Original Research

Short-Term Impacts of Weed Cutting on Physical Habitats in Lowland Rivers – the Importance of Initial Environmental Conditions

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Abstract

We studied the effects of weed cutting at 3 reaches in two Danish lowland rivers with the objectives of examining the response to cutting in rivers with contrasting physical conditions, macrophyte diversity, and assemblage patterns. Physical characteristics and abundance of macrophyte species were registered 3 or 4 times throughout the study period on all reaches.

Weed cutting did not affect the total coverage of stone, gravel and sand and substratum homogeneity, and no common response was found among the reaches. This result is likely to reflect both initial differences in the physical environment among the reaches as well as differences in macrophyte coverage and assemblage patterns. Water depth, variability in current velocity and the coverage of stone and sand were affected by coverage independent of assemblage patterns, whereas the river bed substratum homogeneity was affected by coverage, as well as assemblage pattern.

The analysis indicated that diverse macrophyte communities with several growth morphologies enhance the spatial variability in substratum characteristics compared to reaches with a less diverse and more homogeneous distribution of species.

Keywords: macrophytes, substratum homogeneity, current velocity, weed cutting

Introduction

Submerged macrophytes are abundant in shallow lowland streams and rivers that are common in the cultivated lowlands of northwestern Europe [1-3]. Macrophytes modify physical habitat conditions both spatially and temporally. Growth of macrophytes generally decreases mean current velocity and increases the water level [4, 5]. However, substantial variability in flow patterns may arise with accelerated flow velocities around macrophyte stands and reduced velocities within the stands [3, 5, 6]. Concomitant with changes in current velocity patterns, sed-

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iment composition on the riverbed also changes. Deposition of fine sediments and retention of organic detritus is enhanced in areas with low flow, whereas coarse substrata are exposed in areas with high flow velocities [4].

The intensification of agriculture during the past 100 years has increased the necessity of weed cutting and dredging in many macrophyte-rich lowland rivers. Mechanical removal of macrophyte biomass in the stream channel ensures efficient drainage of water from agricultural land adjacent to streams and reduces the risk of flooding. Plant re-growth may, however, be vigorous and the biomass may recover within the same growing season [7]. Therefore, many streams are weed-cut frequently (>2 times per year) to keep drainage efficient [8]. Weed cutting affects the structure of in-stream habitats, biotic communities, and ecosystem function (e.g. [9]). Macrophyte communities become poorer in species and spatially more homogeneous following several years of weed cutting [10]. In addition, substantial changes in community composition patterns may develop with an enhanced abundance of fast-growing species with a high dispersal capacity [11, 12]. The diversity and structural complexity of macrophytes is important for the river ecosystem. Studies have shown that greater structural diversity results in more varied invertebrate communities [13], probably reflecting that the spatial and temporal heterogeneity of the physical habitat increases with increasing structural diversity of the macrophyte community. Therefore, loss of macrophyte species and homogenization of communities as a result of weed cutting may have severe effects at multiple trophic levels in the river ecosystem.

The above-mentioned impacts of weed cutting relate to the long-term alterations in composition and structural complexity of the macrophyte community. But weed cutting will also affect the physical environment temporarily as removal of macrophyte biomass strongly alters depths, current velocity, and substratum conditions [14]. Despite the widespread application of weed cutting in lowland rivers, only a few experimental studies have addressed the extent and duration of these physical changes. Kaenel and Uehlinger [14] demonstrated that effects of cutting on the physical environment can persist throughout summer and that the vegetation may not recover within the same growing season. In addition, their results indicated that the response can vary in rivers with contrasting macrophyte composition. In the present study we investigate these issues further. Our objectives were:

1) to examine the response pattern to weed cutting in lowland rivers with contrasting physical environmental conditions,
2) to elucidate how macrophyte diversity and assemblage patterns affect the response in physical habitats.

Materials and Methods

Site Description and Experimental Set-Up

This study was conducted in summer 2001 (May to August) in three river reaches situated in two adjoining catchments, River Jordbro (hereafter named river 1) and River Lerkenfeld (hereafter named river 2) in northern Jutland, Denmark. Both rivers are situated on clayey glacial moraine deposits. River 1 drains into Hjarbæk Fjord, whereas river 2 drains into Limfjorden at Lovns Bredning (Fig. 1). Mean annual discharge was measured at hydrometric stations located near the study reaches and mean annual discharge varied between 1.04 and 1.18 $m^3 \cdot s^{-1}$ and between 0.87 and 1.00 $m^3 \cdot s^{-1}$ in rivers 1 and 2, respectively. The discharge regimes are dominated by groundwater during summer (May-September) and by precipitation during winter (October-April). One study site was located in river 1 at 9.16ºE, 56.49ºN (hereafter named reach 1) and two study sites were located in river 2 at 9.49ºE, 56.74ºN (here-

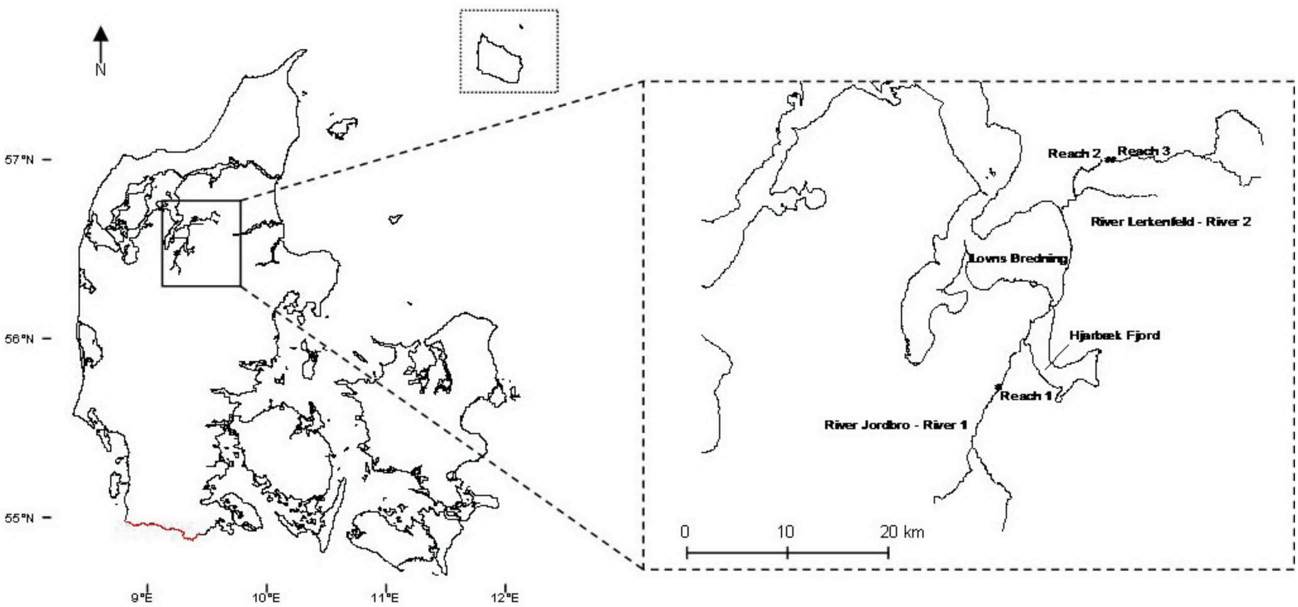

Fig. 1. Location of the surveyed rivers and reaches.

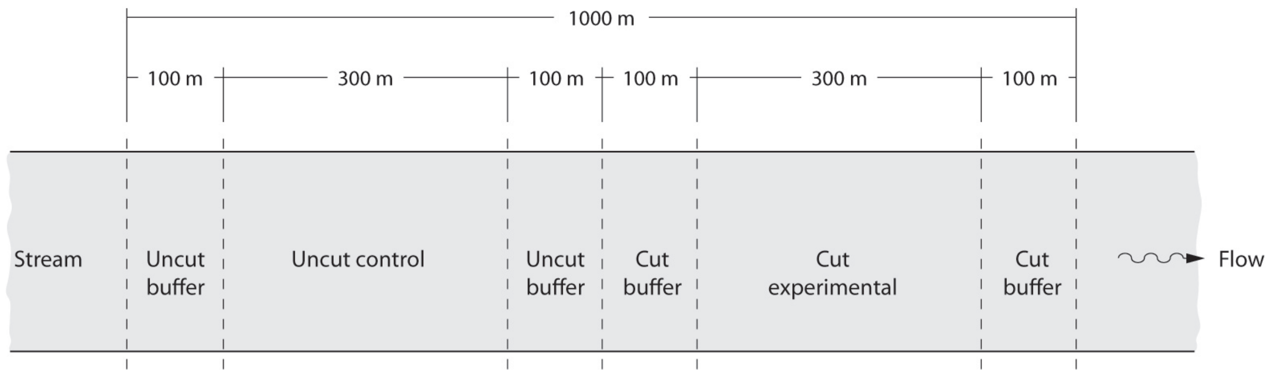

Fig. 2. Set-up of control and experimental reaches on the three sites.

after named reach 2) and 9.40ºE, 56.73ºN (hereafter named reach 3). The catchment areas were 111 km^2, 115 km^2, and 75 km^2 in reaches 1, 2, and 3, respectively. The study reaches were all 1000 m long and were subdivided into several sub-sections as follows: 100 m upstream uncut buffer, 300 m uncut control reach, 100 m uncut buffer zone, 100 m cut buffer, 300 m cut experimental reach, and 100 m cut buffer (Fig. 2). Weed cutting is performed regularly on all reaches twice a year. The cutting is performed by boat and the biomass is cut in a central channel approximately two thirds of the total width of the river reaches. The regional water authorities are responsible for performing the cutting. The cut biomass drifts downstream and is retained on a grill and subsequently removed from the channel by a crane operated from the river bank. The experimental reaches were weed-cut as described above, whereas control reaches were left uncut throughout the study period. In river 1 the first cutting was performed 5 July and the second cutting on 7 August. In river 2, the first cutting was performed on 14 to 18 June and the second on 3 August.

Macrophyte Survey and Measurement of Physical Habitat Characteristics

Abundance registration of plant species (submerged and emergent macrophytes, amphibian and terrestrial) and measurements of physical characteristics were performed 4 times throughout the study period in both experimental and control reaches in river 1, and 3 times throughout the study period in river 2. The experimental design was directed at detecting short-term (within the growing season) changes in the physical characteristics following weed cutting. Therefore, one pre-measurement was performed at the beginning of the growth period (4 weeks prior to the first weed cutting) to provide a physical baseline environment in control and experimental reaches. Subsequently, measurements were performed after each weed cutting, i.e. 1 week following the first weed cutting, 4 weeks following the first weed cutting, which equals 1 week before the second weed cutting and 1 week after the second weed cutting (only reach 1). This gives a total of 20 surveys during the study period.

The surveys were performed in plots (25×25 cm) placed side by side across the river in 11 evenly distributed and permanently marked transects in each experimental and control reach. The total number of plots varied between 221 and 341, depending on the transect widths of the reaches. A glass-bottom bucket was used to aid underwater observations of macrophyte coverage and substratum characteristics. Water depth was measured to the nearest centimetre in the centre of the plots. The mean depth of a river reach was calculated from all depth observations. Mean river width was calculated from measurements of the wetted width in the 11 transects. The dominant substratum type in each plot was categorized using a modified Wentworth-scale [15] as either stone (>60 mm diameter), gravel (3-60 mm), coarse sand (1-3 mm), fine sand (0.25-1 mm), mud (<0.25 mm), hard clay, or peat. The relative frequency of the various substrata on each reach was calculated from registrations in all plots. A cover score was allocated to each macrophyte species present in the plots using the following scale: 1<5%, 2=5-25%, 3=25-50%, 4=50-75%, and 5>75%. Nomenclature followed [16, 17]. If identification of species could not be achieved due to the absence of seasonal diagnostic features, then the identification was only performed to genus level.

To achieve total coverage values for each species present, the sum of plot coverage values was divided by the total number of plots investigated multiplied by the maximum score (in this case 5). Hereafter, these values were multiplied by 100 to reach percentage coverage for the species. Total macrophyte coverage was calculated as the sum of coverage of all species present. Current velocity was measured at two depths in each plot, 5 cm above the river bed ($v_{near\ bed}$) and at 60% of water depth ($v_{0.6D}$), using a Nautilus C 2000 current meter (OTT Germany). The reach scale mean current velocity was measured by dilution gauging [18]. Mean current velocity on both control and experimental reaches was calculated from the time elapsed for half the volume of a 5-litre saltwater solution (12% w/w) to pass through the 300 m reach. Discharge was calculated from the cross sectional area and the plot measurements of water velocities in the most downstream transect on the investigated reach. The slope of the water surface was measured once during the experiment by means of levelling equipment as the difference in height between the upstream and downstream end of the reach, divided by the distance between the points (300 m). Control and experimental reaches were levelled separately (Zeiss Instruments, Germany).

Table 1. Physical properties of experimental and control reaches prior to the experiment.

	Reach 1		Reach 2		Reach 3	
	Control	Experimental	Control	Experimental	Control	Experimental
Discharge ($m^3 \cdot s^{-1}$)	0.93±0.08	0.94±0.07	0.76±0.08	0.82±0.05	1.40±0.2	1.31±0.08
Slope (%)	0.052	0.052	0.045	0.056	0.073	0.113
River width (m)	4.37	5.10	6.53	5.56	5.44	5.27
River depth (m)	0.73±0.08	0.67±0.08	0.62±0.05	0.69±0.03	0.64±0.17	0.56±0.12
Current velocity$_{near\ bed}$ ($m \cdot s^{-1}$)	0.33±0.02	0.33±0.02	0.34±0.02	0.31±0.02	0.33±0.02	0.30±0.03
Current velocity$_{0.6D}$ ($m \cdot s^{-1}$)	0.51±0.24	0.37±0.03	0.39±0.03	0.36±0.02	0.45±0.24	0.35±0.02
CV current velocity$_{near\ bed}$ (%)	29.9±3.22	21.3±2.04	17.2±1.00	17.8±1.00	24.40±6.5	19.4±2.7
CV current velocity$_{0.6D}$ (%)	16.2±3.6	16.5±5.6	16.8±3.2	14.0±2.2	19.1±3.8	16.6±3.8
Depth Homogeneity	0.23±0.04	0.23±0.07	0.19±0.00	0.19±0.03	0.26±0.08	0.32±0.10
Substratum Homogeneity	0.68±0.07	0.77±0.03	0.70±0.02	0.82±0.03	0.68±0.03	0.79±0.00
Stone coverage (%)	3±2	0	6±2	0	4±2	0
Gravel coverage (%)	9±1	15±7	47±4	2±1	18±1	9±5
Sand coverage (%)	60±7	68±14	44±8	93±1	65±6	74±7
Mud coverage (%)	7±3	5±2	3±2	1±1	5±2	7±2

Data Analysis

The composition, diversity, and spatial distribution of the macrophyte communities in the investigated river reaches were described at each survey date using the total number of species encountered (S) and the number and abundance of submerged, amphibious, and terrestrial species [19]. The evenness index ($E_{1/D}$) was used as a measure of the spatial distribution of the macrophytes on the reach, and the Shannon index (H') was used to express macrophyte diversity. In addition, a detrended correspondence analysis (DCA) was used to analyze the similarity in species composition within and between the investigated river reaches and to analyze if changes in composition occurred within the period of study. Rare species (less than 1% coverage) were omitted from the data set before running the DCA ordination, leaving the matrix with 25 species and 20 samples. This analysis was carried out in PC-ORD [20].

Reach-scale means of current velocity, coverage of substrata and depth were calculated after each sampling. The high spatial resolution (>200 sample plots per site) enabled us to obtain representative measurements of the physical heterogeneity and temporal variability within the reaches. The coefficient of variance of all measurements of velocity was calculated and used to characterize the variation in current velocity near the bed and at 60% of the depth. The heterogeneity in the distribution of different substratum types and depth measurements was calculated according to [21].

An analysis of covariance was performed to test for a consistent, short-term, seasonal response pattern to weed cutting using treatment and days relative to cutting as factors and coverage of macrophytes as a covariate [22]. In this analysis all reaches were treated together. To elucidate how macrophyte diversity and assemblage patterns can affect the response, we performed a second covariance analysis (reach was treated as a factor, and coverage was treated as a covariate). We ran this analysis on control reaches only because the maximum coverage achieved in the experimental reaches was limited (30-35%), thereby giving rise to an unbalanced statistical design. The covariance analyses were performed in SAS [23].

Results

The investigated river reaches were approximately the same size. The width varied from 4.37 to 5.44 m and the depth between 0.56 and 0.73 m (Table 1). The discharge was higher in reach 3 compared to the other reaches (Table 1). Discharge decreased in the study period from 0.93 to 0.80 $m^3 \cdot s^{-1}$ in reach 1, from 0.84 to 0.59 $m^3 \cdot s^{-1}$ in reach 2, and from 1.4 to 1.1 $m^3 \cdot s^{-1}$ in reach 3. Reach 3 had a higher water surface slope (0.07-0.11%) compared to the other reaches (0.05-0.06%). The near bed current velocity varied little among the reaches, whereas the velocity in 0.6D tended to be slightly higher on the control reaches compared to the experimental reaches (Table 1). The variation in current velocities, expressed as the CV, showed no systematic variation among reaches or between treatments (Table 1). Substratum characteristics varied among the three reaches initially and between experimental and control reaches. Control reach 2 and 3 had higher amounts of coarse substrata on the river bed and all control reaches had a more

Table 2. Coverage of the most abundant species (coverage >5%) in experimental and control reaches at maximum coverage.

		Abundant species		
		First	Second	Third
Reach 1	Control	*Potamogeton crispus* L. (18%)	*Elodea canadensis* L. C. Rich. (12%)	*Ranunculus peltatus* Schrank. (11%)
	Experimental	*Elodea canadensis* L. C. Rich. (10%)	*Sparganium emersum* L. (7%)	*Potamogeton crispus* L. (7%)
Reach 2	Control	*Ranunculus peltatus* Schrank. (35%)	*Glyceria fluitans* (L.) R. Br. (8%)	-
	Experimental	*Ranunculus peltatus* Schrank. (20%)	*Glyceria fluitans* (L.) R. Br. (6%)	-
Reach 3	Control	*Sparganium emersum* L. (31%)	*Potamogeton pectinatus* L. (15%)	-
	Experimental	*Sparganium emersum* L. (19%)	*Potamogeton pectinatus* L. (10%)	*Elodea canadensis* L. C. Rich. (6%)

heterogeneous distribution of substrata compared to the experimental reaches (Table 1).

Macrophyte coverage was similar in the experimental and control reaches at the beginning of the study period (approximately 20%; Fig. 3). In control reaches 1 and 2, macrophyte coverage increased linearly throughout the study period (r=0.99, p>0.05), whereas maximum coverage was achieved in the middle of the study period in reach 3. Maximum coverage was approximately 50% in all control reaches. In all experimental reaches, macrophyte coverage was around 20% one week following cutting (Fig. 3), which was similar to the initial measurements reflecting the baseline situation. After weed cutting, macrophyte coverage increased, and the maximum coverage attained within the study period was 30-35%.

The composition, diversity and spatial distribution of macrophytes differed among the investigated reaches (Tables 2 and 3). Control and experimental reach 1 had high coverages of *Potamogeton cripsus* (18% and 7%, respectively) and *Eleodea canadensis* (12% and 10%, respectively). Besides these two species, *Ranuculus peltatus* had high coverage in control reach 1 (11%), whereas *S. emersum* had high coverage in experimental reach 1. Control and experimental reach 2 had high coverages of *R. peltatus* (35% and 20%, respectively) and *Glyceria fluitans* (8% and 6%, respectively). Control and experimental reach 3 had high coverages of *Sparganium emersum* (31% and 19%, respectively), *Potamogeton pectinatus* (15% and 10%, respectively) and experimental reach 3 also had a high coverage of *E. canadensis*. The number of species found increased throughout the study period in both control reaches (Table 3). In the experimental reaches the number of species declined in response to weed cutting, but increased during the following period of re-growth. In contrast, the diversity and evenness in the distribution of species either remained rather constant (experimental and control reach 1 and 3) or increased throughout the study period (experimental and control reach 2) (Table 3). We found that both the diversity and evenness in control and experimental reaches were significantly higher in reach 1 (t-test, p>0.05) compared to reach 2 and 3. We could not detect any directional changes in assemblage patterns from the DCA within the period of study in either control or experimental reaches, but a clear segregation on DCA1 of the 3 reaches indicating potential differences in initial conditions among the reaches (Fig. 4).

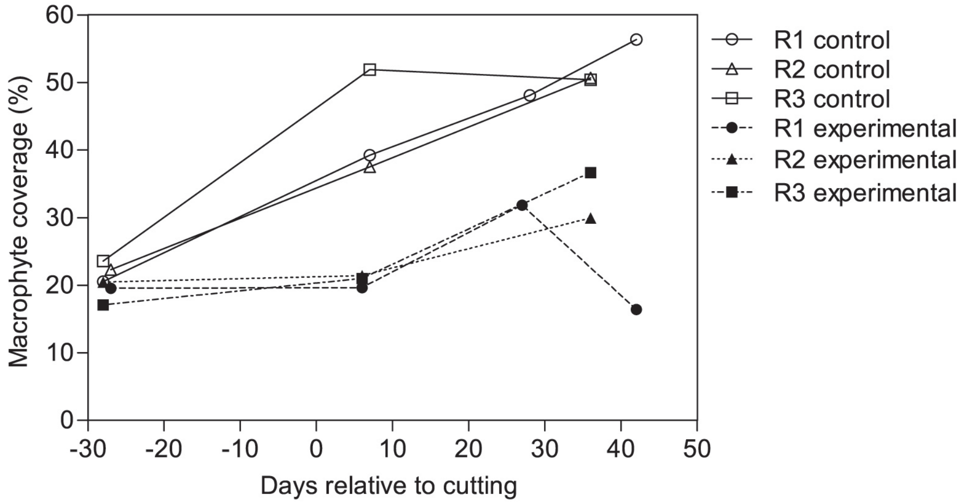

Fig. 3. Macrophyte coverage in experimental reaches 1, 2, and 3 and control reaches 1, 2, and 3 measured before and after weed cutting. In reach 1 the first cutting was performed 5 July and the second on 7 August. In reaches 2 and 3, the first cutting was performed on 14 to 18 June and the second on 3 August.

Table 3. Total number of species, evenness measured as $E_{1/D}$ and the coverage of submerged species in % of total coverage in control and experimental river reaches at varying days before (-) or after (+) weed cutting in the experimental sites.

		Days relative to cutting	Coverage (%)	S	E	H	Submerged (%)
Reach 1	Control	-28	21	9	0.711	1.562	80
		7	39	9	0.664	1.458	88
		28 (-8)	48	10	0.659	1.516	88
		7	55	11	0.653	1.566	87
	Experimental	-27	20	9	0.784	1.724	89
		6	20	9	0.818	1.798	79
		27 (-7)	32	12	0.732	1.82	86
		7	16	10	0.732	1.685	87
Reach 2	Control	-27	22	8	0.342	0.711	86
		7	38	8	0.421	0.876	83
		36 (-7)	51	10	0.454	1.046	81
	Experimental	-28	20	7	0.454	0.884	73
		6	21	6	0.629	1.127	75
		36 (-7)	29	9	0.559	1.229	68
Reach 3	Control	-28	23	6	0.425	0.761	97
		7	52	11	0.445	1.067	96
		36 (-7)	50	13	0.417	1.068	95
	Experimental	-27	17	7	0.489	0.952	91
		6	21	11	0.442	1.06	95
		36 (-7)	37	11	0.45	1.079	95

We did not find a common effect of weed cutting on the physical parameters. Thus, the found effect of treatment (i.e. weed cutting) on the total coverage of stone, gravel and sand and substratum homogeneity was neither related to coverage nor days relative to cutting (Table 4). The lack of significance may reflect initial differences among the reaches. Recovery was limited in the experimental reaches, therefore we were unable to investigate directly how coverage and assemblage patterns contributed to the result. However, by analyzing the effect of coverage and reach and the interaction between these, we may infer its significance. We found that macrophyte coverage significantly affected water depth and the variability in current velocity in the water column, and that the response was similar in the investigated reaches (Table 5; Figs. 5a and 5b). Macrophyte coverage also affected the coverage of stone and sand (Table 5). The coverage of stone increased with increasing macrophyte coverage, whereas the coverage of sand decreased with increasing macrophyte coverage. Macrophyte coverage also affected the homogeneity in the distribution of substrata on the river bed, and a significant interaction between coverage and reach was found, indicating that macrophyte assemblages affect this variable (Table 5, Fig. 6a). The substratum homogeneity was found to decrease with increasing macrophyte coverage in reaches 1 and 2, and to increase with increasing coverage in reach 3. In reach 3, the substratum homogeneity continued to increase following maximum macrophyte coverage (Figs. 6a and 6b).

Discussion

Macrophytes are important for the structure and functioning of many Western European rivers and streams, and the impacts of macrophyte presence are visible at various spatial and temporal scales [3]. Therefore, regular removal of biomass through weed cutting can have significant effects on the function of the lowland river ecosystem [9], reflecting that habitats disappear, but also that the physical river environment changes. In the present study we did not find a common short-term response to weed cutting in the river reaches investigated. This is probably the result of a high variability among the reaches regarding the initial physical characteristics, but differences in macrophyte assemblage patterns may also contribute to variability in the response pattern among the reaches. Thus, different macro-

Table 4. Results of the covariance analysis performed where treatment and days relative to cutting were treated as factors and coverage as a covariate. *F* values marked with an asterisk are significant at p<0.05. For more detailed information, see data analysis section.

Parameter	*F*-value			
	Treatment x days relative to cutting	Treatment	Days relative to cutting	Coverage
Width	-	0.03	-	0.17
Depth	0.28	0.12	5.81	0.08
Current velocity$_{near\ bed}$	0.18	2.10	0.11	0.64
Current velocity$_{0.6D}$	0.40	2.05	0.32	1.10
CV current velocity$_{near\ bed}$	0.26	2.99	0.03	0.57
CV current velocity$_{0.6D}$	0.51	2.42	0.76	3.42
Depth Homogeneity	0.46	0.18	0.86	0.16
Substratum Homogeneity	0.08	37.01*	0.37	0.45
Stone coverage	2.38	26.59*	1.99	0.48
Gravel coverage	0.07	6.24*	0.33	0.12
Sand coverage	0.03	12.86*	1.12	0.54
Mud coverage	0.11	0.47	0.05	0.50

phyte communities may exhibit different recovery rates and in combination with differences in growth morphologies and canopy structures, this may give rise to variation in the response [13, 24, 25]. Kaenel and Uehlinger [14] found similar differences in recovery between two Swiss plateau streams. We found that the recovery was limited in the investigated reaches compared to that generally observed in the intensively cut Danish streams. All abundant species encountered in the investigated reaches possess traits that enable them to cope with frequent cuttings [11], and the limited recovery is therefore unlikely to reflect that the macrophyte communities were sensitive to cutting. Rather, abiotic factors (i.e. turbid water) may explain the limited regrowth. This may also explain the relatively low coverages registered in the uncut reaches compared to those found in earlier studies (exceeding 70%) [3, 21].

Our second analysis of covariance can be used to enhance our understanding of how macrophyte coverage and different assemblage patterns can affect the response to weed cutting. Thus, by analyzing the interaction between coverage and reach on the measured and calculated physical properties, we may infer the significance of coverage and macrophyte assemblage patterns for the physical characteristics. We found that several of the physical characteristics were significantly affected by macrophyte coverage, but also that these were unrelated to assemblage patterns.

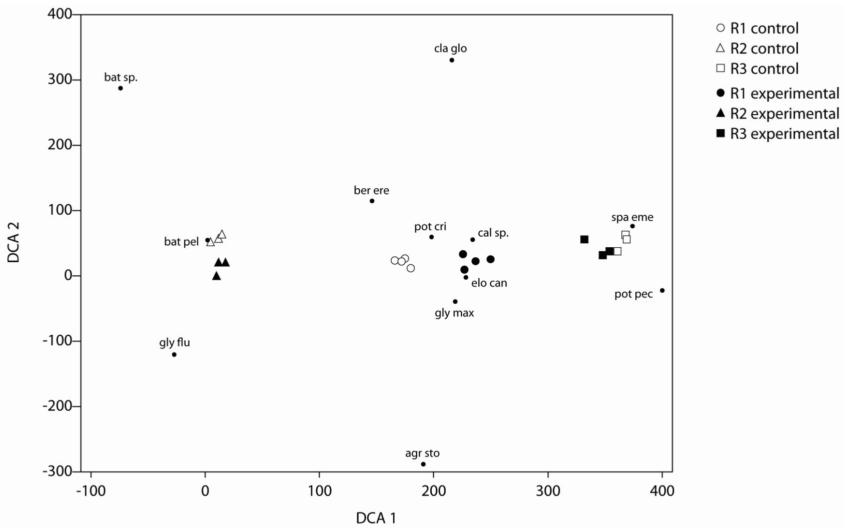

Fig. 4. DCA ordination diagram showing sample and species scores (coverage >1%) in the experimental and control reaches. The ordinations are based on relative frequencies of 25 vascular plant species.

In accordance with other studies, we found that water depth increased with increasing coverage, reflecting that macrophytes reduce current velocities [3, 7]. The finding that the observed response was independent of macrophyte assemblage pattern probably reflects that submerged species with flexible leaves that bend with the flow were predominant in all reaches (80-97%). Had there been significant differences in the abundance of amphibious and/or terrestrial species among the investigated reaches, this would probably have led to a different result as these species have more rigid stalks that increase hydraulic resistance [26]. We also found that the variability in the current velocity increased with increasing macrophyte coverage. The finding that the response of this variable was independent of macrophyte assemblage patterns probably reflects that measurements were performed at the reach-scale and not at the macrophyte patch scale. Thus, measurements at the patch level would probably have led to a different result as the variability in current velocity has previously been found to vary with growth morphology and canopy structure [3, 4, 27]. Documenting the effects on the reach scale or higher however, is a key issue in applied ecology since it is the scale where the rivers and streams are managed.

The variability in the spatial distribution of substratum on the riverbed also responded to macrophyte coverage, but in contrast to water depth and variability in current velocity, the response of this variable varied among the investigated reaches. We found that spatial variability in the substratum distribution increased with increasing coverage in reaches 1 and 2. Reach 1 possessed the most diverse community with the presence of several growth morphologies (e.g. dense patches of *E. canadensis* and more open patches of *P. crispus* and *R. peltatus*) and the most even distribution of species, whereas reach 2 had high coverages of *R. peltatus* (35%) and *G. fluitans* (8%). In contrast to reaches 1 and 2, the variability in substratum distribution declined with increasing coverage in reach 3. Reach 3 had high coverages of *S. emersum* (31%) and *P. pectinatus* (15%). Sediment deposition and hence composition have been found to vary with the morphology and canopy structure of macrophyte species [24]. Dense patches of *Callitruche cophocarpa*, *E. canadensis,* and *R. peltatus* create variable substratum conditions with fine sediment within the upstream two-thirds of the length of the patches, and coarse and more variable sediments outside of the patches and in their downstream parts [24]. Species with streamlined,

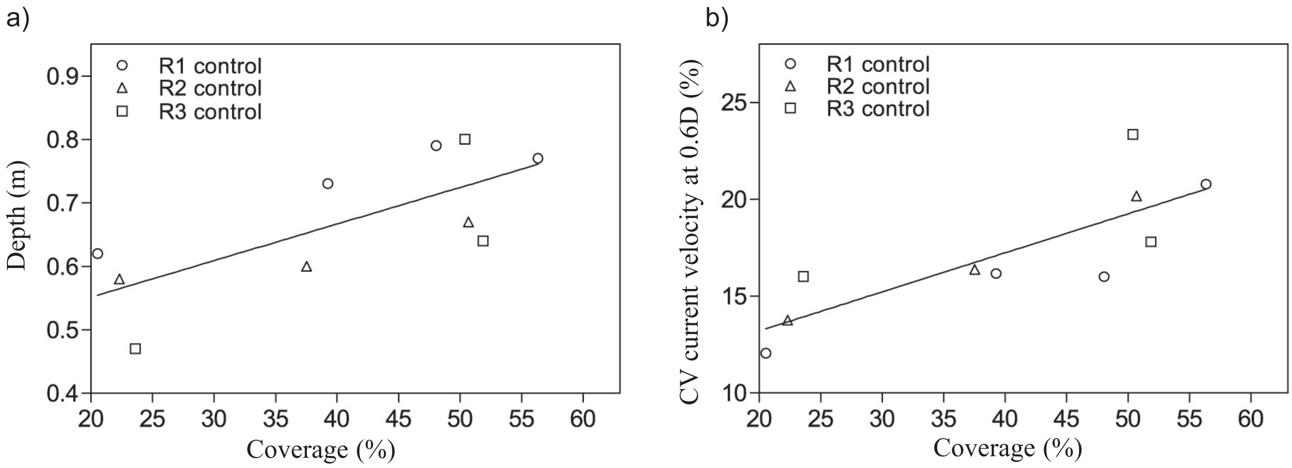

Fig. 5. (a) Relationship between water depth and coverage in the control reaches. The responses did not differ significantly among the reaches and a common linear regression analysis was performed. (b) Relationship between the coefficient of variation and coverage in the control reaches. The responses did not differ significantly among the reaches and a common linear regression analysis was performed.

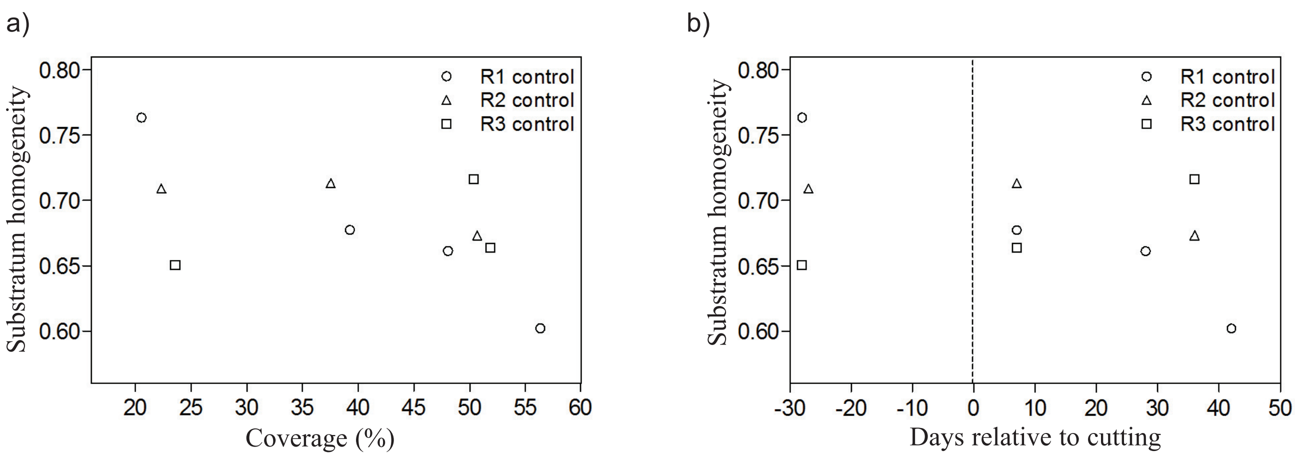

Fig. 6. (a) Relationship between substratum homogeneity and coverage in the control reaches. The responses were found to vary significantly among reaches. (b) Relationship between substratum homogeneity and days relative to cutting in the control reaches.

Table 5. Results of the covariance analysis that was performed to test for differences related to reach characteristics. Reach was treated as a factor and coverage as a covariate. *F* values marked with an asterisk are significant at p<0.05. For more detailed information, see data analysis section.

Parameter	*F*-value			
	Coverage × reach	Coverage (reach)	Coverage	Reach
Depth	0.95	-	11.66*	2.90
Current velocity$_{near\ bed}$	1.20	-	0.14	0.43
Current velocity$_{0.6D}$	0.13	-	0.50	0.30
CV current velocity$_{near\ bed}$	1.51	-	0.51	8.27*
CV current velocity$_{0.6D}$	0.13	-	16.62*	1.85
Depth Homogeneity	0.28	-	1.55	1.77
Substratum Homogeneity	8.70*	8.84*	-	1.28
Stone coverage	0.22	-	49.82*	14.84*
Gravel coverage	1.63	-	3.00	183*
Sand coverage	0.17	-	8.06*	17.43*
Mud coverage	0.65	-	<0.001	1.69

strap-formed leaves that form an open canopy like *S. emersum* only modify the sediment composition insignificantly [24]. The observed response in this study is therefore in line with the above-cited measurements performed at the macrophyte patch level, indicating that whole-reach variability can be predicted from reach assemblage patterns. Thus, our analyses suggest that a diverse community with the presence of several growth morphologies enhances the spatial variability in substratum distribution beyond that found in reaches with a less diverse and more homogeneous distribution of species, especially in cases where open canopies dominate. It is interesting that the homogeneity in the distribution of substratum on the river bed increases despite stagnation in the overall coverage in reach 3 dominated by *S. emersum*. This result can be attributed to a gradual development in river bed substratum properties, which is probably linked to the decline in current velocity during the summer period [3, 28, 29].

Perspectives

Several studies have shown that macrophytes modify the physical river environment in lowland rivers. Therefore, structural and functional properties of the rivers change at various spatial and temporal scales in weed-cut river reaches [9, 14, 30]. The high variability among the reaches regarding the initial physical habitats and macrophyte assemblage patterns seem to be related to different temporal changes in river habitat conditions. The effect is highly dependant on the initial conditions.

Weed cutting will affect diversity and community composition and this will affect the physical conditions in the reaches. The most varied substratum conditions were found in the river reach with the most diverse macrophyte community and the occurrence of several growth morphologies, whereas less varied substratum conditions were achieved in reaches with more homogeneous macrophyte communities. Concomitant with the homogenization of the macrophyte communities following cutting the physical river environment is therefore likely to become more uniform. The substratum conditions became more homogeneous with increasing coverage, and the homogeneity continued to increase following maximum coverage. This may also affect other river biota. Macroinvertebrate communities may be particularly responsive to less heterogeneous substratum conditions. Generally, species living on fine substrata may increase in abundance, whereas the Ephemeroptera, Coleoptera, Trichoptera, and Plectoptera species that are typically associated with coarse substrata may decline in abundance as well as in taxonomic richness [31]. Fast-growing species with a short life-cycle may therefore benefit from continuous intensive weed cutting, and this may lead to fundamental changes in the functions of the ecosystem.

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