetation, physical habitat variables and macroinvertebrates were studied in the spring (March – April) and summer (early or mid August) of 1998 and 2000. Fish were sampled both years in early- or mid-August. Weed cutting was applied in May/June and late August. By sampling prior to weed cutting in late August, the observed differences between stream groups are then the result of the long-term changes in habitats and stream biota and not of short-term influences of recent plant removal. Macrophyte coverage and biomass peak in August in Danish streams (Kelly, Thyssen & Moeslund, 1983) and they should therefore have the maximum ecosystem impact at that time.

In-stream vegetation

In-stream macrophyte species were registered by means of a hydroscope in 150 plots (25 x 25 cm) placed side by side in evenly distributed transects at each site. The number of transects at each site varied depending on stream width (width range: 59-567 cm). Macrophytes were identified to species except for non-flowering individuals of *Callitriche* and *Epilobium*. Non-flowering individuals of *Batrachium aquatile* (L.) *B. baudotti* (Godron) and *B. pletatum* (Schrank) could not be distinguished and were recorded as *Batrachium* spp. (Moeslund *et al.*, 1990). Relative frequency of a species was calculated from the number of plots in which the species was observed relative to the total number of plots with macrophytes. Relative frequencies were used as a measure of species coverage. Total plant coverage at each site was calculated as the percentage of plots with macrophytes. Macrophyte community structure was expressed as species richness and Fisher's α diversity:

$$Fisher's\ \alpha = \frac{N(1-x)}{x}$$, x was iteratively calculated

from: $$\frac{S}{N} = \left[\frac{(1-x)}{x}\right][-\ln(1-x)]$$

where, N is the total number of observed plants (individuals) and S is species richness (Washington, 1984).

Overall species richness (S_{max}) for each stream type was estimated from the 1st order Jack-knife estimate based on re-sampling of the species lists (Palmer, 1990). Confidence intervals for S_{max} were calculated from Smith & van Belle (1984).

Physical habitats

Water depth and dominant substratum type were recorded in all plots used for the vegetation analysis. The substrata were divided into size classes, roughly corresponding to the Wentworth-scale: Stone (>64 mm), gravel (2-64 mm), sand (0.1-2 mm), mud (<0.1 mm, black colour), peat and hard clay. In addition, inorganic substrata covered by mud or debris layers were recorded. Reach-scale coverage of each substratum type was calculated as the relative frequency of all plots examined. The substratum heterogeneity (SH) was quantified (Pedersen, Friberg & Larsen, 2002), because high heterogeneity is likely to increase in-stream habitat variability (Hildrew & Giller, 1994). SH is a number between 0 and 1, with 1 representing maximum spatial substrate heterogeneity.

Depth was measured in the centre of the plots and averaged across all plots. Mean stream width was calculated from the observed width in all transects. Reach scale depth and width

variations were quantified by calculating the coefficient of variance (CV). Ten current velocity profiles were measured across the stream downstream of the studied reach using a propeller current meter. Each velocity profile represented 1/10 of the stream width. The discharge was calculated by integrating the velocity profiles over the depth and multiplying by the width. The average current velocity was calculated as the discharge divided by the wetted cross section area. The sites were levelled using optical levelling equipment (Zeiss Instruments). This enabled calculation of the slope of the stream bed. Sinuosity of the stream channel was calculated from map measurements of the Talweg stream length divided by the length of a straight line. (Leopold, Wolman & Miller, 1964).

In-stream biota

Macroinvertebrates were sampled using kick sampling (25 x 25 cm hand net, 500 μm mesh size) in 4 points in 3 transects spaced approximately 10 m apart. Kick samples were taken across the stream at positions located 10%, 50%, 75% and 100% from the stream bank. All 12 kick samples from each site were pooled to one sample, preserved in 70% ethanol and transported to the laboratory for identification. Macroinvertebrates were identified to species level with a few exceptions: Oligochaeta were identified to family. Simuliidae were identified to genus and Ceratopogonidae to sub-family. Chironomidae and molluscs were identified to species level when possible; otherwise to genus.

Macroinvertebrate community structure and diversity were expressed in several ways. Total number of individuals and number of individuals belonging to Ephemeroptera, Plecoptera and Trichoptera (EPT). Total and EPT species richness were determined and diversity expressed as Fisher's α. Overall species richness (S_{max}) for all streams of a particular stream type (disturbed or undisturbed) was estimated using Jack-knife re-sampling (N=500). To ensure that differences in regional species pools did not affect the results, taxa not occurring in all areas were removed before calculation of any community variables.

Electro-fishing was carried out on a 50 m representative sub-reach in early or mid August. All species present were sampled quantitatively. Trout population estimates were calculated using the method of Seber & Le Cren (1967) based on 2 or 3 samplings. Population densities (numbers m^{-2} stream bed and numbers m^{-1} stream reach) were calculated from the population estimates.

Statistical analyses

Pairwise comparisons of average biotic and physical habitat characteristics between disturbed and undisturbed sites were analysed using standard t-tests. Square-root transformation was applied to substratum cover, variations in depth and width and macroinvertebrate parameters to satisfy assumptions of normality and homogeneity of variances within groups.

Physical habitat structure was analysed using PCA analysis. Differences in habitat structure between stream types were tested using a permutation test on the internal versus external distances in the PCA diagram. A Canonical Correspondence Analysis (CCA) was performed on the macroinvertebrate data using 6 plant species, current velocity and proportion of coarse substrata as environmental variables (ter Braak & Šmilauer, 1998). Monte Carlos simulations (N=199) were used to analyse significance of CCA axes and individual environmental variables. Correlations between the biotic and physical variables were calculated using Spearman rank correlation. Regression analyses were performed using least-squares regression. All statistical tests were carried out in SAS/STAT version 8.2 (SAS Institute Inc., 2000).

Results

Macrophyte communities in streams with different disturbance regimes

Total macrophyte coverage was high (app. 70%) and did not vary between the two stream types (Table 2; t-test, p>0.05). However, Fisher's α-diversity and species richness were significantly higher in undisturbed streams than in streams disturbed by weed cutting (Table 2; t-test, p=0.004). Average species richness per reach was 17.3 in undisturbed streams and 10.9 in disturbed streams. Also combined species richness (S_{max}) was higher on undisturbed sites (146) than on disturbed sites (107).

Berula erecta (Hudson) Coville was the most common species in both stream types occurring in 14% of the surveyed plots. In undisturbed streams *Glyceria fluitans* (L.) R. Br. (7%), *Callitriche* spp. (7%), *Epilobium hirsutum* L. (6%) and *Batrachium* spp.. (5%) were the next most common taxa. In the disturbed streams *Callitriche* spp. (13%), *Lemna minor* L. (6%), *Sparganium* spp. (5%) and *Phalaris arundinacea* L. (2%) were the next most common taxa. Macrophyte patch complexity, calculated as the average number of species present in the investigated plots was significantly higher (2.1) in the undisturbed streams than in streams disturbed by weed cutting (1.9) (Table 2; t-test, p=0.013).

Table 2. Macrophyte community characteristics and averaged species diversity in disturbed streams and in undisturbed streams. Mean values and ranges. Parameter means and ranges given. [¶] Indicates significant higher total estimated species richness (S_{max}) for all streams in a group based on construction of confidence intervals (in parenthesis). * Denotes significant differences (t-test, p<0.05)

Parameter	Undisturbed (n=16)	Disturbed (n=17)
Coverage (%)	72 (21-100)	68 (10-97)
Species richness*	17.3 (8-29)	10.9 (4-24)
S_{max}[¶]	145.9 (142.9-148.8)	106.7 (103.6-109.8)
Fisher's α*	4.5 (2.1-8.2)	2.8 (0.7-6.5)
Species richness per plot*	2.1 (1-11)	1.9 (1-8)

In-stream physical habitats

The studied streams were generally small with a mean width of 1.9 m and a mean depth of 20 cm during summer. Variations in stream width were higher on undisturbed streams than on disturbed streams, but all other physical variables varied little between the groups (Table 3). All streams experienced significant seasonal variations in discharge, current velocity and depth. Summer discharge and current velocity was slightly higher on the undisturbed sites than on disturbed sites. These differences were, however, not significant (Table 3; t-test, p_{disch}=0.286, $p_{velocity}$=0.809).

Table 3. Physical characteristics (mean values) in streams experiencing regular disturbance by weed cutting and undisturbed streams. Ranges for each parameter are given in parentheses. * Denotes significant differences between stream types (t-test, p<0.05).

Parameter	Undisturbed (n=16)	Disturbed (n=17)
Depth (cm)	20 (3-41)	21 (3-49)
$Depth_{CV}$ (%)	62 (30-201)	59 (31-107)
Width (cm)	244 (101-657)	170 (59-311)
$Width_{CV}$ (%)*	27 (6-50)	14 (7-21)
Discharge (l s^{-1})	87 (12-239)	56 (1-235)
Current velocity (cm s^{-1})	13.8 (6.5-31.0)	12.9 (0.6-49.6)
Substrate heterogeneity	0.51 (0.31-0.61)	0.48 (0.30-0.62)

Substratum composition was dominated by sand in both stream groups (app. 38%) and did not differ between stream types (Fig. 1; t-tests, p>0.05). However, coarse substrata were more abundant on undisturbed sites (15%) than on disturbed sites (12%), whereas mud coverage was lower on undisturbed sites (30%) than on disturbed sites (36%). On disturbed sites mud coverage was stable between seasons (t-test, p>0.05), whereas it varied seasonally on undisturbed sites (t-test, p<0.05). Despite over differences in substratum coverages, the spatial substratum heterogeneity was identical between stream types.

Physical habitat structure in summer was analysed using Principal Components Analysis. The first 3 PCA axes had eigenvalues greater than 1. PCA axis 1 separated sites of different width and depth (Fig. 2) and explained 26% of the variation in the data set. The second PCA axis explained 20% of the variation and separated disturbed and undisturbed sites (ANOVA, p=0.001). Disturbed sites had high stream slope, current velocity (V_{Mean}), sinuosity and high coverage of coarse substrata, whereas high mud coverage prevailed on disturbed sites (Fig. 2).
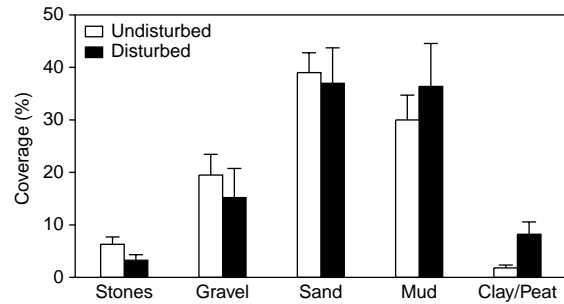
Figure 1. Mean substratum coverage on undisturbed and disturbed sites. Whiskers on bars represent standard errors on the mean value.
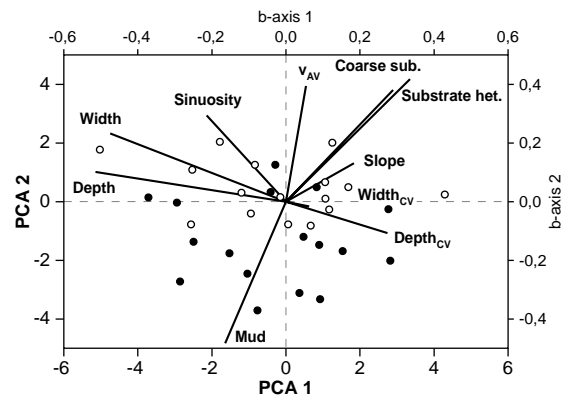
Figure 2. PCA plot of physical habitat structure during summer. •: Sites disturbed by frequent weed cutting; o: Undisturbed sites. Eigenvalues were 2.85, 2.24 and 1.54 for PCA axis 1, 2 and 3 respectively.

Macroinvertebrate communities

A total of 294 benthic macroinvertebrate taxa were present in the 33 studied streams. Undisturbed streams supported the largest number of individuals and the highest species richness. Species richness and abundance were, however,

not significantly different between the two stream types (Table 4; t-test, p>0.05). Average EPT species richness per stream varied significantly between the two stream types (Fig. 3, Table 4; t-test, p<0.001) and was slightly higher in spring than in summer for both stream types. The seasonal difference was not significant however (Fig. 3; p>0.05). The most abundant EPT taxa were *Baetis rhodani* (P.) and *Baetis vernus* C., which together made up 82% and 75% of the EPT individuals on undisturbed and disturbed sites respectively.

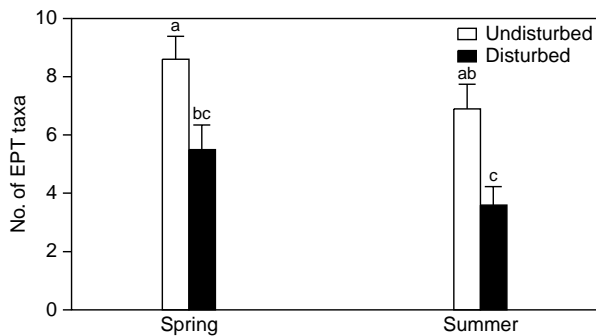**Figure 3.** EPT species richness on disturbed and undisturbed sites in spring and summer. Whiskers on bars represent standard errors on the mean value. Lower case letters indicate significantly different mean values between seasons and disturbance regimes.

Table 4. Macroinvertebrate density, diversity and community composition in undisturbed and disturbed streams. EPT are Ephemeroptera, Plecoptera and Trichoptera species. Mean values and ranges are given. * Denotes significant differences between stream groups (t-test, p<0.05).

Parameter	Undisturbed (n=16)	Disturbed (n=17)
Total abundance	2162 (370-7403)	1492 (205-3371)
Species richness	34.4 (24-47)	29.9 (19-42)
Fisher's α diversity	6.6 (4.2-8.4)	5.9 (3.2-9.3)
Gammarus pulex abundance*	790 (73-2218)	420 (0-2741)
Percentage *G. pulex*	34 (1-58)	21 (0-66)
EPT abundance*	434 (23-1674)	108 (0-727)
EPT species richness*	7.7 (0-12)	3.6 (1-10)

The amphipod, *Gammarus pulex* L. dominated the macroinvertebrate community in both stream types having means of 34% and 21% of the total number of individuals in undisturbed and disturbed streams, respectively. The next most abundant macroinvertebrates in undisturbed streams included the family, Simuliidae (20%), *B. vernus* and *B. rhodani* (15%), the dipteran sub-family Orthocladiinae (4%) and the case-bearing

caddis family Limniphiliidae (2%). On disturbed sites the second most dominating taxa included the burrowing chironomid larva *Micropsectra* spp. (7%), *Baetis* spp. (5%; including the species *B. rhodani* and *B. vernus*), the gastropods, *Potamopyrgus antipodarium* (Smith) and *Pisidium* sp. (each 3%) and Tubificidae (3%).

Macroinvertebrates living on the surface or within the macrophytes are vulnerable to habitat loss by weed cutting. Four macro-invertebrate taxa (*G. pulex*, *Baetis* spp., Simuliidae and Limniphilidae) are associated with in-stream macrophytes and were all less abundant on sites exposed to frequent weed cutting (Fig. 4; t-tests, p<0.05).
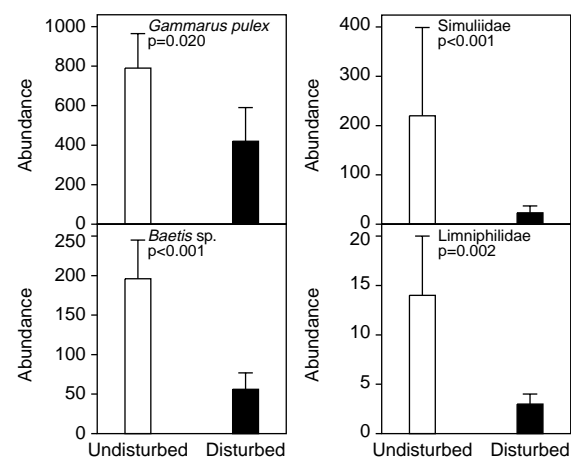
Figure 4. Abundance of macroinvertebrates associated with in-stream vegetation. Whiskers on bars represent standard errors on the mean value. Differences in abundance on disturbed and undisturbed sites were tested by t-tests on square-root transformed data. Test significance levels are shown for each macroinvertebrate taxa.

Macroinvertebrate species traits in relation to physical habitats and macrophytes

The species area relationship predicts that the species richness increases with increasing catchment area. Stream widths correlated with distance form source ($r_{distance}$=0.54, p=0.002) and catchment area (r_{area}=0.58, p=0.001). Therefore, we used stream width as a proxy for catchment area and distance from source. In undisturbed streams EPT species richness and Fisher's α diversity increased with increasing width (r_{EPT}=0.59, p=0.017; $r_{Fisher's\ \alpha\ diversity}$=0.68, p=0.004). On disturbed sites, however, no significant correlation existed between EPT species richness, diversity and stream width. Macrophyte species richness and diversity also increased with increasing stream width and sinuosity in undisturbed streams ($r_{richness}$=0.64, p=0.008; $r_{diversity}$=0.56, p=0.024). As for the macroinvertebrates no correlation existed for the disturbed sites.

Macrophytes and associated EPT taxa were analysed on undisturbed sites, where we expected natural biotic interactions to prevail. Associations were analysed using CCA ordination (Fig. 5). The eigenvalues of CCA axis 1 and 2 were 0.62 and 0.42 respectively and explained 59% of the variance in the data set. Both axes and all environmental parameters in the CCA plot were significant ($p < 0.05$) except the *Batrachium* spp. vector ($p = 0.169$). Three distinct macroinvertebrate groups could be identified in the CCA ordination diagram. Invertebrate group (I) is associated with the presence of *Potamogeton* spp. and moderate current velocities and varying substrata. The presence of the burrowing mayfly *Ephemera danica* Müller, the stonefly, *Isoperla grammatica* (Poda) and the net-spinning caddis larva *Plectrocnemia conspersa* C. indicates a stable in-stream environment. Other macroinvertebrate species in this group include the stonefly genera *Leuctra* and *Nemoura* and the mayfly species, *Baetis vernus*. The presence of *Batrachium* spp. and moderate to high current velocities characterised group II. Macroinvertebrates included *Anabolia nervosa* (C.), *Ephemerella ignita* (Poda) and *Baetis fuscatus*, *B. niger* and *B. rhodani.* Important environmental variables in macroinvertebrate group (III) included coarse substrata and high current velocity. The stonefly, *Amphinemura standfussi* (M.), and the case-bearing caddis larvae *Silo* spp. and two Limniphiliidae species (*Potamophylax latipennis* (Curtis) and *Ecclisopteryx darlecarlica* Kolenati) were present here along with the caseless caddisfly predator *Rhyacophila* spp. and the net-spinning *Hydropsyche* spp.

Effects of weed cutting on fish community

Nine fish species were found on the studied sites. The five most common species were trout (*Salmo trutta* L.), three- and nine spined stickelback (*Gasterostearus aculeatus* L. and *Pungitius pungitius* L.), eel (*Anguilla anguilla* L.), lamprey (*Lampetra planeri* Bloch) and perch (*Perca fluviatilis* L.). Average number of species varied little between stream types and species richness was the same in undisturbed and disturbed streams (Table 5; t-test, $p = 0.442$). Quantitatively trout was the most important species and the only species found in

Table 5. Species richness and trout densities in undisturbed and disturbed streams. Mean values and ranges in parenthesis. * Denotes significant differences between stream groups sites (t-test, $p < 0.05$)

Parameter	Undisturbed (n=16)	Disturbed (n=17)
Species richness	2.5 (1-6)	2.1 (1-6)
Trout density (individuals 100m^{-2})*	108 (2.2-648.1)	22 (0.0-262.2)
Trout density (individuals m^{-1})*	1.6 (0.1-6.7)	0.3 (0.0-3.3)
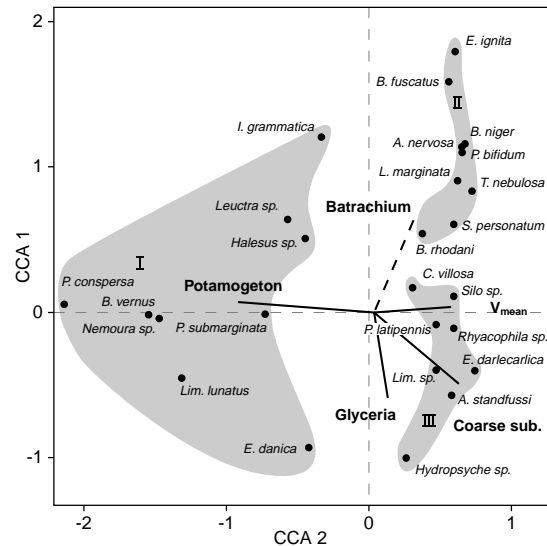
Figure 5. CCA diagram showing species scores of EPT taxa on undisturbed sites. Environmental parameters (plant species, current velocity and coarse substrate coverage) are shown as vectors. Significant vectors ($p < 0.05$) are solid lines and the non-significant ($p = 0.16$) The *Batrachium* vector is dashed. Legend to species names: B. rhodani: *Baetis rhodani* (Pictet); B. vernus: *Baetis vernus* Curtis; B. niger: *Baetis niger* (L.); B. fuscatus: *Baetis fuscatus* (L.); P. bifidum: *Procleon bifidum* (Bengtsson); L. marginata: *Leptophlebia marginata* (L.); P. submarginata: *Paraleptophlebia submarginata* (Stephens); E. danica: *Ephemera danica* Müller; E. ignita: *Ephemerella ignita* (Poda); I. grammatica: *Isoperla grammatica* (Poda); T. nebulosa: *Tanieopteryx nebulosa* (Linneaus); Nemoura sp.: *Nemoura* spp. (including species *N. cinerea* (Retius) and *N. flexuosa* Aubert); A. standfussi; *Amphinemura standfussi* (Ris); Leuctra sp.: *Leuctra* spp. (including species *L. digitata* Kempny, *L. fusca* (Linneaus), *L. nigra* (Olivier)); Rhyacophila sp.: *Rhyacophila* spp. (including species *R. fasciata* Hagen and *R. nubila* Zetterstedt); Hydropsyche sp.: *Hydropsyche* spp. (including species *H. pellucidula* (Curtis) and *H. siltalai* Döhler); E. darlecarlica; *Ecclisopteryx darlecarlica* Kolenati; C. villosa: *Chaetopteryx villosa* (Fabricius); A. nervosa: *Anabolia nervosa* (Curtis); Lim. lunatus: *Limnephilus lunatus* Curtis; Lim. sp.: *Limnephilus* sp.; Halesus sp.: *Halesus sp.* (including species: *Halesus radiatus* (Curtis) and *Halesus digitatus* (Schrank); P. latipennis: *Potamophylax latipennis* (Curtis); Silo sp.: *Silo* sp. (including species *Silo nigricornis* (Pictet)); S. personatum: *Sericostoma personatum* (Specnce).

the majority of the sites. Trout therefore was used in the analysis of effects on the fish community. Trout density measured as individuals per 100m^2 streambed and individuals per meter stream was significantly higher on undisturbed sites than on disturbed sites (Table 5, t-test, $p < 0.05$). Trout density did not correlate with reach-scale macrophyte coverage or diversity ($r_{cover} = -0.10$, $p = 0.577$; $r_{plant\ diversity} = 0.22$, $p = 0.220$). However, trout densities (trout 100m^{-2}) increased with increasing discharge and current velocity ($r_{velocity} = 0.43$, $p = 0.018$; $r_{discharge} = 0.52$, $p = 0.003$).

Discussion

Our study confirmed the prediction that macro-phytes play a key-role in the ecology of lowland streams. We used weed cutting as a large-scale experimental disturbance in streams and found strong long-term effects on the in-stream environment and biota.

Macrophytes were directly affected by disturbance of the habitats. Macrophyte community structure was altered by the continuous disturbance and the effects cascaded through the stream ecosystem affecting in-stream habitats, macroinvertebrates and trout. Macro-invertebrates associated with stable habitats declined. Nursery-and feeding-habitats for trout were degraded as a consequence of weed cutting and potential food resources were removed leading to lower trout density in disturbed streams

Plant communities, species richness, diversity and complexity

We found that species richness, diversity, estimated total species richness (S_{max}) and macrophyte patch complexity all were markedly higher in undisturbed than in disturbed streams. These results suggest that these alterations are long-term detrimental effects of continuous disturbance.

Riis & Sand-Jensen (2001) found that macrophyte species with good dispersal abilities were more abundant in disturbed streams than the more poorly dispersed species. They concluded that this shift in community structure was a consequence of frequent disturbance by weed cutting. The impact of disturbance should be that species with a high colonisation potential profit relative to susceptible, less weedy, species. Dominance patterns should therefore change towards a community of species having rapid growth, fast dispersal and/or a high reproductive output in weed-cut streams (Baatrup-Pedersen *et al.*, 2002). However, we did not find any difference in dominance patterns of macrophyte types between stream types. This result may reflect that there was a predominance of amphibious and terrestrial species in both stream types, which may render the macrophyte community less vulnerable to frequent cutting and may blur effects of disturbance. Thus, amphibious and terrestrial species may colonise not only the near bank zone but also the middle zone in small streams and recruitment from nearby undisturbed bank populations may enhance species re-growth thereby reducing the impact of frequent disturbance of submersed macrophytes. It may be more important, however that the studied stream systems consist of a complex matrix of reaches

with weed cutting and without weed cutting. As a consequence no entire stream is truly undisturbed or disturbed in its entire length. When comparing sites located in this complex of disturbance regimes where colonisation from upstream areas is possible, differences in species richness and diversity will be less marked compared to the differences expected if entirely undisturbed and entirely disturbed streams systems had been available for comparison (Turner, 1998).

Effects of frequent disturbance on in-stream physical habitats

Many short-term studies have identified and quantified changes in physical habitat structure following plant removal (e.g. Kaenel & Uhrlinger, 1998). The effects include higher current velocities, increased hydraulic stress, increased sediment transport and subsequent deposition of sandy substrata. Other studies have focused on the direct removal of macroinvertebrates from the macrop-hytes (Kern-Hansen, 1978; Dawson *et al.*, 1991). Our results suggest that one effect of disturbance is that a larger stream area experiences low flow and enhanced mud deposition in late summer when in-stream plants are re-established. This is probably due to the formation of a dense in-stream plant community consisting of species better at obstructing flow and raising water levels, thereby enhancing deposition of fine sediment. Similar results have been demonstrated in a study of plant community structure on regulated and unregulated streams in Denmark (Baattrup-Pedersen & Riis, 1999).

Variation in stream width has declined in streams disturbed by weed cutting and was the only significant difference between the two stream types. Thereby natural variations in physical appearance and in microhabitats situated in the near-bank zone are lost. This development is similar to that observed in canalised streams that loose their natural morphological structure and develop less variable edge habitats (Brookes, 1988; Garner *et al.*, 1996). A multivariate analysis (PCA) was used to assess differences in physical habitat structure generated by disturbance. Using the linear combinations of several physical habitat variables (the principal component scores for each site) it was possible to highlight differences between streams with different disturbance regimes, which were not recognisable using single physical parameters.

Effects of weed cutting on the macroinvertebrate community

Studies of disturbance by weed cutting on macroinvertebrate communities have either focus-sed on short-term effects or recovery following weed cutting (e.g. Pearson & Jones, 1978; Kaenel *et*

al., 1998). To our knowledge no previous analyses exist of the long-term effects of weed cutting on macroinvertebrate communities. In our study macroinvertebrate communities in disturbed and undisturbed streams were not different with respect to species diversity, species richness and number of individuals. A possible explanation for this similarity between stream types is that no streams are solely weed-cut or undisturbed, all systems are mixed. Undisturbed and disturbed sites are located in a network of stream reaches of different weed cutting practice. Macroinvertebrate drift from upstream undisturbed sites is thus capable of supplying species to downstream weed cut sites, and vice versa, thereby minimising differences in species richness and diversity between the streams types (Williams & Hynes, 1976). It is likely that due to the patchy streams, species diversity and richness can be maintained at comparable levels in the two stream types despite marked differences in disturbance, and physical habitats. Diversity and community indices alone may thus not be good descriptors of disturbances.

Species composition in the two stream types was, however, significantly different. This was probably caused by a substitution of species in the disturbed streams. Physical habitats probably changed as a consequence continuous weed cutting. Muddy deposits are maintained in disturbed streams throughout the year. These are typically found in the sheltered areas along the stream margin and are therefore more likely to be stable compared to a sandy substrata located in the free flow in the middle of the stream. Muddy substrata and slow flow are likely to promote the high number of species of detritus feeders and their abundance on disturbed sites. This substitution is supported by the presence of taxa such as *Micropsectra* spp., *Potamopyrgus antipodarium* and *Pisidium* sp. Generally species living on muddy substrata grow faster and have a shorter life cycle compared to EPT species (Merritt & Cummins, 1996). Very few EPT taxa are capable of living and feeding in the muddy substrata and their abundance was low streams (Ward, 1992).

The lower EPT species richness in disturbed streams indicates vulnerability to frequent habitat disturbance (Merritt & Cummins, 1996). We found a total of 35 EPT species which - with a few exceptions - are associated with stable substrata such as stones, gravel and macrophytes. These substrata are removed during dredging and weed cutting or become covered by the increased sediment transport following the disturbance. Drift from upstream areas will not be able to compensate for this loss because habitats are degraded or missing and the EPT-taxa will be unable to colonise the disturbed sites.

Macroinvertebrate species traits in relation to disturbance

Gammarus pulex has been shown to migrate following disturbance by weed cutting (Kern-Hansen, 1978). The species uses in-stream-sheltered areas and macrophytes as refuge and is likely to be affected by disturbance of the macrophytes. We found a reduced abundance of *G. pulex* on disturbed sites indicating that *G. pulex* has been unable to recover after 2-3 months despite being known to be abundant in drift and a good coloniser (Elliott, 2002). Therefore, the low abundance on the disturbed sites is probably a long-term result of habitat loss in the disturbed streams.

Macrophytes are also an important habitat for Simuliidae, which live attached to plant surfaces in streams with fine substrata (Dawson et al., 1991). Abundance of simulids was 90% lower on disturbed sites probably due to removal of macrophytes. Likewise, Dawson et al. (1991) found that simulid abundance decreased by 22%, when macrophytes were removed in an English chalk stream. Species of *Baetis* are found in association with either coarse substrata or macrophytes and moderate flow. They feed on attached microalgae on macrophyte surfaces and coarse substrata (Wiberg-Larsen, 1984). As with the simulids, abundance of *Baetis* probably decreased as a consequence of habitat loss (macrophytes) and habitat degradation (deposition of fine sediment on coarse substrata) following weed cutting.

Trichopterans belonging to the family, Limniphilidae are mostly shredders of dead and living plant material (Jacobsen, 1993) and they are not adapted to life in a depositional environment (Wood & Armitage, 1997; Wood, Vann & Wanless, 2001). Limniphilid species *Ecclisopteryx dalecarlica*, *Chaetopteryx villosa*, *Potamophylax latipennis* and *Anabolia nervosa* were abundant in undisturbed streams where habitats consisting of stable substrata and experiencing moderate to high current velocities (Merritt & Cummins, 1996).

Macroinvertebrate assemblages associated with macrophytes

Numerous studies have focused on removal of macroinvertebrates and subsequent re-colonisation following disturbance. Few studies have focused on the direct effects (initial habitat loss and food decline) and related these to species traits. Macroinvertebrate herbivory is well documented in the literature (e.g. Jacobsen, 1993). We analysed direct interactions between macrophytes as habitats and food resource and EPT species in undisturbed streams.

The Limniphilids are a diverse family and showed no distinct preference to any macrophyte species or physical variable. The Limniphilid, *Anabolia nervosa* is grouped with the *Batrachium* spp. vector and not with the *Potamogeton* spp.

vector as would probably be expected since it as a herbivore prefers fresh submerged leaves of *Potamogeton perfoliatus* (Jacobsen & Sand-Jensen, 1994). Limniphilids have a large feeding plasticity, however, and are not constrained to certain habitats with preferred macrophytes (Jacobsen, 1993; Merritt & Cummins, 1996).

The *Potamogeton* spp. vector indicates relatively large and deep heterogeneous undisturbed streams (Riis, Sand-Jensen & Vestergaard, 2000) supporting diverse macroinvertebrate communities as indicated by the presence of *Baetis vernus* which lives in the vegetation or on coarse substrata in larger streams. Other macroinvertebrate species found here also indicates the presence of a stable heterogeneous environment. The community includes the stoneflies *Nemoura* spp. and *Leuctra* spp., which are both found in a variety of habitats but prefer inorganic substrata and moderate to fast flow (Elliott, 1987). The presence of *Ephemera danica* and *Isoperla grammatica* indicates stable habitat conditions with high water quality and good oxygen concentrations (Wiberg-Larsen, 1984).

Ephemerella ignita lives associated with dense stream vegetation (Merritt & Cummins, 1996) and is associated with *Batrachium* spp. along with three *Baetis* species, *Procleon bifidum* (B.), *Leptophlebia marginata* (L.), which all use macrophytes as flow shelter and act as facultative shredders on living and dead plant material (Wiberg-Larsen, 1984). *Tanieopteryx nebulosa* (L.) is also found within the vegetation in fast-flowing streams. *Sericostoma personatum* (S.) is often found in the fine sediments in and around the vegetation (Elliott, 1969). Other species such as *Silo* spp., *Hydropsyche* spp. *Amphinemura standfussi* and *Rhyacophila* spp. were not directly associated with the presence of plant species, but they all prefer stable substrata and moderate to high flow (Wiberg-Larsen, 1984; Meritt & Cummins, 1996).

The preliminary analysis of direct biotic interactions in undisturbed streams showed that it was possible to associate distinct macrophytes with certain macroinvertebrate assemblages.

Disturbance affects trout density and habitats
Trout densities were clearly affected by weed cutting. A higher trout density in streams without disturbance agrees with findings from other studies on river canalisation and maintenance (e.g. Moyle, 1976). Fish habitat preferences were not measured directly so only indirect reach-scale effects can be evaluated. Trout is affected differently by disturbance depending on stage in the life cycle. Lower trout densities on disturbed sites were probably the result of either direct trout habitat degradation or an indirect effect of lower prey densities due to degradation of macroinvertebrate habitats.

Mortensen (1977) showed that mortality of young trout increased due to degradation of nursery habitats when macrophytes were cut. Scott (1985) studying degradation of marginal nursing habitat obtained similar results for young fry following total removal of all plants in the stream and on the banks. Large trouts are territorial mid-stream feeders and would thus be affected by loss of sheltered habitats within and around macrophyte stands. Weed cutting should increase the distance between feeding habitats in the streams and may therefore lead to reduced trout densities. Upstream removal of in-stream vegetation could also affect downstream sites by reducing downstream drift of macroinvertebrate prey (Brookes, 1988).

Macroinvertebrates make up a substantial proportion of the diet of trout and many prey species uses macrophytes as habitats. *Gammarus pulex* and *Baetis* species are such important item of trout prey and dominate macroinvertebrate communities of both undisturbed and disturbed streams. The much lower abundance of *G. pulex* in disturbed than undisturbed streams may thus be an important reason for the accompanying lower density of trout. Other potential trout prey include *Ephemerella ignita*, other mayflies and simulids (Elliott, 1967; Andersen *et al.*, 1992). All of the above mentioned taxa are abundant in drift and may thus be readily available as a potential food resource for trout. Potential food sources to trout were app. three-fold lower on disturbed sites indicating a possible food limitation.

Perspectives
Streams are an important part of the European landscape and of great significance for its biodiversity. Habitat diversity in rivers and streams has declined during the past 100 years leading to impoverished habitats with less co-existence of macrophytes and macroinvertebrates. Among the habitats lost are riffle habitats with high flow and coarse sediments and meanders or backwaters with low flow and fine sediments (Brookes, 1988). Our results suggest that macrophyte richness, diversity and patch complexity are lowered as a result of disturbance by weed cutting. A substitution of macroinvertebrates species occurs when habitats are changed. Direct effects on macroinvertebrates include loss of habitats and a decline of food resources. We found that specific plant species supported distinct assemblages of macroinvertebrates, indicating the potential cascading effects of weed cutting. We recommend that weed cutting should be considered detrimental, carefully evaluated and avoided whenever possible. Otherwise water purification initiatives to improve conditions for biotic stream-communities may not achieve the desired purposes.

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References

Andersen TH, Hansen HO, Iversen TM, Jacobsen D, Krøjgaard L & Poulsen N (1992): Growth and feeding of 0+ brown trout (*Salmo trutta* L.) introduced to two small Danish streams. *Archiv für Hydrobiologie*, **125**, 339-346.

Baattrup-Pedersen A, Larsen SE & Riis T (2002): Long-term effects of stream management on plant communities in two Danish lowland streams. *Hydrobiologia*, **481**, 33-45.

Baattrup-Pedersen A & Riis T (1999): Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology*, **42**, 375-385.

Brookes A (1988): *Channelized Rivers - Perspectives for Environmental Management.* John Wiley and Sons, Chichester.

Cattaneo A & Kalff J (1980): The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography, 25*, 280-289.

Copp GH (1990): Effect of regulation on 0+ fish recruitment in the Great Ouse, a lowland river. *Regulated Rivers: Research and Management, 5*, 251-263.

Dawson FH, Clinton EMF & Ladle M (1991): Invertebrates on cut weed removed during weed-cutting operations along an English river, the river Frome. *Aquaculture and Fisheries Management*, **22**, 113-121.

Elliott JM (1967): Food of trout (*Salmo trutta*) in a dartmoor stream. *Journal of Applied Ecology*, **4**, 59-71.

Elliott JM (1969): Life history and biology of *Sericostoma personatum* Spence (Trichoptera). *Oikos*, **20**, 110-118.

Elliott JM (1987): Temperature induced changes in the life cycle of *Leuctra nigra* (Plecoptera: Leuctridae) from a Lake District stream. *Freshwater Biology*, **18**, 177-184.

Elliott JM (2002): A continuous study of the total drift of freshwater shrimps, *Gammarus pulex*, in a small stony stream in the English lake district. *Freshwater Biology*, **47**, 75-86.

Garner P, Bass JAB & Collett GD (1996): The effects of weed cutting upon the biota of a large regulated river. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **6**, 21-29.

Harrod JJ (1964): The distribution of invertebrates on submerged aquatic plants in a chalk stream. *Journal of Animal Ecology*, **33**, 335-341.

Hearne JW & Armitage, PD (1993) Implications of the annual macrophyte growth-cycle on habitat in rivers. *Regulated Rivers: Research and Management, 8*, 313-322.

Hildrew AG & Giller PS (1994): Patchiness, species interactions and disturbance in the stream benthos. In: *Aquatic ecology - scale, pattern and process. The 34th Symposium of the British Ecological Society University College, Cork* (Eds. P.S. Giller, A.G. Hildrew & D.G. Raffaelli), pp. 21-62. Blackwell Scientific Publications, Oxford.

Iversen TM, Kronvang B, Madsen BL, Markmann P & Nielsen MB (1993): Reestablishment of Danish streams - restoration and maintenance measures. *Aquatic Conservation: Marine and Freshwater Ecosystems, 3*, 73-92.

Jacobsen D (1993): *Invertebrate herbivory on submersed freshwater macrophytes* (In Danish). Ph.D. Thesis. Freshwater Biological Laboratory, University of Copenhagen, Copenhagen.

Jacobsen D & Sand-Jensen K (1994): Invertebrate herbivory on the submerged macrophyte *potamogeton perfoliatus* in a Danish stream. *Freshwater Biology, 31*, 43-52.

Kaenel BR, Matthaei CD & Uehlinger U (1998): Disturbance by aquatic plant management in streams: Effects on benthic invertebrates. *Regulated Rivers: Research and Management, 14*, 341-356.

Kaenel BR & Uehlinger U (1998): Effects of plant cutting dredging on habitat conditions in streams. *Archiv für Hydrobiologie, 143*, 257-273.

Kelly MG, Thyssen N & Moeslund B (1983): Light and the annual variation of oxygen- and carbon-based measurements of productivity in macrophyte-dominated river. *Limnology and Oceanography*, **28**, 503-515.

Kern-Hansen U (1978): Drift of *Gammarus pulex* L. in relation to macrophyte cutting in four small Danish lowland streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie, 20*, 1440-1445.

Kern-Hansen U & Dawson FH (1978): The standing crop of aquatic plants of lowland streams in Denmark and their inter-relationships of nutrients in plants, sediment and water. In: *Proceedings of European Weed Research Society Fifth Symposium on Aquatic Weed, Amsterdam*, pp. 143-150.

Leopold LB, Wolman MG & Miller JP (1964): *Fluvial processes in geomorphology.* W. H. Freeman & Co., San Francisco.

Mann KH (1988): Production and use of detritus in various freshwater, estuarine, and coastal

marine ecosystems. *Limnology and Oceanography,* **33**, 910-930.

Merritt RW & Cummins KW (Eds.) (1996): *An introduction to the aquatic insects of North America* 3ed. Kendall∕Hunt Publishing Company, Dubuque, Iowa.

Moeslund B, Løjtnant B, Mathiessen H, Mathiessen L, Pedersen A, Thyssen N & Schou JC (1990): Danske Vandplanter (in Danish). *Environmental News* No. **2**. Danish Environmental Protection Agency, Copenhagen.

Monohan C & Caffrey JM (1996): The effect of weed control practices on macroinvertebrate communities in Irish Canals. *Hydrobiologia,* **340**, 205-211.

Mortensen E (1977): Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to management of small streams. *Journal of Fish Biology,* **11**, 613-617.

Moyle PB (1976): Some effects of channelization on the fish and macroinvertebrates of Rush Creek. Modoc County, California. *California Fish and Game,* **63**, 179-186.

Palmer MW (1990): The estimation of species richness by extrapolation. *Ecology,* **71**, 1195-1198.

Pearson RG & Jones NV (1978): The effects of weed-cutting on the macroinvertebrate fauna of a canalised section of the river Hull, a northern English chalk stream. *Journal of Environmental Management,* **7**, 91-97.

Pedersen ML, Friberg N & Larsen SE (2002): Physical habitat structure in Danish lowland streams. *River Research and Applications* (Accepted).

Percival E & Whitehead H (1929): A quantitative study of the fauna of some types of stream-bed. *Journal of Ecology,* **17**, 282-314.

Riis T & Sand-Jensen K (2001): Historical changes in species composition and richness accompanying pertubation and eutrophication of Danish lowland streams over 100 years. *Freshwater Biology,* **46**, 269-280.

Riis T, Sand-Jensen K & Larsen SE (2001): Plant distribution and abundance in relation to physical conditions and location within Danish stream systems. *Hydrobiologia,* **448**, 217-228.

Riis T, Sand-Jensen K & Vestergaard O (2000): Plant communities in lowland Danish streams: Species composition and environmental factors. *Aquatic Botany,* **66**, 255-272.

Rooke JB (1984): The invertebrate fauna of four macrophytes in a lotic system. *Freshwater Biology,* **14**, 507-513.

Sand-Jensen K (1998): Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology,* **39**, 663-679.

Sand-Jensen K, Jeppesen E, Van Der Bijl L, Nielsen K, Wiggers-Nielsen L, Iversen TM (1989): Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology,* **22**, 15-32.

Sand-Jensen K & Madsen TV (1989): Invertebrates graze submerged rooted macrophytes in lowland streams. *Oikos,* **55**, 420-423.

Sand-Jensen K & Mebus JR (1996): Fine-scale patterns of water velocity within macrophyte patches in streams. *Oikos,* **76**, 169-180.

SAS Institute (2000): *The SAS System Version 8.2.* SAS Institute. Cary, USA.

Scott A (1985): Distribution, growth and feeding of postemergent grayling *Thymallus thymallus* in an English river. *Transactions of the American Fisheries Society,* **114**, 525-531.

Seber GAF & LeCren ED (1967): Estimating population parameters from catches large relative to population. *Journal of Animal Ecology,* **36**, 631-643.

Smith EP & Vanbelle G (1984): Nonparametric-estimation of species richness. *Biometrics,* **40**, 119-129.

Smock LA & Harlowe KL (1983): Utilization and processing of freshwater wetland macrophytes by the detrivore *Asellus Forbesi. Ecology,* **64**, 1556-1565.

ter Braak CJF & Šmilauer P (1998): *CANOCO Reference manual and User's Guide to Canoco for Windows Version 4.* Microcomputer Power, Ithaca, USA.

Tuner MG (1998): Landscape ecology – living in a mosaic. In: *Ecology* (Ed. SI Dodson), pp. 77-122. Oxford University Press, New York.

Ward JV (1992): *Aquatic insect ecology,* Vol. I. John Wiley and Sons, New York.

Washington HG (1984): Diversity, biotic and similarity indexes - a review with special Relevance to aquatic ecosystems. *Water Research,* **18**, 653-694.

Watson D (1987): Hydraulic effects of aquatic weeds in U.K. Rivers. *Regulated Rivers-Research and Management,* **1**, 211-227.

Wiberg-Larsen P (1984): *Plecoptera and Ephemeroptera – keys and ecological notes* (In Danish). National Environmental protection Agency, Copenhagen.

Williams DD & Hynes HBN (1976): The recolonization mechanisms of stream benthos. *Oikos,* **27**, 265-272.

Wood PJ & Armitage PD (1997): Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**, 203-217.

Wood PJ, Vann AR & Wanless PJ (2001): The response of *Melampophylax mucoreus* (Hagen) (Trichoptera: Limniphilidae) to rapid sedimentation. *Hydrobiologia* **455**, 183-188.

Spatio-temporal variations in substratum stability and macroinvertebrates in lowland stream riffles

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Abstract

The physical structure of two riffles in a lowland Danish stream was studied and its importance for the composition and density of the macroinvertebrate communities was evaluated. The two riffles were visually assessed to be very similar, but measurements revealed that they differed in overall hydraulic conditions, stability, substratum composition and consolidation. These differences affected abundance of both burrowing and surface dwelling macroinvertebrates. The unstable unconsolidated riffle had higher total macroinvertebrate abundance (4137 m^{-2} vs. 1698 m^{-2}), diptera abundance (2329 m^{-2} vs. 386 m^{-2}) and total species richness (31.7 vs. 28.8) and lower evenness (0.77 vs. 0.83) than the compact riffle. Among samples within the unconsolidated riffle, variations in macroinvertebrate communities were related to differences in mean substratum particle size. Here, a linear log-log relationship existed between macroinvertebrate abundance and the abundance of Ephemeroptera, Plecoptera and Trichoptera and the median particle size (r^2_{total}= 0.46, p=0.002; r^2_{EPT}= 0.73, p<0.001). No similar relationships were evident on the consolidated riffle. Moreover, macroinvertebrate communities on the unconsolidated riffle were dominated by species with a high colonising potential. Despite being assessed to the same geomorphological unit, inter-riffle variation was surprisingly high as the riffles differed substantially with respect to consolidation and overall hydraulic structure. These differences resulted in different macroinvertebrate community structure from the same species pool. The findings address the question if macroinvertebrate communities can be assessed at the scale of the geomorphological unit or meso-habitat.

Keywords

Streams, riffle substrata, physical habitats, spatial variation, macroinvertebrates

Introduction

Variations in catchment geology, channel morphology, discharge and sediment transport determine streambed structure and create distinct hydromorphological units such as riffles and pools within streams (Church, 1996). High-flow events exert strong physical forces that are believed to structure the overall stream morphology. The magnitude and distribution in time of these high-flow events therefore determines the overall stability of hydromorphological units. The hydro-morphological units are consequently a result of contemporary processes as well as historical hydraulic conditions.

Many lowland streams are meandering with hydromorphological units such as riffles being relatively stable over decades (Ward, 1989). Local variations in channel morphology, sediment transport and in-stream hydraulic conditions may, however, cause significant variation in the hydromorphological units. While the overall physical structure of the stream remains constant, the finer structure of the hydromorphological units may vary considerably due to changes in upstream morphology and local variations in hydraulics and sediment input to the stream. The habitat structure in streams is therefore the result of many physical processes acting on a number of nested spatial and temporal scales (Cummins *et al.*, 1984; Frissell *et al.*, 1986; Hildrew & Giller, 1994).

Riffles are normally perceived as homo-geneous hydromorphological units consisting of coarse substrata (*sensu* Grant *et al.*, 1990) and their value as habitats for macroinvertebrates has been studied in comparative studies of riffles and pools (Brussock & Brown, 1991; Scarsbrook & Townsend, 1993) or in relation to sand intrusion into salmonoid spawning gravel (e.g. Sear, 1993; Acornley & Sear, 1999; Kondolf, 2000). To our knowledge, no studies have, however, directly analysed interactions between riffle structure, sub-stratum composition and macroinvertebrate com-munities in lowland streams.

In-stream macroinvertebrate distribution is governed by the availability of different habitats and food resources and by biotic interactions (Giller & Malmquist, 1998). However, streams are

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heterogeneous systems with significant variations in macroinvertebrate communities over short distances. Substratum characteristics such as particle size (e.g. Pennak & Van Gerben, 1947), stability (Stanford & Ward, 1983) and heterogeneity (Hynes, 1970; Tolkamp, 1980) are likely to influence macroinvertebrate distribution and colonisation in the streams. Substratum texture may be another important factor (Harman, 1972; Lamberti & Resh, 1979; Erman & Erman, 1984). Some studies analyse the physical structure of different hydromorphological units or habitats and relate these to the macroinvertebrate community structure (e.g. Wood *et al.*, 1999; Kemp *et al.*, 2000) but detailed studies of specific hydromorphological units are to our knowledge non-existent.

Our main objective was to study how physical variations in two natural riffles in a Danish lowland stream affected the macroinvertebrate community. Meandering lowland streams are thought to be relatively stable with large-scale morphology being stable over decades (Church, 1996). If so, inter-riffle variability in physical structure should be low both on the spatial and temporal scale and macroinvertebrate community structure should reflect these stable conditions.

Methods

Study sites

Two riffles placed about 100 m apart in Tange stream, Denmark were studied (Fig. 1). The two riffles are located on a 1-km reach where natural channel morphology has been preserved. The riffles were located at similar points just downstream of a meander and stream slope was 2 ‰ at both riffles. Sediment transport and upstream hydraulic conditions were also identical at the two riffles. The overall morphological conditions were thus identical between the riffles and both riffles also had identical macroinvertebrate colonisation potentials. Tange stream is 4 to 6 m wide with a mean depth of 40 cm. Mean annual discharge at the site is 0.8 $m^3 s^{-1}$ (range 0.3 – 7.1 $m^3 s^{-1}$). The Tange stream catchment is characterised by a relatively quick response to precipitation events and the river thus has a peak-dominated hydrologic regime (Fig. 2). The stream flows in a valley with steep slopes, which are dominated by deciduous forest. Both riffles are partly shaded from tree canopies extending from the stream bank. Overall channel morphology is characterised by natural irregular meanders and the stream is morphologically active and capable of migrating freely within the river valley.
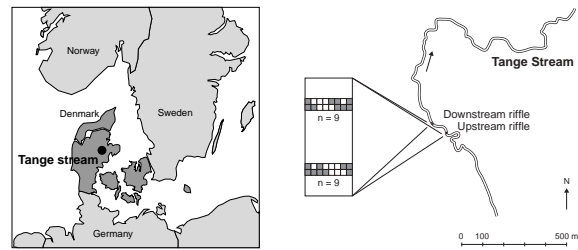
Figure 1. Location of the field sites and sampling methodology on the riffles in Tange stream. The insert shows sampled fields in the two transects (grey colour).
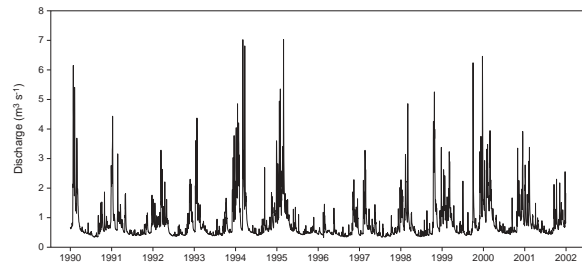
Figure 2. Daily mean discharge time series from Tange stream 1990-2001.

Riffle characteristics

Sampling was carried out during a period of low flow on two consecutive days in May 2001. Ten transects were evenly spaced along each entire riffle. Each transect was divided into plots, each 0.5 m wide and extending 1 m upstream from the transect line. In the centre of the plot, water depth was measured to nearest cm and current velocity was measured 5 cm above the streambed with an inductive current meter (OTT, Nautilus C2000). In each plot the substrate distribution was determined using the following categories: Stones (> 64 mm), coarse gravel (8-64 mm), fine gravel (2-8 mm), coarse sand (1-2 mm) and fine sand (0.1-1 mm). The presence of hard clay, peat and mud (<0.1 mm black) was recorded along with the coverage of organic debris such as dead plant tissue and leaves. Data were used for an overall characterisation of the two riffles. A total of 105 plots were sampled on the upstream riffle and 122 on the downstream riffle.

The discharge was measured using a propeller current meter (OTT instruments, Germany). Ten current-velocity profiles were measured across the stream downstream of the studied reach using a propeller current meter. Each velocity profile represented 1/10 of the stream width. The discharge was calculated by integrating the velocity profiles over the depth and multiplying by the width. The slope was calculated from optical levelling of the stream bed (Levelling instrument: Zeiss Instruments, Germany).

To assess substratum stability of the riffles, 50 stones of equal size (approx. 35 mm x 60 mm) painted with yellow dye on the upper side were placed in 5 clusters in different parts of the riffles

at different velocities. The stones were placed a month prior to the experiment and were examined and removed on the first day of sampling. Each stone was given a score in the field prior to removal from 0 to 4 based on the dye removal as a consequence of scouring. The following scoring system was used: (0) no visible scouring; (1): 0-25% of the painted surface scoured; (2): 25-50% of the painted surface scoured; (3) more than 50% of the dye removed by scouring; (4) turned – dye-side faced down.

As an additional measure of riffle surface stability, the algal biomass was used. The painted stones were transported to the laboratory in opaque plastic containers and 96% ethanol was added to the plastic containers until the stones were covered. All samples were extracted at 5ºC and kept in darkness for 12 h following 15 min of ultrasound treatment. Thereafter they were filtered through a GF/C filter and the volume of ethanol used for each stone was measured. The chlorophyll content was determined spectro-photometrically as described by Søndergaard & Riemann (1979).

Riffle consolidation was measured by means of a penetrometer (Sear, 1995). The resistance to penetration is a function of the density of sediment packing and the degree of interlock. By applying a consistent force 3 times to an iron rod (length: 50 cm) and measuring the penetration depth a semi-quantitative measure of consolidation is achieved. Penetrometer measure-ments were carried out in 36 points on each riffle.

Physical habitat and macroinvertebrate sampling
Two transects were randomly selected for the intensive study of physical habitats and macro-invertebrates. Each transect was divided into 4 quadrates (1 m x 1 m) evenly distributed across the wetted width. Each quadrate was further sub-divided into 4 fields (0.5 m x 0.5 m). Nine fields out of 16 were sampled in each transect using a nested randomised design, sampling 3 out of 4 fields in 3 of 4 quadrates (Fig. 1). In each selected field, sampling depth and current velocity 5 cm above the bed were measured in the each corner and in the centre of the field. Macroinvertebrates were sampled using a 200 cm^2 surber-sampler (200 μm mesh size). The streambed was disturbed and all material to a depth of 5 cm was retained in the mesh bag. Subsequently, the material from each sample was transferred to a container, preserved in 70% ethanol and transported to the laboratory where all macroinvertebrates were identified to either species or genus level, except for dipterans that were identified to sub-family level.

The organic fraction was separated from the sample, and CPOM (>1 mm) and FPOM (<1 mm) were separated by sieving. The organic fractions were dried for at least 6 hours at 60° C until constant weight. After dry combustion at 550°C for 1 hour the ash-free dry weight (AFDW) was calculated for each fraction. The inorganic substratum was then wet-sieved through a series of stainless steel sieves (diameter = 20 cm, Endecotts, London). The following fractions were dried and weighed: 64 mm, 32 mm, 16 mm, 8 mm, 4 mm, 2 mm, 1 mm, 0.5 mm and <0.5 mm. Particle size distribution and median particle size were calculated for each sample.

Data analyses and statistical methods
The spatial distribution of water depth and current velocity was calculated and a 2D-plot for each riffle was generated using a kriging method in the Surfer v. 7.0 software package (Golden Software, 1999). Mean values and standard deviation of depth and current velocity between riffles were compared using standard t-tests on log-transformed data to satisfy assumptions of normality and equal variances (Snedecor & Cochran, 1989). The reach-scale distributions between riffles were compared using Kolomogorov-Smirnoff tests (Conover, 1980).

The substratum distribution based on the survey of the entire riffle was calculated and compared using a Kolomogorov-Smirnoff test and the median particle size was compared between riffles using a t-test. To assess the stability of the riffles, the scouring-scores for each riffle were compared using a Kolomogorov-Smirnoff test. A Spearman rank correlation analysis was performed on physical habitat variables (Conover, 1980).

Macroinvertebrate community structure and diversity were expressed in several ways. Mean abundance and abundance of Ephemerop-tera, Plecoptera and Trichoptera (EPT), Shannon-Wiener diversity (H') and Pielou's evenness (J') were calculated for each riffle (Washington, 1984). Taxonomic richness was also calculated as the mean number of taxa (S) on each riffle and the overall species richness (S_{max}) estimated from the 1st order Jack-knife estimate based on re-sampling of the species lists (Palmer, 1990). Confidence intervals for S_{max} were calculated from Smith & van Belle (1984). The abundance of dipterans and their proportion in each sample were also calculated.

Samples were classified for each riffle separately using two-way indicator species analysis (TWINSPAN). TWINSPAN analysis was carried out on presence-absence data in the PC-ORD Version 4.23 software package (McCune & Mefford, 1999). The TWINSPAN groups were tested for significance calculating Bray-Curtis similarities between samples and testing these among the TWINSPAN groups. All statistical tests were performed in the SAS system version 8.2 (SAS Institute, 2000). Differences in environmental

variables (depth, current velocity and median particle size) were tested among the TWINSPAN groups by means of ANOVA. Pair-wise differences in environmental variables were tested using standard t-tests on log-transformed data.

and 34 cm s^{-1}). Median particle size in the 18 macroinvertebrate samples was not significantly different between the riffles (Table 1; t-test, $p>0.05$).

Results

Overall characterisation of riffle habitats
Discharge at the study sites was 0.6 m^3 s^{-1} which is close to mean summer discharge. The length of the upstream- and downstream riffle was 18 m and 10 m, respectively. Mean depth and current velocity were significantly higher (22 cm and 44 cm s^{-1}) on the downstream than on the upstream riffle (19 cm
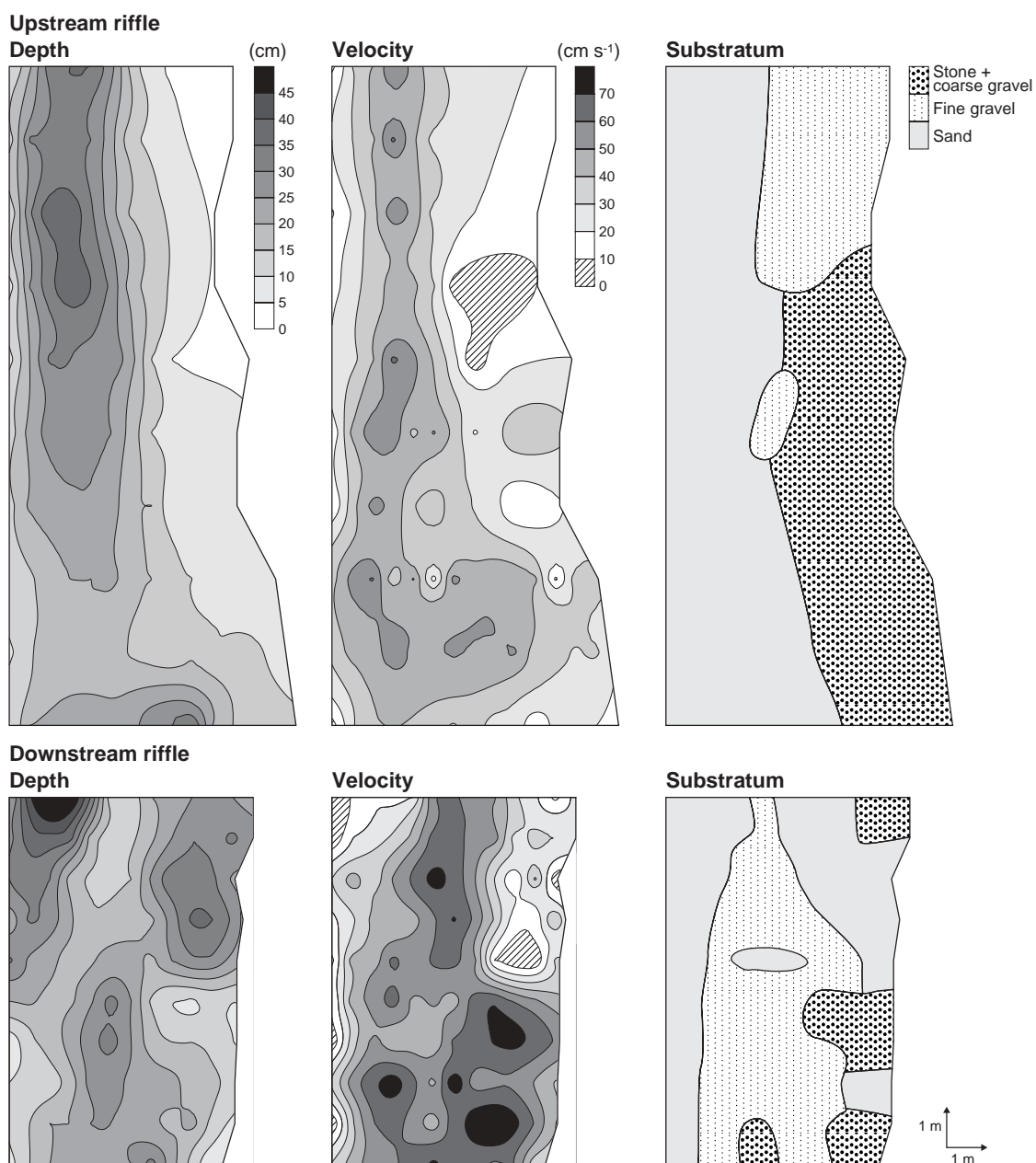

Figure 3. Contour plots of depth (cm), near bed current velocity (cm s^{-1}) and substrata on the upstream and downstream riffle.

Variation in habitat structure

The physical habitat structure on the riffles, as assessed by contour plots of depth, current velocity and substratum, demonstrated large differences (Fig. 3). On the upstream riffle the majority of the flow (approx. 80%) was concentrated in a relatively deep channel with high current velocity in one side of the riffle, while the other shallow part had low current velocity (Fig. 3). On the downstream riffle the flow pattern was more heterogeneous with high velocities and shallow and deep areas irregularly distributed throughout the riffle (Fig. 3). On the upstream riffle, the distribution of substrata showed a similar pattern, stones and gravel were located in the shallow part of the riffle with low current velocity, whereas the sandy substrata were found in the deep and fast flowing part of the riffle. On the downstream riffle the substrata were more mixed and there was an irregular pattern in the substratum composition (Fig. 3).

The spatial differences in physical riffle structure between the two sites were also reflected in the frequency distribution of depth and current velocity (Fig. 4). There was a high frequency of shallow depths (< 10 cm) on the upstream riffle, whereas depths close to the mean value (20 –30 cm) dominated the downstream riffle. Velocities of 20-40 cm s^{-1} dominated on the upstream riffle, whereas about 50% of all velocities on the downstream riffle exceeded 40 cm s^{-1} (Fig. 4). The distribution of depth and current velocities were significantly different between the two riffles (Kolomogorov-Smirnoff test, p<0.001).

The substratum distribution was significantly different between the two riffles (Fig. 4; Kolomogorov-Smirnoff test, p<0.05). Fine gravel was the dominant substratum on the upstream riffle (49%), whereas fine gravel (35%) and fine sand (34%) were equally dominant on the downstream riffle (Fig. 4). The fine sand cover was higher and the fine gravel coverage was lower on the downstream riffle than on the upstream riffle. All other substrata were not significantly different between the riffles (Fig. 4).

Current velocity and the presence of coarse substrata (stones and gravel) was positively correlated among sampling fields on the downstream riffle (r = 0.39, p < 0.001). On the upstream riffle this correlation was negative (r= 0.18, p = 0.07). On both riffles, however, the highest velocities were found in areas with high coverage of fine gravel and coarse sand ($r_{upstream}$ = 0.54, p < 0.001; $r_{downstream}$ = 0.64, p < 0.001).

The spatial distribution of depth and current velocity on the riffles demonstrated that depth and current velocity was significantly negatively correlated on the downstream riffle, whereas a slightly positive correlation existed on the upstream riffle (Fig. 5).
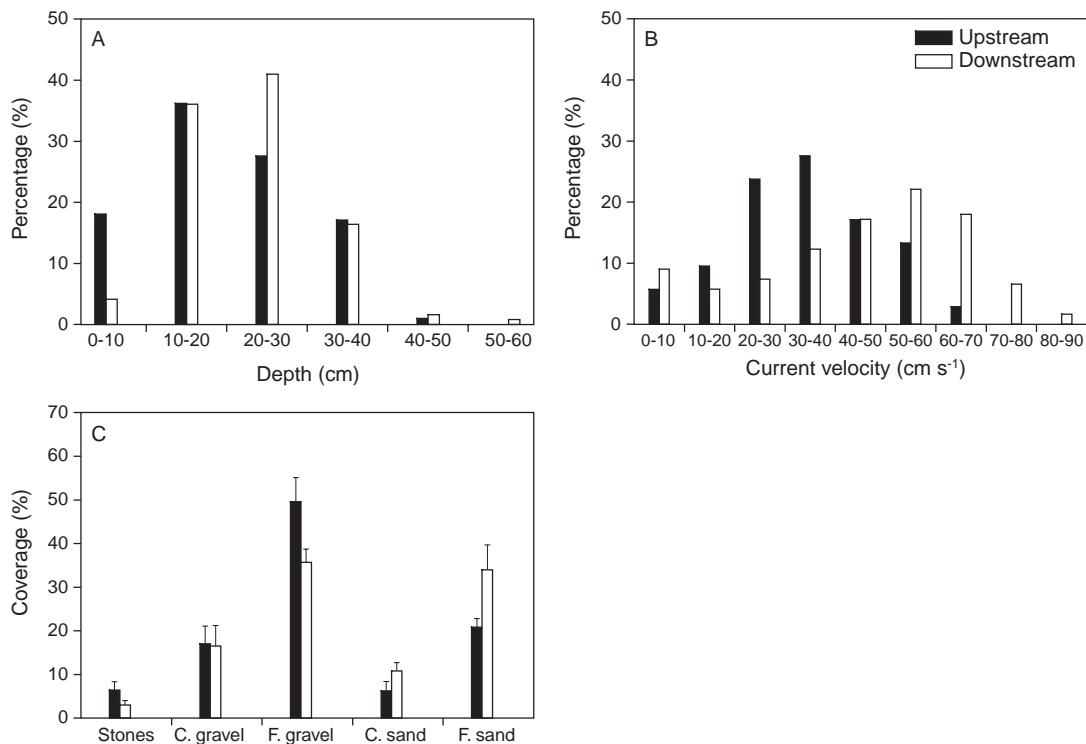

Figure 4. Depth (A), current velocity (B) and substratum distributions (C) on the two riffles in Tange stream.
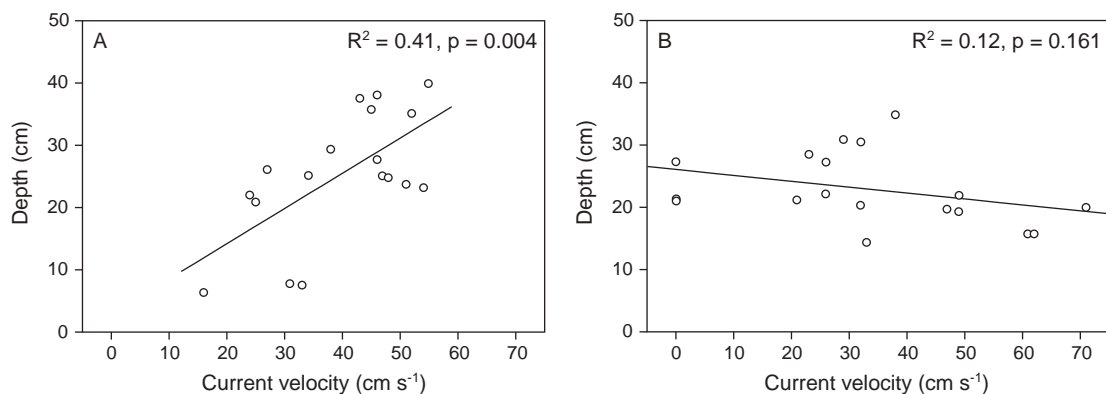
Figure 5. Relationship between depth and current velocity on the upstream (A) and downstream riffle (B).

Riffle substratum stability and consolidation

Riffle stability was expressed as the scour of 50 stones placed in each riffle a month prior to sampling. On the downstream riffle, a significantly larger percentage of stones had been turned over (30%) than on the upstream riffle (10%) (Fig. 5; Kolomogorov-Smirnoff test, p<0.001). Stones with no scouring constituted 44% of all stones on the upstream riffle, whereas only 4% were left without any scour on the downstream riffle (Fig. 6). On 20 naturally embedded stones of equal size on each riffle the algal biomass was significantly lower on the downstream riffle (65 mg chl. $\underline{a}$ m^{-2}) than on the upstream riffle (105 mg chl. $\underline{a}$ m^{-2}; t-test, p<0.001).
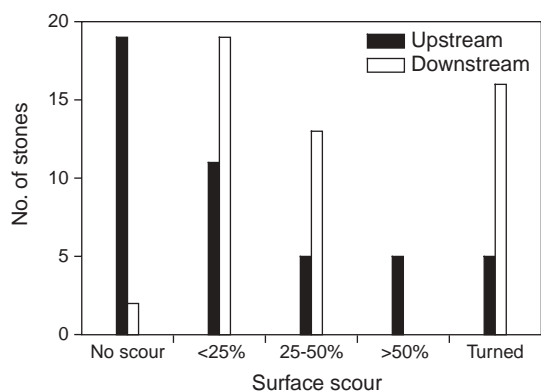
Figure 6. Riffle stability measured as the percentage of stone surface impacted by scour on the two riffles.

Riffle consolidation varied significantly between the two riffles (Table 2; t-test, p<0.001). Consolidation measured as the penetration depth was approximately 2.5 times higher at the downstream riffle than at the upstream riffle.

Macroinvertebrate communities

A total of 31 macroinvertebrate species were found on the two riffles. Species richness was 26 for the upstream riffle and 27 for the downstream riffle. Mean species richness per sample was identical on the two riffles, but total estimated species richness was significantly higher (31.7) on the downstream

riffle than on the upstream riffle (28.8) (Table 3) as seen from the confidence limits. Mean macroinvertebrate abundance was much higher on the downstream riffle than on the upstream riffle (Table 3; t-test, p < 0.05). This difference was primarily due to a 6-fold higher diptera abundance (t-test, p < 0.05). The community diversity and the diversity and abundance of EPT species on the two riffles were identical (Table 3). Pielou's evenness was, however, significantly higher (0.83) on the upstream riffle than on the downstream riffle (0.77), thus reflecting the lower abundance on the upstream riffle and the dominance of few abundant species on the downstream riffle (Table 3; t-test, p < 0.05).

The mayfly *Baetis* spp. dominated the macroinvertebrate community on the upstream riffle (31%). The second most abundant species was *Gammarus pulex* L. (24%), followed by the dipteran predator *Dicranota* spp. (11%) and chironomids (9%). The stoneflies *Amphinemura standfussi* Ris and *Leuctra* spp. together made up 10% of the macroinvertebrate community. On the downstream riffle chironomids were the most abundant macroinvertebrates (29%). The second most common species were *Dicranota* spp. (25%) and *G. pulex* (15%) followed by *A. standfussi* and *Leuctra* spp. (13%). *Baetis* spp. constituted only 5% of the macroinvertebrate community on the downstream riffle.

Correlations between physical variables and macroinvertebrate community variables were restricted to correlation between median sub-stratum particle size and EPT species richness, EPT abundance, species richness and total abundance in the sample (Fig. 7). Both overall abundance and EPT abundance were correlated linearly to the median particle size in the sample on the downstream riffle (Fig. 7BD). No significant linear correlation existed on the upstream riffle (Fig. 7AC).

TWINSPAN classification of macroinvertebrate samples

The macroinvertebrate TWINSPAN classification (presence-absence data) separated samples into 3 groups on both riffles (Fig. 8; ANOVA, p<0.05). On the upstream riffle a group (III) of 3 samples with low species richness and without *Leuctra* spp. and Naididae was separated in the first division (Fig. 8). The other two groups were characterised by either high species richness (group I, n = 7) or moderate species richness (group II, n = 8). Macroinvertebrates indicator species in group I included *Elmis aenea* (Müller) and *Heptagenia* spp. On the downstream riffle, 6 samples with high species richness were separated in the first division (group III, Fig. 8). Simulids and *Baetis* spp. were indicator species for this group. The remaining 12 samples were divided into a group with a core-community of the most common species (group II, n = 8) and a group (n = 4) with low species richness and low EPT taxa richness (Table 4 and Fig. 8).

Macroinvertebrate community structure in the TWINSPAN groups on the upstream riffle was only different with respect to number of individuals, evenness and EPT taxa richness. TWINSPAN group (I) had higher abundance, lower evenness and higher EPT taxa richness than the other two groups. TWINSPAN group (II) and (III) had similar macroinvertebrate community structures (Table 4). Macroinvertebrate community group (III) was significantly different from group (I) and (II) communities on the downstream riffle. Species richness, macroinvertebrate abundance and Shannon diversity were higher in TWINSPAN group (III) than in group (I).
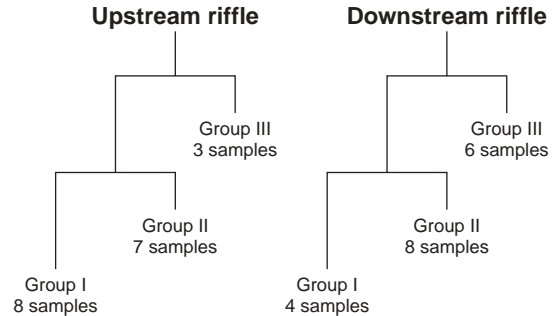

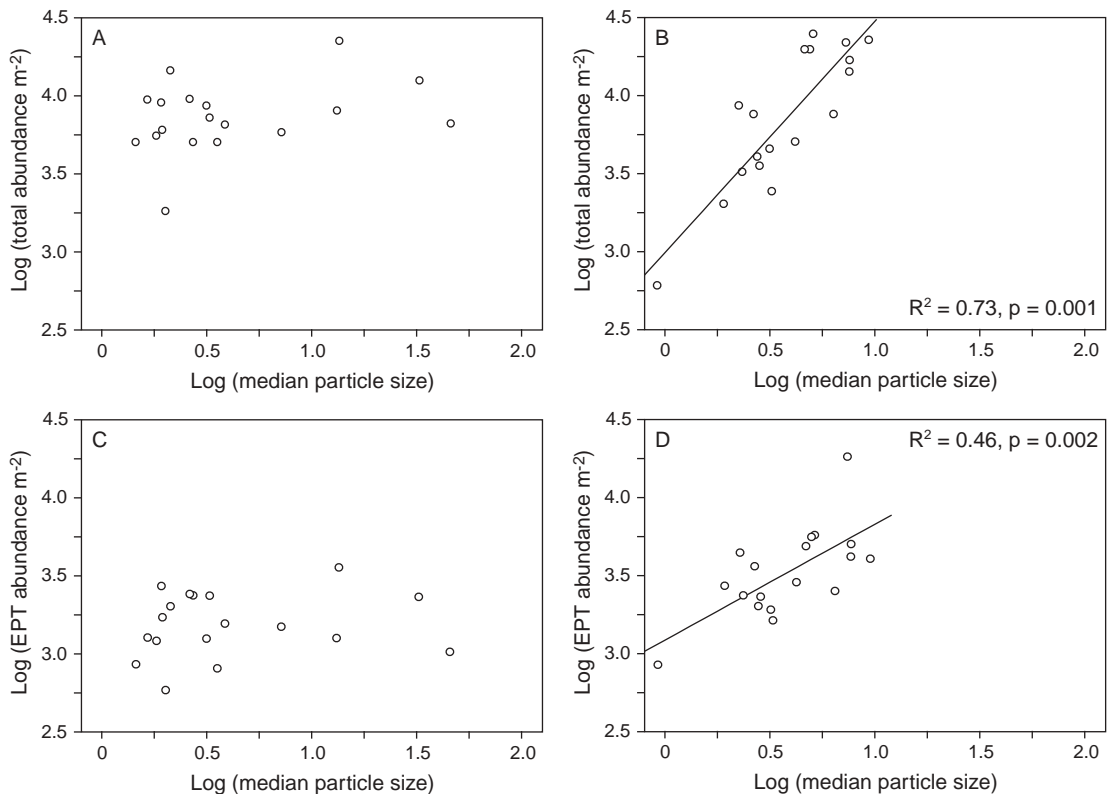**Figure 8.** TWINSPAN analyses on the upstream and downstream riffle.

Figure 7. Relationship between median particle size and total macroinvertebrate abundance and between median particle size and EPT taxa abundance on the upstream (A, C) and downstream (B, D) riffle.
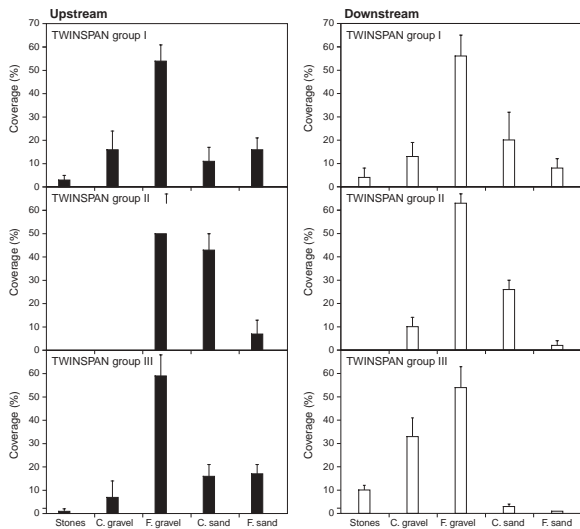
Figure 9. Substratum distribution in the TWINSPAN groups on the riffles.

The samples were not grouped systematically in relation to hydraulic conditions or amount of POM on either riffle. Thus, the current velocity and the amount of POM in the sediment were not significantly different among TWINSPAN groups. However, on both riffles the substratum distribution varied among TWIN-SPAN groups. On the upstream riffle, the substratum distribution in group (II) was different from the distribution in group (I) and (III), and on the downstream riffle, all three distributions were significantly different (Fig. 9; Kolomogorov-Smirnoff test, $p < 0.05$). No further physical differences were apparent on the upstream riffle. In contrast large differences in in-stream habitat parameters were present on the downstream riffle. The primary difference among the groups was related to the substratum distribution and the coarseness of the substratum. The median particle size was significantly higher in TWINSPAN group (III) than in TWINSPAN groups (I) and (II). (Table 5). The group (II) samples were taken in significantly deeper areas of the riffle than the samples in the third group (III). The range in physical habitat parameters was generally wider on the downstream riffle than on the upstream riffle, thus reflecting the diverse physical habitat structure on this riffle.

Discussion

Overall physical structure in streams
The two riffles in Tange stream were located at identical points in the stream and the discharge regime, sediment transport through the riffles and slope varied little between the riffles. Nonetheless, the physical structure on the two riffles varied considerably due to differences created by local variations in streambed morphology, structure and hydraulic conditions within the individual riffle.

Local variations in in-stream physical structure
We mapped near-bed flow and depth along the two riffles and could therefore demonstrate a significant variation the overall hydraulic structure between them. The upstream riffle had the majority of the flow concentrated in one part of the riffle. In contrast, the downstream riffle had the flow distributed across the entire riffle in an irregular pattern. Under low-flow conditions, flow lines in riffles diverge and this irregular flow pattern is therefore how the flow structure is normally perceived in lowland riffles (Church, 1996).

On the upstream riffle the presence of coarse substrata was maintained in areas of low current velocity due to higher velocities at other seasons. As discharge increases during the winter the flow is no longer constrained to one side of the riffle. The entire riffle will be engaged in the flow, and high current velocities over the coarse substrata will remove deposited fine material (Carling, 1996). On the downstream riffle current velocities will increase across the entire riffle as discharge increases, resulting in higher stress on the streambed across the riffle. The riffle structure is thus controlled by previous historic flow events, but local differences in stream bed sediment structure and morphology on the two riffles have caused significantly different reactions to these events, with different contemporary flow patterns and parameter relations as a result (Schumm, 1977; Church, 1996).

Riffle stability and substratum structure
The hydraulic conditions on the riffles were reflected in the distribution of substrata across the riffles. On the upstream riffle, sand dominated in the fast flowing section of the riffle. Gravel and stones had either been eroded from this part or buried beneath sand. The sandy streambed deposits thus represent a temporary deposition as it is in transport along the streambed. The downstream riffle had a more complex spatial distribution of substrata, thus reflecting the variation in riffle hydraulic structure. Substratum composition was noticeably finer and more sand was present, reflecting the higher velocities capable of moving coarser material. The patchy environment on this riffle creates patches of lower current velocities and shear stress where different particle sizes remain stable on the streambed. However, the overall current velocities are highest on this riffle and 44% of the stones were turned, indicating an unstable environment. The sand dominance on the streambed therefore reflects a temporary deposition, as sand is dominant in

transport along the streambed (Brookes, 1988; Thompson, 1986).

The lower coverage of coarse substrata and the dominance of fine material on the downstream riffle indicate a lower stability here (Mangelsdorf *et al.*, 1990). Low stability was observed by *in situ* use of stone clusters, which have proved a reliable and flexible method for estimating surface stability in streams (Matthaei *et al.*, 1999; Ferguson *et al.*, 2002). On the downstream riffle, stones in all five stone clusters were turned over. In contrast, only stones in two clusters were turned over on the upstream riffle. The unstable conditions on the downstream riffle were further suggested by the low concentration of chlorophyll <u>a</u> on stable natural stones in the riffle, indicating either significant scour from sediment in transport or more frequent movements of the stones (Giller & Malmqvist, 1998). However, as macroinvertebrate abundance was higher on the downstream riffle, the low algal biomass can also be result of higher grazer pressure. This possibility cannot be excluded since the grazer *Elmis aenea* and the chironomid family Orhocladiinae, which includes a number of grazer species were more abundant on the downstream riffle (Merrit & Cummins, 1996).

The upstream riffle sediment structure was very compact. In contrast, sediments were loosely structured on the downstream riffle. Reliable and robust methods for evaluating the structure of the stream bed sediments from field methods measuring *in situ* structure and texture are few (Cummins, 1964). Therefore we used a simple one-dimensional method that we believe is applicable in lowland streams where the stream bed sediments are heterogeneous and consists of a number of different particle fractions. Median particle size in the two riffles was identical. The difference in surface sediment size was thus not reflected in the sub-surface sediments when sampling to a depth of 5 cm. This indicates a substantial coverage of sandy substrata in the sub-surface layers on both riffles. The compact surface structure on the upstream riffle indicate that this riffle had a pavement of coarse surface stones arranged in a compact pattern, whereas this pavement was irregular at the downstream riffle, thereby opening up a larger part of the sub-surface sediments for colonisation of macroinvertebrates.

The compact sediment structure in one side of the upstream riffle has affected the local streambed morphology and caused alteration of the flow pattern. This has thus enhanced stabilisation by concentrating the physical stress to a confined flow channel. The hydraulic regime in Tange stream is peak-dominated and the streambed is therefore exposed to high shear stress all year. Even during summer the discharge can increase two-fold. These high-flow events can potentially cause instability within the stream given the right unconsolidated conditions. The downstream riffle is in a transitional unstable phase with fast flow and fine substrata, despite the riffle-pool sequences usually being considered stable over decades (Frissell *et al.*, 1986; Ward, 1989).

Macroinvertebrate communities on riffles

Differences in macroinvertebrate communities were caused by a significantly higher abundance of chironomids and *Dicranota* spp. on the downstream than the upstream riffle. The unconsolidated nature of the downstream riffle enhances the possibility of colonisation by the multi-voltine, burrowing r-strategists such as *Dicranota* spp., and most chironomids (Merritt & Cummins, 1996). *Dicranota* spp. is a predator and its high abundance indicates favourable habitat conditions and high prey density. The flux through the riffle of prey for *Dicranota* spp. and fine particulate organic matter (FPOM) for the chironomids (Tanytarsini and some Orthocladiinae) need to be high to keep the relative abundance at 25% and 29% of all individuals for the two taxa. *Gammarus pulex* and *Baetis* spp. were abundant on the upstream riffle, indicating the existence of a widespread sheltered zone of low flow (Wiberg-Larsen, 1984; Dahl & Greenberg, 1996). *Amphinemura standfussi* and *Leuctra* spp. are usually found in areas of relatively stable substrata (Wiberg-Larsen, 1984). The presence of these taxa on the downstream riffle reflects that sheltered refuge areas are present on parts of the riffle, despite the low stability (Lancaster & Hildrew, 1993). Only part of the riffle surface is presumably moving and an intermediate stability regime is perhaps present here (Stanford & Ward, 1983).

Interactions between macroinvertebrates and substratum are well documented and many studies have focused on relating macroinvertebrate species composition and abundance to substratum types, flow and depth (e.g. Brunke *et al.*, 2001). Most of these studies have concentrated on measuring colonisation on substrata of different particle sizes and on uniform and mixed substrata (Pennak & Van Gerben, 1947; Ward, 1975). The results from these studies show that species richness, diversity and macroinvertebrate abundance increase with particle size. We found identical substrata on both studied riffles and a substantial species overlap was observed among samples and between riffles.

Variation in macroinvertebrate abundance was linearly related to median particle size on the unconsolidated downstream riffle. No linear correlation existed on the upstream riffle, indicating that abundance on the consolidated

riffle might have a limited macroinvertebrate colonisation (Minshall, 1984). We analysed within riffle variations in macroinvertebrate communities (TWINSPAN) and found that the macroinvertebrate distribution reflected the substratum characteristics. The strongest relationship was found on the unconsolidated riffle, where both substratum distribution and median sediment particle size varied among TWINSPAN groups. The linear relationship between median particle size and total macroinvertebrate abundance and EPT abundance indicates that the substratum is important for both the surface and sub-surface macroinvertebrate communities. Our results suggest that the compact sediment structure on the upstream riffle limited the macroinvertebrate abundance and reduced colonisation of the riffle. Knowledge of the detrimental effect of compact sediment on macroinvertebrate community abundance and diversity is largely circumstantial, however, (Minshall, 1984) and the possibility of further evaluation of our results is limited.

Conclusions and perspectives

In summary, our results show that sediment structure and compactness and particle size distribution can have a substantial effect on macroinvertebrate community diversity, structure and abundance in riffles. We found larger variations in hydraulic structure and physical structure between the riffles than expected in a stable lowland stream. Local variations in physical conditions on a scale below the hydrolomorphological unit explained macroinvertebrate community compositions. Without in situ measurements of stability and texture we would have over-looked the substantial physical differences between the two riffles which are important for understanding the hydraulic structure and the colonisation of macroinvertebrates. These small-scale variations limit our ability to predict macroinvertebrate communities from features assessed at the scale of the hydromorphological unit. Our results clearly show that in order to create reliable dynamic models that predict macroinvertebrate communities from physical variables, information on the stability of the different meso-habitats and information on particle size distribution of stream bed sediments need to be included.

Acknowledgements

References

Acornley RM & Sear DA (1999): Sediment transport and siltation of brown trout (salmo trutta l.) spawning gravels in chalk streams. *Hydrological Processes*, **13**, 447-458.

Brunke M, Hoffmann A & Pusch M (2001): Use of mesohabitat-specific relationships between flow velocity and river discharge to assess invertebrate minimum flow requirements. *Regulated Rivers: Research and Management*, **17**, 667-676.

Brookes A (1988): *Channelized Rivers - Perspectives for Environmental Management*. John Wiley and Sons, Chichester.

Brussock PP & Brown AV (1991): Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. *Hydrobiologia*, **220**, 109-117.

Carling PA (1996): In-stream hydraulics and sediment transport. In: *River flows and channel forms* (Eds. GE Petts & P Calow), pp. 160-184. Blackwell Scientific Publications, Oxford.

Church M (1996): Channel morphology and typology. In: *River flows and channel forms* (Eds. GE Petts & P Calow), pp. 185-202. Blackwell Scientific Publications, Oxford.

Conover WJ (1980): *Practical Nonparametric statistics. 2nd edition*. John Wiley and Sons, New York.

Cummins KW (1964): An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturlist*, **67**, 477-504.

Cummins KW, Minshall GW, Sedell JR, Cushing CE & Petersen RC (1984): Stream ecosystem theory. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 1818-1827.

Dahl J & Greenberg L (1996): Effects of habitat structure on habitat use by gammarus pulex in artificial streams. *Freshwater Biology*, **36**, 487-495.

Erman DC & Erman NA (1984): The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia*, **108**, 75-82.

Ferguson RI, Bloomer DJ, Hoey TB & Werritty A (2002): Mobility of river tracer pebbles over different timescales. *Water Resources Research*, **38**, art. no.-1045.

Frissell CA, Liss WJ, Warren CE & Hurley MD (1986): A hierarchical framework for stream habitat classification - viewing streams in a watershed context. *Environmental Management*, **10**, 199-214.

Giller PS & Malmqvist B (1998): *The biology of streams and rivers.* Oxford University Press, Oxford.

Golden Software (1999): *Surfer 7.0 User's Guide.* Golden Software Inc., Golden, Colorado, USA.

Grant GE, Swanson FJ & Wolman MG (1990): Pattern and origin of stepped-bed morphology in high-gradient streams, Western Cascades, Oregon. *Geological Society of America Bulletin,* **102**, 340-352.

Harman WN (1972): Benthic substrates - their effect on freshwater mollusca. *Ecology,* **53**, 271-276.

Hildrew AG & Giller PS (1994): Patchiness, species interactions and disturbance in the stream benthos. In: *Aquatic ecology - scale, pattern and process. The 34th Symposium of the British Ecological Society University College, Cork* (Eds. PS Giller, AG Hildrew & DG Raffaelli), pp. 21-62. Blackwell Scientific Publications, Oxford.

Hynes HBN (1970): *The ecology of running waters.* University of Toronto Press, Toronto.

Kemp JL, Harper DM & Crosa GA (2000): The habitat-scale ecohydraulics of rivers. *Ecological Engineering,* **16**, 17-29.

Kondolf GM (2000): Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society,* **129**, 262-281.

Lamberti GA & Resh VH (1979): Substrate relationships, spatial-distribution patterns, and sampling variability in a stream caddisfly population. *Environmental Entomology,* **8**, 561-567.

Lancaster J & Hildrew AG (1993): Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society,* **12**, 385-393.

Mangelsdorf J, Scheurmann K & Weiss FH (1990): *River morphology. A guide for geoscientists and engineers.* Springer-Verlag, Berlin.

Matthaei CD, Peacock KA & Townsend CR (1999): Patchy surface stone movement during disturbance in a New Zealand stream and its potential significance for the fauna. *Limnology and Oceanography,* **44**, 1091-1102.

McCune B & Mefford MJ (1999): PCORD *User's Guide, version 4. Multivariate analysis of ecological data.* MjM software Design, Gleneden Beach, Oregon, USA.

Merritt RW & Cummins KW (Eds.) (1996): *An introduction to the aquatic insects of North America 3rd edition.* Kendall/Hunt Publishing Company, Dubuque, Iowa.

Minshall GW (1984): Aquatic insect-substratum relationships. In*: The ecology of aquatic insects* (eds. V.H. Resh & D.M. Rosenberg), pp. 358-400. Praeger Scientific, New York.

Palmer MW (1990): The estimation of species richness by extrapolation. *Ecology,* **71**, 1195-1198.

Pennak RW & Van Gerpen ED (1947): Bottom fauna production and physical nature of the substrate in a northern Colorado trout stream. *Ecology,* **28**, 42-48.

SAS Institute (2000): *The SAS System Version 8.2.* SAS Institute. Cary, USA.

Scarsbrook MR & Townsend CR (1993): Stream community structure in relation to spatial and temporal variation - a habitat templet study of 2 contrasting New Zealand streams. *Freshwater Biology,* **29**, 395-410.

Schumm SA (1977): *The fluvial system.* John Wiley and Sons, New York.

Sear DA (1993): Fine sediment infiltration into gravel spawning beds within a regulated river experiencing floods: ecological implications for salmonoids. *Regulated Rivers: Research and Management,* **8**, 373-390.

Sear DA (1995): Morphological and sedimentological changes in a gravel-bed river following 12 years of flow regulation for hydropower. *Regulated Rivers: Research and Management,* **10**, 247-264.

Smith EP & Vanbelle G (1984): Nonparametric-estimation of species richness. *Biometrics,* **40**, 119-129.

Snedecor GW & Cochran WG (1989): *Statistical Methods.* Iowa State College Press. Ames, Iowa.

Stanford JA & Ward JV (1983): Insect species diversity as a function of environmental variability and disturbance in stream systems. In: *Stream ecology: application and testing of general ecological theory* (Eds. JR Barnes & GW Minshall), pp. 265-278. Plenum Press, New York.

Søndergaard M & Riemann B (1979): Ferskvandsbiologiske analysemetoder (In Danish). Akademisk Forlag, Copenhagen.

Thompson A (1986): Secondary flows and the pool-riffle unit: a case study of the processes of meander development. *Earth Surface Processes and Landforms,* **11**, 631-641.

Tolkamp HH (1980): *Organism-substrate relationships in lowland streams.* Agricultural Research Report 907, Agricultural University, Wageningen, The Netherlands.

Ward JV (1975): Bottom fauna-substrate relationships in a northern Colorado trout stream - 1945 and 1974. *Ecology,* **56**, 1429-1434.

Ward JV (1989): The 4-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society,* **8**, 2-8.

Washington HG (1984): Diversity, biotic and similarity indexes - a review with special Relevance to aquatic ecosystems. *Water Research,* **18**, 653-694.

Wiberg-Larsen P (1984): *Plecoptera and Ephemeroptera – keys and ecological notes* (In Danish). National Environmental Protection Agency, Copenhagen.

Wood PJ, Armitage PD, Cannan CE & Petts GE (1999): Instream mesohabitat biodiversity in three groundwater streams under base-flow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **9**, 265-278.

Appendix 1

	Upstream riffle (N=18)	Downstream riffle (N=18)
Non-insects		
Dugesia gonocephala	16	15
Naididae indet	32	38
Eiseniella tetraedra	3	15
Gammarus pulex	200	287
Ephemeroptera		
Baetis rhodani	134	39
Baetis spp.	127	59
Heptagenia sulphurea	9	10
Ephemerella ignita	0	2
Plecoptera		
Brachyptera risi	0	1
Amphinemura standfussi	35	108
Leuctra spp.	46	140
Coleoptera		
Dytiscinae indet	0	1
Elmis aenea	19	121
Trichoptera		
Rhyacophila nubila	29	39
Hydropsyche siltalai	12	1
Potamophylax latipennis	3	0
Halesus spp.	1	1
Diptera		
Dicranota spp.	90	484
Hexatominae indet	0	3
Psychodidae indet	0	1
Simuliidae indet	2	5
Tanypodinae indet	7	14
Orthocladiinae indet	56	258
Chironomini indet	7	16
Tanytarsini indet	4	281
Hemerodromia spp.	4	22
Wiedemannia spp.	1	0
Atherix ibis	4	4
Mollusca		
Lymnaea peregra	2	0
Anisus vortex	4	0
Pisidium sp.	1	0
Total abundance	848	1965

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Variations in riffle habitat structure and effects of disturbances on riffles and pools in lowland Danish streams

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Abstract

A study of riffle and pool habitats in 14 small semi-natural lowland Danish streams was carried out in spring and autumn 2002 with the aim of quantifying within-stream differences in riffle habitat structure. The effects of anthropogenic disturbances on habitat structure in riffle and pools were also studied.

Depth, width, current velocity and median particle size were used to determine the riffle habitats in a PCA ordination. Euclidean distances in the PCA ordination diagram eliminated inter-correlation between discharge and the habitat variables and were used as a measure of differences in riffle structure. Differences in physical structure between adjacent riffles increased as discharge increased (R^2 = 0.50, p= 0.005) but differences in riffles were not significantly influenced by disturbance.

Riffle and pool habitats differed with respect to frequency distributions of depth, current velocity and substratum. In disturbed streams, the differences in current velocity and depth between riffles and pools were significantly lower (0.10 m, 0.15 m s^{-1}) than in undisturbed streams (0.14 m, 0.26 m s^{-1}). Frequency distribution of depth and current velocity in riffles varied significantly between disturbed and undisturbed streams, whereas distribution in pools did not differ.

This study showed that variations in physical structure on meso-scale units (riffles) depended on large-scale parameters, such as discharge. Anthropogenic physical disturbance affected riffles more severely than pools. The study highlights the importance of generating new knowledge on discrete morphological units such as riffles and pools, and how they vary in terms of physical structure and stability in lowland streams in time and space.

Keywords

Lowland streams, riffle-pool structure, physical habitats, disturbance

Introduction

Riffle-pool sequences are distinct morphological units within the stream system that have been surveyed to describe and understand their large-scale dynamics in relation to stream geomorphology (Thompson, 1986; Hooke & Harvey, 1983; Church, 1996). Differences in macroinvertebrate communities between riffle and pool habitats have also received much attention (e.g. Scarsbrook & Townsend, 1993). In contrast, few studies have focused on small-scale variations in physical conditions in riffles and pools and little is known about their dynamic structure and stability at different spatio-temporal scales (Poole, 2002). The riffle and pool units have been severely affected by anthropogenic disturbance in lowland streams due to channelization and dredging. The loss of riffle-pool sequences in channelized streams have made these a focus of multiple river restoration projects (Brookes, 1988; Smith *et al.*, 1995).

Stream regulations such as channelization, dredging and weed cutting have changed in-stream physical structures in lowland streams.

Channelization affects the overall morphological structure of the stream as well as in-stream habitats by reducing the variation in depth, current velocity and substrata between riffles and pools and between different stream reaches (Brookes, 1988). Increased stress on the streambed and the bank enhances sediment erosion and subsequent sediment transport in channelized streams (Thorne, 1997). Dredging and weed cutting in stream regularly take place to ensure runoff from surrounding agricultural areas (Iversen *et al.*, 1993). These continuous disturbances maintain a reduced physical habitat heterogeneity and thereby affect the in-stream biota (Kaenel & Uehlinger, 1998; Baattrup-Pedersen & Riis 1999; Pedersen & Friberg, 2002a).

More than 90% of the Danish streams have been channelized, widened and deepened over the past 100 years, thereby altering the natural physical structure (Brookes, 1987). The majority of Danish streams are small (<2.5 m wide), nutrient-rich and have low channel slopes resulting in relatively low current velocities, fine substrata and marked seasonal growth of submerged macro-phytes (Sand-Jensen *et al.,* 1989; Sand-Jensen,

1998). Anthropogenically induced disturbance of stream morphology, riparian areas and macrophytes have resulted in a declining spatial physical variability in Danish lowland streams (Iversen et al., 1993).

Variations in the physical structure of riffles and pools within a stream are controlled by either natural dynamics or by anthropogenic activities. In order to understand differences in stability of these hydromorphological units and the distribution of macroinvertebrates, it is necessary to analyse the mechanisms causing differences in riffles and pools. The overall objective of this study was therefore to analyse variations in the physical structure of riffles and pools in lowland Danish streams. The first specific objective was to analyse how the physical structure of individual riffles and inter-riffle variability depended on large-scale hydraulic conditions and large-scale stream geomorphology. The second specific objective was to quantify the differences in physical structure between riffles and pools and to evaluate these differences in relation to large-scale physical characteristics of the streams and the extent of anthropogenic disturbance.

Methods

Physical stream features were studied in 14 streams in the spring and autumn 2002. The streams were located within a radius of 50 km in eastern Jutland, Denmark. The stream sites were located in small tributaries to three larger rivers in the area: River Gudenå, River Egå and River Aarhus. All catchments have loamy soils and are dominated by agricultural land use, but have different riparian land use. Average precipitation in the region is 750 mm y^{-1} and average annual stream runoff is 250 mm.

In each stream two adjacent riffle-pool sequences (two pools and two riffles) were randomly selected for this study. The sites were visited twice under identical flow conditions. The riffle habitats were intensively studied in spring and a comparative study of riffles and pools was carried out in autumn.

Physical habitat structure on riffles
Twelve transects were placed at regular intervals along the length of each riffle. Each transect was divided into 4 plots. Plot width varied depending on wetted-width and the length of all plots was set at 1 m. Measurements in each of the 48 plots for every riffle included depth and current velocity (1.5 cm above the streambed) using a propeller current meter (Model ZS/18, Höntzch Instruments, Waiblingen, Germany). The dominant substratum in each plot was registered as stones (>64 mm diameter), gravel (2 – 64 mm

diameter), sand (0.1 – 2 mm diameter) and mud (< 0.1 mm diameter, black colour).

Ten of the 48 plots were randomly selected for intensive physical measurements. Sediment samples were collected from the streambed to a depth of 5 cm and analysed for particle size distribution in the laboratory. The sediment was sieved through a sequence of steel sieves (64 mm, 32 mm, 16 mm, 8 mm, 4 mm, 2 mm, 1 mm and < 1 mm, Endecott, London). In each of the 10 plots, depth and current velocity were measured in the corners and in the centre of the plot.

The discharge in each stream was calculated from measurements of current velocity profiles across the stream using a propeller current meter (Klein Flügel, OTT Instruments). Stream slope was measured in each stream by means of optical levelling of the stream bed along a 100 m reach (Levelling instrument: Zeiss Instruments, Germany).

Riffle and pool physical structure
Differences in physical structure between riffles and pools were quantified in all 14 streams in autumn. Depth, current velocity and dominant substratum were measured in 8 randomly selected plots of the 48 plots in the riffles. In the pools, a similar grid of 48 plots was laid out, and 8 plots were also randomly selected for sampling in the pools.

Assigning streams to disturbance groups
The streams were divided into disturbed and undisturbed streams based on a survey of riparian land use, cross section morphology and longitudinal morphology along a 100 m reach upstream and a 100 m reach downstream from the selected riffle-pool sequences. Streams are usually channelized and regulated due to either agricultural or urban land use (Brookes, 1988; Iversen et al., 1993). Consequently, streams were assigned to the undisturbed group if natural riparian land use (forest, shrubs/trees and wet meadows) prevailed along with natural sinuous or meandering stream morphology and no impact of channelization on the cross sections. In contrast, disturbed streams had agricultural land use in the riparian zones and were channelized and incised with rectangular cross sections.

Data analysis
Mean values and standard deviations (SD) of depth, width and current velocity were calculated for each riffle along with substratum distribution and median particle size. Riffle habitats are naturally structured by the available energy at a site, which is either generated from the volume (and depth) of water that passes the riffle and from the force from the acceleration of the water

generated by the stream slope (Leopold *et al.*, 1964). Therefore a correlation analysis (Pearson product moment correlation) was performed to evaluate the importance of large-scale stream characteristics such as discharge and slope for the physical variables of the riffles (Conover, 1980). Riffle structure was assessed by means of a multivariate PCA analysis using riffle depth, width, current velocity and median particle size as parameters (ter Braak, 1995). Differences in physical structure of adjacent riffles were quantified as the Euclidean distance between their location in the two-dimensional PCA plot. The differences were analysed as a function of discharge, slope and stream power. Stream power has been identified as an important parameter when overall morphological instability in meandering streams is assessed (Leopold *et al.,* 1964; Sear, 1995). Stream power was calculated as:

$$\Omega/w = Q \, S \, g \, \rho$$

where Ω is stream power per unit width (W m^{-1}), w is width (m), Ω/w is stream power per unit area (W m^{-2}), Q is discharge (m^3 s^{-1}), S is stream slope (m m^{-1}), g is acceleration due to gravity (9.82 m s^{-2}) and ρ is density of water (10^3 kg m^{-3}).

Residual variation from the regression lines relating discharge to physical parameters was analysed for systematic differences related to disturbed and undisturbed conditions. Differences in residual were tested by means of standard t-tests (Snedecor & Cochran, 1989). Distributions of riffle and pool depth, substratum and current velocity were tested for differences between disturbance groups by means of a Kolomogorov-Smirnoff Goodness-of-fit test (Conover, 1980). All statistical test were performed using SAS system version 8.2 (SAS Institute, 2000).

Results

Riffle habitats
Discharge correlated positively to stream depth and width and current velocity. The variations in current velocity on the riffles correlated positively to stream slope (Table 1). Riffle substratum particle size was not correlated to discharge nor stream slope, but variations in the median particle size were positively correlated to discharge (Table 1).

The multivariate ordination of physical riffle structure resulted in two PCA axes with eigenvalues higher than 1, which explained 66% of the variation in the data (Fig. 1). Three different groups of streams could be identified by PCA ordination, reflecting differences in stream width and overall stream morphology. Streams in group

(I) were larger and streams in group (II) and (III) were smaller than 2.5 m. The two streams in group (III) were the smallest and located in a deep narrow trench about 2 m below the surrounding landscape (Fig. 1).

Variations in riffle habitats were expressed as the Euclidean distance between the two riffles in the PCA plot. There was no significant effect of stream width on differences in riffle habitats (t-test between groups I and II combined and III, p=0.100). Stream slope was not correlated to the riffle habitat differences either (r=-0.08, p=0.778). Stream power combines the effect of both discharge and stream slope and was correlated to riffle habitat differences between adjacent riffles, though not significantly (Fig. 2). In contrast, discharge significantly affected the difference in
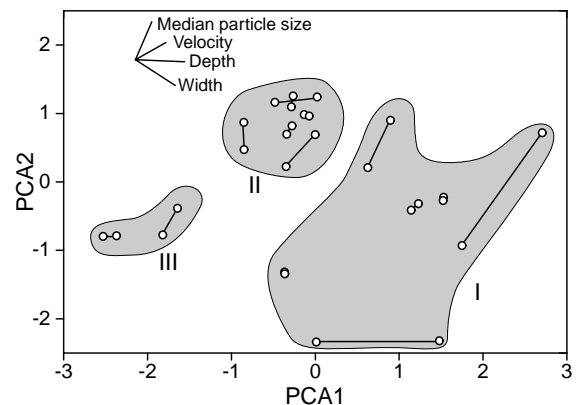
Figure 1. PCA ordination plot of the physical habitat structure on 28 riffles in 14 lowland Danish streams. Eigenvalues for PCA-axes 1 and 2 were 1.55 and 1.08, respectively. The two PCA-axes explained 66% of the variation in the data set. Each point in the plot represents a riffle and neighbouring riffles are connected by a straight line.

habitat structure as differences in riffle habitats increased at higher discharge (Fig. 2).

Physical structure in riffles and pools
Discharge at the study sites ranged from 0.019 to 0.596 m^3 s^{-1} and stream width ranged from 0.8 to 8.0 cm. Stream slopes varied from 0.7‰ to 15.7‰, covering the range found in the upper and middle parts of Danish lowland streams (Table 2). Depth varied significantly between riffles (0.17 m) and pools (0.29 m; t-test, p<0.001). Near-bed current velocity also varied significantly in accordance with the riffle-pool structure (t-test, p<0.001). Mean current velocity was 0.29 m s^{-1} on riffles and 0.08 m s^{-1} in pools. Sand dominated in pools (56%) whereas gravel was the dominant substratum in riffles (59%). Substratum characteristics varied considerably between riffle and pool habitats and among the 14 streams as indicated by the ranges (Table 2).

67
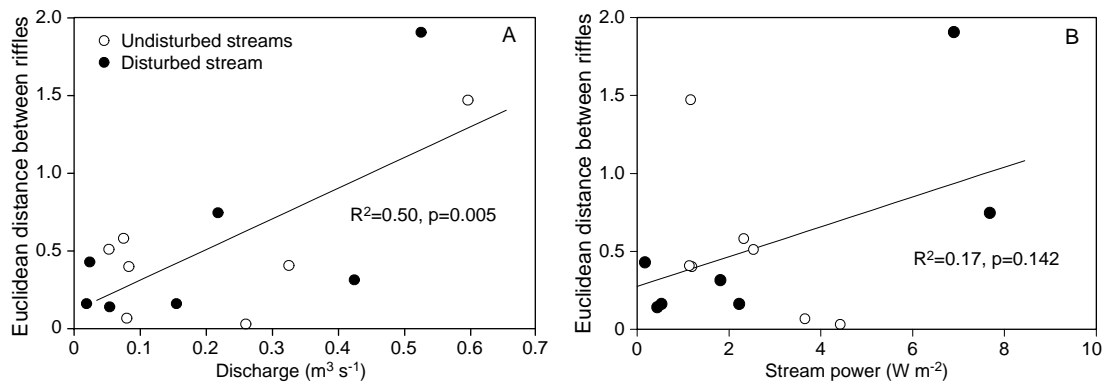
Figure 2. Differences in physical habitat structure on the riffles expressed as the Euclidean distance between points in the PCA ordination diagram as a function of (A) measured discharge and (B) estimated stream power.

Effects of disturbance on riffle habitat structure
Since discharge affected the in-stream habitat variability (expressed as the Euclidean distance), effects of anthropogenic disturbance on physical riffle parameters were evaluated after first taking the discharge gradient into account. The residuals from regressions of width, depth, current velocity and median particle size with discharge as the independent variable were analysed for significant differences between disturbed and undisturbed sites. No effect of disturbance was apparent for any of these variables, however (Table 3; t-test, $p > 0.05$). In contrast, the residuals of regressions of riffle-pool differences in depth and current velocity with discharge did differ systematically between disturbance groups (Fig. 3). Differences in depth and current velocity between riffles and pool were both significantly (t-test, $p < 0.05$) higher in undisturbed streams (0.14 m, 0.26 m s^{-1}) than in disturbed streams (0.10 m, 0.14 m s^{-1}) suggesting a

significant effect of anthropogenic disturbance on these parameters.

The differences in physical variables between disturbed and undisturbed streams were not significant, indicating that stream groups did not differ systematically at the reach scale (Table 4). Frequency distributions of depth and current velocity in disturbed and undisturbed streams were significantly different in riffles, but not in pool habitats (Kolomogorov-Smirnoff tests, $p < 0.05$). In riffles in undisturbed streams, higher current velocities (> 0.50 m s^{-1}) were found more frequently than in disturbed streams. Current velocities below 0.10 m s^{-1} were only found in disturbed streams (Fig. 4). Riffles were generally deeper in disturbed streams and depths above 0.40 m were therefore more common in disturbed streams (Fig. 4). In pools, the distribution of depth and current velocity was similar between disturbed and undisturbed streams (Kolomogorov-Smirnoff tests, $p > 0.05$).
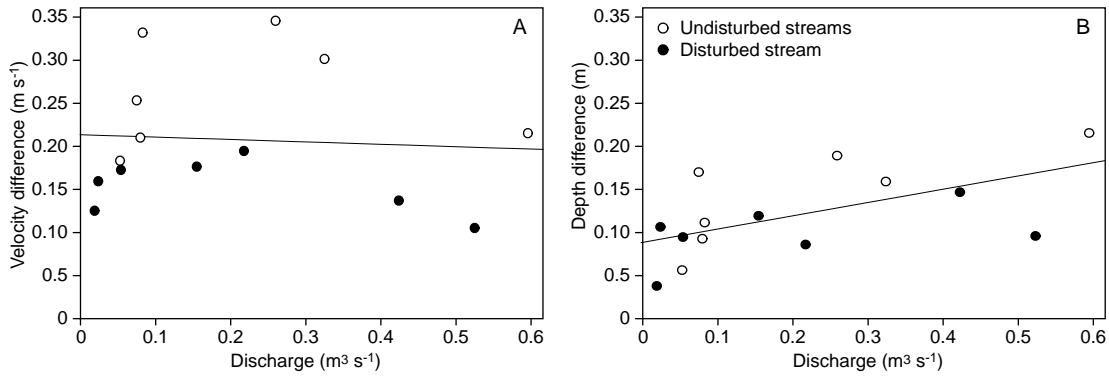
Figure 3. Current velocity difference between riffles and pools (A) and depth differences between riffles and pools (B) as function of measured stream discharge on undisturbed and disturbed streams. Lines show the linear regression. Residuals for each point equals the vertical distance between individual point and the regression line.
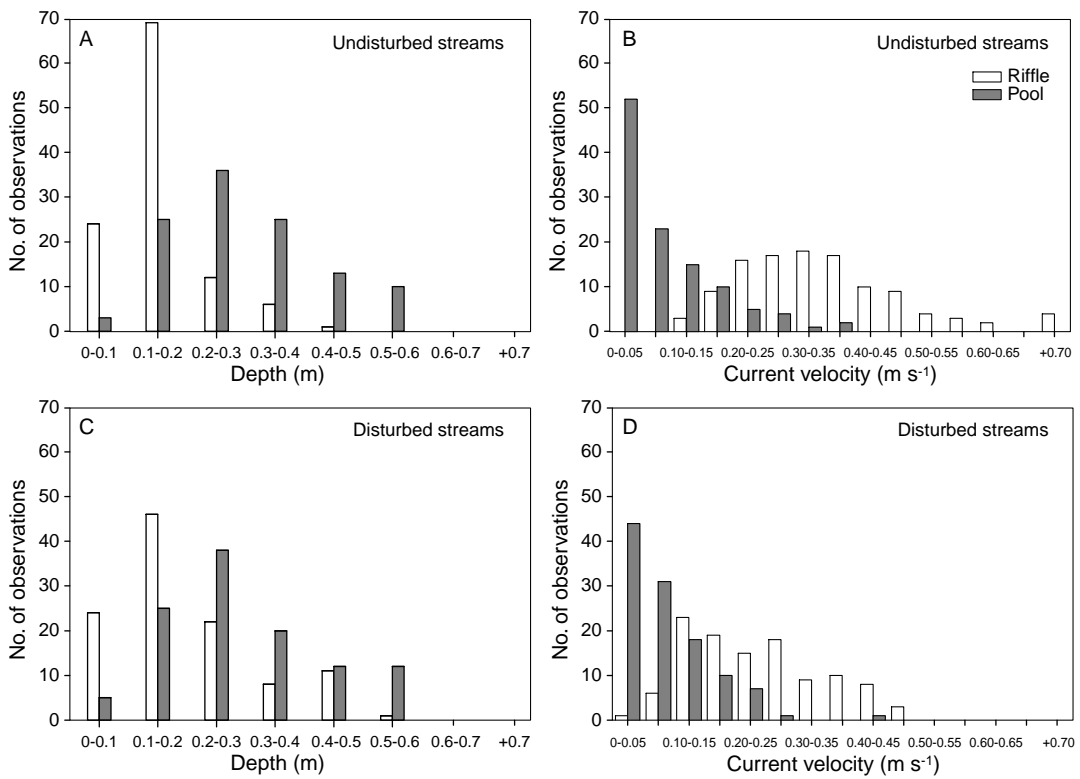
Figure 4. Frequency distribution of depth and current velocity in riffles and pools on disturbed and undisturbed sites.

Substratum distribution was not significantly different between disturbed and undisturbed streams (Fig. 5; Kolomogorov-Smirnoff tests, p>0.05). In both stream groups gravel dominated on the riffles (approx. 75%). Sand and gravel were equally abundant in the pools, both covering approx. 50% of the streambed (Fig. 5).
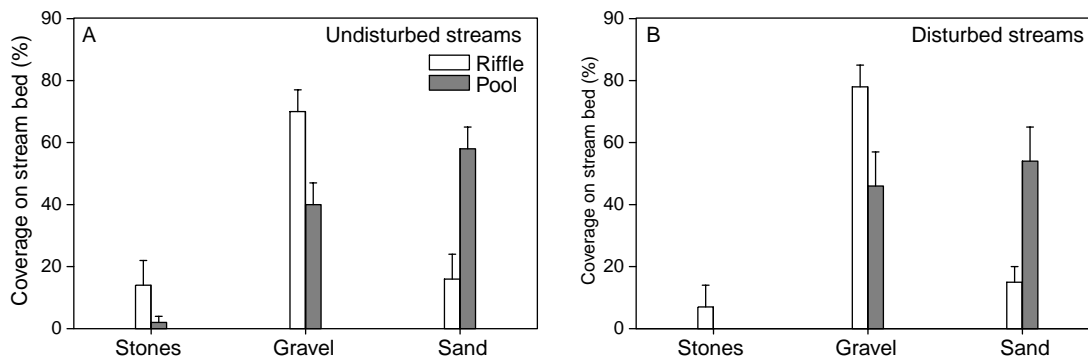
Figure 5. Frequency distributions of substrata in riffles and pools on disturbed and undisturbed sites.

Discussion

Within-stream variability in riffle habitat was most pronounced in large streams with high discharge. Riffle habitat differences increased with increasing discharge reflecting the direct physical importance of discharge on variation in riffle structure. Variations in median particle size also increased with increasing stream width and discharge. This may be due to the ability of streams to transport and deposit particles of more varied sizes as discharge and sediment transporting competence increase along the stream (Leopold *et al.*, 1964; Schumm, 1977).

In larger streams, the increased discharge and the increased riffle area will probably support more diverse depth, flow and substratum conditions. Increasing discharge probably permits the transport of a wider range of particle sizes; the physical competence of the streams is thus increased (Schumm, 1977). The increasing large-scale forces may result in a potential increase in small-scale physical differences on the riffles. The control of variations in riffle structure by large-scale parameters such as discharge, supports the hierarchically based stream ecosystem theory proposed by Frissell *et al.* (1986) and Minshall (1988). According to this theory, parameters at large scales impose constraints and control on parameters at lower scales just as discharge controls physical riffle variation in this study.

Stream morphology research has concentrated on either large-scale studies of stream development or on large-scale processes such as sediment transport. Little information is available on how different meso-scale hydromorphological units, such as riffles and pools vary in terms of physical structure and stability along the stream and over time (Lane and Richards, 1994). Interest in studies of small- and meso-scale variations in physical structure around distinct morphological units is growing (e.g. Kemp *et al.*, 2000; Booker *et al.*, 2001).

The importance of the in-stream environment for macroinvertebrate species inter-actions are well known (e.g. Hildrew & Townsend, 1977). In order to increase our understanding of these morphological units as habitats for macroinvertebrates, the aspects of physical structure and stability need to be studied in detail. The present study and the study by Pedersen & Friberg (2002b) clearly demonstrate that variations in a hydromorphological unit can be substantial and we need increase our knowledge on the stability and variability of these dynamic units.

Stream power was not correlated to the variation in riffles within streams, which probably indicates that stream power is a suitable parameter for evaluating large-scale morphological stability (Leopold *et al.*, 1964; Richards, 1982). But, it is apparently of limited value when used to explain variations in physical structure of discrete morphological units such as riffles. The multivariate riffle structure analysis indicated that depth and current velocity played a major role in determining the physical riffle structure. These parameters are not directly affected by the power exerted on the stream bed and might therefore help to explain the low predictive power of the stream power.

Depth and current velocity in riffles and pools varied significantly and independently of disturbance. Despite overall differences in disturbance, natural channel dynamics prevailed and created a substantial physical variation between riffles and pools. The differences in current velocity and depth between riffles and pools were significantly higher in undisturbed streams than in disturbed streams. Channelization homogenised variations in depth and current velocity between riffles and pools in disturbed streams. This is similar to the results found in other studies (Brookes, 1988). Frequency distributions of current velocity and depth were altered most radically on the riffles, which demonstrate their greater sensitivity to disturbance. Channelization mainly affects riffles

by increasing depth and levelling the streambed, thereby shifting the stream to a uniform channel with greater mean depth. As a consequence, riffles are more strongly affected than pools. Levelling of the stream bed is most effectively carried out by removing coarse gravel beds forming the riffles and this operation will enhance the destruction of the natural riffle structure (Brookes, 1987). Similar results indicating destruction of riffle-pools sequences have been reported in other streams impacted by stream regulation (Brookes, 1988). Riffles had naturally been regenerated in the disturbed streams by actively eroding and transporting exposed gravel thereby creating new riffles over a long period of time. This has been caused by natural recovery, since the riffles have not been restored in the disturbed streams.

Conclusion and perspectives

In conclusion, the results show that discharge, stream size and position within the stream system affect the variation in riffle morphology. These results support the idea of a hierarchically nested physical stream ecosystem. Further, the study showed that disturbance affected the riffle habitats most severely, but depth, current velocity and substratum varied between riffles and pools in both disturbed and undisturbed streams.

This study highlights the importance of generating new knowledge on small-scale spatial and temporal differences in discrete morphological units such as riffles and pools, and how anthropogenic and natural disturbances affect these small-scale physical conditions. More knowledge is also needed on how riffles and pools vary in terms of physical structure and stability in lowland streams in time and space. We need to link process and form across multiple scales to understand the complex nature of the in-stream habitats and explain the distribution of the in-stream biota.

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References

Baattrup-Pedersen A & Riis T (1999): Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology*, **42**, 375-385.

Booker DJ, Sear DA & Payne AJ (2001): Modelling three-dimensional flow structures and patterns of boundary shear stress in a natural pool-riffle sequence. *Earth Surface Processes and Landforms*, **26**, 553-576.

Brookes A (1987): The distribution and management of channelized streams in Denmark. *Regulated Rivers: Research and Management*, **1**, 3-16.

Brookes A (1988): *Channelized Rivers - Perspectives for Environmental Management*. John Wiley and Sons, Chichester.

Church M (1996): Channel morphology and typology. In: *River flows and channel forms* (Eds. GE Petts & P Calow), pp. 185-202. Blackwell Scientific Publications, Oxford.

Conover WJ (1980): *Practical Nonparametric statistics. 2nd edition*. John Wiley and Sons, New York.

Frissell CA, Liss WJ, Warren CE & Hurley MD (1986): A hierarchical framework for stream habitat classification - viewing streams in a watershed context. *Environmental Management*, **10**, 199-214.

Hildrew AG & Townsend CR (1977): Influence of substrate on functional response of *Plectrocnemia conspersa* (Curtis) larvae (Trichoptera, Polycentropodidae). *Oecologia*, **31**, 21-26.

Hooke JM & Harvey AM (1983): Meander changes in relation to bend morphology and secondary flows. In: *Fluvial systems* (eds. JD Collinson & J Lewin), pp. 121-132. Special Publication No. 6, International Association of Sedimentologists. Blackwell Scientific Publications, Oxford.

Iversen TM, Kronvang B, Madsen BL, Markmann P & Nielsen MB (1993): Reestablishment of Danish streams - restoration and maintenance measures. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **3**, 73-92.

Kaenel BR & Uehlinger U (1998): Effects of plant cutting dredging on habitat conditions in streams. *Archiv für Hydrobiologie*, **143**, 257-273.

Kemp JL, Harper DM & Crosa GA (2000): The habitat-scale ecohydraulics of rivers. *Ecological Engineering*, **16**, 17-29.

Lane SN & Richards KS (1997): Linking river channel form and process: time space and causality revisited. *Earth Surface Processes and Landforms*, **22**, 249-260.

Leopold LB, Wolman MG & Miller JP (1964): *Fluvial processes in geomorphology*. WH Freeman & Co., San Francisco

Minshall, GW (1988): Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*, **7**, 263-288.

Pedersen ML & Friberg N (2002a): Physical habitats and diversity of biological communities in low-

land streams with contrasting disturbance (submitted to *Freshwater Biology*).

Pedersen ML & Friberg N (2002b): Spatio-temporal variations in stability, substratum and macroinvertebrates in lowland stream-riffles (Submitted to *Journal of the North American Benthological Society*).

Pool GC (2002): Fluvial landscape ecology addressing uniqueness within the river discontinuum. *Freshwater Biology, 47, 641-660.*

Richards KS (1982): *Rivers: Form and process in alluvial channels.* Methuen, London.

Sand-Jensen K (1998): Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology, 39*, 663-679.

Sand-Jensen K, Jeppesen E, Van Der Bijl L, Nielsen K, Wiggers-Nielsen L & Iversen, TM (1989): Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology, 22*, 15-32.

SAS Institute (2000): *The SAS System Version 8.2.* SAS Institute. Cary, USA.

Scarsbrook MR & Townsend CR (1993): Stream community structure in relation to spatial and temporal variation - a habitat templet study of 2 contrasting New Zealand streams. *Freshwater Biology*, **29**, 395-410.

Schumm SA (1977): *The fluvial system.* John Wiley and Sons, New York.

Sear DA (1995): Morphological and sedimentological changes in a gravel-bed river following 12 years of flow regulation for hydropower. *Regulated Rivers: Research and Management*, **10**, 247-264.

Smith C, Youdan T & Redmond C (1995): Practical aspects of restoration of channel diversity in physically degraded streams. In: *The ecological basis for river management* (eds. DM Harper & AJD Ferguson), pp. 269-273. John Wiley and Sons, Chichester.

Snedecor GW & Cochran WG (1989): *Statistical Methods.* Iowa State College Press. Ames, Iowa.

ter Braak CJF (1995): Ordination. In: *Data analysis in community and landscape ecology* (Eds. RHG Jongman, CJF ter Braak & OFR van Tongeren), pp. 91-173. Cambridge University Press, Cambridge.

Thompson A (1986): Secondary flows and the pool-riffle unit: a case study of the processes of meander development. *Earth Surface Processes and Landforms*, **11**, 631-641.

Thorne CR (1997): Channel types and morphological classification. In: *Applied fluvial geomorphology for river engineering and management* (Eds. CR Thorne, RD Hey & MD Newson), pp. 175-222. John Wiley and Sons, Chichester.

Physical habitat structure and effects of riparian land use along the upper continuum in Danish lowland stream systems

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Abstract

Physical stream characteristics were measured in 143 stream reaches along the upper continuum in lowland Danish stream systems between 1993 and 2002. The measured physical parameters included discharge, stream slope, width, depth, current velocity, substrata, coverage of coarse organic debris (CPOM) and macrophytes. Headwater streams were either forested or open land streams. In contrast, the riaprian areas of the streams in the middle and lower parts of the stream systems were dominated by agricultural or abandoned agricultural land use.

Discharge, current velocity, width and depth increased with distance to the source, thus responding to continuous addition of water from a larger catchment area (r>0.3, p<0.05). Stream slope decreased with distance to the source, reflecting the change from high gradient topography in headwater streams (max: 51.1‰) to moderate gradients further downstream (2.7‰ - 6.3‰). CPOM coverage was highest in the forested headwater streams and decreased as land use changed to open land. Coverage of coarse substrata varied little along the continuum (mean: 30-35%). The variations in coarse substrata and mud were compared to larger Danish streams. The results suggest that homogeneous geomorphological and geological conditions in the small Danish catchments create a discontinuous system, where changes to the stream substrata are governed by physical thresholds within the system.

The physical structure of forested headwater streams was significantly different from the structure in open land streams. Substratum characteristics remained more stable between seasons in forested headwater streams than in-stream in the open land. Discharge and macrophyte coverage significantly affected seasonal differences in physical habitat structure in streams located in open land, indicating a complex influence of discharge and macrophyte cover on physical habitats along the stream system.

Knowledge of the physical habitat structure and the controlling parameters along the continuous stream system is important when a quality assessment of the physical habitats is needed. In the Water Framework Directive physical stream quality has to be established along with an outline of reference conditions. Therefore, analyses of longitudinal gradients and variations in physical stream features in relation to land use are a vital part of establishing the required knowledge of the physical stream environment.

Keywords

Lowland streams, stream morphology, habitats, substratum, river continuum, land use

Introduction

Conceptual models of river channel morphology predict systematic variations in morphology and physical structure through the river system, thus reflecting the changes in available energy (Schumm, 1977). Natural river systems are in a dynamic equilibrium, which leads to consistent changes in stream depth, width, discharge, current velocity and sediment transport through the system from source to outlet (Leopold *et al.*, 1964; Church, 1996).

The physical stream structure and hydrological regime form a template for biological responses in river systems (Southwood, 1977). This template creates consistent changes in community structure and functions along with loading of organic matter, transport and utilisation along the river continuum. These continuous changes in biotic and physical structure form the River Continuum Concept (RCC) (Vannote *et al.*, 1980). The RCC has been a useful tool for analysis of longitudinal changes in biotic communities and large-scale physical conditions in large river systems. Important features at meso-scale, such as riffles and pools, along the continuum are, however, only indirectly included in the RCC and a comprehensive description of stream morphology is not offered with this concept. Studies of catchment-scale stream morphology have primarily concentrated on large-scale patterns and processes in large river systems (Schumm, 1977). The structure, spatial and temporal stability and function of riffles and pools

at lower scales have been described by Frissell *et al.* (1986) as a nested hierarchical system, but few studies have actually included these concepts in large-scale studies of physical conditions and habitat structure. Geomorphological studies have concentrated on large-scale patterns in downstream fining of stream bed sediments (Petts *et al.*, 2000).

Danish stream systems are generally small as 70% of the country's area is drained by rivers with catchment areas less than 500 km^2, and only two rivers are longer than 100 km. About 75% of all streams (total natural stream length is 36 000 km) are less than 2.5 m wide and the majority of the open land is used for agricultural production and is heavily drained by underground tiles. The natural drainage density (stream length in a catchment divided by catchment areas) in Denmark is 0.9 km km^{-2} of which 98% is physically modified. This modification intensity is 15 times higher than in England and Wales (Brookes *et al.*, 1983) and 300 times higher than in the USA (Brookes, 1988). The Danish landscape and stream systems are fundamentally very different from the large systems, from where the RRC and the geomorpholological concepts have emerged. The majority of Danish streams are characterised by low-gradient environments with low current velocity, fine sediments and marked seasonal growth of submerged macrophytes, often subject to weed cutting (Sand-Jensen *et al.,* 1989). More than 90% of the Danish streams have been channelized, widened and deepened to improve drainage of the agricultural land. As a result, Danish streams have lost most of their natural variations in depth, current velocity and substratum (Brookes, 1987; Iversen *et al.*, 1993).

The dominance of small streams and small catchments and the widespread anthropogenic disturbance of physical conditions in lowland Danish streams is likely to mask the natural variations in physical parameters along the continuum. The overall objective was therefore to study physical parameter variations along the upper continuum and relate these to the general geomorphological concepts. This study further aimed at analysing variations in physical features along the upper continuum in Danish lowland streams in relation to differences in riparian land use. The study also aimed at analysing general relationships between physical variables and seasonal variations in the physical habitat structure in streams with substantial macrophyte growth in the summer.

Methods

Physical stream characteristics were sampled in 143 small and medium-sized streams evenly distributed throughout Denmark. All streams were visited in both spring/winter (December – March) and in summer (May – August) in one of the years between 1993 and 2002.

Field survey
In each stream a number of equally spaced transects were placed along the stream reach. The stream reach length was approximately 50 m. Transects were sub-divided into plots (0.5 m x 0.5 m). A minimum of 5 transects and 50 plots were sampled at each site. Water depth and dominant substratum type were recorded in all plots. The substrata were divided into size classes roughly corresponding to the Wentworth-scale (Wenthworth, 1922): Stone (>64 mm), gravel (2-64 mm), sand (0.1-2 mm), mud (<0.1 mm, black colour), peat and hard clay. In addition, the presence of debris layers consisting of leaves (CPOM) and large woody debris (e.g. roots, trees etc.) was recorded in each plot. Reach-scale coverage of each substratum type was calculated as the relative frequency of all plots examined. In order to analyse the spatial variations in the stream bed substrata, the substratum heterogeneity (SH) was quantified (see Pedersen *et al.*, 2002). SH is a number between 0 and 1 with 1 representing maximum spatial substrate heterogeneity. Depth was measured in the centre of the plots and averaged across all plots. Mean stream width was calculated from the observed wetted width in all transects. Reach scale depth and width variations were quantified by calculating the coefficient of variance (CV).

The discharge was measured using a propeller current meter (OTT instruments, Germany). Ten current velocity profiles were measured across the stream downstream of the studied reach using a propeller current meter. Each velocity profile represented 1/10 of the stream width. The discharge was calculated by integrating the velocity profiles over the depth and multiplying by the width. The average current velocity was calculated as the discharge divided by the wetted cross section area. If stream depth was lower than 0.07 m, mean current velocity was measured by means of dilution gauging (White, 1978). The method was typically used in forested streams. A volume of water with a known concentration (10% w/w) of NaCl was added instantaneously at the upstream end of the sampling reach. Conductivity was measured continuously at the downstream end of the reach. Mean current velocity was then calculated from the time elapsed for half of the NaCl solution to pass through the reach. Discharge was calculated as wetted cross sectional area multiplied by the mean current velocity.

The slope was calculated from optical levelling of the stream bed along the entire length of the surveyed reach (Levelling instrument: Zeiss Instruments, Germany). The cross sections were divided into three groups based on their morphology: Natural (no signs of channelization or dredging), semi-natural (formerly channelized reach, with signs of natural cross section development) or channelized (cross sections are rectangular). The dominant riparian land use within the first 10 meters from the bank was identified in the field as either agricultural, forest or other open land. Other open land comprised several natural and semi-natural land uses.

Map survey

For each stream the catchment area and the distance from sampling reach to the source were extracted from digital topographic maps (1:25,000). Stream order was also determined from the digital maps. Using the digital catchment boundary, the dominating catchment land use (agriculture or forest) and dominant soil type (sand or loam) were extracted from the Danish Area Information System (Nielsen *et al.*, 2000).

Data analysis

Stream sites were assigned to three equally sized groups depending on the distance from source to the sampled reach (0-2000 m; 2000-4000; >4000 m). The first group, which consisted of headwater streams, was further sub-divided into forested and non-forested sites due to significant differences in physical stream structure between forested streams and streams located in the open land. Variations in physical parameters with distance from source were analysed using least-squares regression analysis. Frequency distribution of riparian land use in the distance groups and cross section type in the riparian land use groups were tested for differences using χ^2-tests (Snedecor & Cochran, 1989).

Physical structure in streams with different land use was assessed by means of a multivariate PCA analysis of depth, width, current velocity, CV of depth, CV of width, macrophyte coverage, CPOM coverage, substratum heterogeneity and coverage of coarse substrata and mud (ter Braak, 1995). Similarities in physical habitat structure among land use stream groups were tested using an analysis of variance on similarities (ANOSIM) between points within the groups (Clarke & Warwick, 1994). These analyses were performed in the Primer Software Package (Primer-E Ltd., 2001). All other statistical analyses were carried out in SAS/STAT version 8.2 (SAS Institute Inc., 2000).

Differences in substrata and physical stream characteristics (depth, with, current velocity etc.) were tested among the distance groups using 3-factor ANOVAs with Bonfferoni-correction applied, and t-tests were used for pair-wise comparisons. The three factors were cross section type, distance group and riparian land use. Three-factor analysis was used because all three parameters potentially affected the physical stream structure. Inter-correlation between the factors was taken into account when the results were analysed. Discharge, current velocity and stream dimensions were log-transformed and substratum data were arc sine transformed to satisfy assumptions of normality and homogeneity of variances within groups (Snedecor and Cochran, 1989).

Seasonal differences in physical habitat structure in streams located in the open land were assessed by means of a PCA analysis (ter Braak, 1995). Depth, width, current velocity, CV of depth, CV of width, substratum heterogeneity and coverage of coarse substrata and mud were used as input variables. Seasonal differences (between summer and winter/spring) in the physical habitat structure were calculated as the Euclidean distance between the summer point and the spring/winter point in the PCA plot for each stream. This measure of seasonal difference was then correlated to higher-scale parameters such as stream slope, land use, discharge and macrophyte coverage by means of least squares regression.

Results

Catchment characteristics

Catchment areas varied between 0.1 km^2 and 67.4 km^2 and averaged 10.7 km^2. Loam and sandy soils were equally dominant in the catchments. Catchment land use was dominated (71%) by agriculture, whereas forests dominated in 29% of the catchments. The dominance of agriculture was also reflected in the riparian land use, as agriculture dominated along 51% of all streams. Streams with forested riparian areas made up 27% and other types of open land use constituted the remaining 22%. Natural cross sections were present in 41% of all streams, whereas streams with semi-natural and disturbed cross sections were present in 33% and 26% of the streams, respectively (Table 1).

Table 1. Overall characteristics of the 143 catchments.

Catchment feature	Frequency distribution (%)
Dominant soil type (sand/loam)	(42 / 58)
Catchment land use (agricultural/forest)	(71 / 29)
Riparian land use (agriculture/open land/forest)	(51 / 22 / 27)
Stream profile (natural/semi-natural/disturbed)	(41 / 33 / 26)

The riparian land use in streams in the upper parts of the systems was dominated by

forests, whereas riparian land use in streams located further downstream was dominated by agriculture. Agriculturel and other types of open land use increased while forests decreased with increasing distance from the source. The land use distributions was significantly different among the distance groups (Fig. 1; χ^2-test, p<0.001). Natural cross sections were more frequent in streams with forest riparian land use, and these were primarily located in the upper parts of the stream systems. In contrast, streams surrounded by agriculture or open land use were dominated by disturbed and semi-natural cross sections. These types of land use dominated in the middle and lower parts of the stream systems. About one third (19 out of 52) of streams in the upper parts of the stream systems were also dominated by agricultural or open land use. These streams mostly had disturbed cross sections. The frequency distributions of cross section types among streams of different riparian land use was thus significantly different (Fig. 1; χ^2-test, p=0.002). The results thus show a strong correlation between cross section type, riparian land use and distance from source.

Stream characteristics
Discharge in the streams ranged from 0 to 0.53 $m^3 s^{-1}$ (mean: 0.08 $m^3 s^{-1}$) and current velocity ranged from 0 to 0.56 $m s^{-1}$ (overall mean: 0.18 $m s^{-1}$). Mean stream width ranged from 0.37 m to 6.57 (overall mean: 1.76 m) and mean depth ranged from 0.02 m to 0.52 m (overall mean: 0.19 m). Stream slopes ranged from 0.1 ‰ to 42.1 ‰ (overall mean: 14.4‰). In open land streams mean macrophyte coverage ranged from 0 to 100% (overall mean: 50%) in summer (Table 2).

Physical habitat structure in streams with different riparian land use
The physical stream structure in forested streams was significantly different from the structure in

Table 2. Overall characteristics (mean and range) of the studied streams (N=143).

Parameter	Mean	Range
Discharge ($m^3 s^{-1}$)	0.082	0.000 – 0.532
Stream slope (‰)	14.4	0.1 – 242.1
Mean current velocity ($m s^{-1}$)	0.18	0.00 – 0.56
Width (m)	1.76	0.37 – 6.57
Depth (m)	0.19	0.02 – 0.52
Distance from source (km)	3.8	0.1 – 20.1
Summer macrophyte coverage (%)	50	0 – 100

streams with riparian areas dominated by agriculture or abandoned agriculture and wetlands (Fig. 2). The first three PCA axes had eigenvalues higher than 1 and explained a combined 67% of the variation in the data. PCA axis 1 separated large, deep streams with high macrophyte coverage from small, shallow streams with high coverage of CPOM. High values on PCA axis 2 corresponded to high coverage of coarse substrata and high substratum heterogeneity (SH). The third PCA axis separated streams with extensive variations in depth and width from the more homogeneous streams (Fig. 2). The forested streams were significantly different from the streams located in the open land (ANOSIM, p<0.001). Streams with agricultural riparian land use overlapped significantly in the PCA ordination with streams with semi-natural riparian land use (Fig. 2; ANOSIM, p=0.100). In the open streams, riparian land use was thus not manifested in the physical habitat structure.

The results of the PCA analysis showed that small forest streams located close to the stream source had a significantly different physical stream structure from streams in the open land. Forested headwater streams were therefore treated as a separate group in the analyses.
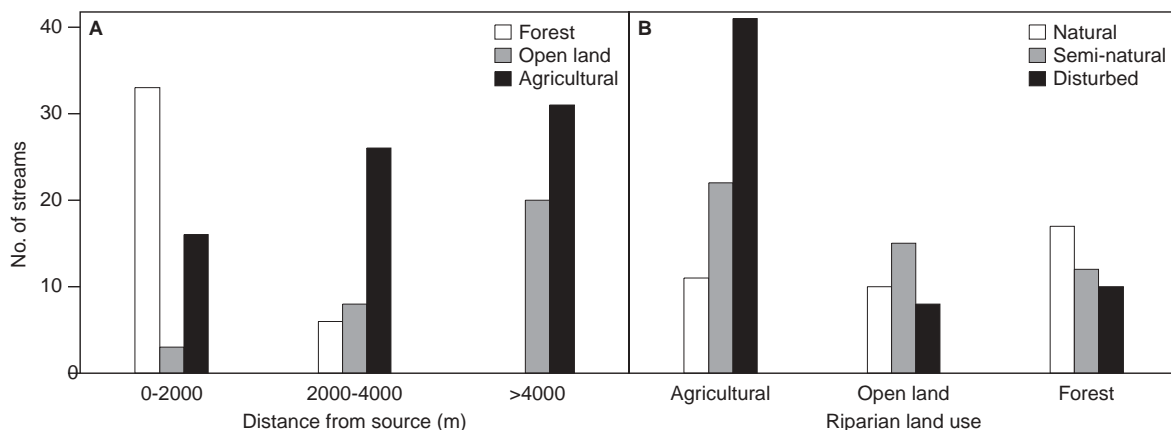

Figure 1. (A) Riparian land use in streams along the upper continuum in different intervals from the source. (B) Distribution of cross section types in streams with different riparian land use.
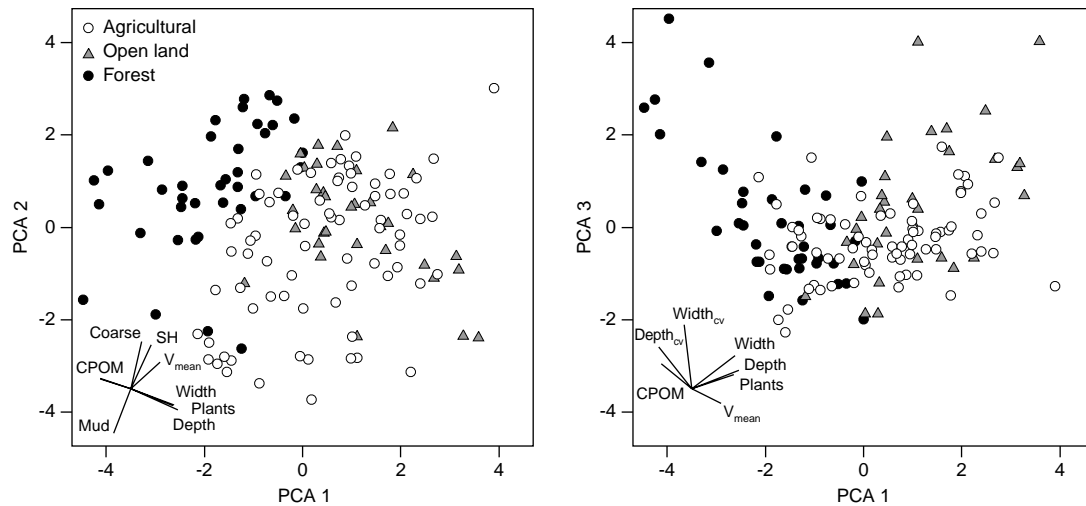
Figure 2. PCA ordination of physical habitat structure. (A) PCA axis 1 vs. PCA axis 2. (B) PCA axis 1 vs. PCA axis 3.

Physical stream characteristics along the upper continuum

Catchment area increased significantly with increasing distance from the source (Fig. 3). In contrast, stream slope decreased exponentially with distance from the source (Fig. 3). Therefore, forested streams close to the source (Group I) had significantly higher mean slopes (51.1‰) than streams in the other groups, including open land headwater streams (6.3‰, Table 3; t-tests, p<0.05). Stream depth and width varied significantly along the upper continuum (Fig. 3). Depth and width were significantly higher (0.23 m and 2.13 m) in streams located furthest away from the source (Group IV) than in forested stream close to the source (0.05 m and 0.81 m) (Table 3; t-tests, p<0.05). Open land headwater streams (Group II) and streams in the middle part of the continuum

(Group III) had identical mean depths and widths, indicating limited physical variation in the upper and middle parts of open land catchments (Table 3).

Discharge and mean current velocity increased with distance to the source (Fig. 3). However, discharge was not significantly different among the upper streams (Group I to III). Only streams located furthest downstream had significantly higher discharge (0.111 m^3 s^{-1}) than streams in the other groups (I: 0.007 m^3 s^{-1}; II: 0.037 m^3 s^{-1} and III: 0.056 m^3 s^{-1}; Table 3; t-tests, p<0.05). Mean current velocity was significantly different between group I (0.09 m s^{-1}) and group IV streams (0.19 m s^{-1}), whereas groups II and III had intermediate current velocities (Table 3).

Table 3. Mean annual characteristics of the streams in the 4 groups along the upper river continuum (mean and range). Lower case letters indicate significant mean values (t-test, p<0.05).

Parameter	Group I	Group II	Group III	Group IV
	(Forest, < 2000m) (n=33)	(Open, < 2000m) (n=19)	(Open, 2000 - 4000m) (n=40)	(Open, > 4000m) (n=49)
Discharge (m^3 s^{-1})	0.007[a] (0.001 − 0.081)	0.037[a] (0.006 − 0.103)	0.056[a] (0.001 − 0.186)	0.111[b] (0.007 − 0.370)
Stream slope (‰)	51.1[a] (1.5 − 242.1)	6.3[b] (0.5 − 25.7)	3.8[b] (0.5 − 20.0)	2.7[b] (0.1 − 8.3)
V_{Mean} (m s^{-1})	0.09[a] (0.01 − 0.27)	0.16[ab] (0.02 − 0.41)	0.16[ab] (0.01 − 0.44)	0.19[b] (0.04 − 0.40)
Width (m)	0.81[a] (0.32 − 1.77)	1.38[b] (0.51 − 2.20)	1.50[b] (0.76 − 2.85)	2.13[c] (0.75 − 5.53)
Depth (m)	0.05[a] (0.01 − 0.25)	0.15[b] (0.07 − 0.28)	0.16[b] (0.04 − 0.35)	0.23[c] (0.06 − 0.50)
Width$_{CV}$ (%)	23[a] (7 − 63)	17[b] (0 − 36)	18[b] (0 − 39)	20[b] (5 − 48)
Depth$_{CV}$ (%)	83 (42 − 183)	58 (33 − 99)	61 (27 − 171)	53 (28 −75)
Macrophyte coverage (%)	1[a] (0 − 15)	41[b] (2 − 95)	39[b] (0 − 97)	63[c] (2 − 100)
SH	0.38[a] (0.00 − 0.64)	0.30[b] (0.00 − 0.52)	0.34[ab] (0.00 − 0.58)	0.37[ab] (0.05 − 0.68)
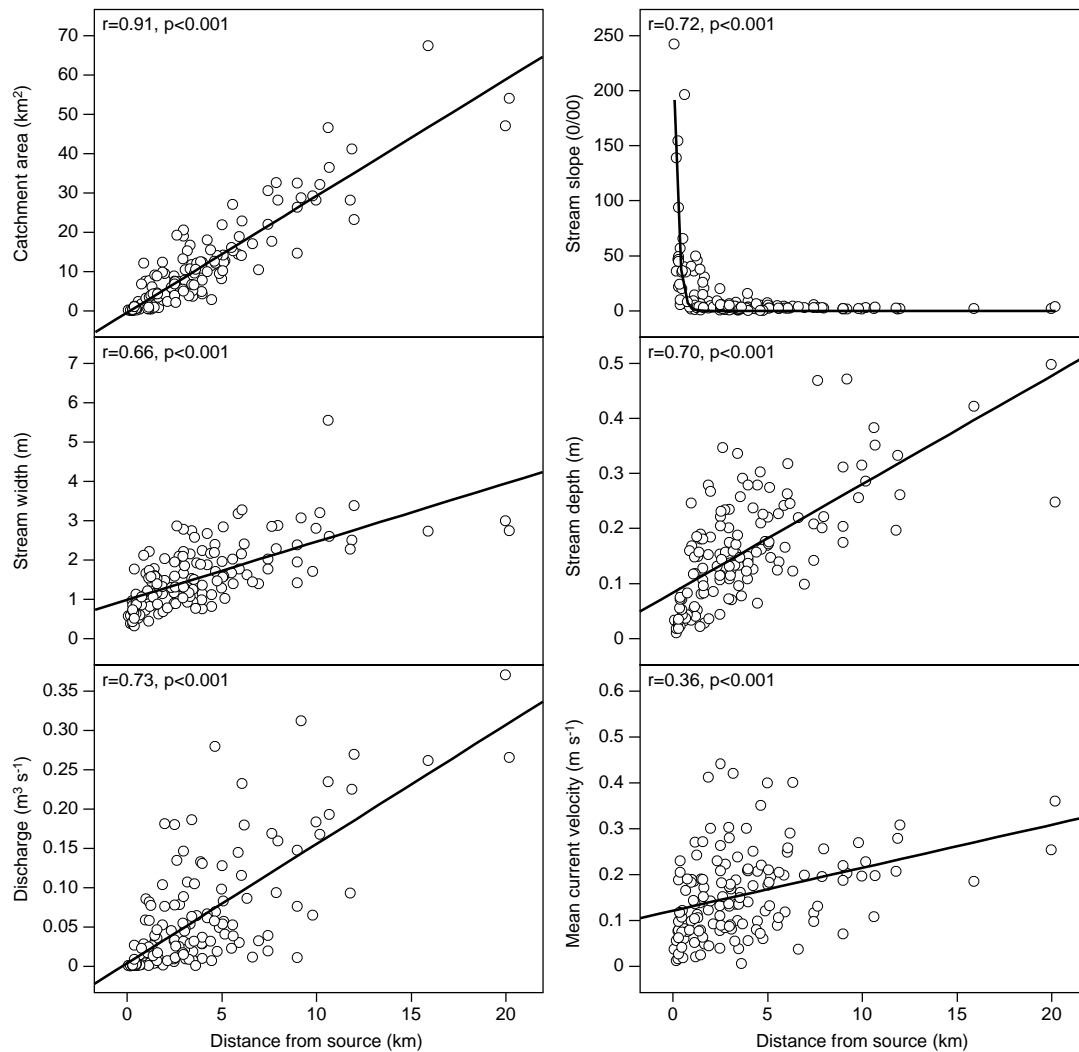
Figure 3. Variations in physical stream features with distance from the source. Catchment area, Stream slope, Stream width, Stream depth, Discharge and Mean current velocity. Least squares correlation coefficients and p-values are shown in each plot.

Variations in depth ($Depth_{CV}$) were not significantly different among the groups. $Depth_{CV}$ was higher (83%) in the forested headwater streams than in the other three groups (mean: 57%, Table 3). Variations in width ($Width_{CV}$) were significantly higher (23%) in forested headwater streams than in the other three groups (Table 3; t-tests, $p<0.05$). The substratum heterogeneity (SH) was highest (0.38) in the forested headwater streams and lowest in the open headwater streams (0.30; Table 3; t-tests, $p<0.05$). Intermediate SH-values were found in the larger streams further downstream (Group III, IV).

The cover of CPOM decreased exponentially with increasing distance to the source, reflecting changes in riparian land use and stream characteristics from small forested headwater streams to open larger streams (Fig. 4A). The coverage of coarse substrata (gravel + stones) was constant along the upper continuum (Fig. 4B & Fig. 5). Macrophyte coverage was low (1%) in forested streams and increased with distance to the source (Table 3).

Seasonal differences in physical habitat structure in open land streams

The coarse substrata varied little among stream groups in both summer and winter/spring (Fig. 5). In spring there was no significant difference in coverage of any substrata among the groups (Fig. 5; t-tests, $p>0.05$). In summer, however, mud coverage was significantly lower and sand coverage significantly higher in Group I and IV than in Group II and III (Fig. 5; t-tests, $p>0.05$). The substrata in the forested headwater streams vary little between summer and spring/winter (Paired t-test, $p>0.05$). In all other stream groups, mud and sand coverage varied significantly between seasons (Fig. 5; Paired t-test, $p>0.05$). The highest seasonal variations in substrata were found in the open headwater streams and variations decreased with distance to the source (Fig. 5; ANOVA, $p<0.05$).

The seasonal pattern in substratum cover clearly indicated that some streams varied more than others. In order to analyse if large-scale parameters controlled these seasonal differences,

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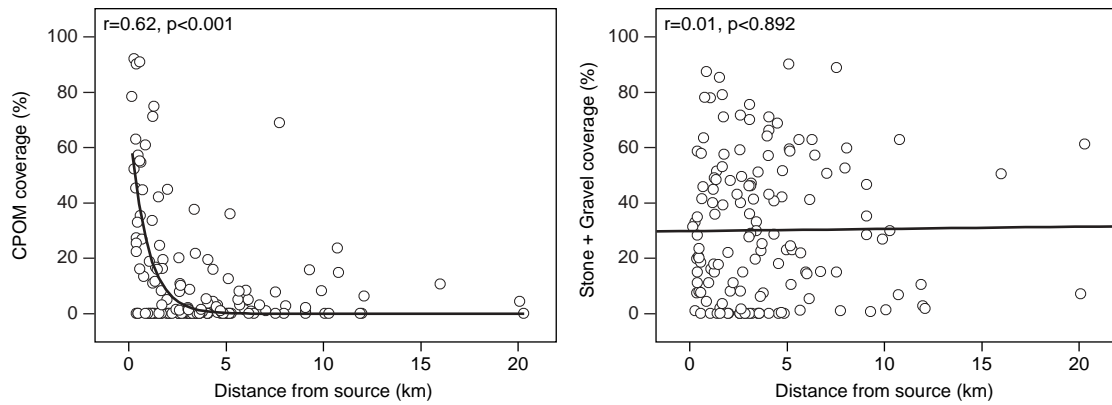
Figure 4. Variations in CPOM cover and cover of coarse substrata (stone + gravel) with distance from the source. Least squares correlation coefficients and p-values are shown in the plots.
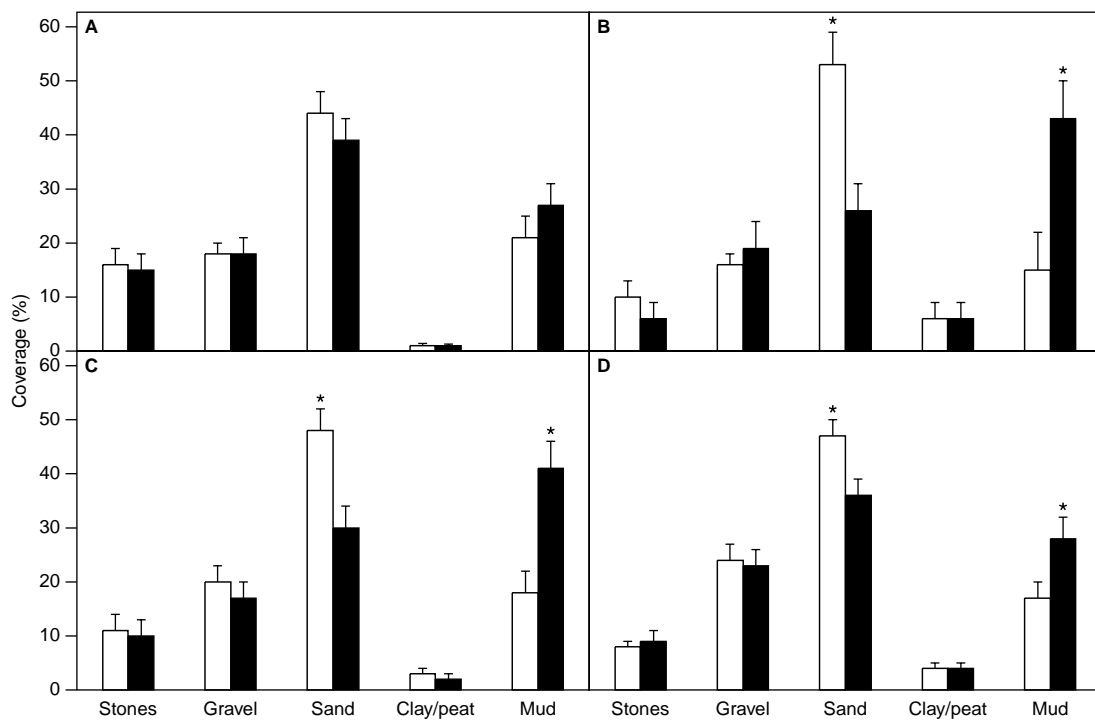
Figure 5. Substratum characteristics in spring / winter and summer with increasing distance from the source. Open bars represent winter/spring substratum coverage and filled bars represent summer coverage. (A) Forested streams, 0-2000 m from the source, (B) Non-forested streams, 0-2000 m from the source. (C) Streams, 2000 – 4000 m from the source. (D) Streams, >4000 m from the source. (*) Denotes significant differences in coverage between summer and winter/spring (Paired t-test, p<0.05).

an analysis of the seasonal difference in physical habitat structure in open land streams was performed. All physical parameters in the streams varied significantly between summer and winter/spring (Table 4; Paired t-test, p<0.05). Generally, stream dimensions, discharge, current velocity and SH were highest in spring/winter, whereas variations in depth and width were significantly highest in summer (Table 4).

The PCA analysis of physical habitat structure in streams located in open land explained 70% of the variation in the data, and the first three PCA axes had eigenvalues greater than 1. Euclidean distance was used as a measure of physical habitat difference between summer and

Table 4. Physical characteristics (mean ± standard error) of the streams located in the open land (N=111) in summer (May – August) and winter/spring (December – March). P-values from the paired t-test are also shown.

Parameter	Summer	Winter/Spring	p-value
Width (m)	1.69 ± 0.09	1.82 ± 0.07	< 0.001
CV of width (%)	20 ± 1	18 ± 1	0.004
Depth (m)	0.16 ± 0.01	0.22 ± 0.01	< 0.001
CV of depth (%)	61 ± 3	54 ± 1	0.018
Discharge ($m^3 s^{-1}$)	0.043 ± 0.006	0.116 ± 0.011	< 0.001
Current velocity ($m s^{-1}$)	0.11 ± 0.01	0.24 ± 0.01	< 0.001
SH	0.32 ± 0.02	0.37 ± 0.01	0.003

winter/spring and was based on all three PCA axes. Seasonal differences in physical habitats were higher in streams with natural cross sections than streams with disturbed and semi-natural cross sections (t-tests, p<0.05).

Streams with relatively high summer discharge generally experience smaller seasonal variations in physical habitat structure than streams with low summer discharge (Fig. 6). Discharge increased with distance to source and the seasonal variations were therefore highest in the smaller streams close to the source. High macrophyte growth generally decreased seasonal differences in habitat structure (Fig. 6). Macrophyte growth and discharge were inter-correlated since discharge and macrophyte coverage increased with distance from the source. The most stable habitat conditions were found in the larger streams with high macrophyte coverage and high discharge.

Discussion

Physical habitat structure along the upper continuum

The variations in physical parameters along the upper continuum in lowland Danish streams generally followed the patterns described in the geomorphologic concepts from large river systems (Schumm, 1977). Discharge in Danish streams is normally dominated by groundwater and streams have relatively stable hydrologic conditions. These stable conditions and uniform catchment topography and geology are believed to result in gradual changes in dimensions and flow conditions along the continuum (Ward & Robinson, 1999). Stream width, depth, discharge and mean current velocity increased with increasing distance from the source. Stream slope decreased exponentially with distance to the source.

In natural stream systems the CPOM coverage would vary along the continuum in response to forest cover and type as well as stream size (Friberg, 1996). In the forested upland areas the CPOM coverage should be high due to large inputs from the forest. In the macrophyte-rich reaches further downstream, the CPOM coverage should be lower and primarily consist of macrophyte detritus or transported CPOM from upstream-forested areas. If Danish lowland streams had been natural, most if not all of the studied sites would have been located in forests (Friberg, 1996), and CPOM cover would thus be a function of the ability of the streams to retain CPOM on the stream bed. I found that CPOM decreased exponentially with distance to the source. This pattern is therefore not the one expected in natural lowland stream areas, but has primarily to do with the fact that forested streams are constrained to the headwater areas.

Geomorphologic studies in many major river systems have shown characteristic variations in streambed substratum along the river continuum (e.g. Leopold *et al.*, 1964; Petts *et al.*, 2000). The headwater streams contain coarse substratum because the available stream power is insufficient to transport coarse substrata while finer substrata are removed and deposited further downstream. Median substratum size has been shown to decrease along the continuum as stream transport capacity increases and larger particle sizes and sediment volumes can be eroded (Leopold *et al.*, 1964; Schumm, 1977). The coverage of coarse substrata varied little along the upper continuum, whereas mud cover was high in small and medium-sized open streams (group II and III), but it was also high in forested streams and larger open streams. These results could reflect the narrow gradient studied. In order to put these findings into perspective, substratum charac-teristics from two larger streams and two rivers
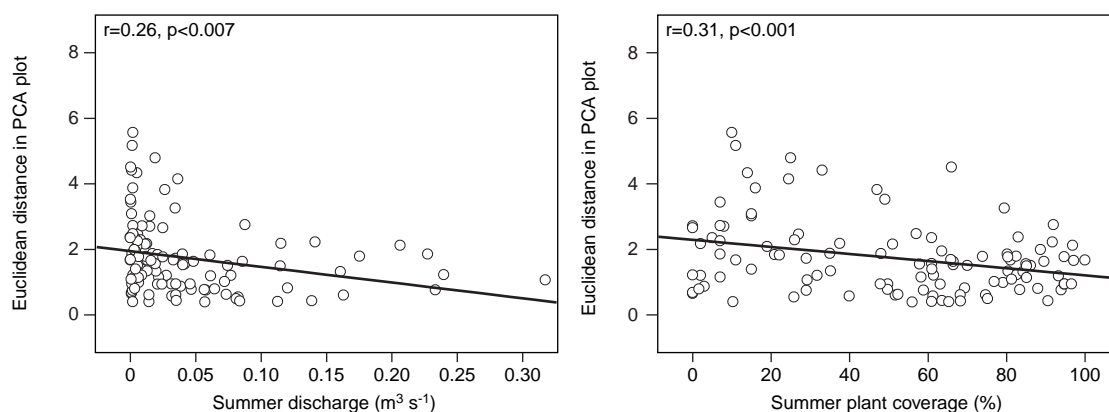

Figure 6. Differences in physical habitat structure between summer and spring/winter as a function of (A) summer discharge and (B) summer macrophyte cover. The difference is expressed as the Euclidean distance between the summer and spring/winter point for each stream in the PCA ordination.

were included in the discussion (Table 5). The results show that coarse substrata are a dominant feature of streams up at least 11 m wide. Mud cover decreased significantly when the stream width exceeded 4.3 m.

The presence of coarse substrata is also partly governed by the fact the upland areas in most large rivers of the world are located in relatively high altitude areas (usually mountains) where bedrock is present. Lowland areas dominate the Danish landscape, which has been formed by glaciers. No bedrock is present except on the island of Bornholm, which was not included in this survey. In contrast to the large river systems of the world, the small Danish catchments are geologically uniform, primarily consisting of sandy melt water deposits or moraine tills (Sugden & John, 1976). The coarse substrata in Danish lowland streams are therefore derived from erosion of similar sediments uniformly distributed from source to outlet. The combination of low power streams these uniform large-scale features may govern a more evenly distribution of the substrata along the continuum.

Naturally limited variation in coarse substrata along the lowland Danish streams due to homogeneous geologic conditions may also explain this pattern. Some of the most significant concentrations of coarse substrata have been reported from main channels in the large Danish streams, such as the river Gudenå (Madsen & Gregersen, 1998). In a global perspective the larger streams in Denmark are medium sized and probably belong to the upper erosion zone in the geomorphological continuum concept (Schumm, 1977). The apparently continuous substitution of coarse substrata with fine substrata along the river continuum may thus be true for large streams covering a larger range of geological conditions, but not necessarily for relatively small groundwater-fed lowland streams.

These results indicate that Danish lowland stream systems are not real continua, but systems where a number of physical thresholds determine morphological characteristics, such as substratum characteristics. For example, a threshold seems to exist at a certain point within the catchments where mud cover on the stream bed becomes insignificant and is then limited to the vegetated zone near the stream bank. This proposal of a threshold controlled system is in agreement with a concept describing the river system as a mosaic of patches, as argued by other researchers (e.g. Townsend, 1996; Poole, 2002).

Habitat structure in relation to cross section morphology and effects of riparian land use

Stream width, depth, discharge and mean current velocity increased with increasing distance from the source. Many of the studied streams have undergone significant habitat degradation by channelization and subsequent dredging (Brookes, 1987; Iversen et al., 1993), but this did not affect the large-scale pattern.

The majority of high-gradient streams were located in forests and low-gradient streams in agricultural areas and in areas with other open land use. High-gradient headwater streams have remained surrounded by forests due to difficulties in turning these areas into productive agricultural land. The high frequency of undisturbed cross sections in the forested streams underline this. The highest frequency of disturbed cross-sections was found in the low-gradient areas, which relatively easily have been turned into productive agricultural areas. Stream slope variations are therefore closely interrelated to profile type and riparian land use.

I found a significant difference in physical stream structure between forest streams and streams located in the open land. Streams located in forests were small headwater streams. The streams dominated by agriculture were generally located further downstream and were thus larger and had higher discharge. The largest seasonal variations in substratum characteristics were found in upper open land streams and in intermediate streams despite a relatively high

Table 5. Substratum characteristics in Danish streams located at different distances from the source. Values for forested and other small upland streams are mean values based on the number of observations indicated in the table. Values for Mattrup stream, Tange stream, River Gelså and River Skjernå are based measurements in two reaches and in at least 10 transects (approx. 150 points) in each reach.

	Forest streams N=33	Small streams N=110	Mattrup stream	Tange stream	River Gelså	River Skjernå
Catchment area (km^2)	1	14	45	70	311	2500
Distance to source (km)	1.3	4.6	9.9	16.7	41.0	97.5
Width	0.8	1.9	4.3	6.5	11.0	30.0
Stone	15	10	2	1	5	0
Gravel	15	17	20	21	25	8
Sand	40	43	60	42	62	88
Mud	25	25	18	2	6	4
Clay/peat	5	5	0	4	2	0

percentage of natural and semi-natural cross sections. These results indicate that the natural dynamics in the forest streams stabilises the substratum. Large-scale parameters such as discharge and sediment transport probably overrule the significance of the naturalness of the cross sections in the streams in the open land. Variations in physical structure in these streams may be caused by large-scale instability on unstable upstream reaches. The higher stability in forest streams was probably caused by a greater spatial substratum heterogeneity (SH), which could dissipate the energy from the flow.

Seasonal differences in physical habitat structure
Relatively high flow during summer, and thus higher mean current velocities, help stabilise the streambed in the larger streams. The results showed that high summer discharge and high macrophyte coverage reduced differences in the physical structure of the streams between summer and winter/spring. Macrophytes and discharge are, however, intercorrelated and the quantitative significance of each parameter is therefore difficult to separate. The lower seasonal differences in streams with high discharge and high macrophyte coverage suggest that accelerated near-bed current velocities around the macrophytes are capable of eroding fine sediments and thereby minimise seasonal variations in substrata coverages (Sand-Jensen, 1998). In this way there is a spin-off of high discharge and high macrophyte cover to stabilise the habitat conditions.

In the small streams in the open land and intermediate streams low discharge during summer enhanced mud deposition, which is then eroded during the higher flows in winter. This situation creates large seasonal variation in the coverage of different substrata. Terrestrial plants with different morphology than submersed macrophytes tend to dominate stream plant communities in small lowland streams. These plants potentially create more flow friction and thus enhance deposition of fine sediments, thereby affecting the seasonal variations in the smaller streams (Riis *et al.*, 2001). The seasonal pattern in the substrata was also supported by the analysis of the entire physical habitat structure. The key-role of macrophytes in lowland streams has been reported by many researchers (e.g. Sand-Jensen *et al.*, 1989; Riis, 2000). My results indicate that relationships between discharge, macrophyte coverage (biomass) and physical habitats are very complex and change through the stream systems. The results also points at the importance of low-flow conditions for the physical habitat structure (Wood *et al.*, 1999; Miyake & Nakano, 2002). The largest habitat variations (and thus the most

seasonally variable) can be expected in streams with low discharge

The seasonal variations in physical stream conditions along the upper continuum indicate the existence of hierarchical system in which higher order parameters, such as discharge and macrophyte growth act as important controls on seasonal variations in lower-scale physical stream parameters (Schumm, 1977; Frissell *et al.*, 1986).

Perspectives

According to the Water Framework Directive streams have to be managed at a catchment basis and correct management of water resources therefore requires knowledge of variations in biological and physical characteristics along the continuum. Physical habitat quality, in particular, must be determined for all streams and the reference condition defined. It is therefore important to acquire knowledge of variations in physical habitat quality and quantity. Analysis of parameter relationships along the continuum may therefore provide useful information of the physical basis of the stream ecosystem. The WRD will to be used throughout Europe and across large gradients in catchment size, physical features, geology and climate. It is therefore essential to collect information about parameter changes along small as well as large river systems in order to ensure proper management of the European water resources in the future.

Acknowledgements

References

Brookes A, Gregory KJ & Dawson FH (1983): An assessment of river channelization in England and Wales. *Science of the Total Environment*, **27**, 97-112.

Brookes A (1987): The distribution and management of channelized streams in Denmark. *Regulated Rivers: Research and Management,* **1**, 3-16.

Brookes A (1988): *Channelized Rivers - Perspectives for Environmental Management.* John Wiley and Sons, Chichester.

Church M (1996): Channel morphology and typology. In: *River flows and channel forms* (Eds. GE Petts & P Calow), pp. 185-202. Blackwell Scientific Publications, Oxford.

Clarke KR & Warwick RM (1994): *Change in marine communities. An approach to statistical analysis and interpretation.* National Environmental Research Council, Plymouth, UK.

Friberg N (1996): *Biological structure of forest streams and effects of afforestation.* Ph.D. Thesis. National Environmental Research Institute, Silkeborg, Denmark.

Frissell CA, Liss WJ, Warren CE & Hurley MD (1986): A hierarchical framework for stream habitat classification - viewing streams in a watershed context. *Environmental Management,* **10**, 199-214.

Iversen TM, Kronvang B, Madsen BL, Markmann P & Nielsen MB (1993): Reestablishment of Danish streams - restoration and maintenance measures. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **3**, 73-92.

Leopold LB, Wolman MG & Miller JP (1964): *Fluvial processes in geomorphology.* W. H. Freeman & Co., San Francisco.

Madsen BL & Gregersen J (1998): *Streams in Denmark* (In Danish). Gad, Copenhagen.

Miyake Y & Nakano S (2002): Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. *Freshwater Biology,* **47**, 219-230.

Nielsen K, Stjernholm M, Olsen BØ, Müller-Wohlfeil DI, Madsen I, Kjeldgaard A, Groom G, Hasen HS, Rolev AM, Hermansen B, Skov-Petersen H, Johansen VK, Hvidberg M, Jensen JE, Bacher V & Larsen H (2000): *Area Information System - AIS* (In Danish). Danmarks Miljøundersøgelser, Silkeborg.

Pedersen ML, Friberg N & Larsen SE (2002): Physical habitat structure in Danish lowland streams. *,River Research and Applications* (Accepted).

Petts GE, Gurnell AM, Gerrard AJ, Hannah DM, Hansford B, Morrissey I, Edwards PJ, Kollmann J, Ward JV, Tockner K & Smith BPG (2000): Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **10**, 249-266.

Poole GC (2002): Fluvial landscape ecology: addressing uniqueness within the river continuum. *Freshwater Biology,* **47**, 641-660.

Primer-E Ltd. (2001): *Primer Software Package, version 5.* Primer-E Ltd, Plymouth, UK.

Riis T (2000): *Distribution and abundance of macrophytes in Danish streams.* Ph.D. Thesis.

National Environmental Research Institute, Silkeborg, Denmark.

Riis T, Sand-Jensen K & Larsen SE (2001): Plant distribution and abundance in relation to physical conditions and location within Danish stream systems. *Hydrobiologia,* **448**, 217-228.

Sand-Jensen K (1998): Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology,* **39**, 663-679.

Sand-Jensen K, Jeppesen E, Van der Bijl L, Nielsen K, Wiggers-Nielsen L & Iversen, TM (1989): Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology,* **22**, 15-32.

SAS Institute (2000): *The SAS System Version 8.2.* SAS Institute. Cary, USA.

Schumm SA (1977): *The fluvial system.* John Wiley and Sons, New York.

Snedecor GW & Cochran WG (1989): *Statistical methods.* Iowa State College Press. Ames, Iowa.

Southwood TRE (1977): Habitat, the template for ecological strategies? *Journal of Animal Ecology,* **46**, 337-365.

Sugden DE & John BS (1976): *Glaciers and landscape.* Edward Arnold, London.

ter Braak CJF (1995): Ordination. In: *Data analysis in community and landscape ecology* (Eds. RHG Jongman, CJF ter Braak & OFR van Tongeren), pp. 91-173. Cambridge University Press, Cambridge.

Townsend C R (1996): Concepts in river ecology: pattern and process in the catchment hierarchy. *Archiv für Hydrobiologie Supplement,* **113**, 3-21.

Vannote RL, Minshall GW, Cummins KW, Sedell JR & Cushing CE (1980): The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37**, 130-137.

Ward RC & Robinson M (1999): *Principles of hydrology.* McGraw-Hill, London.

Wentworth CK (1922): A scale of grade and class terms for clastic sediments. *Journal of Geology,* **30**, 377-392.

White KE (1978): Dilution methods. In: *Hydrometry* (ed. RW Herschy), pp. 47-55. John Wiley and Sons, Chichester.

Wood PJ, Armitage PD, Cannan CE & Petts GE (1999): Instream mesohabitat biodiversity in three groundwater streams under baseflow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **9**, 265-278.

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Appendix A

Morten Lauge Pedersen & Nikolai Friberg

Forslag til opstilling af fysisk indeks

Baggrund

Forringede fysiske forhold i vandløbene er estimeret som hovedårsagen til at mange målsatte vandløb ikke opfylder deres målsætning i dag. Dansk Vandløbsfaunaindeks-værdien beskriver en given vandløbsstræknings biologiske tilstand, dvs. summen af alle påvirkninger af strækningen – fysisk, biologisk og kemisk. I tilfælde af at målsætningen på en vandløbsstrækning ikke er opfyldt, skal det vurderes hvad grunden her til er. For at kunne skille de fysiske forholds betydning for tilstanden fra, er det nødvendigt med en standardiseret metode til beskrivelse af disse forhold. Praksis i dag ved prøvetagning efter DVFI-metoden er at forsøge at tage faunaprøven så repræsentativt som muligt i forhold til de fysiske forhold, der forekommer på strækningen (dog skal én af tre sparkeprøver udtages i et stryg). Samtidig registreres eventuel lugt eller farvning af vandet. Desuden registreres substrattyper og strømforhold.

Opstillingen af et standardiseret Vandløbsfysisk Indeks vil kunne hjælpe til en bedre tolkning af de fysiske forholds betydning for vandløbskvaliteten i vores vandløb. Her beskrives en metode til en objektiv vurdering af de fysiske forhold i vandløb, dels med udgangspunkt i danske og udenlandske erfaringer og dels ud fra de aktuelle forhold i de danske vandløb.

Erfaringer med opstillinger af fysiske indeks

I England er der udviklet et system til en klassificering/beskrivelse af vandløbsfysiske forhold og habitater – the River Habitat Survey (RHS). RHS benytter en standardiseret metode hvor prøvetageren på en 500 meter vandløbsstrækning skal vurdere bl.a.:

– Brummens udseende og planter
– Vandløbsmorfologiske forhold
– Fysiske forhold i vandløbets forskellige habitater
– Forhold i oplandet til strækningen

Alle data indføres i standardiserede skemaer og en fysisk habitatvurdering, der ikke er relateret til et biologisk samfund, foretages. Vandløbsstrækninger over hele England kan således sammenlignes da der er udført det samme måleprogram på dem. RHS er baseret på inspektion af vandløbsstrækningerne og vurdering af de fleste parametre. Dette betyder at man har haft svært ved at opnå reproducerbare resultater – forskellige prøvetagere har ikke kunnet komme frem til samme resultater på de samme strækninger. Dette skyldes at systemet er baseret på mange vurderinger og på få målinger. RHS er således ikke foreløbigt objektivt og robust mht. prøvetagning og der er ikke i systemet en klar kobling mellem den fysiske habitatkvalitet og den biologiske vandløbskvalitet målt vha. smådyr.

Men også andre europæiske lande og initiativer beskæftiger sig med vurdering af den fysiske vandløbskvalitet. Både i Frankrig og Tyskland findes systemer der er sammenlignelige med RHS. Den europæiske standardiseringsorganisation, CEN, arbejder på at udvikle en fælles europæisk standard for måling af fysisk habitatkvalitet. Denne standard er fortrinsvis baseret på de engelske og franske erfaringer på området.

Danske erfaringer

Flere amter har benyttet sig af at vurdere de fysiske forhold i vandløbet i forbindelse med udtagningen af faunaprøver. Her præsenteres to danske bud på et Vandløbsfysisk indeks.

Århus-indekset

Indekset er bygget op omkring vurderingen af en lang række fysiske forhold i vandløbet. Tilstedeværelsen af forskellige formelementer og substrattyper skal vurderes sammen med intensiteten i tilstedeværelsen. I modsætning til Fyns-indekset indgår der en negativ vægtning af elementer der regnes for negative i forhold til vandløbsmiljøet. Indeksværdien beregnes som summen af alle værdierne for de enkelte elementer (tabel 1). Indekset kan antage værdier mellem –20 og 48. Indeksværdien vurderes herefter i forhold til vandløbets målsætning. De fysiske forhold beskrives som hhv. gode, acceptable, ikke acceptable eller dårlige inden for visse intervaller af det fysiske indeks. Der skal ikke så høj en indeksværdi til at opnå god kvalitet for et B3-målsat vandløb som for et A-målsat vandløb. Omvendt skal indeksværdien ikke være ret lav, før de fysiske forhold på en A-målsat strækning angives som ikke acceptable eller direkte dårlige.

Tabel 1. Århus-indekset.

Parameter	Intensitet (I)	Faktor (F)	Værdi (=FxI)
Høller og stryg		x2	
Mæandrering		x1	
Gydegrus		x2	
Grus		x2	
Sten		x2	
Rødder		x1	
Grødebanker		x1	
Underskårne brinker		x2	
Udhængende vegetation el. træer		x1	
Anden fysisk variation		x2	
Negative parametre Sandvandring		x-2	
Blød ustabil bund		x-1	
Bredt vandløbsprofil i.fht. vandføring		x-1	
Nyligt opgravet (lille indgreb = 1 stort indgreb =2)		x-1	
Reguleret/udgravet		x-1	
Okker		x-1	
Indeksværdi			Sum af hele kolonnen
Intensitet angives som: 1 lille forekomst 2 middel forekomst 3 dominerende			

Fyns-indekset

Det fynske indeks er forholdsvist simpelt bygget op, og vurderingen af de fysiske forhold kan relativt hurtigt gennemføres. Indeksværdierne fastlægges ved vurdering, og der foretages ingen målinger i vandløbet. Vandløbets grad af regulering beskrives ved en klassificering i tre grupper: ureguleret, noget reguleret og reguleret. Tilstedeværelsen af forskellige substrattyper beskrives i tre grupper – jo grovere substrat jo højere værdi. Indeksværdien findes ved at værdierne for de substrater der er tilstede summeres (maksimalt 11) og ganges med reguleringsværdien. Indekset kan antage værdier mellem 0 og 22 – højest er bedst. Indekset er skitseret i tabel 2.

Tabel 2. Fyns-indekset

Slyngningsgrad	Værdi	Substrat	Værdi
Ureguleret	2	Sten	3
Noget reguleret	1,5	Grus, døde grene	2
Reguleret	1	Slam, detritus, sand, vandplanter	1

Opstilling af fysisk indeks for danske vandløb

De fysiske forhold på en given vandløbsstrækning er et produkt af de naturgivne forhold, indgreb direkte på strækningen samt forholdene i oplandet til strækningen. Ved opstillingen af det fysiske indeks er det vigtigt at man i videst muligt omfang kan skille disse tre typer af påvirkninger fra hinanden og således kvantificere dem hver for sig.

Det fysiske indeks skal kunne relateres til DVFI-værdien eller andre biotiske forhold på strækningen. Dvs. en høj DVFI-værdi skulle gerne afspejle en stor fysisk variation og dermed en høj værdi for det fysiske indeks. Strækninger der er fysisk påvirkede, skulle således gerne få en lavere indeksværdi end de upåvirkede strækninger af samme type. Ud fra det fysiske indeks og viden omkring faunaelementernes (smådyr og fisk) udbredelsesmønster skal man kunne forudsige strækningens potentielle faunaklasse og smådyrs- og fiskesamfundets sammensætning og tæthed. Dette gøres ud fra en antagelse om at der er knyttet karakteristiske faunasamfund til uforstyrrede vandløb indenfor samme region. Det er desuden vigtigt at indeksets værdier afspejler hvilke indgrebsmuligheder, der kan anvendes for at ændre på den givne tilstand.

Belært af erfaringerne fra det engelske RHS, som udelukkende er baseret på vurderinger af de fysiske forhold, er det vigtigt, at et dansk indeks er baseret på reelle målinger af fysiske parametre i vandløbet, kombineret med vurderinger af forholdene omkring vandløbsstrækningen. En anden vigtig lære der kan drages af de engelske erfaringer er at de vurderinger der skal foretages, skal være så simple at de til en hver tid kan reproduceres af en anden prøvetager – systemet skal med andre ord være robust.

Opbygning

Det vandløbsfysiske habitatindeks (kaldet VFHI) består som udgangspunkt af 3 dele der hver for sig udtrykker en indeksværdi der kan relateres til vandløbet eller dets nære miljø (figur 1). De tre del-indeks er som følger:

– Vandløbsindeks (opmålt på en strækning med en bredde-afhængig længde på mindst 20 m)
– Strækningsindeks / ådals (vurderinger af parametre knyttet til vandløbets udseende, brinken, bræmmen og ådalen foretaget på en strækning der mindst er 100 m lang)
– Oplandsindeks

Opdelingen i tre indeks er et udtryk for at kvaliteten af en given vandløbsstrækning er styret af forskellige processer og mekanismer der hver for sig yder en påvirkning på vandløbets miljø på forskellige skalaer. Det er også et udtryk for at forskellige forhold i vandløbet varierer med forskellig frekvens og derfor skal vurderes / måles med forskellige intensitet: Den overordnede morfologi i vandløbet ændres kun meget langsomt mens hastigheds-, bredde- og dybdeforholdene i vandløbet kan ændres fra dag til dag hvis vandføringen ændres. Endelig følger planter og andre af vandløbets organismer typisk en sæsonvariation mht. udbredelse og vækst.

Som udgangspunkt arbejdes der på en 100 m ekstensiv strækning (strækningsindekset) hvis vandløbet er bredere end 4m dog på en længere strækning. I selve vandløbet benyttes en intensiv strækning beliggende i midten af den ekstensive strækning til målinger af parametrene til vandløbsindekset.
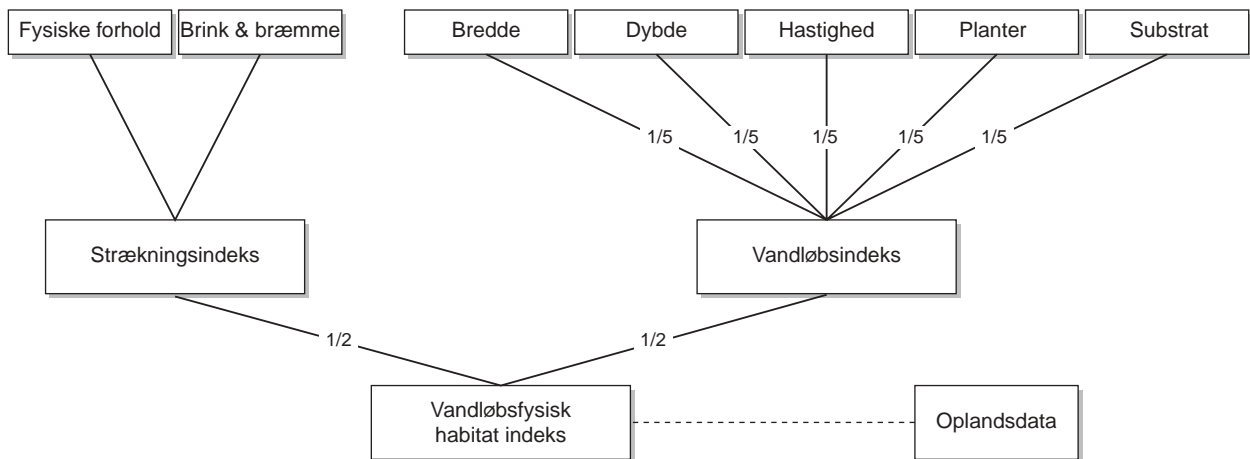
Figur 1. Principskitse af beregningsrutinerne i det vandløbsfysiske habitat indeks

Strækningsindekset (typisk, 100, 200 eller 300 m)				
				Vandløb
		Vandløbs- indeks		Brink (vandspejl til kronekant)
				Bræmmen /ådal (kronekant – 50 m)

Figur 2. Principskitse af delstrækninger og målekvadrater til brug i det fysiske indeks

Oplandsindeks

På oplandsniveau indsamles data om jordbundsforhold: arealanvendelse, tilstedeværelsen af punktkilder og spredt bebyggelse. Desuden identificeres eventuelle mulige påvirkninger fra by-mæssig bebyggelse. Disse data indgår ikke direkte i det fysiske indeks, men fungerer som bag-grundsdata der skal være med til karakterisere forholdene i oplandet til den undersøgte stræk-ning. Oplandsdata indsamles én gang, og genindsamling foretages kun i det omfang der sker væ-sentlige ændringer i forholdene i oplandet. Disse oplysninger vil typisk skulle indsamles med års mellemrum.

Parametre
– jordbundsforhold
– arealanvendelse
– punktkilder
– spredt bebyggelse

Strækningsindekset

Følgende parametre skal vurderes i strækningsindekset:

- Længdeprofil
- Tværprofil
- Fald
- Brink vegetation
- Bræmmebredde

- Bræmme vegetation
- Mesohabitater – substrattyper

Alle del-elementer skal vurderes hvis det er muligt. Skulle der være enkelte elementer som ikke kan vurderes med de kategorier og parametre der bruges i det fysiske indeks, så udelades disse blot. Indeksberegningen foretages derefter på et reduceret antal parametre hvor vægtningen er justeret efter det reducerede antal parametre.

Strækningen bør udvælges så repræsentativt som overhovedet muligt for den vandløbsstrækning. Længden af strækningen varieres alt efter hvor bredt vandløbet er (tabel 3).

Tabel 3. Den undersøgte stræknings længde som funktion af vandløbets bredde.

Vandløbsbredde (meter)	Strækningslængde (meter)
1	100
2	100
3	100
4	200
5	200
6	200
7	300
8	300
9	300
10	400

I nedenstående tabel 4 er angivet strækningslængden og det ideelle antal af mæanderbuer / høl- og strygsekvenser som funktion af vandløbets bredde. Generelt forholder det sig sådan at man ikke bør have mindre end 4-5 sekvenser i datamaterialet. Der er i tabellen regnet med en afstand mellem buer / høl- og strygsekvenser på 7 gange vandløbets bredde. For at holde antallet af vurderinger nede, skal der ideelt være under 30 sekvenser pr. strækning.

Tabel 4. Antal høl/sekvenser som funktion af vandløbets længde og bredde.

Bredde i m Stræknings-længde i m.	1	2	3	4	5	6	7	8	9	10
100	14	7	5	4						
200	28	14	7	7	6	5	4			
300		21	14	11	9	7	6	5	5	4
400		29	19	14	11	9-10	8	7	6	6
500			24	18	14	12	10	9	8	7
600			29	21	17	14	12	11	9-10	8-9
700				25	20	17	14	13	11	10
800				29	23	19	16	14	13	11

Længdeprofil
Vandløbets længdeprofil karakteriseres vha. tilstedeværelsen af høl- og strygsekvenser samt graden af slyngning. En kombination af de to parametre benyttes ved beregningen af indeksværdien.

Høller og stryg
Antallet af høller og stryg forekommer naturligt med en afstand på 3-4 gange bredden af vandløbet. Således er afstanden mellem to på hinanden følgende stryg ca. 5-7 gange bredden af vandløbet. Det samlede antal stryg og/eller høller opgøres på strækningen. Antallet sammenlignes med det optimale antal angivet i tabellen ovenfor. Stryg er kendetegnet ved relativ lav vandddybe, hurtig strøm (krusninger på vandoverfladen og/eller brudt overflade) og groft substrat. Høller er karakteriseret ved at være dybere, lav strømhastighed (som regel med sekundær cirkulær strøm) og fint bundsubstrat. I mæandrerende vandløb findes høller i ydersiden af sving medens stryg er beliggende på strækningerne mellem svingene. I mindre slyngede vandløb kan sekvenserne være sværere at identificere, men kan identificeres på forskelle dybde og substrat.

Feltprocedure
Antallet af høller og stryg tælles på strækningen og indføres i skema. Dette sammenlignes ved indeksberegningen med det optimale antal høller og stryg på strækningen.

Indeks score

Antal høller og stryg	Score
Ingen høller eller stryg	-10
Under 25% af det optimale antal høller og stryg til stede	0
25- 50% af det optimale antal høller og stryg til stede	10
> 50% af det optimale antal høller og stryg til stede	20

Især i mindre vandløb med meget stort fald kan det forekomme at hele strækningen henligger som ét langt stryg. Dette registreres separat og giver scoren 7.

Slyngning
Vandløbenes slyngningsgrad varierer alt efter hvor i vandløbssystemerne de er beliggende, faldet og jordtypen. Derfor skal slyngningsgraden også vurderes i forhold til vandløbets bredde. Slyngningsgraden vurderes på vandløbets overordnede udseende. Et lige vandløb vil ingen buer eller slyngninger have. I sinuøse og mæandrerende vandløb vil bølgelængden på buerne være 10-14 gange bredden af vandløbet. Slyngningsgraden kan med fordel bestemmes på 4cm kort (1:25.000) og derefter verificeres i felten. Længden af vandløbets overordnede strømningsretning måles ved at lægge en lige linie gennem eksempelvis strygene. Herefter måles vandløbets samlede længde. Forekommer der overordnede retningsændringer i vandløbet lægges knækpunkter ind på fugleflugtslinien. De to tal divideres med hinanden og et udtryk for slyngningsgraden haves:

SI = Vandløbslængde / Ådalslængde

Følgende værdier identificerer de forskellige typer af vandløb:

SI < 1,05   Lige vandløb
1,05 < SI <1,50   Sinuiøse vandløb
SI> 1,50   Mæandrerende vandløb
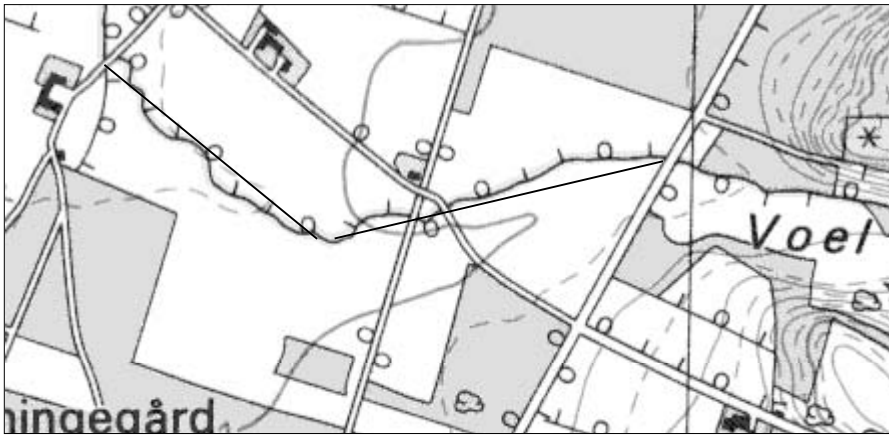
Figur 3. Beregning af slyngningsgraden. Længde langs vandløb: 829m. Længdeaksens længde: 790m. SI=1,05. Vandløbet kan således klassificeres som sinuiøst.

Felprocedure
Slyngningsgraden vurderet på kort suppleres med en vurdering i felten da især mindre vandløb kan optræde lige på kortmaterialet medens de rent faktisk er slyngede. I skemaet indføres slyngningsgraden som:

Indeks score

Slyngning	Skemaværdi	Score	
		Bredde < 2m	Bredde > 2m
Lige	0	10	2
Sinuiøst	1	10	7
Mæandrerende	2	5	15

Et vandløb der på et kort ser lige ud kan vise sig at være sinuøst eller omvendt når man kigger på det i felten. Vandløb hvor der er skabt en strømrende i et kanaliseret forløb, betegnes som kanaliserede da det er vandløbets kronekant der afgør om vandløbet snor sig.

Tværsnitsprofil
Tværsnitsprofilets udseende vurderes på strækningen. Det kan oftest være en fordel at foretage vurderingen i en række tværsnit.

Tværsnitsprofilets udseende indikerer om der har været foretaget indgreb i vandløbet hvilket vil afspejle sig i manglende variation i vandløbets tværsnit. Ved vurderingen er det hele vandløbets tværsnit fra bund til kronekant der vurderes. Tværsnittet kategoriseres i tre kategorier: naturlig, semi-naturlig og kanaliseret. De semi-naturlige tværsnit udgøres af tværsnit med udpræget undergravning af brinken (udenfor høller) og tillige kanaliserede vandløb der er på vej mod en naturlig variation. Stærkt udgravede vandløb hvor afstanden fra bund til kronekant er stor og profilet rektangulært, kategoriseres som kanaliserede. Se desuden nedenstående figur for eksempler på de forskellige tværprofiler.
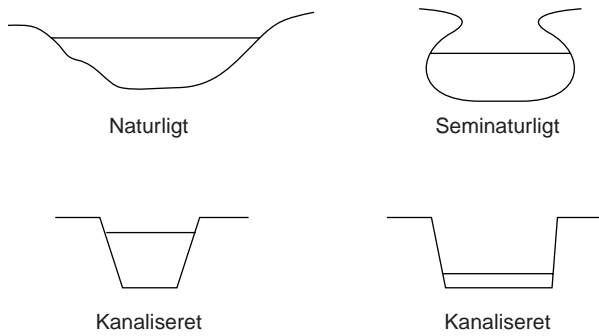
Figur 4. Tværprofiltyper.

Feltprocedure

Tværprofilerne vurderes i felten og indføres i skema. Bredden af det vanddækkede areal måles et antal gange og gennemsnitsbredden indføres i skema

Indeks score

Tværprofil type	Skemaværdi	Score
Kanaliseret	0	-10
Semi-naturligt	1	10
Naturligt	2	20

Fald

Faldet kan have stor betydning for substratets sammensætning og strømhastigheden på strækningen og dermed for smådyrenes tilstedeværelse

Feltprocedure

Strækningens fald kan opgøres på 2 måder, enten ved direkte måling af bundens hældning på strækningen i felten vha. nivelleringsudstyr eller ved at måle vandløbets længde mellem to højdekurver på et 4 cm kort. Ved opmåling på kort beregnes faldet som højdeforskellen divideret med afstanden langs vandløbet. Et fald der er vurderet på kortmateriale, er væsentligt mere usikkert end et målt fald. Hvis man ligger inde med oplysninger om bundhældningen fra tidligere målinger kan disse med fordel bruges. Faldet i promille indføres i skemaet

Indeks score

Fald	Score
<1 ‰	0
1-5 ‰	2
5-10 ‰	5
>10 ‰	10

Brink udseende og vegetation

Vegetationen på brinken (dvs. fra vandoverfladen til kronekanten) kan have betydning for om et vandløb kan karakteriseres som værende naturligt. En vegetationsløs brink vil tælle negativt medens lav græsbevoksning er neutral. Udhængende vegetation (høj vegetation og grene) kan fungere som skjulested for fisk og vil derfor tælle positivt medens alt for kraftig vækst af planter fra brinken vil tælle negativt hvis vandløb totalt skygges.

Feltprocedure

Brinken struktur vurderes som: Antallet af forskellige vegetationstyper, Ingen vegetation (I), 1 type – enkel (E), 2-3 typer – simpel (S), 4-5 typer –kompleks (K), Udhængende (U)

Vegetatitionen vurderes som: Den dominerende vegetationstype registreres, Ingen vegetation (I), Lave urter (LU), Høje urter (HU), Træer (T), Buske/krat (B), Mos (M), Kulturafgrøde (KA)

Desuden vurderes den udhængende vegetation efter følgende skema:

Udhængende vegetation	Dækning af vandløbs areal			
	0-25 %	25-50 %	50-75 %	>75 %
Dækningen under 25 % af brinken dækket	10	7	5	5
Mellem 25 % og 50 % af brinken dækket	10	5	2	0
Mellem 50 % og 75 % af brinken dækket	5	2	0	-5
Over 75 % af brinken dækket	5	0	-5	-10

Tilstedeværelsen af træer vurderes som: Skov (S); >50 % træ (U), 25-50 % træ (N), Enkelte træer (E), Ingen træer (I)

Alle vurderinger foretages på både højre og venstre side af vandløbet.

Indeks score
Er pt. ikke helt fastlagt

Bræmmen
Bræmmens vegetation, struktur og arealanvendelsen vurderes indenfor de første 5 m fra vandløbet.

Feltprocedure
Bræmme vegetation vurderes som: Ingen vegetation (I), Lave urter (LU), Høje urter (HU), Træer (T), Buske/krat (B), Mos (M), Kulturafgrøde (KA)

Bræmmens struktur vurderes som: Antallet af forskellige vegetationstyper, Ingen vegetation (I), 1 type – enkel (E), 2-3 typer – simpel (S), 4-5 typer –kompleks (K)

Arealanvendelsen vurderes indenfor følgende kategorier: Løvskov (LS), Nåleskov (NS), Vådområde (V), Urban/have (U), Hede (H), Græsset (G), under plov – omdrift (D), Krat (K).

Indeks score
Er ikke fastlagt p.t.

Ådalen
Ådalens udseende kan give en ide om hvorvidt vandløbet har været berørt af menneskehånd. Desuden vil vegetation og arealanvendelse indikere om der stadig er en potentiel påvirkning.

Feltprocedure
Ådalens udseende vurderes som: Ingen (I), Bred (B), Smal (S)

Arealanvendelsen vurderes som: Løvskov (LS), Nåleskov (NS), Vådområde (V), Urban/have (U), Hede (H), Græsset (G), under plov – omdrift (D), Krat (K).

Indeks score
Er ikke fastlagt p.t.

Vandløbets substrat
Substraternes udbredelse vurderes på hele strækningen. Der er i alt 5 point at uddele mellem de enkelte substrater, svarende til at 1 point er lig med 20% dækning på strækningen. De forskellige substrater er angivet i nedenstående tabel.

Tabel 5. Substrattyper

Sten:	> 60 mm
Grus:	3 – 60 mm
Sand:	0,25 – 3 mm
Mudder / Slam:	Sort farvet materiale <0,25 mm, som regel meget blødt
Ler:	Kompakt meget finkornet materiale, typisk < 0,063 mm
Tørv:	Organisk materiale, mere eller mindre omsat

Feltprocedure og indeks score
Substraternes score fås ved at gange antallet af point for substrattypen med værdien i nedenstående liste.

Substrattype	Score
Sten	3
Gydegrus	4
Sand	2
Mudder / silt – blød bund	-1

Da sten typisk er meget ujævnt fordelt på vandløbsstrækninger, foretages der, udover ovenstående karakteristik af substratet, også en vurdering af hvor mange sten der er tilstede på strækningen. Denne score lægges til substratscoren. Sten vurderes desuden som selvstændig parameter på hele strækningen som:

Vurdering	Kvantitativ beskrivelse	Feltværdi	Score
Ingen	0 sten	0	
Få	1 til 10 sten pr strækning	1	
Enkelte	10 til 20 sten pr strækning	2	
Udbredt	20 til 50 sten pr. strækning	3	
Mange	flere end 50 sten pr strækning	4	

I de tilfælde hvor stendækningen vurderes til 1 eller højere i substratregistreringen, svarer dette til at der skal være mange sten.

Vandplanter
Vandplanter skaber fysisk variation i vandløbet ved at ændre strømforholdene i vandsøjlen og influerer dermed også på bundsubstratet. Planternes form har også betydning for hvorledes de påvirker strømmen i vandløb. Derfor vurderes dækningen af emergente og neddykkede vandplanter separat.

Feltprocedure og indeks score
Dækningen af de to typer af vandplanter vurderes som følger.

Plantedækning	Felt værdi	Neddykkede vandplanter	Emergente vandplanter
Ingen grødedækning	0	0	0
Op til 10% af bunden er dækket af grødeøer	1	2	2
10-50% af bunden er dækket af grødeøer	2	10	5
50%-75% af bunden er dækket af grødeøer	3	7	2
over 75% af bunden er dækket af grødeøer	4	2	0

Grene, rødder og træer

Rødder, træ og grene i selve vandløbet kan medvirke til at øge habitatdiversiteten og de fysiske forhold generelt og desuden virke som skjul for fisk og levesteder for smådyr. Det er nok at disse optræder i forbindelse med den ene brink.

Feltprocedure og indeks score

Dækningen vurderes som følger.

Feltregistrering	Værdi	Score
Ingen dækning	0	0
10% dækning	1	2
10-25% dækning	2	5
over 25% dækning	3	10

Vandløbsindekset

Indekset består af 5 parametre som vurderes i 4 kvadrater i 10 transekter ækvidistant udlagt på en strækning der har en længde på 10 gange bredden af vandløbet, således at både høller og stryg dækkes i klassifikationen. Den intensive strækning placeres så vidt muligt på den del af strækningen hvor DVFI eller faunaprøven udtages, alternativt placeres denne midt på strækningen. Nedenfor er længden af denne givet ved forskellige af vandløbets bredder. Desuden er afstanden mellem de enkelte transekter på den intensive strækning også angivet.

Vandløbsbredde (m)	Intensiv strækningslængde (m)	Afstand mellem transekter (m)
1	20	2
2	20	2
3	30	3
4	40	4
5	50	5
6	60	6
7	70	7
8	80	8
9	90	9
10	100	10

Hvert transekt deles i den vanddækkede bredde i 4 lige store felter. Hvert felt er lige så langt som det er bredt, dog maks. 1 m. Der startes i det nedstrøms beliggende transekt. I hvert transekt spændes en snor tværs over vandløbet. Observatøren står nedstrøms snoren med front mod denne. Første kvadrat i hvert transekt starter ved venstre bred set i strømmens retning, se figur 3.
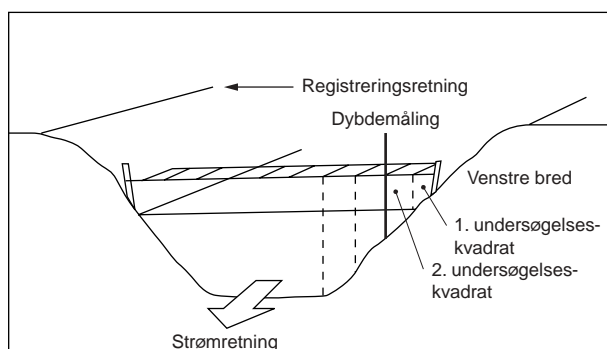
Figur 5. Opstilling af transekterne

Følgende parametre skal vurderes i hvert kvadrat:

- Bredde
- Dybde
- Planter, træ, rødder, grene
- Strømhastighed
- Substrat

De enkelte dele vægter ligeligt i indeksberegningen. Hvis én eller flere af parametre ikke kan vurderes på en strækning, udgår denne/disse af beregningen af indekset og vægtene fordeles på de parametre der kan måles.

Bredde
Den vanddækkede bredde måles med 1 cm nøjagtighed i hvert af de udlagte transekter. Bredde indeksværdien beregnes som variationskoefficienten (CV) på alle 10 målinger af bredden. Hvis variationskoefficienten er højere en 100% sættes denne til 100%.

B.I. = B_{CV}

Indekset kan antage værdier mellem 0 og 100

Dybde
Dybden måles med 1 cm nøjagtighed i midten af hvert kvadrat. Dybde indeksværdien beregnes som variationskoefficienten (CV) for alle 40 målinger af dybden. Hvis variationskoefficienten er højere en 100% sættes denne til 100% i beregningen af indeksværdien.

D.I. = D_{CV}

Strømhastighed
Hastigheden er meget svær at vurdere som absolut størrelse, og det vil gøre indekset for felt krævende at operere med en målt hastighed. Derfor vurderes hastigheden i hvert kvadrat på en skala med tre værdier:

Ingen vandbevægelse	(0)
Flydende vandbevægelse – vandoverfladen er flad og strømmen svag	(1)
Strømmende vandbevægelse – vandoverfladen er brudt og uregelmæssig evt. med stående bølger	(2)

Andelen af kvadrater med høj strømhastighed = (2) beregnes som procentandel af det totale antal kvadrater, dvs. 40:

H.I. = Antal kvadrater med høj hastighed = (2)/40 * 100

Indekset kan antage værdier mellem 0 og 100

Substrat
Substratet vurderes i hvert felts totale bredde samt i samme længde opstrøms herfor, dog maks. 1 m. I hvert felt vurderes dækningsgraden af de forskellige substrattyper på en skala fra 1 til 5. Der er i alt 5 point at uddele, svarende til at hvert point angiver en dækning på 20 % af feltets areal. Følgende substrattyper vurderes:

Sten:	> 60 mm
Grus:	3 – 60 mm
Sand:	0,25 – 3 mm
Mudder / Slam:	Sort farvet materiale <0,25 mm, som regel meget blødt
Ler:	Kompakt meget finkornet materiale, typisk < 0,063 mm
Tørv:	Organisk materiale, mere eller mindre omsat

På baggrund af observationerne beregnes den samlede dækning af de enkelte substrater på hele strækningen. Dette bruges til beregning af den anden del af substratindekset. Generelt tæller tilstedeværelsen af substraterne positivt indtil en vis dækning hvorefter en højere dækning ikke bidrager yderligere til indeksværdien. Disse grænseværdiers størrelse er afhængige af substrattypen og er angivet i nedenstående tabel.

Faktorer til beregning af substratindekset

	F (positiv=1)	F (neutral=0)
Sten	60 %	>60 %
Grus	70 %	>70 %
Sand	40 %	>40 %
Tørv / ler	20 %	>20 %
Mudder / slam	10 %	>10 %

Substratet registreres i alle kvadrater, og den procentvise fordeling af substraterne beregnes. Dækningerne omsættes herefter til en score ved at tage hensyn til grænseværdierne. Således vil et vandløb med 10 % sten, 20 % sand og 70 % mudder, få 10 point for sten, 20 point for sand, og 10 point for mudder.

Ved ekstremt homogene substratdækninger bruges følgende undtagelser fra ovenstående skema.

Hvis sand, ler, eller tørv udgør 100 % af substratet tildeles substrat scoren 5. Hvis mudder eller slam udgør 100 % af substratet på strækningen tildeles scoren 0. Hvis tørv / ler / mudder og slam tilsammen udgør 100 % tildeles scoren 5.

Heterogeniteten beregnes som antallet af nabokvadrater med forskelligt dominerende substrat divideret med det totale antal sammenligninger af nabokvadrater. Det samlede antal sammenligninger på en strækning er 30. Heterogeniteten findes så ved:

Substrat heterogenitet = antal forskellige substrat obs./30

Substrat indekset beregnes som:

S.I. = (Substrat score + Substrat heterogenitet) / 2

Indekset kan antage værdier mellem 0 og 100

Vandplanter
Makrofytterne influerer på strøm- og sedimentationsforholdene i vandløbet. Kompleksiteten af makrofytternes vækstformer og antallet af arter (graden af samvækst) influerer ligeledes på hvorledes strømforholdene påvirkes. Således vil en kompleks grødeø med mange arter yde en mere varieret påvirkning end enkeltstående planter.

I hvert felt vurderes dækningen af alle vandplanter. Samtidig vurderes det om den dominerende vækstform er emergent eller neddykket. Desuden vurderes det om der er tale om en monokultur eller om der er flere arter til stede. Vurderingen foretages i hvert felt. Scoren for dækningen ganges med arts scoren og korrigeres med scoren for vækstformen

Indeks score

Dækning	Værdi	Score
Ingen planter	0	0
< 20 % dækning	1	1
< 40 % dækning	2	2
< 60 % dækning	3	3
< 80 % dækning	4	2
> 80 % dækning	5	1

Samvækst	Værdi	Score
1 Art	1	1
2 eller flere arter	2	2

Plantetype	Værdi	Score
Emergent	1	1
Neddykket	2	2

Indeksværdien beregnes som procentandelen af den maksimale score det er muligt opnå, dvs. summen af scoren for hvert transekt / Maksimal score

P.I. = Dækning * Samvækst * Plantetype / Maks.score * 100

Indekset kan således antage værdier mellem 0 og 100

Træ, rødder, grene og blade
Træer mv. skaber variation i leverstederne for fisk og smådyr og kan virke som skjul. Bladpakker kan specielt i skovvandløb udgøre en signifikant habitat for mange smådyr. Denne medtages fordi den kan have særdeles stor udbredelse. Tilstedeværelsen vurderes i hvert felt på strækningen. Tilstedeværelsen af træ, rødder og grene vurderes som følger:

	Værdi	Score
Intet træ, stammer eller grene	0	0
Få objekter (1-2)	1	4
Mange objekter (3 eller flere)	2	8
Ingen blade	0	0
Udpræget dækning af nedfaldne blade	1	2

Indeksværdien beregnes som procentandelen af den maksimale score det er muligt opnå, dvs. summen af scoren for hvert kvadrat / Maksimal score

P.I. = Træscore + baldscore /maks. score *100

Indekset kan antage værdier mellem 0 og 100

Vandløbsfysiske habitat indeks

Det vandløbsfysiske habitatindeks beregnes som en vægtet sum af vandløbsindekset og stræk-ningsindekset. P.t. er vægter de to indeks lige, dvs.

VandløbsFysisk Habitat Indeks = ½ Vandløbsindeks + ½ Strækningsindekset

Dataindsamling og feltmålinger

Oplandsdata kan indsamles fra diverse digitale kortværk samt ved inspektion af kortblade. Disse data bør være de første der indsamles før en eventuel feltregistrering, således at man har overblik over de overordnede forhold på strækningen og i oplandet. Indekset er sammensat således at det skulle kunne bruges uanset årstiden. Der er i strækningsindekset taget højde for at der i nogle vandløb eksisterer forhold som ikke umiddelbart kan indekseres efter metoden der er brugt her. Ved at justere antallet af parametre når nogle vurderinger falder, kan der tages højde for svært in-dekserbare forhold.

Opstilling og aftestning af indekset

Indekset testes i løbet af foråret 2003 i forbindelse med det generelle vandløbstilsyn på en række lokaliteter fordelt over det meste af landet. I forbindelse med selve fauna-prøvetagningen opmåles parametrene til vandløbsindekset. Oplandsdata, ådalsdata og data i den ekstensive del af vand-løbsprogrammet indsamles ligeledes.

Indeksets robusthed skal testes i forhold til prøvetager. Det er som nævnt ovenfor vigtigt at to uaf-hængige prøvetagere kan nå frem til samme resultat, når målingerne i vandløbet og bedømmelsen af forholdene på brinkerne og i ådalen skal vurderes. Det er nødvendigt i denne proces løbende at redigere og evaluere de målinger og vurderinger der lægges til grund for indeksberegninger for netop at sikre objektiviteten.

Indekset skal testes på en række strækninger med meget forskellige fysiske forhold for at finde ud af, om det er robust nok til at virke på strækninger med enten meget gode eller meget dårlige fysi-ske forhold.

Når der er fastlagt et indeks som er robust i forhold til prøvetagning og målemetoder, er det vig-tigt at få kommunikeret anvendelsen ud til så mange som overhovedet muligt, så det kan integre-res i det landsdækkende vandløbstilsyn. Derfor påregnes at afholde en workshop på DMU i efter-året 2003 for amter og andre interesserede.

Indekset skal yderligere testes for sæsonvariationer. Dette må dog gøres løbende efter indeksets introduktion, da ressourcerne p.t. ikke er tilstede til denne aftestning.

Der skal sandsynligvis ske en yderligere evaluering af indekset ved at samle alle indeksregistre-ringer f.eks. hos DMU og derefter analysere på tværs af amter og regioner i Danmark. De nærmere omstændigheder og forudsætninger for denne evalueringsprocedure skal dog aftales på et senere tidspunkt mellem de parter der skal gøre brug af indekset.

Tidsplan for test af indekset

Januar 2003:	Opstart af arbejdsgruppe der arbejder med aftestning af fysiske in-deks
Marts – maj 2003:	Felttestning af indeks på forskellige vandløbsstrækninger
September 2003:	Arbejdsgruppens indstilling vedr. felttest af det fysiske indeks fore-ligger opstilling af færdigt indeks
September/oktober 2003:	Workshop på DMU.

Litteratur

Boon, P. J., J. Wilkinson, et al. (1998). "The application of SERCON (System for Evaluating Rivers for Conservation) to a selection of rivers in Britain." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 597-616.

Bult, T. P., R. L. Haedrich, et al. (1998). "New technique describing spatial scaling and habitat selection in riverine habitats." Regulated Rivers-Research & Management **14**(1): 107-118.

Friberg, N., P. Græsbøll, et al. (1999). "Fysiske forhold og tilstand i mindre vandløb." Vand og Jord **6**(3): 117-120.

Harper, D. and M. Everard (1998). "Why should the habitat-level approach underpin holistic river survey and management?" Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 395-413.

Holmes, N. T. H., P. J. Boon, et al. (1998). "A revised classification system for British rivers based on their aquatic plant communities." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 555-578.

Jeffers, J. N. R. (1998). "Characterization of river habitats and prediction of habitat features using ordination techniques." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 529-540.

Jeffers, J. N. R. (1998). "The statistical basis of sampling strategies for rivers: an example using River Habitat Survey." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 447-454.

Kaarup, P. (1999). "Indeks for fysisk variation i vandløb." Vand og Jord **6**(4): 136-139.

Raven, P. J., P. J. Boon, et al. (1998a). "Towards an integrated approach to classifying and evaluating rivers in the UK." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 383-393.

Raven, P. J., N. T. H. Holmes, et al. (1998b). "Quality assessment using River Habitat Survey data." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 477-499.

Raven, P. J., N. T. H. Holmes, et al. (1998c). River Habitat Quality - the physical character of rivers and streams in the UK and Isle of Man. Bristol, Environment Agency**:** 85.

Wilkinson, J., J. Martin, et al. (1998). "Convergence of field survey protocols for SERCON (System for Evaluating Rivers for Conservation) and RHS (River Habitat Survey)." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 579-596.

Wright, J. F., M. T. Furse, et al. (1998). "River classification using invertebrates: RIVPACS applications." Aquatic Conservation-Marine and Freshwater Ecosystems **8**(4): 617-631.

Windolf, J. (red):, (2000). Vandløb 1999. Vandmiljøovervågning. Fyns Amt.

Feltarbejde og feltskemaer

Stations identifikation
Stationsidentifikationen tjener to formål, dels at få en præcis stedfæstelse af hvor målingerne er udført, dels at være sikker på at der er muligt at identificere den fysiske habitat vurdering og sammenligne den med en eventuel biologisk prøvetagning. Stations identifikationen indeholder følgende:

– Prøvetager
– Datoen for feltarbejdets udførelse
– Vandløbets navn
– Lokaliteten
– Strækningens vandløbsorden (vandløbsorden efter Strahler og vurderet på 4 cm kort)
– Strækningen markeres på et kort og koordinaterne (UTM) for strækningens nedstrøms ende noteres.
– Koten på nærmeste højdekurve der krydser vandløbet noteres
– Koten på udspringet noteres
– Faldet på strækningen
– Under bemærkninger noteres alle relevante oplysninger som ikke registreres ved habitat vurderingen

VandløbsFysisk Habitat Indeks
Strækningsindeks

Længdeprofil						
Antal stryg og Høller		Høller:		Stryg:		
Strækningen er ét langt stryg	J/N					
Slyngningsgrad	L/S/M					
Ådalstype	I/S/B					
Tværprofil	K/S/N					
Bredde (m)						
Sektion		1	2	3	4	5
Substrat (5 point pr. sektion)						
Sten						
Grus						
Sand						
Tørv / Ler						
Blødbund / mudder / Slam						
Stendækning	I/E/N/U/M					
Vandplanter						
Neddykkede planter	I/E/N/U/M					
Emergente planter	I/E/N/U/M					
Rødder, grene, træer	I/F/N/U					
Højre brink "face" struktur	I/E/S/K/U					
Højre brink vegetation	I/LU/HU/T/B/M/KA					
Træer	S/U/N/E/I					
Struktur	I/E/S/K/U					
Højre Bræmme vegetation	I/LU/HU/T/B/M/KA					
Træer	S/U/N/E/I					
Struktur	I/E/S/K					
Arealanvendelse	LS/NS/V/U/H/G/O/K					
H. ådal arealanvendelse	LS/NS/V/U/H/G/O/K					
Venstre brink "face" struktur	I/E/S/K/U					
V. brink vegetation	I/LU/HU/T/B/M/KA					
Træer	S/U/N/E/I					
Struktur	I/E/S/K/U					
V. bræmme vegetation	I/LU/HU/T/B/M/KA					
Træer	S/U/N/E/I					
Struktur	I/E/S/K					
Arealanvendelse	LS/NS/V/U/H/G/O/K					
V. ådal arealanvendelse	LS/NS/V/U/H/G/O/K					

Substrat: Der tildeles i alt 5 point pr. sektion (1 p. svarer til ca. 20% dækning)

Vegetation: Den dominerende vegetationstype registreres, Ingen vegetation (I), Lave urter (LU), Høje urter (HU), Træer (T), Buske/krat (B), Mos (M)

Vegetations struktur: Antallet af forskellige vegetationstyper, Ingen vegetation (I), 1 type – enkel (E), 2-3 typer – simpel (S), 4-5 typer –kompleks (K), Udhængende (gælder kun brinker) (U)

Udhængende vegetation: Sæt ring omkring den dækningskombination der passer bedst på strækningen. Scoren er angivet i hvert felt. Hvis der ingen udhængende vegetation er tilstede skrives "0" ud for feltet ingen vegetation

Arealanvendelse: Løvskov (LS), Nåleskov (NS), Vådområde (V), Urban/have (U), Hede (H), Græsset (G), under plov – omdrift (D), Krat (K).

Ådalstype: Ingen (I), Bred (B), Smal (S)

Træer: Skov (S); >50% træ (U), 25-50% træ (N), Enkelte træer (E), Ingen træer (I)

Vandplanter: Ingen (I), 0-10% (E), 10-50% (N), 50-75% (U), >75% (M)

Tværprofil: Kanaliseret (K), Seminaturligt (S), Naturligt (N)

Slyngningsgrad: Lige (L), Sinuiøst (S), Mæandrerende (M)

Stendækning: Ingen (I), Enkelte (E), Nogle (N); Udbredt (U); Mange (M)

Langt stryg: Ja (J), Nej (N)

Rødder, grene træ i vandløbet: Ingen (I), 0-10% (E), 2:10-25% (N), >25% (M)

Trans		Felt 1	Felt 2	Felt 3	Felt 4	Bredde
1	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
2	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
3	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
4	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
5	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
6	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
7	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
8	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
9	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					
10	Hastighed					
	Planter					
	Antal arter					
	Plantetype					
	Træ, grene					
	Blade					

Trans		Felt 1	Felt 2	Felt 3	Felt 4
1	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
2	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
3	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
4	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
5	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
6	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
7	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
8	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
9	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				
10	Dybde				
	Sten				
	Grus				
	Sand				
	Mudder/ slam				
	Tørv / ler				

Appendix B

Grødeskæring nedsætter artsrigdommen i Gels Å (Weed cutting reduces species richness in Gelså Stream)

Pedersen, M.L., Baattrup-Pedersen, A., Sand-Jensen, K., Friberg, N. & Kronvang, B. 2001: Grødeskæring nedsætter artsrigsommen i Gels Å. Vand & Jord, 8: 67-69

Appendix C

Ørreders gydning på udlagt gydegrus (Trout spawning on re-instated spawning gravel beds).

Pedersen, M.L., Dieperink, C., Kronvang, B. & Hansen, C.R. 2001: Ørreders gydning på udlagt gydegrus. Miljø- og Vandpleje, 27: 5-7

Appendix D

EFFECTS OF RE-INSTATING SPAWNING GRAVEL IN DANISH LOWLAND STREAMS

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Background

During the 20th century spawning of brown trout (*Salmo trutta* L.) has declined as a result of the straightening and culverting of 96% of the Danish watercourses. Subsequent excess sediment transport has further led to the destruction of spawning sites by sedimentation, and natural trout reproduction has therefore decreased.

Re-establishing the natural spawning sites in the streams has been a priority for the Danish stream authorities for the past 10 years. However, spawning gravel has been re-introduced into the streams by means of trial and error methods and no effect studies of the spawning site restorations have been carried out.

This project has focused on evaluating a number of restoration projects carried out between 1989 and 1994 in a number of streams of varying sizes. The primary objective of the study was to evaluate these restoration efforts, and to investigate the limiting factors for reproduction of trout on re-instated gravel.

Methods

Spawning activity during winter, abundance of fry in May and August, and physical conditions (depth, velocity, macrophyte coverage and substrate) were measured in 3 streams (Stream Stensbæk, River Ryds Å & River Gels Å) on 2-3 reaches per stream and on an equal number of up-stream control reaches during 2000. The effects of re-instating spawning gravel in streams on spawning, activity, fry emergence and survival were analysed as were the habitat preferences of the surviving fry in August.

Spawning activity and fry emergence

The spawning activity was significantly positively correlated to the gravel coverage (R=0.79), as was the density (per 100 m²) of fry in May to the spawning redd area per 100 m² (R=0.65). These results indicated a link between gravel coverage and fry emergence.

Density of fry in August was significantly negatively correlated to current velocity in the stream margin habitat (R=0.50). The depth and density of fry in May was also positively correlated to the density of fry in August. These correlations were not significant though.
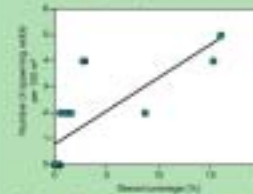
Figure 1. Relationship between the number of spawning redds per 100 m² and the gravel coverage in spring.
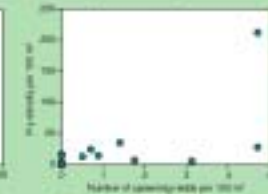
Figure 2. Plot of fry density in May and the number of spawning redds per 100 m².

Fry habitat preferences in August

The fry primarily prefer depths of 20 to 40 cm (60%) and velocities of 0 to 4 cm s⁻¹ (36%) in August. The empirical depth and velocity distributions preferred by the fry were tested against the overall distribution in the streams. Both the preferred velocity and depth distributions were significantly different from the distributions in the streams studied (Kolmogorov-Smirnoff Goodness of fit test, 5%-level).
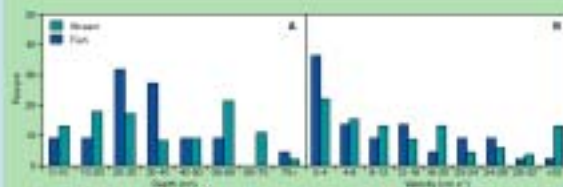
Figure 3. Depth (a) and current velocity (b) distributions from the 3 streams and the corresponding fish preference curves.

Table 1: Average physical and hydrological conditions in the 3 streams

	River Gels Å	Stream Stensbæk	River Ryds Å
Width (m)	3.2	1.7	3.7
Depth (cm)	36	23	58
Reach length (m²)	30	50	50
Reach area (m²)	110	90	283
Velocity (cm s⁻¹)	59	37	36
Discharge (l s⁻¹)	20 - 2000	20 - 120	400 - 1000

Table 2. Spawning activity and fry density in May and August. * indicate significant difference on 5% level. The numbers in brackets are total numbers of spawning redds. The fry densities are calculated as average number of fry per 100 m² streambed and as average number per meter stream length.

	River Gels Å		Stream Stensbæk		River Ryds Å	
	Restored	Control	Restored	Control	Restored	Control
Spawning redd area (m²)	92.7 (11)*	5.4 (4)	4.8 (8)*	0.7 (4)	5.6 (2)	0.0 (0)
Gravel coverage (%)	48	84	12	18	37	38
Percentage gravel used for spawning (%)	24*	1	20*	1	10*	0
Fry density in May						
(avg. number 100 m²)	20.3	19	72.1*	0	10.7	0
(avg. number m⁻¹)	1	0.8	1.4*	0	0.4	0
Fry density in August						
(avg. number 100 m²)	31.0	22	29.7	18.7	13.7	0
(avg. number m⁻¹)	1.7	1.1	6.6	0.2	6.6	0

Binomial tests were used to test for significant differences between the restored reaches and the control reaches. Significant differences in fry density were only found in Stream Stensbæk in May.

The spawning redd areas were significantly larger on the restored reaches in Stream Stensbæk and River Gels Å compared to the control reaches. The percentage of gravel used for spawning was significantly higher on the restored reaches compared to the control reaches, in spite of the generally higher coverage of gravel on the control reaches. Gravel on the control reaches was mixed with sand and therefore seemed unsuitable for spawning.

Conclusion

This study indicates that re-instating spawning gravel into Danish streams enhances the spawning activity and the number of trout fry emerging from the spawning redds. Spawning activity was enhanced significantly in two streams following restoration. Furthermore, a larger percentage of the introduced gravel is actually used for spawning activity. Differences in fry densities, between the restored and control reaches, were only significant in Stream Stensbæk in May. The results indicate that the introduced gravel provides a better potential for spawning success.

The most significant parameter to explain the number of fry in May was the spawning redd area. The gravel coverage correlated positively to the spawning activity thereby mediating a link to the fry density. Microhabitat selection by the fry in August indicated clear preferences with respect to depth and velocity.

National Environmental Research Institute

The National Environmental Research Institute, NERI, is a research institute of the Ministry of the Environment. In Danish, NERI is called *Danmarks Miljøundersøgelser (DMU)*.
NERI's tasks are primarily to conduct research, collect data, and give advice on problems related to the environment and nature.

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The first overall objective of the PhD-study was to study variations in physical habitats and macroinvertebrates across multiple scales in Danish lowland streams. The second objective was to study the effects of anthropogenic and natural disturbances on physical habitats and biota. The thesis is comprised of an introduction and 5 accompanying papers which all deals with different aspects habitats and biota in lowland streams. Discharge, near bed currently velocities were found to influence stream substratum patterns in general and the coverage mud substratum in particular. Physical habitats varied in a consistent way through the upper part of the lowland river systems in Denmark. Habitats and biota were influenced by a number of variables acting and interacting on multiple scales within the stream ecosystem. Human influence on the habitats and biota was analysed using weed-cutting as a disturbance. Biotic communities were significantly less varied in weed cut streams than in streams without weed cutting. Stream channelization influenced habitat variability, esspecially in riffle habitats where depth and current velocity was lower and less varied in disturbed and channelized streams than in near-natural streams. Danish lowland streams have been heavily modified over the past 200 years causing a significant degradation in biotic communities.

Physical habitat structure in lowland streams and effects of disturbance