

# Effect of cattail (*Typha* spp.) mowing on water beetle assemblages: changes of environmental factors and the aerial colonization of aquatic habitats

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**Abstract** Some studies found no, or weak evidence that dense monotypic cattail (*Typha* spp.) stands exclude water beetle species from aquatic habitats, or modify aquatic beetle assemblages. Other studies suggest that cattail may reduce the chance of aerial water beetle colonization, and decreases water temperature; negatively affecting these insects. We examined the response of aquatic beetle assemblages to the mowing of cattail (*Typha angustifolia* L., *T. latifolia* L.) in a freshwater marsh. Following removal of cattail at the water level in experimental plots, aquatic beetles were sampled both in mowed and intact (control) plots weekly, through a month in the spring of 2008. Aquatic beetles were more abundant in mowed plots. Species richness was the same, but it showed different patterns in mowed and intact plots. Shannon's diversity was similar between treatments, while evenness was lower

in mowed plots. 29% of the aquatic beetles showed a strong preference for mowed plots, and 15% preferred the control plots. Water temperature was an important factor, with mowed plots having higher water temperatures because of increased solar radiation. Polarization visibility of the water surface was also a factor, since aerially colonizing (flying) aquatic beetles use horizontally polarized light reflected from the water surface to seek potential locations. Using imaging polarimetry, we showed that mowing strongly enhanced the water-reflected polarized light signal, because it reduced the screening effect of cattail leaves, which made the visual detection of water easier. Our results suggest that cattail mowing is a useful method in aquatic beetle conservation: it increases the chance of aerial colonization due to the enhanced polarization visibility of the water surface, and creates a habitat for more abundant assemblages otherwise excluded by the monodominant dense cattail stands. Thus, sustaining hemi-marsh conditions with vegetated and mowed areas is advisable to maximize overall aquatic beetle diversity.

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## Introduction

Cattails (*Typha* spp.) often cause conservation problems, because their dense, monotypic stands exclude other wetland-dependent plant species, waterfowl (Anseriformes) and shorebirds (Charadriiformes) (Kantrud 1986; Linz et al. 1996; Kostecke 2002; Kostecke et al. 2004), due to the reduced open water surface (Ball 1990), even where cattails are native (Kercher and Zedler 2004). Previous studies on the impact of cattail and cattail removal on

aquatic macroinvertebrates found no, or little significant differences in aquatic beetle assemblages between waters with and without cattail cover (Murkin et al. 1982; Linz et al. 1996; Kostecke 2002; Kostecke et al. 2005). Other results predict that cattail may exclude aquatic beetle species from aquatic habitats for the following reasons:

- (i) Emergent vegetation, and thus also cattail stands, may shade the water from direct sunlight, and thus reduce the water temperature (DeBusk and DeBusk 2000). Developmental time and vulnerable larval stages in warmer waters may be shorter (Nilsson and Soderstrom 1988; Fairchild et al. 2003), and adult size, fecundity, growth rate, survivorship, and timing of reproduction (Sweeney 1993; Cayrou and Céréghino 2005) may vary with temperature. Thus, the majority of aquatic beetles prefer relatively warmer waters and responds quickly to changes in temperature (Eyre 2006), and if cattail decreases water temperature, it may affect inhabiting aquatic beetles negatively.
- (ii) When positively polarotactic aquatic beetles seek their habitats by aerial colonization, the horizontally polarized light reflected from the water surface provides the major optical signal for habitat detection from a remote distance (Schwind 1991, 1995; Wildermuth 1998; Horváth and Varjú 2004; Horváth and Kriska 2008). If emergent cattail cover is relatively dense, the polarized optical signal is weak, and aquatic beetles may fail to detect the water surface, whilst less screened waters may be easier to find (Nilsson and Svensson 1995; Lundkvist et al. 2001). Removing emergent vegetation strongly increases the open water surface in mowed plots, affecting the visibility. Visibility here means not simply the view of the glittering water surface, because aquatic insects generally find water by means of positive polarotaxis rather than the colour and intensity of reflected light (Schwind 1991, 1995). Horizontally polarized light can be reflected towards flying polarotactic water insects only from vegetation-free regions of the water surface. In this work, the optical availability of horizontally polarizing open water surfaces for flying polarotactic aquatic insects is called the “polarization visibility”.

Mowing is an accepted, conventional management technique to decrease the negative impacts of cattail (Ball 1990; Sojda and Solberg 1993). Although Murkin et al. (1982) investigated the effect of cattail mowing on aquatic invertebrates, they considered it as a food resource of waterfowl. From the viewpoint of aquatic beetle ecology and conservation there is no recent information on the effect of cattail mowing. The flying capacity and the various microhabitat requirements of aquatic beetles

(Fairchild et al. 2000; Davy-Bowker 2002) predict rapid responses of these insects to environmental changes especially removal of emergent vegetation.

Here, we test the hypothesis that cattail mowing in a freshwater marsh changes the composition, increases the abundance and diversity of aquatic beetle assemblages due to the reduced negative effects of the dense monotypic stands. Since microhabitat preferences of aquatic beetles may differ (Fairchild et al. 2000, 2003) and they should not respond in the same way to cattail mowing, we use indicator species analysis (Dufrêne and Legendre 1997) to identify species preferring mowed and intact plots. We also investigate the role of environmental factors, such as depth, pH, conductivity and temperature of water, furthermore the reflection-polarization characteristics (polarization visibility) of the water surface changed by cattail removal, to see whether the change of these factors due to mowing influenced aquatic beetles.

## Materials and methods

### Study site

Our study was conducted at the Nyík-rét Reservoir II located in the Tápió-Hajta Protected Landscape Area in the eastern part of Pest county, Hungary (47° 23' 15" N, 19° 48' 50" E). In Tápió-Hajta Protected Landscape Area mean yearly air temperature is 9.7–10.3°C. Mean yearly precipitation is 553 mm, 30–40% of which falls from April to June. The Nyík-rét Reservoir II is a 150 ha freshwater marsh, flooded by the Hajta stream. The dominant vegetation is reed (*Phragmites australis* (Cav.) Trin.) and cattail (*Typha latifolia* L. and *T. angustifolia* L.). Water depth is approximately 70–100 cm in early spring, which decreases during summer as the area dries out.

### Experimental design

In April 2008 ten experimental plots, each 10 m × 10 m, were established in an area dominated by *T. angustifolia*. Plots were randomly located. The vegetation was hand-mowed with a brushcutter in 5 plots, 15 cm above the water surface (water level varied between 70 and 80 cm). Cut vegetation was removed by raking to the border of the plots. Despite of our efforts, small amounts of shred remained in the plots. Five control plots remained intact. The average distance between plots and between shoreline was 12 m, and the minimum distance between any pair was 10 m.

Based on the results of a previous pilot study with 3 mowed and 3 intact (control) plots, a 10 m distance appeared to be large enough for beetles to perceive plots as

distinct microhabitats. This distance was small enough to minimize the effect of landscape variability, which was considered also in estimating the number of replicates. Results from the pilot study, and sample size calculation methods (Morrison et al. 2001) suggested that 5 mowed and 5 intact (control) plots measured repeatedly five times provide adequate data for analysis.

### Sampling

Aquatic beetles have an en masse dispersal at late spring (Boda and Csabai 2009) and by timing our experiment at May we expected the maximal response from aquatic beetles to cattail removal as most of them disperse and search for the most suitable habitat at this time. The dispersal activity of aquatic beetles has a daily rhythm and most frequently there is an activity peak in the evening (Bernáth et al. 2004; Csabai et al. 2006; Boda and Csabai 2009). Therefore, by sampling aquatic beetle species composition in the morning we minimized the distorting effect of daily dispersion events.

To reduce the possible effects of disturbance due to wading, sampling was started 3 weeks after the mowing. Samples were taken weekly, altogether on five sampling dates (2, 10, 18, 24 and 30 May). Intervals of at least 6 days between samplings decreased the disturbance due to the previous sampling. Temperature, conductivity and pH of water were measured at each site on each sampling occasion with Hanna Combo HI 98130 combined tester, and water depth was also measured. Measurements were done in the center of the plots, 20 cm under the water surface. As water temperature is a very labile parameter, we also monitored it every hour (20 cm under the water surface) with a HOBO Pendant Data Logger during the first 3 weeks of sampling.

Aquatic beetles were captured by sweeping with a D-frame sweep net (mesh size = 200  $\mu\text{m}$ , mouth area = 23 cm, depth = 12 cm) just above the substrate and among the submerged or emergent vegetation. Sampling started in the center of the plots, and continued in a spiral around the center to avoid sampling the same area over multiple times. Sampling time was 20 min on each occasion, including sweeping and removing beetles from the sample. Captured specimens were preserved with 70% ethanol. Only adult beetles were collected and identified in the laboratory using keys and descriptions by Csabai (2000) and Csabai et al. (2002) with nomenclature following Csabai (2003). Because *Helophorus aquaticus* (Linnaeus 1758) versus *H. aequalis* (Thomson 1868) and *H. minutus* (Fabricius 1775) versus *H. paraminutus* (Angus 1986) are not identifiable with the use of morphological keys (Csabai et al. 2002), they were identified only at the species-group level. Abundance was estimated as the total number of collected beetles at each sampling site and date.

### Data analysis

A repeated measures ANOVA model was used to compare abundance, species richness, Shannon's diversity, Pielou-evenness and environmental factors among treatments and sampling dates. In the case of conductivity and pH of water the assumption of sphericity was violated (i.e. Mauchly Sphericity Test,  $P < 0.05$ ). Therefore, Greenhouse-Geisser (G-G) corrections were made on their degrees of freedom and  $P$ -values. Comparisons of dates and treatments were made using Fisher's least significant difference (LSD) test using Statistica 7.0 (Statsoft Inc. 2007).

To compare species assemblages between mowed and intact (control) plots, we calculated Shannon's diversity (Zar 1984), Pielou-evenness (Pielou 1966) and Bray-Curtis dissimilarity index (Podani 2000). Associations of species with either mowed or intact (control) plots were evaluated with indicator species analysis (ISA), which is a combination of the fidelity and specificity of the species to a treatment type (Dufrêne and Legendre 1997). Indicator value is maximal (100%) if all individuals of a species are found only in one treatment type and the species occurred in all plots of that treatment. Evaluation of the statistical significance of the maximum indicator values for each species was done by Monte Carlo randomization tests, in which species abundance data were randomized among treatment types (100 iterations).

Relationship between aquatic beetle species and environmental variables was analyzed by direct gradient analysis (Canonical Correspondence Analysis, CCA, ter Braak 1986). A Monte Carlo randomization test (100 iterations) was used to calculate the statistical significance of species-environment correlations. To decrease the distorting effect of multicollinearity (i.e. correlation within explanatory variables), water conductivity was excluded from the CCA, because conductivity correlated both with pH ( $P = 0.005$ ,  $r = 0.386$ ) and water temperature ( $P = 0.002$ ,  $r = 0.411$ ). Other correlations between the measured environmental factors were not significant ( $P > 0.05$ ). Shannon's diversity, evenness, Bray-Curtis dissimilarity, ISA and CCA were calculated using the R statistical environment (R-Development Core Team 2007).

### Imaging polarimetry

The reflection-polarization characteristics of water surfaces were measured by imaging polarimetry in the red ( $650 \pm 40$  nm = wavelength of maximal sensitivity  $\pm$  half bandwidth of the CCD detectors of the polarimeter), green ( $550 \pm 40$  nm) and blue ( $450 \pm 40$  nm) parts of the spectrum. The method of imaging polarimetry is detailed by Horváth and Varjú (1997, 2004). Here we mention only the fact that when a linearly polarizing filter is rotated in

front of a camera, the intensity and colour of the recorded scene change sinusoidally if the incident light is partially linearly polarized. By taking three pictures from the scenery through the polarizer at three different orientations of its transmission axis we obtained the so-called polarization pictures. After the evaluation of these pictures by our self-written computer program, we obtain the colour-coded, two-dimensional spatial distributions of the intensity  $I$ , degree of linear polarization  $d$ , and angle of polarization  $\alpha$  (e.g., from the vertical, as a reference direction) of light coming from the investigated scenery in the red, green and blue spectral range, where the camera's detectors are maximally sensitive.

An area of the water surface is sensed as water by a polarotactic aquatic insect, if (i) the degree of linear polarization  $d$  of water-reflected light is higher than a threshold  $d^*$ , and (ii) the deviation  $\Delta\alpha = |90^\circ - \alpha|$  of the angle of polarization  $\alpha$  from the horizontal is smaller than a threshold  $\Delta\alpha^*$  (Horváth and Varjú 2004). Both thresholds  $d^*$  and  $\Delta\alpha^*$  may be species specific and wavelength-dependent. As examples, in Figs. 1 and 2 we used  $d^* = 5\%$  and  $\Delta\alpha^* = 10^\circ$ . Although these threshold values are arbitrary, the use of other values did not influence qualitatively our conclusions. In this work the quantitative measure of polarization visibility is the proportion  $Q$  of the area (relative to a given region of the scene) detected polarotactically as water, for which  $d > d^*$ , and  $\Delta\alpha = |90^\circ - \alpha| < \Delta\alpha^*$ .

Our polarimetric measurements were performed under clear sky in sunshine, in intact (control) plots, in mowed, but not raked plots, and in mowed and raked plots. In Figs. 1 and 2 we present only the polarization patterns measured in the blue spectral range. Similar patterns were obtained in the red and green parts of the spectrum. However, the data in Table 2 are based on reflection-polarization characteristics measured in the red, green and blue spectral ranges.

## Results

### Environmental factors

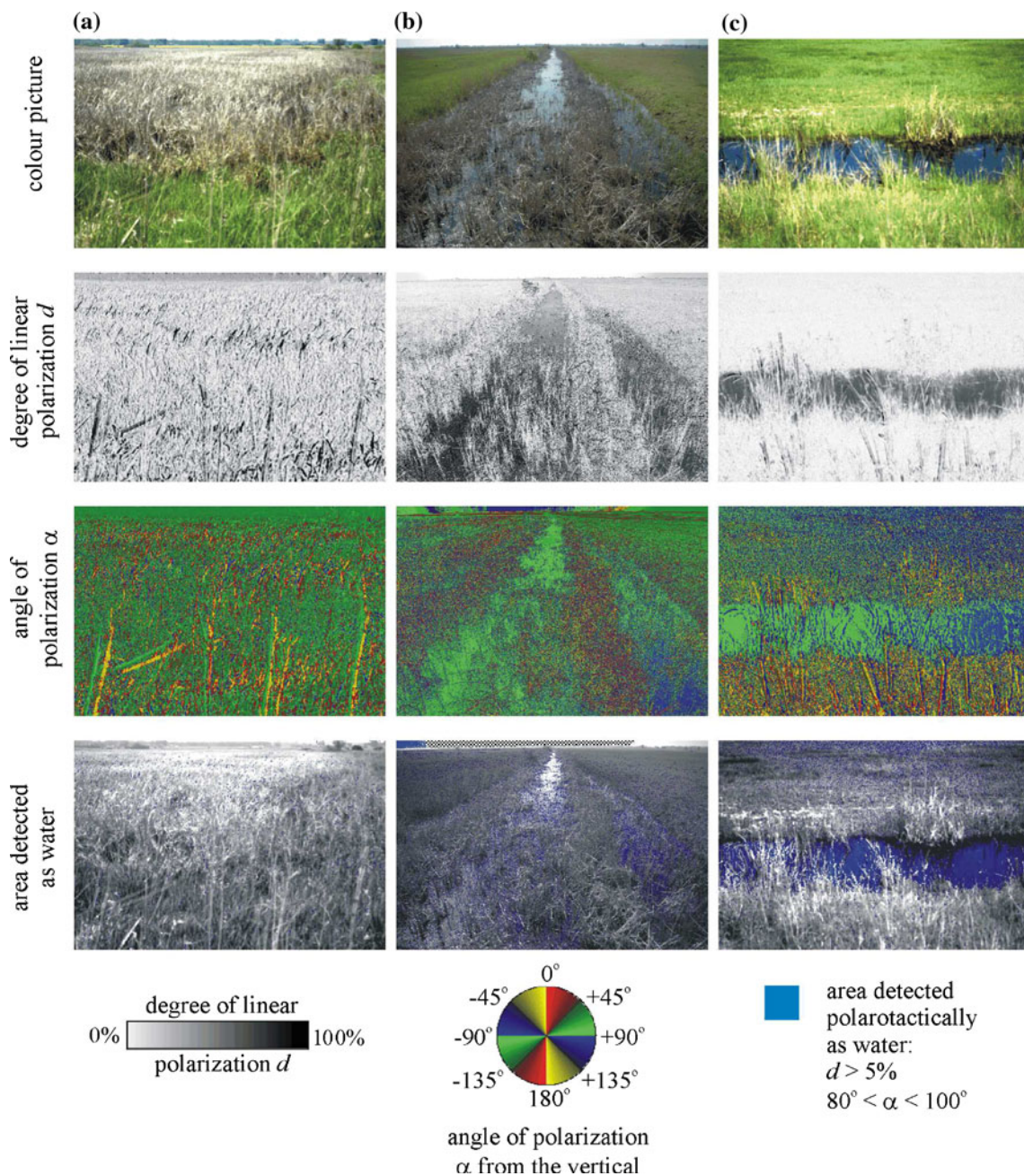
Repeated measures ANOVA indicated that water depth decreased significantly during the study (Table 1), but no statistically significant differences were found between treatments. The water temperature  $T$  measured at sampling occasions was significantly higher in the mowed plots than in control (intact) plots (Table 1, Fig. 3a) over all sampling dates (Fisher's LSD:  $P < 0.001$ ), the difference (mean  $\pm$  standard deviation) between mowed and control plots was  $1.3 \pm 0.57^\circ\text{C}$ . The water-temperature data monitored hourly also showed that  $T$  was higher in mowed plots. The difference was  $2.2 \pm 0.71^\circ\text{C}$  at noon (12:00) when thermal

differences between treatments were the most pronounced. There were also significant temperature differences between sampling dates (Table 1).

Although treatment effect in water conductivity was statistically significant (Table 1), Fishers's LSD tests found no differences between treatments on individual sampling dates. There were differences in conductivity within treatments between dates. No statistically significant differences were found in water pH between treatments, but sampling dates differed significantly (Table 1). Significant treatment-by-date interactions were not found for any of the environmental factors.

Reflection-polarization patterns of different water bodies measured by imaging polarimetry in the blue part of the spectrum are shown in Fig. 1. Brown dry cattail (covering/screening totally the underlying water surface) and the green grass (on the shore of the water body) reflect weakly polarized light (encoded by light grey and white shades) with directions (angles) of polarization changing strongly spatially due to the different orientations of cattail leaves (Fig. 1a). Such reflected light is unattractive to positively polarotactic aquatic insects (Horváth and Varjú 2004). Regions of the water surface not covered by cattail reflect highly polarized (encoded by dark grey and black shades) and horizontally polarized (encoded by bright green and bright blue colours) light (Fig. 1b), which is very attractive to polarotactic aquatic insects (Schwind 1991, 1995). Dark open water surfaces without vegetation (Fig. 1c) always reflect highly and horizontally polarized light when viewed at the Brewster angle (at which the surface-reflected ray of light is perpendicular to the refracted ray penetrating into water;  $\theta_{\text{Brewster}} = \arctan n \approx 37^\circ$  from the horizontal for the refractive index  $n = 1.33$  of water).

In Fig. 2 the reflection-polarization patterns of a region of a water body are shown for three different conditions: (1) when the water surface was almost totally covered by cattail (Fig. 2a), (2) when it was covered by mowed cattail (Fig. 2b), and (3) when the mowed cattail was raked away (Fig. 2c). Depending on the wavelength of light, the proportion  $Q$  of the highly and horizontally polarizing regions of the water surface (sensed as water by flying, water-seeking polarotactic aquatic beetles) increased from 18.2–24.0 to 42.2–49.5% after the cattail was mowed, and  $Q$  increased further to 44.3–51.9% after the mowed cattail was raked away.  $Q$  was highest in the blue part of the spectrum (24.0–51.9%), and it decreased through the green (20.6–47.6%) toward the red (18.2–44.3%) spectral range (Table 2). The physical reason for this is that the water-reflected light was the blue skylight, and the light coming from under the water surface was most intense in the red spectral range. Hence, depending on its density, the cattail (and other plant) coverage can more or less reduce the polarization visibility  $Q$  (horizontally polarized light



**Fig. 1** Colour pictures, patterns of the degree  $d$  and angle  $\alpha$  (clockwise from the vertical) of linear polarization, and areas detected polarotactically as water (for which  $d > 5\%$  and  $80^\circ < \alpha < 100^\circ$ ) of different water bodies measured by imaging polarimetry in the blue part of the spectrum. The angle of elevation of the optical axis of the

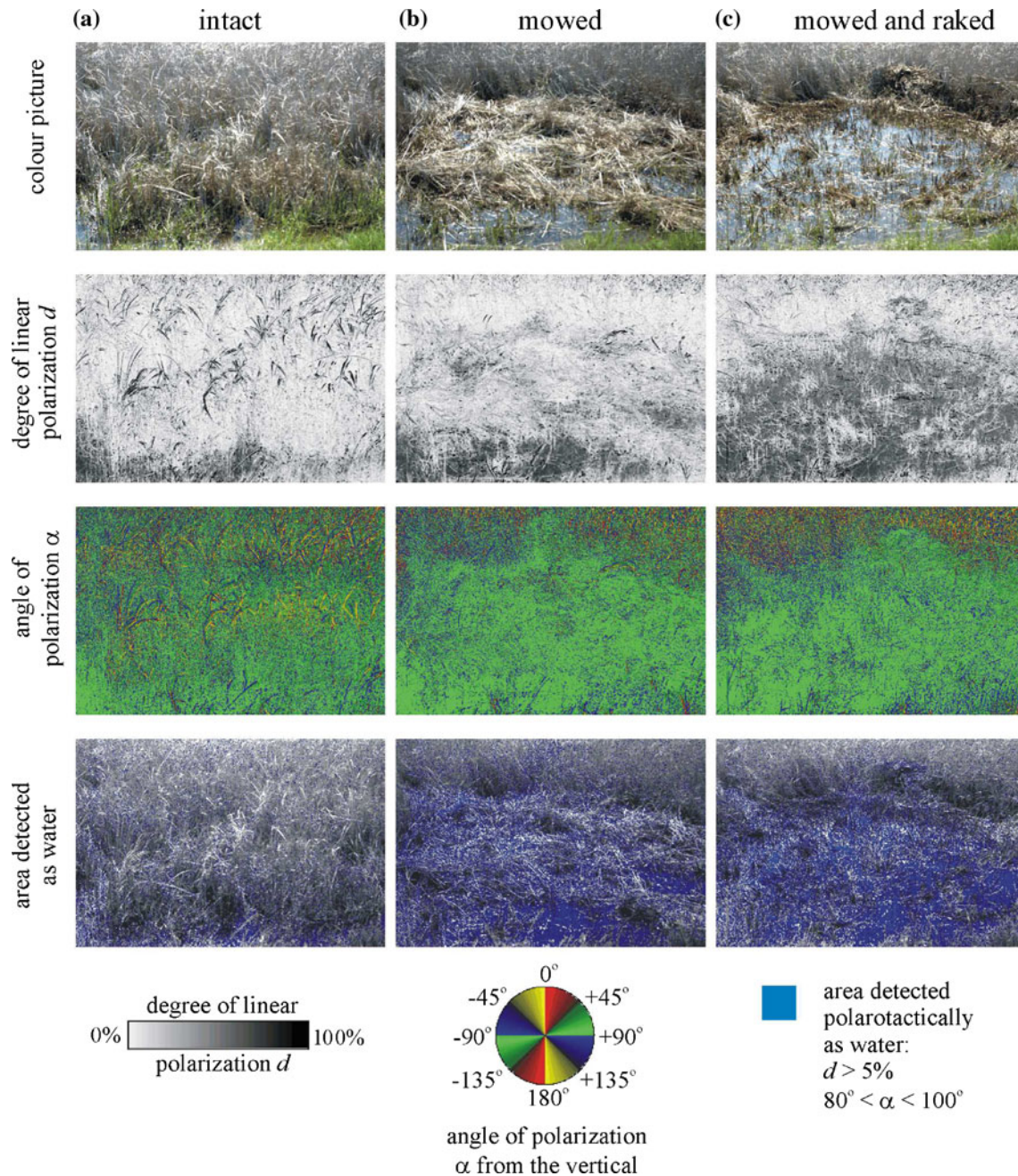
polarimeter was  $-35^\circ$  from the horizontal. **a** A water surface which is totally covered by cattail. **b** A water channel, the surface of which is partly covered by cattail. **c** Another water channel, the surface of which is open (without water plants)

signal) of the water surface (Fig. 2, Table 2), and thus can make more or less difficult the aerial colonization of waters by aquatic beetles.

#### Aquatic beetle assemblages

A total of 1606 individuals of aquatic beetles (mowed plots, 931; unmown plots 675) belonging to 44 species and

3 genera were collected (Table 3). The dominance of the most frequent species *Noterus crassicornis* was 33.7%. The proportions of subdominant species were as follows: *Hygrotus decoratus*: 11.7%, *Enochrus coarctatus*: 7.9%, *Helophorus minutus/paraminutus* group: 6.79%, *Enochrus testaceus*: 5.3%. The proportions of the remaining 42 taxa were below 5%. There was a significant difference in the abundance between treatments (Table 1). Fishers’s LSD



**Fig. 2** As Fig. 1 for a region of a water body, when **a** it is almost totally covered by cattail, **b** it is covered by the mowed cattail, and **c** the mowed cattail is raked away

tests run on each date found that the beetle abundance was higher in mowed plots on the 3rd sampling date ( $P = 0.014$ ). There were also differences between dates (Table 1). Treatment-by-date interaction was not significant (Fig. 3b).

No significant differences between treatments or sampling dates were found for species richness, but there was a significant treatment-by-date interaction (Table 1). When species richness increased in mowed plots, it decreased in control (intact) plots and vice versa (Fig. 3c). The rarefied

species richness of mowed plots was 42.2, whereas that of the controls was 34.

Shannon's diversity ( $H'$ ) did not differ between treatments or sampling dates. Also treatment-by-date interaction was not different. The Pielou's evenness ( $J'$ ) was significantly lower in mowed plots than in control plots (Table 1) indicating that the assemblages were dominated by a few abundant species, while control plots supported assemblages with more balanced species distribution. Bray-Curtis dissimilarity index values (mean  $\pm$  standard

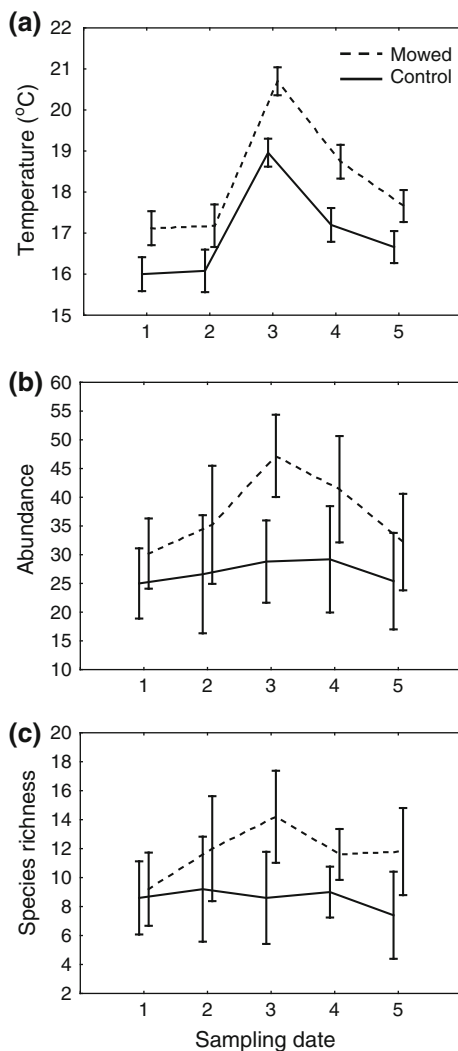
**Table 1** Results of repeated measures ANOVA comparing abundance, species richness, Shannon’s diversity, Pielou-evenness and environmental factors of different treatments and sampling dates

	F <sub>1,28</sub>		
	Between dates	Between treatments	Treatment by date interaction
Water level	5.86**	NS	NS
Water temperature	93.1**	555.9**	NS
Conductivity	19.51**	9.5*	NS
pH	21.95**	NS	NS
Abundance	3.22**	14.75**	NS
Species richness	NS	NS	6.16**
Shannon diversity	NS	NS	NS
Pielou evenness	NS	6.408*	NS

Statistically significant differences are marked (\*  $P < 0.05$ ; \*\*  $P < 0.01$ )

**Table 2** Proportion  $Q$  of the area (relative to the regions below the horizon in the picture) detected polarotactically as water (for which degree of polarization  $d > 5\%$ , and angle of polarization  $80^\circ < \alpha < 100^\circ$ ) for the water body in Fig. 2 measured by imaging polarimetry in the red, green and blue parts of the spectrum

Spectral range	Covered by cattail (Fig. 2a) (%)	Covered by mowed cattail (Fig. 2b) (%)	Mowed cattail raked away (Fig. 2c) (%)
Red	18.2	42.2	44.3
Green	20.6	46.0	47.6
Blue	24.0	49.5	51.9



**Fig. 3** Comparisons of means ( $\pm 95\%$  confidence intervals) of water temperature, aquatic beetle abundance (i.e. number of individuals), and species richness (i.e. number of species) between mowed and control (intact) plots

deviation) indicated rather high differences in species assemblages between treatments ( $0.608 \pm 0.088$ ), and smaller differences either within mowed ( $0.285 \pm 0.062$ ) or control plots ( $0.299 \pm 0.056$ ).

The indicator species analysis (ISA) showed that 14 species (29% of the total species richness) were significant indicators of the mowed plots, whereas 7 species (15%) were significant indicators of the control plots (Table 3). The positions of symmetric indicator species (i.e. indicator value  $> 55\%$ ) in the ordination are highlighted in Fig. 4 and agree with the results of ISA.

CCA revealed a strong relation among environmental factors and aquatic beetle abundance and species composition. The triplot scores of axis 1 for water temperature, axis 2 for water pH, and axis 3 for water depth were high, however, the Monte Carlo randomization test showed that only the scores of temperature differed significantly from that of randomized data (Table 4). The separation of the convex polygons of treatments was large along axis 1, suggesting that the treatments differed particularly by their temperature (Fig. 4).

**Discussion**

There might be two major sources of aquatic beetles colonizing the studied plots: either from other parts of the marsh or from other similar marshes within a radius of a few kilometres. As aquatic beetles must find waters during their flight within about 1 h to avoid dehydration (Bernáth et al. 2004; Horváth and Varjú 2004), it is unlikely that a significant part of the beetles came from larger distances, because there were no wetlands in the wider surroundings.

Our findings suggest that the considerably increased polarization visibility  $Q$  of water due to mowing (Table 2, Fig. 2) was the main factor which enhanced the chance of aerial colonization by aquatic beetles, and thus modified aquatic beetle assemblages. From a remote distance a water-seeking flying aquatic insect cannot sense the temperature, pH, conductivity, oxygen content, etc. of water,

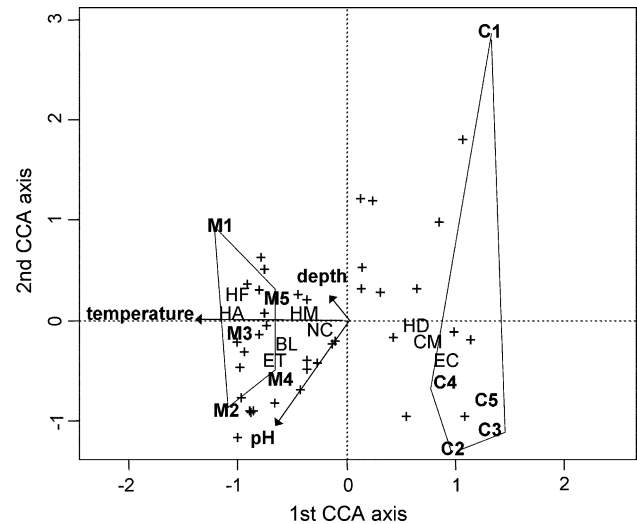
**Table 3** Associations of significant indicator species with either mowed or control (intact) plots by indicator species analysis and mean abundance  $\pm$  standard deviation values. Indicator value  $V$  is 100%, if all individuals of a species are found in one treatment type and the species occurred in all plots of that treatment

	$V$ (%)	Mean $\pm$ SD
Control (intact) plots		
<i>Enochrus coarctatus</i> (Gredler, 1863)	87**	4.68 $\pm$ 0.76
<i>Hygrotus decoratus</i> (Gyllenhal, 1810)	72**	5.68 $\pm$ 0.73
<i>Cymbiodyta marginella</i> (Fabricius, 1792)	62**	2.64 $\pm$ 0.62
<i>Anacaena limbata</i> (Fabricius, 1792)	52**	1.88 $\pm$ 0.54
<i>Liopterus haemorrhoidalis</i> (Fabricius, 1787)	45**	1.00 $\pm$ 0.23
<i>Hydaticus seminiger</i> (De Geer, 1774)	22*	0.32 $\pm$ 0.11
<i>Hydrochara caraboides</i> (Linnaeus, 1758)	12**	0.12 $\pm$ 0.07
<i>Helophorus nubilus</i> Fabricius, 1777	21	0.32 $\pm$ 0.13
<i>Hydroporus tristis</i> (Paykull, 1798)	12	0.36 $\pm$ 0.16
<i>Hydroporus angustatus</i> Sturm, 1835	9	0.12 $\pm$ 0.07
<i>Enochrus fuscipennis</i> (Thomson, 1884)	9	0.12 $\pm$ 0.07
<i>Coelostoma orbiculare</i> (Fabricius, 1775)	5	0.08 $\pm$ 0.06
<i>Ilyius quadriguttatus</i> (Lacordaire, 1835)	4	0.04 $\pm$ 0.04
<i>Rhantus grapii</i> (Gyllenhal, 1808)	4	0.04 $\pm$ 0.04
Mowed plots		
Helophorus minutus species group	81**	4.08 $\pm$ 0.97
<i>Berosus luridus</i> (Linnaeus, 1761)	72**	1.92 $\pm$ 0.31
<i>Noterus crassicornis</i> (O.F.Müller, 1776)	71**	15.16 $\pm$ 1.49
<i>Enochrus testaceus</i> (Fabricius, 1775)	67**	2.52 $\pm$ 0.36
Helophorus aquaticus species group	61**	1.92 $\pm$ 0.51
<i>Haliplus furcatus</i> Seidlitz, 1887	60**	0.84 $\pm$ 0.17
<i>Helochares obscurus</i> (O.F.Müller, 1776)	38**	0.60 $\pm$ 0.19
<i>Hydrobius fuscipes</i> (Linnaeus, 1758)	37**	0.92 $\pm$ 0.24
<i>Laccophilus poecilus</i> Klug, 1834	28**	0.28 $\pm$ 0.09
<i>Hydrophilus piceus</i> (Linnaeus, 1758)	24*	0.52 $\pm$ 0.26
<i>Enochrus bicolor</i> (Fabricius, 1792)	24*	0.32 $\pm$ 0.13
<i>Hydroglyphus geminus</i> (Fabricius, 1792)	24**	0.28 $\pm$ 0.11
<i>Hydrochara flavipes</i> (Steven, 1808)	22*	0.36 $\pm$ 0.15
<i>Berosus signaticollis</i> (Charpentier, 1825)	20*	0.20 $\pm$ 0.08
<i>Hygrotus impressopunctatus</i> (Schaller, 1783)	21	0.76 $\pm$ 0.27
<i>Hygrotus inaequalis</i> (Fabricius, 1776)	20	0.20 $\pm$ 0.08
<i>Graptodytes granularis</i> (Linnaeus, 1767)	19	0.36 $\pm$ 0.13
<i>Hydroporus erythrocephalus</i> (Linnaeus, 1758)	12	0.20 $\pm$ 0.08
<i>Spercheus emarginatus</i> (Schaller, 1783)	11	0.20 $\pm$ 0.10
<i>Graphoderus austriacus</i> (Sturm, 1834)	9	0.12 $\pm$ 0.07
<i>Berosus frontifoveatus</i> Kuwert, 1888	8	0.08 $\pm$ 0.06
<i>Haliplus flavicollis</i> Sturm, 1834	8	0.20 $\pm$ 0.16
<i>Enochrus affinis</i> (Thunberg, 1794)	6	0.12 $\pm$ 0.09
<i>Hydrovatus cuspidatus</i> (Kunze, 1818)	5	0.08 $\pm$ 0.06
<i>Enochrus melanocephalus</i> (Olivier, 1792)	4	0.04 $\pm$ 0.04
<i>Enochrus ochropterus</i> (Marshall, 1802)	4	0.16 $\pm$ 0.16
<i>Graphoderus cinereus</i> (Linnaeus, 1758)	4	0.04 $\pm$ 0.04
<i>Haliplus variegatus</i> Sturm, 1834	4	0.04 $\pm$ 0.04
<i>Hydaticus transversalis</i> (Pontoppidan, 1763)	4	0.08 $\pm$ 0.06

**Table 3** continued

	$V$ (%)	Mean $\pm$ SD
<i>Hydrochus elongatus</i> (Schaller, 1783)	4	0.08 $\pm$ 0.06
<i>Limnoxenus niger</i> Zschach, 1788	4	0.04 $\pm$ 0.04
<i>Hydrochus crenatus</i> (Fabricius, 1792)	2	0.04 $\pm$ 0.04
<i>Hydraena</i> sp.	2	0.04 $\pm$ 0.04

Statistically significant associations are marked (\*  $P < 0.05$ ; \*\*  $P < 0.01$ )



**Fig. 4** Triplot of canonical correspondence analysis. M1–M5 denote the five mowed plots, while C1–C5 denote control (intact) plots. Environmental factors are vectors, and “+” indicates the species. The names of symmetric indicator species (i.e. indicator value  $>55\%$ ) are abbreviated by the first letter of the genus and the first letter of the species names in Table 1

but can perceive the horizontally polarized light reflected from open areas of the water surface (Schwind 1991). This polarized signal guides the insect to a water body. After entering into water, the insect may sense physico-chemical parameters and decide whether they are appropriate or not. If the environmental factors are appropriate, the insect may remain in the chosen water body, otherwise it leaves the water in order to seek another, more appropriate location (Schwind 1995; Horváth and Varjú 2004).

In our field experiment, mowed plots received more solar radiation than intact plots, and this increased the water temperature. Temperature is a major environmental factor for invertebrate species distribution (Batzler and Wissinger 1996; Eyre 2006), and small changes in temperature may greatly affect important life history characteristics of macroinvertebrates (Sweeney 1993). As a secondary driver, different water temperatures might be responsible for the different beetle assemblages between



**Table 4** The output of canonical correspondence analysis and Monte Carlo randomization test for constraining variables

	Triplot scores for constraining variables			<i>df</i>	<i>F</i>	P
	Axis 1	Axis 2	Axis 3			
Water depth	−0.103	0.182	−0.977	1	0.81	0.59
Water temperature	−0.999	−0.000	0.038	1	6.30	0.01
Water pH	−0.460	−0.716	−0.525	1	1.39	0.19

shaded, relatively cool waters and heavily insolated warmer waters.

Neither conductivity, nor pH of water was affected by mowing. Arnott et al. (2006), and Juliano (2006) also found that pH had little or no influence on aquatic beetles. Thus, we could assume that polarization visibility  $Q$  and temperature differences  $\Delta T$  were the two major (primary and secondary) environmental factors that resulted in the different patterns in aquatic beetle assemblages. Mowing might also influence the following environmental parameters affecting water beetles:

1. A small amount of shred remaining in mowed plots after raking might increase detrital food resources. However, decay of cattail litter is a relatively slow process as it lasts for a few years (Welsch and Yavitt 2003; Álvarez and Bécares 2006; de Neiff et al. 2006), while our experiment finished after 2 months of cattail mowing. Therefore, the detrital increase due to the remained leaf litter seems to be insignificant in our short-term study. Murkin et al. (1982) also found little influence of detrital food resources on invertebrate abundance in cattail stands.
2. Removing emergent vegetation causes higher light intensity that affects the quantity of green algae and thus oxygen-level and productivity. Flechtner (1986) found that crawling water beetles (Halipilidae) are showing affinity to waters with high productivity, and they have a high demand for oxygen combined with the existence of green algae. Crawling water beetle species found in our study (*Halipilus furcatus*, *H. flavicollis* Sturm 1834, and *H. variegatus* Sturm 1834) were present only in mowed plots, and *H. furcatus* was a significant indicator species of that treatment, confirming the findings of Flechtner (1986). However, as other aquatic beetle families are not algophagous, we assume that productivity is a minor factor adjusting water beetle assemblages. Differences in oxygen level seem also less important because aquatic beetles respire with atmospheric oxygen and use temporary air stores in water.
3. If mowing reduces the negative effects of cattail, an increase in both the abundance and diversity of other plant species is quite possible. Increased submerged

vegetation may support more diverse and dense macroinvertebrate assemblages (Kurashov et al. 1996; Strayer and Malcom 2007; Stewart and Downing 2008), because it provides food, protection from predators, increased physical heterogeneity and additional living spaces (Gregg and Rose 1985). However, our experiment was probably too short to allow considerable changes in the submerged vegetation.

4. Mowing may have affected aquatic beetles through their food resources. Studies in other types of vegetation showed that mowing increases midge (Chironomidae) density (Batzler and Wissinger 1996; de Szalay and Resh 1997, 2000). This may cause an increased number of predaceous aquatic beetles. Phytophagous beetles may prefer mowed plots because of the extended submerged vegetation, but also control (intact) plots, due to the higher amount of leaf litter. To answer this question, further studies focusing on the food web changed by mowing are necessary.

Since there are conflicting results in relation to vegetation and aquatic macroinvertebrate density and diversity; we hypothesize that cattail mowing may affect aquatic beetles both negatively and positively: negatively, because mowing reduces the amount of plants, which provides food and cover for aquatic beetles (Hebauer 1986; Verberk et al. 2001). The risk of predation imposed by visual predators, and also the surface turbulence caused by wind should be higher in mowed plots (de Szalay and Resh 2000). However, as adult aquatic beetles use temporary air stores, they do not need to live near the water surface, and are less exposed to surface predation and turbulence than taxa breathing atmospheric oxygen (de Szalay and Resh 2000). Thus, they are not restricted to the dense vegetated waters, but can expand to the mowed water bodies, if there are more favourable conditions. Solar radiation, and thus water temperature is usually higher in mowed plots, furthermore mowing creates open water surface with an increased polarization visibility  $Q$ , enhancing the chance of aerial colonization by polarotactic aquatic insects (Young 1960; Galewski 1971; Fairchild et al. 2003).

Although we cannot precisely identify which factor has the stringest influence, it is clear that conservation of aquatic beetles in *Typha* stands in a freshwater marsh can

be enhanced by mowing relatively small plots, since this produces favourable conditions for many aquatic beetle species. However, some species prefer intact plots. Consequently, to maximize aquatic beetle diversity it is advisable to create both mowed and unmown areas. It is possible to affect water beetle assemblages with relatively small mowed areas. Where resources (financial or human) are limited, small intervention plots are a viable option for maximizing opportunities for aquatic beetles. According to Balcombe et al. (2005) and Sartoris and Thullen (1998), approximately even proportions of vegetated and open water habitats (i.e. hemi-marsh) create optimal conditions for aquatic invertebrates, though our study indicates this may not be necessary. Repeats of our work need to be undertaken to substantiate our findings.

An important practical consequence of our work is that mowed cattail need not be raked away, if the only aim is to enhance the polarization visibility  $Q$  of water surfaces, as it increases more after mowing than after mowed cattail is raked away. Such raking is very difficult, and time and energy can be spared by leaving the mowed cattail in situ. Studying the possible negative or positive effects of mowed cattail (increased plant debris) on aquatic insects should be undertaken in the future.

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