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The structure and dynamics of a water beetle community in a semipermanent wetland (Vrbenské rybníky Nature Reserve, South Bohemia)

Bachelor Thesis

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Annotation

In my thesis I examined the structure and dynamics of a water beetle community in a semipermanent wetland in an alder carr. The results are based on three years of my field work and processing of material collected by a light trap at the study site during five years. The thesis focuses on: 1. Comparison of selectivity and efficiency of several widely used sampling methods; 2. Seasonal dynamics and effects of environmental variables on flight acitivity; 3. Spatiotemporal dynamics and effects of habitat structure and fluctuations in water levels. General patterns and relationships are highlighted.

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Contents

1 Introduction **5**

2 Topic one – Selectivity and efficiency of four methods for sampling water beetles **6**

- 2.1 Review of the literature – Methods for sampling insects in stagnant waters 7
- 2.2 Material and methods 10
  - 2.2.1 Study site description 10
  - 2.2.2 Sampling 11
  - 2.2.3 Processing material 12
  - 2.2.4 Data processing 12
- 2.3 Results 13
- 2.4 Discussion 19

3 Topic two – Flight activity of water beetles – seasonal dynamics and effects of environmental variables **21**

- 3.1 Review of the literature – Dispersal by flight in aquatic insects 22
- 3.2 Material and methods 24
- 3.3 Results 26
- 3.4 Discussion 35

4 Topic three – Spatiotemporal dynamics of a water beetle community **37**

- 4.1 Review of the literature – Spatiotemporal dynamics, habitat associations, biotic and abiotic factors shaping insect communities of stagnant waters 38
- 4.2 Material and methods 41
- 4.3 Results 42
- 4.4 Discussion 50

5 Conclusions **52**

6 References **53**

Appendix – List of species **60**

1 Introduction

This thesis evaluates data from a survey of water beetles in a semipermanent wetland close to the Černiš pond in southern Bohemia. In this survey, I attempted to cover a number of questions related to the ecology of water beetles as well as the underlying methodology needed to study these questions.

In the Czech Republic, water beetles are well studied but most of the previous research focused on faunal surveys, some of them very extensive. Globally, ecological studies on water beetle communities are by far not as numerous as those targeting other dominant aquatic insects, e.g. Diptera, Odonata, Ephemeroptera, and Plecoptera. Knowledge of processes shaping the aquatic insect communities is still growing, but a lot of questions are awaiting answers both in the field of general processes affecting the structure and dynamics of these systems and in specific topics of ecology of different taxonomical and ecological groups.

The study site is of international significance and belongs to the most important wetlands in South Bohemia. Altogether 922 species of moths, accounting for more than 30% of Czech moth's fauna and including several very rare species, were found here during last decades (Spitzer & Lepš 1988, Lepš et al. 1998, Jaroš & Spitzer 1999). Recently, research of Neuroptera, ground beetles (Coleoptera: Carabidae) (Bezděk 2002, Bezděk et al. 1997, Čížek 1999) and other groups of beetles (Čížek 1999) has been carried out here as well. Water beetles were included in the study of Čížek (1999), but the method used and the taxonomical scope of his work did not provide detailed data on the structure and dynamics of the water beetle community. Water beetles are the dominant predatory group in the wetland. Other predatory insects (e.g. Odonata, Heteroptera) and fish are virtually absent.

My thesis focuses on three topics:

a. **Selectivity of several standard sampling methods**. A wide range of methods for sampling aquatic invertebrates have been developed, hence their evaluation is necessary. I hypothesized that the light trap operating in the wetland would be most selective and gain the lowest number of species in comparison to activity traps, box trap and handnet sampling. Overall, I expected to find clear differences in species composition among the methods, attributable to differential activity of the species.

b. **Flight activity.** Seasonal aspects of dispersal by flight and effects of environment have been studied repeatedly. I have focused mainly on differences in seasonality and effects of environmental variables on flight activity among dominant families. Moreover, I expected mass emigration of water beetles during periods of rapid desiccation and supposed to confirm that air temperature is the other key factor determining the flight activity of water beetles.

c. **Spatiotemporal dynamics.** Seasonal dynamics of aquatic insect communities are traditionally studied, but little attention has been paid to spatial structuring. Hydrological conditions variable in time and space were supposed to be of great importance for the spatiotemporal dynamics of the water beetle community. With retreat in water level, shift in spatial distribution towards concentration in the centre of the wetland was expected. Drain geometry (water depth and width) and density of vegetation were supposed to influence the local density as well composition of the water beetle community.

2 Topic one

Selectivity and efficiency of four methods for sampling water beetles

2.1 Review of the literature – methods for sampling insects in stagnant waters

A wide variety of sampling methods is used for sampling water insects because of their great variability in microhabitat occupation and mobility. D-frame handnet and kitchen strainer are usually used for qualitative collecting (Boukal et al. 2007). A variety of quantitative methods have been developed for collecting specific groups or for general research of macroinvertebrate communities with as little bias as possible. Several of them used in stagnant waters are briefly discussed here.

Box trap

A number of devices for enclosing a defined area and extracting animals were proposed, but as most of them are complicated. Over the years, a box trap of the simplest construction has become a common standard in quantitative research of invertebrates of stagnant water bodies for its simplicity and reasonable accuracy. It is a box without the bottom and top and with sides 0.3–0.7 m long, made of metal sheets, plexiglas or other sturdy material. The trap is placed into the water, pushed into the bottom, and the enclosed area is thoroughly swept by a handnet. This method allows evaluating the density of a wide spectrum of invertebrates.

Some authors caution that this method can underestimate the density of large highly mobile taxa (Fairchild et al. 2000; O'Connor et al. 2004). If the trap is placed quickly and the animals not disturbed, this bias is likely to be negligible (J. Klečka pers. obs.). Problems may arise in dense and rough vegetation (e.g. reed, sedges), where the manipulation with box trap is difficult. A box sampler developed by Gerking (1957) enables to cut the vegetation in the enclosed area, but it was originally designed for use in soft vegetation. A modification for its use in dense rough vegetation was recently proposed by Sychra & Adámek (J. Sychra pers. comm.). They however conclude that mobile taxa are severely underestimated by this trap in such habitats.

Corers and grabs

These methods are used for colleting zoobenthos inhabiting the bottom sediments (e.g. Chironomidae, Oligochaeta, Hirudinea). The principle is extracting invertebrates from a fixed volume of sediments. A core sampler is basically a metallic tube which is pushed into the bottom to a given depth and lifted with a sediment sample. It is used especially in shallow waters. Grabs of various, often complicated construction can be used also in deep waters, where they are casted from a boat. Invertebrates are extracted by flushing the softest portion of sediments from a sample on a sieve and by manual sorting of remaining material (see Southwood & Henderson 2000 for further information). Landin (1976) tested a core sampler for sampling small water beetles inhabiting the water/shore boundary and considered this method as effective but reported an underestimation of abundance of the smallest species from the family Hydraenidae, caused likely by damage during sampling, transport of sampled material, and extraction in Berlese-Tullgren funnels.

Standardized effort-based methods

One of the most commonly used method for its simplicity is standardized handnet sampling. The collector simply sweeps the habitat using a handnet for a given period of time (e.g. Nilsson & Svensson 1995) or a given area (without any solid boundaries as compared to the box trap) (e.g. Nilsson & Soderberg 1996). For the purpose of detecting the highest possible number of species inhabiting the locality (as required for biomonitoring) it is ideal to identify present mesohabitats (e.g. part of a pond overgrown by reed, muddy-bottomed shallows without vegetation, inflow area etc.) and allocate equal sampling time to all of them

(Environment Agency and Pond Conservation Trust 2002). Standardizing by time leads to gaining semiquantitative data roughly comparable among sites. For quantitative analyses, it seems more reasonable to sample a fixed area, but this may lead to non-detection of species inhabiting mesohabitats with small relative areas. If sampling of a given area is done quickly to avoid undersampling of highly mobile taxa and consistently among sites, it may provide reasonably good quantitative data. Because of the lack of published tests regarding the effectivity and selectivity of this method, we can only speculate about a possible bias towards less mobile taxa (Becerra Jurado et al 2008), size selectivity, or the effect of vegetation density and other habitat variables on the performance of this method. Turner & Trexler (1997) found handnetting standardized by area as good as the box trap. Becerra Jurado et al (2008) found a negative correlation between vegetation density and proportion of taxa sampled exclusively by handnetting compared to activity traps, which may be explained by difficult manipulation with handnet in dense vegetation (see also Murkin 1983). Poor performance of handnetting in dense vegetation at least for some groups of insects is well known among collectors (e.g. O'Connor et al. 2004; J. Sychra pers. comm). On the other hand, some authors report that handnetting performs well even in highly vegetated habitats (García-Criado & Trigal 2005). Handnet sampling may be especially useful in bioassessment surveys, where accurate information about density is not required, because sweeping a variety of microhabitats within a water body provides good information about the community composition and is quick and cheap (García-Criado & Trigal 2005).

Activity traps

A variety of traps is used for collecting mobile swimming taxa of water beetles especially from the family Dytiscidae (both adults and larvae) (e.g. Nilsson et al. 1994; Lundkvist et al. 2001) and other aquatic macroinvertebrates. The simplest version is made from plastic bottles by cutting the upper third and inserting it inversely into the lower part, which creates a funnel leading swimming invertebrates inside the trap. Other modifications are a glass jar with attached plastic funnel or the so-called surface-associated activity trap designed by Hanson et al. (2000). Traps are usually laid horizontally near the bank and are exposed for several days with or without bait (chicken liver etc.). This method performs well for various invertebrate taxa in a variety of environments such as lakes (e.g. Nilsson et al. 1994; Hyvonen & Nummi 2000), ponds (e.g. Becerra Jurado et al. 2008) and wetlands (e.g. Lundkvist et al. 2001).

The size selectivity of activity traps was rarely assessed directly. Nilsson & Soderberg (1996) did not find any difference in mean individual body size when compared to handnetting, but Hilsenhoff (1987, 1991) reported positive size selectivity of activity traps. Another drawback of this method is that the relative abundance of a given species in the samples obviously depends on its activity and may not reflect its relative abundance in the community. Equal mobility of different species and different sexes are the underlying assumptions in quantitative analyses of data from activity traps. These assumptions have never been tested formally to my knowledge. Activity traps have very low time costs, provide samples free of detritus and plant fragments unlike most other methods, and are easy to standardize among researchers, which makes them advantageous for long-term or extensive studies (Murkin 1983).

An interesting, but only several times used modification is an aquatic light trap (Williams et al. 1996; Dennett & Meisch 2001), which is based on attraction of water beetles to light. This is basically a conventional activity trap equipped with a light source (chemical lightstick or electrical light specially designed for underwater usage). The attraction to light might be species specific, which would make quantitative interpretation difficult.

Light trap

Light traps of various designs are often used for research of insect flight activity (Southwood & Henderson 2000). Most families of water beetles are known to fly at light (e.g. Zalom et al. 1979, 1980). Light trap was used in a variety of studies focused on seasonal dynamics. According to Zalom et al. (1979, 1980), light trap provides unbiased estimates of the flight activity of Dytiscidae and Hydrophilidae. No other studies addressing the question of possible bias caused by species-specific attraction to light are available in water beetles, but in other insects, it is known that light catches are biased for many reasons including species- and sex-specific reactions to the light (see Southwood & Henderson 2000 for further information). Weather conditions are known to affect flight activity of water insects and thus also light trap catches (see Chapter 3.1). As light traps are usable only during the night, species flying during the day would not be detected. Daily flight periodicity is still an open question, but most species of water beetles seem to flight preferably after the sunset and are thus detectable by light trap (see Chapter 3.1).

Other methods for collecting flying water insects

Another commonly used method is the window trap (or flight-intercept trap), collecting flying insects passively without any attraction and thus providing an unbiased picture of relative abundance of different taxa in the air in relation to their flight activity. The trap is composed of a vertical sheet of glass or plexiglass and a collecting vessel filled with conservation liquid where the insects accumulate after hitting the vertical plate (see Southwood & Henderson 2000 for further information).

A rotary net machine composed of nets attached to an automatically rotating boom was used e.g. by Zalom et al. (1979, 1980), who believed that this method provides unbiased estimates of flight activity of insects.

Water insects see polarized light, which can be used in collecting using traps of various designs and containing a plate made of a material reflecting polarized light similarly as a water surface (Schwind 1991, 1995; Lundkvist et al. 2002; Csabai et al. 2006). This method was also used by earlier researchers, who thought that isects are attracted by shiny surfaces before the importance of polarized light was recognized (e.g. Landin & Stark 1973; Landin & Vepsäläinen 1977, Landin 1980; see also Chapter 3.1).

Comparison of methods

Although some of the methods described above are very frequently used, the efficiency and selectivity of most of them was only scarcely tested. Only a few attempts have been made so far to compare several methods. Differences in species composition between corers and handnetting or box trap are substantial (e.g. García-Criado & Trigal 2005). O'Connor et al. (2004) considered box trap as a clearly superior alternative to handnetting in the terms of efficiency and accuracy, but other such as Turner & Trexler (1997) considered these methods as equal. According to Becerra-Jurado et al (2008), both activity traps and handnetting standardized by time yield species not sampled by the other method, and for species richness estimation they consider the combination of these methods as desirable. Sychra & Adámek (J. Sychra pers. comm.) found out that box trap specifically designed for the use within dense stands of rough vegetation underestimated the abundance of highly mobile taxa compared to handnetting, as a consequence of difficult manipulation with the box trap within dense stands of vegetation; on the other hand, net sampling underestimated the abundance of slowly mobile taxa inhabiting the bottom surface and the vegetation. In the study of Nilsson & Soderberg (1996), samples from activity traps and handnetting did not differ in the size composition of dytiscid beetles, which contradicts the common belief that handnetting underestimates abundance of large mobile species (Becerra Jurado et al 2008) and that activity traps underestimate abundance of small and less mobile taxa (Hilsenhoff 1987, 1991). Turner & Trexler (1997) evaluated several methods for sampling wetland invertebrates and found large differences in total number of species, specimens and species composition among methods. Handnet and box trap collected the most diverse array of invertebrates and performed equally well. Differences among results obtained by different methods were reported by most authors. For biomonitoring programs, combination of several methods is thus recommended.

Among the methods for collecting flying insects, Zalom et al. (1979, 1980) found out no significant difference between the relative composition of catches of water beetles obtained by light trap and rotary net machine. This does not correspond to the results of studies in other groups of insects, which detected species-specific attraction of light (see Southwod & Henderson 2000 for further information).

Concluding remarks

Unbiased sampling methods are crucial for ecological studies that require reliable estimates of abundance across a range of species or individual states (e.g. sex, maturity). Further studies of the selectivity of various methods used to sample aquatic insects in stagnant water bodies are thus needed, because biased field data may lead to false conclusions obscuring our understanding of population- and community-level processes in aquatic habitats.

2.2 Material and methods

2.2.1 Study site description

The studied wetland, an alder carr of an area of ca. 1 km², is located in the Vrbenské rybníky NR at the NW outskirts of České Budějovice in South Bohemia, Czech Republic. It is located in a mainly agricultural landscape composed of a mosaic of fields, meadows, forests, and ponds used for aquaculture (Fig. 1). The wetland is a part of a peasantry operated by the company “Lesy a rybníky města Českých Budějovic s.r.o.“. The meadows surrounding the wetland are thus under extensive agricultural regime. The altitude is ca. 380 m a.s.l., the mean annual temperature is 8.2 °C, and the mean annual precipitation is 582.8 mm (means for years 1961-1990; data from the Czech Hydrometeorological Insitute).

Most of the area is overgrown by alder (*Alnus glutinosa*), along the edges mixed with other, partly planted tree species (pine, birch, oak, and fir). The herb layer is dominated by sedges (*Carex* spp.) and reed (*Phragmites australis*).

The central part of the wetland is inundated during spring (depth usually up to ca. 30 cm). The wetland is intersected by drains up to ca. 1 m deep, and additional drains bound the wetland. Most of the area desiccates during summer but some of the drains retain water for most or whole season (depending on rainfall). In dry years, the wetland completely dries out in summer before it fills again in autumn to spring by water from rain and melting snow. Other types of water bodies found near the wetland are represented by wet meadows, pools and ponds.

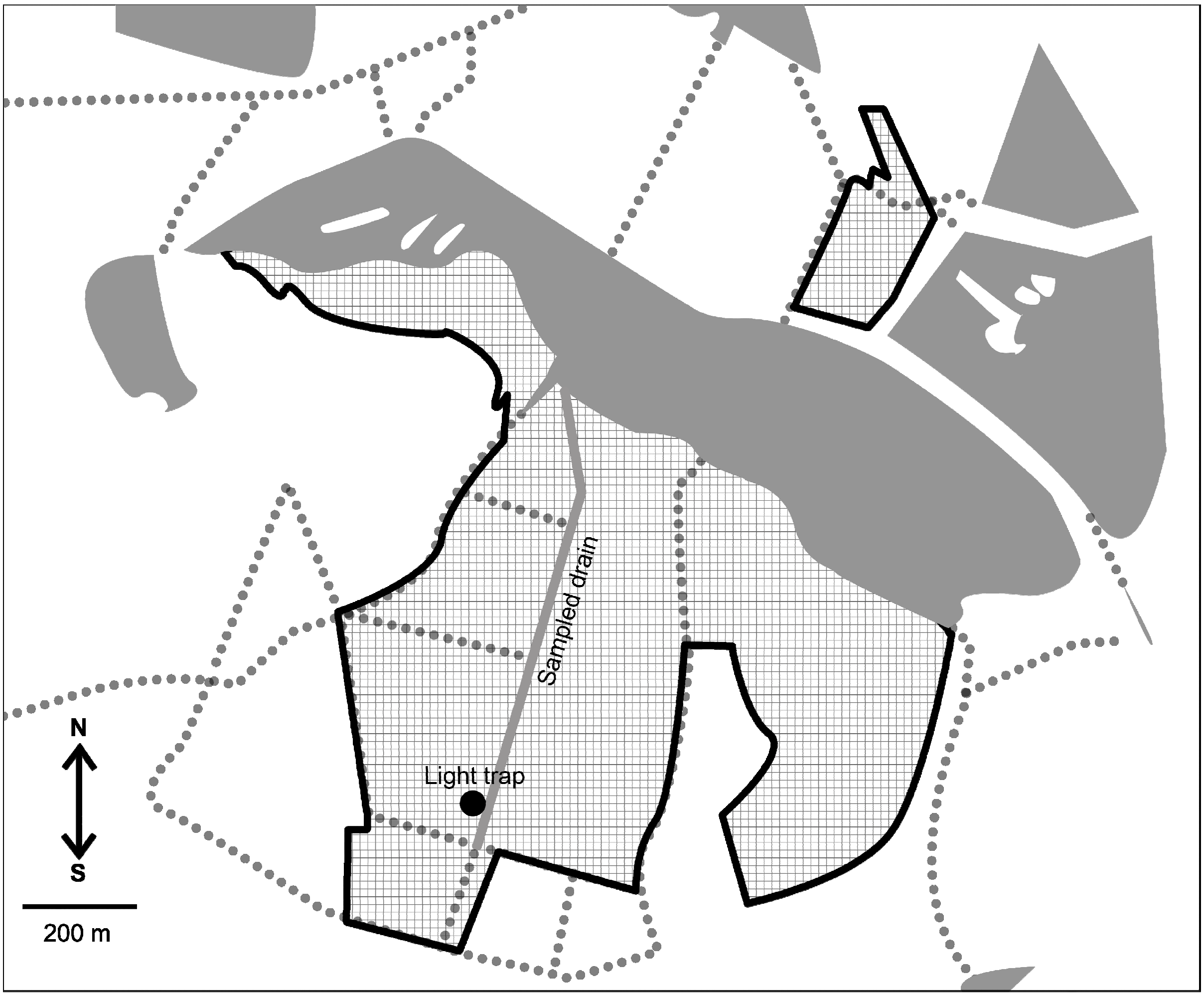

Fig. 1 – The study site (ponds in grey, alder carr in grey meshes, drains as grey dotted lines, meadows, fields and other land in white).

2.2.2 Sampling

Quantitative sampling took place in a 800 m long drain intersecting the wetland in approximately north-south direction and its near surroundings (Fig. 1). I used several quantitative sampling methods: activity traps, light trap, box trap, and standardized handnet sampling. Additional data were obtained by qualitative collecting using handnet and kitchen strainer in the alder carr and also in other water habitats near the wetland. All these methods except the light trap were used for collecting adult beetles as well as larvae.

Activity traps

Unbaited activity traps were made from 1.5 l plastic bottles with an 82 mm diameter at the outer end and 22 mm at the narrow inner end (see Collecting methods for additional details). Traps were placed into the drain just under the water surface near the bank at 20 m intervals and exposed for 48 hours. They were set weekly from snowmelt till late autumn (or until the drain dried out completely) in 2004-2006. In 2004, 18 traps were set in outer (southern) half of the drain, and 36 traps covering the whole length of the drain except a very shallow 120-m long stretch in the middle of the wetland were used in 2005 and 2006.

Light trap

A light trap located near the beginning of the same drain is used for monitoring of moths since 1981 and maintained by Karel Spitzer and Josef Jaroš (Jaroš & Spitzer 1999), I have been obtaining water beetles from this trap since 2002, and data from 2002–2006 are used in this thesis. The trap operates every night from early spring till the end of autumn, and captured insects are collected three times a week. During the study period, technical problems caused several short-term losses of data, but the losses are negligible (less than 3% of total sampling nights).

Box trap

Box trap was used in 2004 in the outer half of the same drain. Six samples were taken weekly, three of them in the drain and three in the flooded area outside the drain in the wetland interior. The wetland was divided into three segments perpendicularly to the drain. In each segment, a pair of randomly located samples was taken (one sample in the drain adjacent to the bank, one outside the drain up to 20 m apart). A plastic box trap covering an area of 60 x 40 cm was placed into the water and the enclosed area was thoroughly swept. Large plant fragments were sorted out in the field; detritus and small plant remains with collected beetles were taken to the lab in cloth bags and dried in dry extractors consisting of a container with a little of water and a tightly fitting frame with the bottom made from wire mesh, on which I placed a thin layer of substratum. The upper part was covered by a cloth and the substratum was let to dry for 48 hours. Adult beetles and larvae were collected in the lower container with water.

Handnet sampling

Standardized handnet sampling was carried out in 2006. Four 20 m long segments spread regularly over the full length of the drain were sampled every two weeks. One randomly located sample was taken in each segment and the area of approximately 0.5 x 0.5 m adjacent to the bank was thoroughly swept by a handnet. Large plant remains were sorted out in the field and soft detritus was preserved in 96% ethanol and collected invertebrates were sorted out in the lab. This method is conceptually very similar to the box trap and was used to overcome problems with manipulation with box trap in the hardly accessible centre of the wetland.

2.2.3 Processing material

I have identified all collected beetles to species level, except the larvae of *Cyphon* spp. and a few other larvae, which could be identified only to genus. Adults were divided in two age groups labelled as mature (tough, fully pigmented cuticle on the ventral body side) and immature (soft pale cuticle at least on abdominal ventrites). In all species of the Dytiscidae, sex was determined using secondary sexual characters or by extraction of genitalia.

Adults are stored dry except those collected by standardized handnet sampling, which are stored in ca. 80% ethanol as are with the larvae.

2.2.4 Data processing

Unless otherwise stated, data analyses and graphs were executed in the R 2.6.0 software (R Development Core Team 2007). The species richness and diversity of assemblages sampled by individual methods were analyzed using EstimateS software (Colwell 2006). Comparison of sampling methods is based only on species with aquatic adults (light trap collects also species with terrestrial adults). Sample-based rarefaction was computed using analytical formulas given by Colwell et al. (2004) for data from individual methods separately and for the combined data set containing pooled data from all methods. Observed numbers of species were compared with species richness predicted by two commonly used nonparametric estimators – Chao2 (Chao 1984, 1987) and ICE (Lee & Chao 1994). As a measure of diversity, Simpson's diversity index (i.e., the inverse of Simpson's dominance index) was computed along with every rarefaction analysis on all sizes of subsets of samples together with standard deviation (based on 100 resampling runs with sampling with replacement). To facilitate comparison of species richness among methods, results were rescaled from numbers of samples to numbers of individuals following recommendation of Gotelli & Colwell (2001). To avoid bias caused by an increasing number of collected species with increasing sampling effort, direct comparisons of methods were performed on subsets of equally sized samples (numbers of individuals), based on rarefaction resampling procedure. Their size was 400 individuals in both adults and larvae, i.e. ca. the lowest total number of specimens collected by any method. Activity traps and light trap were also compared for samples containing 23,000 specimens. Because of sample-based rarefaction, estimates were available for all levels of numbers of samples, but not for exactly given numbers of individuals. Values for subsets of samples most closely matching given numbers of specimens were used (departures were only several specimens in all cases; thus this approximation has no effect on the results). In all of these analyses, one sample means one activity trap, one ca. 0.25 m^2 sample of box trap or handnet sampling, and one 2–3 days long period of light trap collecting.

The difference in the relative composition of the assemblages of individual methods was tested using CCA in CANOCO 4.5 (ter Braak & Šmilauer 2002). All samples taken at one sampling date were pooled for each method except the light trap, for which I pooled three successive samples from a 7-day period around the date when samples were taken by the other methods. Sampling date was used as a categorical covariable. For testing significance, Monte Carlo test with 9999 permutations was used; samples were permuted randomly within blocks defined by sampling date. Significance of all canonical axes was evaluated.

2.3 Results

In total 53,913 specimens of adults and 3,000 specimens of larvae were collected by the four sampling methods. During three years, 2004-2006, 2,261 samples were taken by activity traps. Adults of 62 species (n=23,018) and larvae of 25 species (n=1763) were collected. The light trap was operating during 1,160 nights in 2002-2006 (510 samples) and collected 43 species of aquatic adults and 12 species of terrestrial Scirtidae and Sphaeridiinae (total n=29,250). Using the box trap (51 samples in 2004), 41 species of adults (n=1238) and 12 species of larvae (n=432) were collected. Finally, handnet sampling (46 samples in 2006) yielded 32 species of adults (n=407) and 27 species of larvae (n=805). Altogether 90 species were collected by the four quantitative methods during my survey, 12 of them with terrestrial adults. Larvae of 35 species were also found. In total, 109 species of water beetles from 10 families are known at the study site and in its environs (Appendix 1). This constitutes almost 30% of Czech water beetle fauna (Boukal et al. 2007).

Based only on adults, only 18% of all species with aquatic adults were common to all methods. Each method sampled some unique species not sampled by other methods; mostly activity traps (13%, especially medium-sized to large Dytiscidae) and light trap (10% species with aquatic adults and other seven species with terrestrial adults from the Scirtidae and five terrestrial species of the Hydrophilidae: Sphraeridiinae). Box trap sampled 2% of unique species, handnet sampling 1%, and the two methods together had 4% of unique species calculated from the total number of species with aquatic adults (note, however, that sampling effort was very different among methods). In larvae, 29% of species was common to all methods, 14% of species was collected exclusively by activity traps (especially large Dytiscidae), 3% by box trap, 29% by handnet sampling, and 31% of species was unique for box trap and handnet sampling taken together. The highest number of species of adults was sampled by activity traps; in larvae, handnet sampling collected the highest number of species, followed by activity traps (Appendix 1).

Rarefaction analyses revealed that the sample sizes obtained by each method were sufficient to gain good estimates of the total number of species detectable by the method (Table 1). In adults as well as in larvae, the rarefaction curves and species richness estimators ICE and Chao2 converge (Figs. 2 and 3; other popular estimators ACE and Chao1 performed very similarly). In rarefaction-based analyses, the light trap had the lowest number of species of aquatic adults as well as the lowest adult diversity at the level of 400 individuals. Other methods yield considerably higher numbers of species and diversity values and perform similarly at this level. In the larvae, the number of species was lowest in the box trap data and highest in the handnet data. The diversity of larvae sampled by activity traps was considerably higher than by box trap and handnet (Figs. 4 and 5).

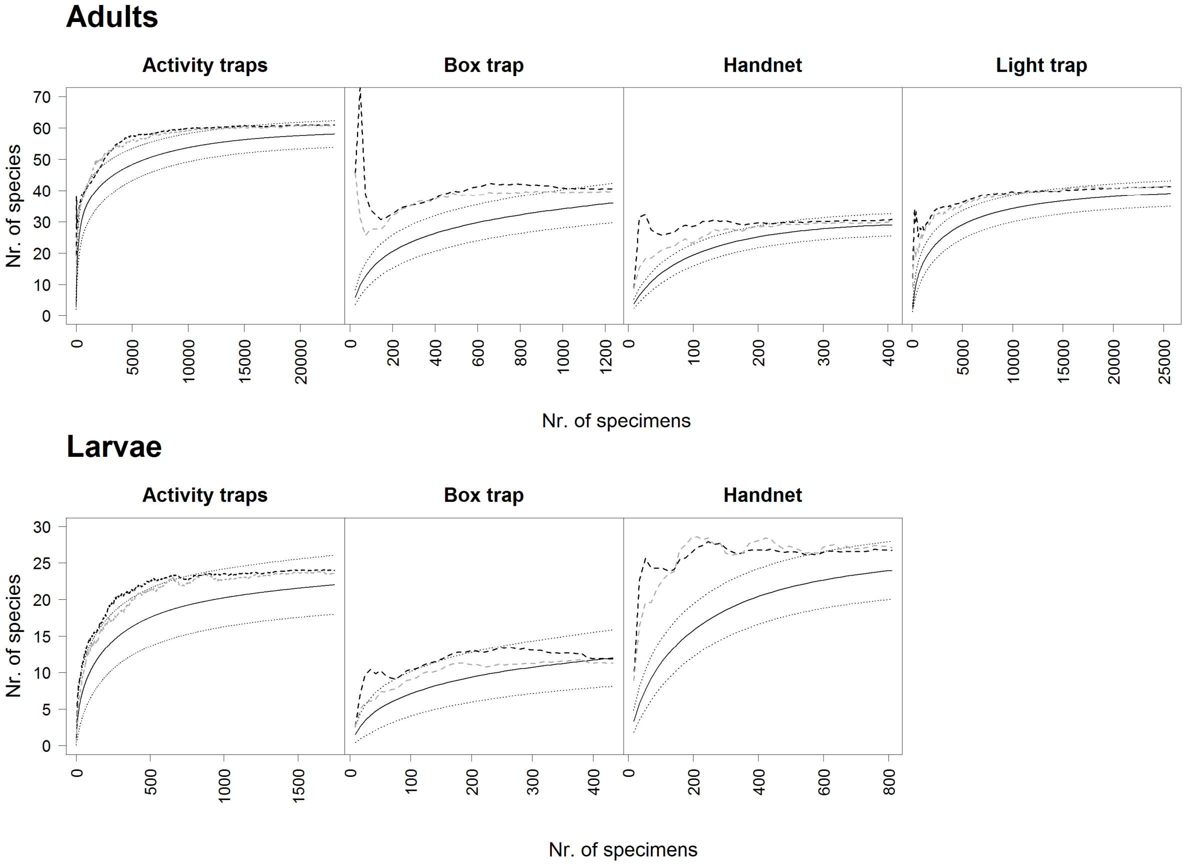

Fig. 2 – Sample-based rarefaction curves for data from the four collecting methods (mean observed number of species and 95% confidence interval as thin black lines, ICE=thick dashed black line, Chao2=thick dashed gray line).

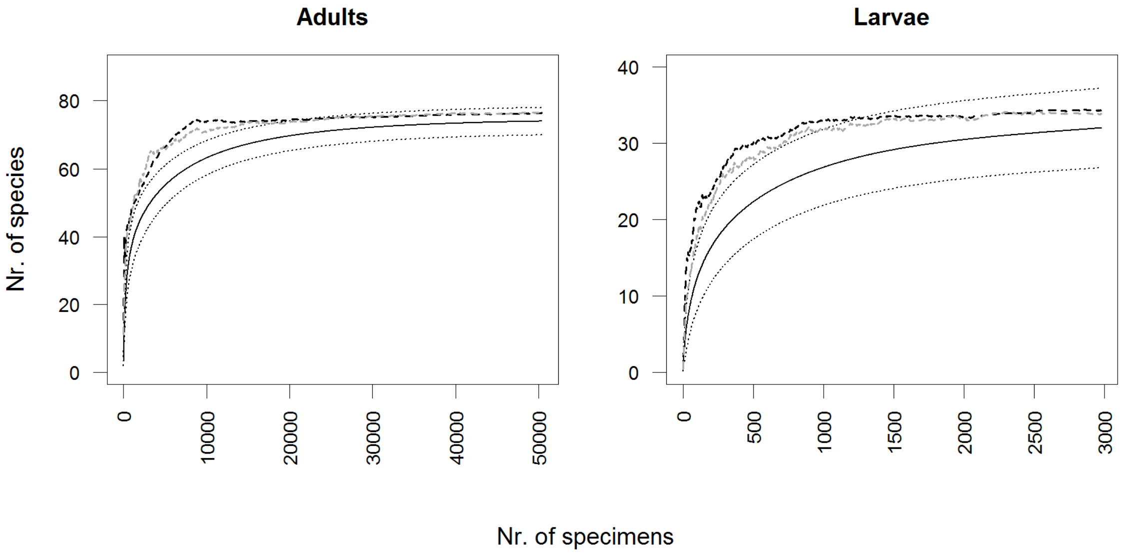

Fig. 3 – Sample-based rarefaction curves for combined data from all methods (mean observed number of species and 95% confidence interval as thin black lines, ICE=thick dashed black line, Chao2=thick dashed gray line).

Table 1 – Sampling effort required to find 70% and 90% of total number of species detectable by the tested methods as estimated by ICE and Chao2, given as number of samples and specimens (in parentheses).

	adults				**larvae**		
	Activity traps	**Box trap**	**Handnet**	**Light trap**	**Activity traps**	**Box trap**	**Handnet**
70% ICE	246 (2508)	21 (510)	15 (132)	95 (4932)	546 (422)	17 (144)	18 (317)
70% Chao2	239 (2467)	20 (486)	14 (124)	95 (4932)	503 (389)	15 (127)	18 (317)
90% ICE	1163 (11859)	51 (1238)	33 (291)	318 (16511)	1981 (1530)	35 (297)	46 (810)
90% Chao2	1111 (11328)	49 (1190)	30 (265)	323 (16770)	1701 (1314)	30 (255)	46 (810)

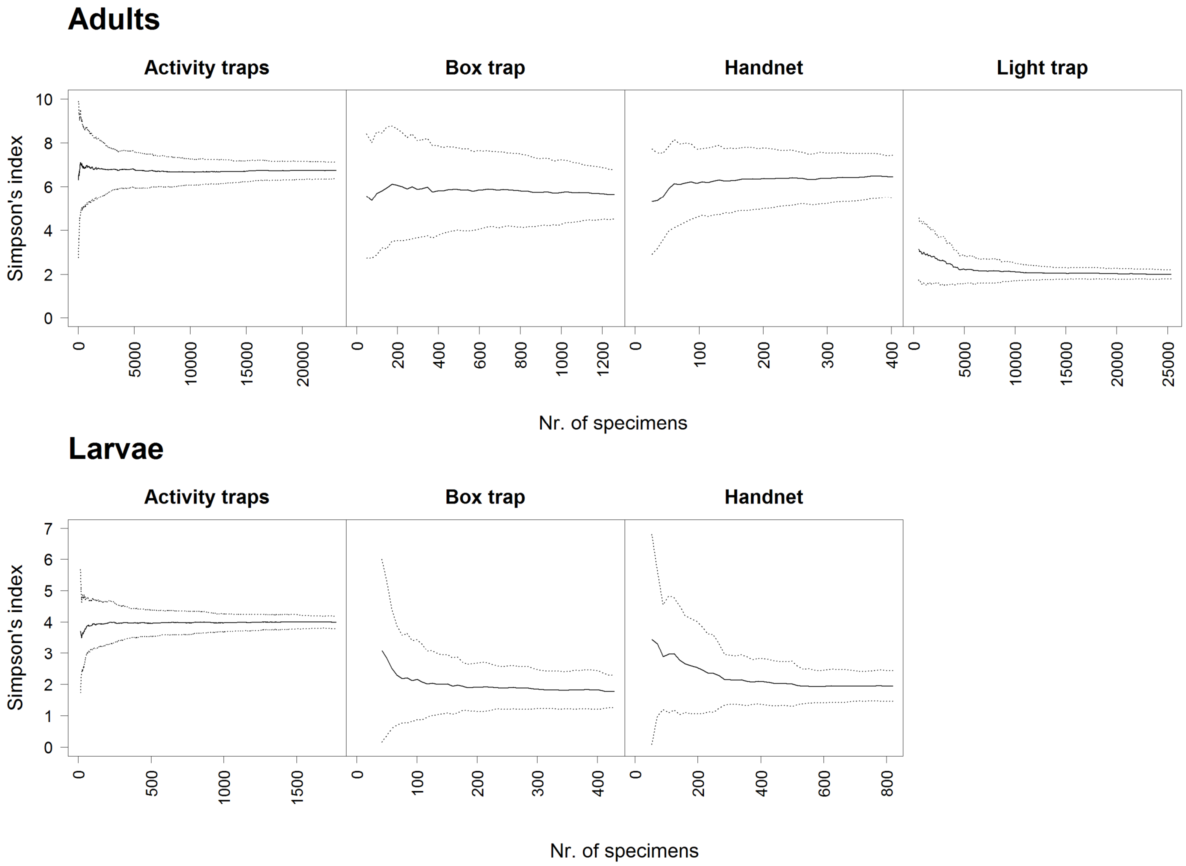

Fig. 4 – Simpson's diversity index in relation to the number of specimens sampled by the four collecting methods (mean ± SD).

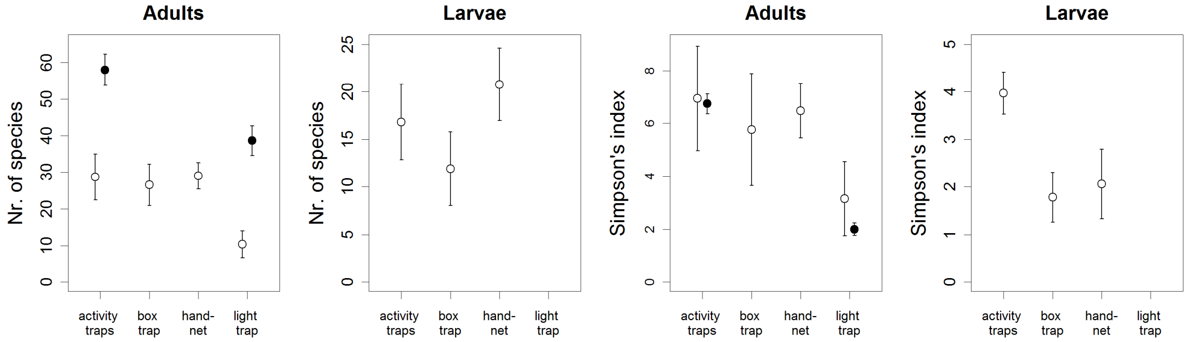

Fig. 5 – Comparison of species richness (mean and 95% confidence interval) and diversity (Simpson's index, mean ± SD) across the collecting methods on the level of 400 (empty circles) and 23,000 individuals (solid circles).

The relative species composition differed significantly among the methods both in the case of aquatic adults (CCA, F=13.561, P<0.0001, explained variance=36.4%) and aquatic larvae (CCA, F=4.077, P<0.0001, explained variance=28%) (Fig. 6). The differences in the relative abundance of common species among methods are summarized in Table 2. Box trap and handnet sampling are based on a similar principle and yield similar results, as shown by the proximity of the centroids for both methods in the CCA plot for the adults (however, this is an indirect comparison through activity traps and the light trap; moreover, the box trap and handnet sampling were not used in the same year). In the larvae, a group of mostly large species of Dytiscidae prevailed in the samples from the activity traps, whereas other

Dytiscidae together with the Scirtidae and Hydrophilidae prevailed in the box trap and handnet samples (right panel in Fig. 6). In adults, several species of the Hydrophilidae and Dytiscidae clearly dominated in the light trap data. However, most Dytiscidae and some Hydrophiloidea were, to a various degree, split between activity traps and box trap+handnet sampling. For most large Dytiscidae, the activity traps were clearly most efficient, while small species from the subfamily Hydroporinae were more represented in the box trap and handnet samples relative to the other methods. All Hydrophiloidea were most efficiently collected by the box trap+handnet sampling or at light. Only the large *Hydrochara caraboides* was captured almost exclusively by activity traps (left panel in Fig. 6).

Results of CCA (Fig. 6) also show that the presence and abundance of species in the light trap samples does not follow a simple pattern. Apart from the Scirtidae and Heteroceridae, which have terrestrial adults and were collected exclusively at light (not used in the CCA, see Appendix 1) a few species of Hydrophilidae constitute a large proportion of the light trap catches (the most numerous species, *Hydrobius fuscipes*, makes up more than 70% of collected specimens with aquatic adults; Table 2). All species of Hydrophilidae were collected at light, which shows their generally high attraction to the light. On the other hand, no Hydraenidae and Hydrochidae and only 45% of species of Dytiscidae were captured by the light trap. Interestingly, none of the seven recorded *Agabus* species were collected at light. Several other dytiscid species commonly found in activity traps were not recorded at light (e.g. *Acilius canaliculatus*, *Colymbetes fuscus*, *Hydaticus seminiger*) (Appendix 1).

Table 2 – Relative abundances of the most common species found by the four sampling methods (given as percentage of total numbers of specimens collected by each method). Question marks indicate species in which some of the larvae could not be properly identified. Adult Scirtidae were excluded from this analysis.

	adults				**larvae**		
	Activity traps	**Box trap**	**Handnet**	**Light trap**	**Activity traps**	**Box trap**	**Handnet**
Dytiscidae							
Acilius canaliculatus	29.57%	1.21%	10.32%	0%	35.68%	0.69%	3.48%
Agabus congener	4.56%	0.16%	0.25%	0%	1.42%	0.23%	1.24%
Dytiscus marginalis	2.36%	0%	0%	0.04%	31.76%	0%	0%
Hydaticus seminiger	18.91%	0.24%	4.91%	0%	4.25%	0%	0.62%
Hydroporus neglectus	0.86%	14.06%	5.90%	0.50%	?	0%	?
Hydroporus striola	1.00%	2.18%	0.98%	0.07%	0%	0%	1.99%
Ilybius ater	6.21%	0.57%	0.98%	2.55%	1.08%	0%	1.86%
Ilybius fuliginous	0.13%	0.24%	0.25%	4.15%	0%	0%	0.62%
Ilybius guttiger	4.79%	0.24%	0.72%	0.38%	0.34%	0%	0.99%
Ilybius subtilis	10.88%	5.25%	1.23%	3.24%	10.04%	0.46%	0.12%
Rhantus suturalis	0.16%	0%	1.47%	2.45%	0.06%	0%	0.25%
Hydrophilidae							
Anacaena lutescens	0.58%	37.24%	31.70%	3.45%	0%	0%	?
Cercyon convexiusculus	0.05%	2.75%	1.47%	0.16%	0%	0%	?
Enochrus coarctatus	0.01%	0.40%	0%	8.26%	0%	?	0%
Hydrobius fuscipes	0.98%	6.06%	16.46%	70.93%	0.11%	5.55%	1.12%
Hydrochara caraboides	4.54%	0.08%	0.74%	0.02%	2.10%	0%	0%
Scirtidae							
Cyphon sp.					1.25%	78.24%	73.67%
Microcara testacea					1.42%	11.1%	7.33%

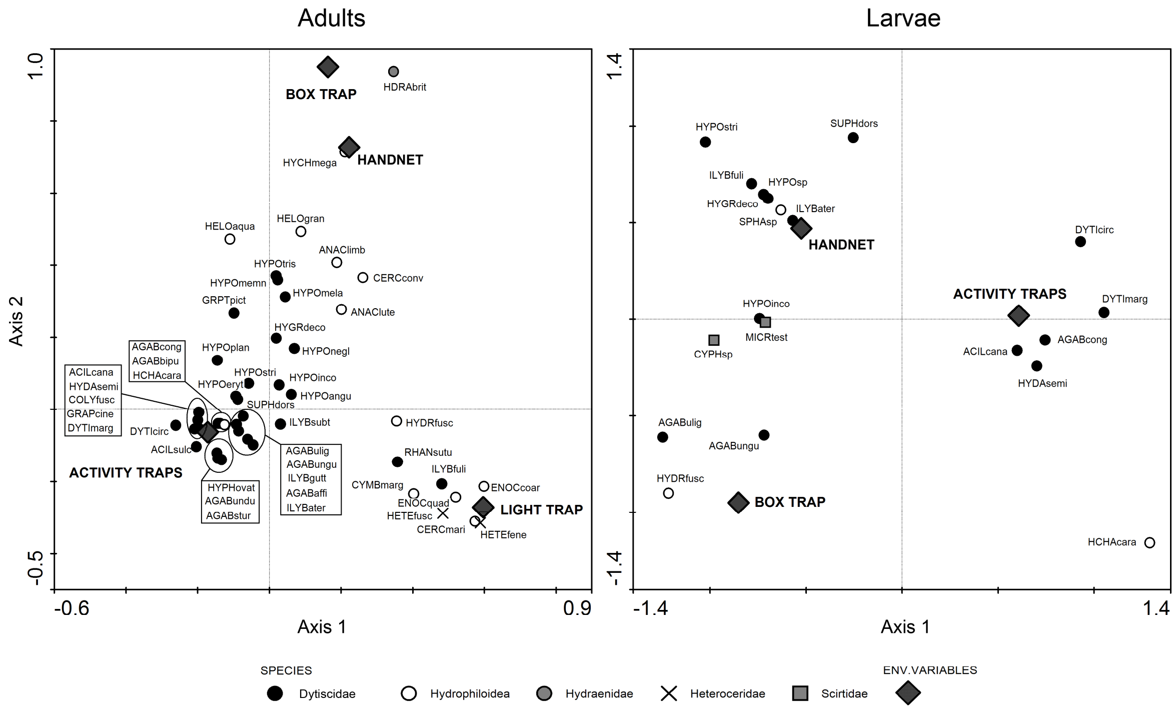

Fig. 6 – Relative species composition in the different sampling methods, tested by CCA separately for adults and larvae. Species with low frequency or no relation to ordination axes are not displayed. See Appendix 1 for species names.

2.4 Discussion

My survey showed that the four sampling methods are not equivalent. All four methods sampled some unique species not sampled by other methods, which demonstrates that they can be all useful and a single method cannot provide a full picture of the composition of water beetle communities.

Light trap seems to attract relatively few species and the data therefore show low diversity. This corresponds to published results demonstrating that attraction to light is species specific in various insect groups (Southwood & Henderson 2000) but contradicts the results of Zalom et al. (1979, 1980), who did not detect any significant difference between the relative composition of catches of the Hydrophilidae and Dytiscidae collected at light and by a supposedly unbiased rotary net machine. Since most species of water beetles can fly (Jackson 1952, 1956a, 1956b; Foster 1979) and the wetland dried out in dry years, I suppose that the low percentage of the Dytiscidae and the absence of the Hydraenidae and Hydrochidae is caused mainly by indifference to light sources. At the same site, several species of water beetles of these families were collected in a window trap (Čížek 1999) but not at light. This discrepancy could be alternatively explained by different daily flight patterns – species with a diurnal flight activity will not be detected by a light trap at night. This is however an unlikely explanation, because water beetles are known to fly preferably after the sunset (Fernando & Galbraith 1973; Zalom et al. 1979, 1980; Csabai et al. 2006).

Acilius canaliculatus and *Hydaticus seminiger*, which are the most abundant species in activity traps collections, were not captured at light or in the window trap operated by Čížek (1999), but they have well developed hind wings and flight muscles and are capable of flight (J. Klečka pers. observ.). It is possible that both species do not emigrate from the locality even if it completely desiccates and survive the drought buried into wet substrate on the bottom. Jackson (1952) and Davy-Bowker (2002) observed a similar behaviour in *Agabus bipustulatus*, and during my survey, both species were very abundant even in very shallow and small puddles during the dry-out. Absence of large Dytiscidae in the window trap of Čížek (1999) may also have been caused by their ability to escape from the trap, but this explanation is unlikely as the only slightly smaller *Ilybius subtilis* was among the most numerous species in his samples.

In larvae, a significantly lower number of species detected by box trap compared to net sampling may also be caused by differences in sample processing. In both cases, samples contained a large amount of detritus and small plant fragments, but the box trap samples were taken to the lab without conservation and animals were extracted using a dry extractor. During the transport or the extraction procedure, small and delicate larvae could have been killed. On the other hand, net samples were preserved in ethanol and manually sorted under the stereomicroscope, which reduces such a bias. A similar problem was encountered by Landin (1976) in the case of adults of small Hydraenidae. The higher diversity of samples of larvae in activity traps is caused by the more even species abundances (evenness is a component of Simpson's diversity index). Samples from the box trap and handnet were dominated by larvae of *Microcara testacea* and *Cyphon* sp., which are slowly moving on the bottom and crawling over leaves and branches and only rarely captured by activity traps.

A relationship between body size and activity leading to a bias towards large species has troubled entomologists working with various activity traps for a long time (e.g. Mommertz et al. 1996). Size selectivity of samples of water beetles from activity traps is thus to be expected. Adults and larvae of large Dytiscidae (e.g. *Dytiscus*, *Acilius* and *Hydaticus*) are clearly better sampled by activity traps as compared to box trap and handnet sampling. Predation on smaller species in the traps seems very unlikely, based on occasionally checks of the entire trap contents. Previous results concerning the size selectivity of these methods in water beetles were unclear. Probably the only proper test was made by Nilsson & Soderberg (1996), who did not find any difference between activity traps and handnet sampling, which contradicts previous findings that handnetting underestimates large mobile species (Becerra Jurado et al 2008) and activity traps underestimate small and less mobile taxa (Hilsenhoff 1987, 1991). Despite some concerns (Becerra Jurado et al 2008; Fairchild et al. 2000; O'Connor et al. 2004), I believe that box trap and handnet sampling provide estimates of density with little bias. Large number of species of medium-sized to large Dytiscidae undetected by these methods might reflect their low density in the wetland and their presence in activity traps is rather the result of high efficiency of the traps for these species (Hilsenhoff 1987, 1991) than the result of a poor performance of the other two methods.

I found out that to gain reasonable estimates of total species richness, fairly high effort using a combination of sampling methods is required in such species-rich habitats. Usual sampling schemes consisting of monthly sampling by a single method would not be sufficient. One year of intensive research combining activity traps (hundreds of samples) and handnet sampling or box trap (tens of samples) was necessary for gaining an insight into the composition of the community in this wetland. It is to be expected that in similar types of wetlands, such intensity would be desirable. Much lower effort may be sufficient in other types of water bodies. In a group of heavily vegetated ponds, Becerra-Jurado et al. (2008) considered only three samples of three minutes of multihabitat handnetting and nine activity traps as enough for detecting 70% of the estimated total number of species. This is an order of magnitude lower effort than suggested by my results.

Results of my tests of selectivity of four commonly used sampling methods show that none of them is sufficiently effective and when the aim is to collect as many species as possible, several methods should be used. Light trap appears to sample well species with terrestrial (Scirtidae) or semiaquatic (Hydrophilidae: Sphaeridiinae) adults but provides poor data on the Hydraenidae and Hydrochidae and many species of Dytiscidae. Activity traps and handnet sampling (or a box trap) seem to be complementary (see also Hilsenhoff 1991; Turner & Trexler 1997; Becerra-Jurado et al. 2008). Finally, habitat structure, density of animals and other factors should be taken into account when planning sampling procedures.

3 Topic two

Flight activity of water beetles – seasonal dynamics and effects of environmental variables

3.1 Review of the literature – Dispersal by flight in aquatic insects

Capacity for flight

Insect orders differ considerably in flight capacity: in some of them, all species are flightless while in others all known species are capable of flight (Wagner & Liebherr 1992). Species of various taxa inhabiting temporary habitats are more prone to migrate by flight than related species inhabiting permanent habitats, because the key advantage of migration is the ability to keep up with the pace of changes in spatial distribution of the habitats; dispersal thus forms an important part of life histories of most insect species (Southwood 1962; Wagner & Liebherr 1992). Theoretical models have shown that dispersal can be advantageous even in homogeneous habitats stable in time (Hamilton & May 1977), which may explain why flightlessness in rather uncommon in insects and is usually associated with specific habitat conditions. Habitat stability, isolation, the necessity to save energy in cold habitats and parasitism are among the causes of flightlessness in insects (Wagner & Liebherr 1992).

Most insects with aquatic adults are capable of flight; however, some species are known to be flightless both in the Coleoptera and the Heteroptera (Jackson 1952, 1956a, 1956b; Foster 1979; Hutchinson 1993). It was suggested that flightless species are typical dwellers of permanent habitats whereas inhabitants of temporary habitats are better fliers (Southwood 1962). This pattern was also observed between populations, e.g. in the Gerridae (Heteroptera), in which summer populations inhabiting permanent waters have a high proportion of brachypterous specimens, whereas almost all individuals in populations inhabiting temporary habitats have fully developed wings (Southwood 1962; Vepsäläinen 1973; Vepsäläinen & Nieser 1977). Changes in morphological traits connected to flight ability along an altitudinal gradient in *Agabus bipustulatus* (Coleoptera: Dytiscidae) were attributed to the tendency to lose flight capability in harsh environment to save energy (Drotz et al. 2001). Flight ability can also change over an individual's lifetime: Kirby & Foster (1991) reported flight capability in freshly emerged *A. uliginosus*, followed by flight muscle degeneration and flightlessness for the rest of life, and the same phenomenon was observed in several species of aquatic Heteroptera (Southwood 1962).

Some water beetles as well as bugs, mosquitoes and midges are known to cover long distances and thus belong to the first colonizers of new water bodies. Good flight ability is also one of the mechanisms enabling some insect species to live in ephemeral habitats such as vernal pools (Popham 1964; Pajunen & Jansson 1969; Wiggins et al. 1980; Layton & Voshell 1991).

Seasonal and daily patterns of the flight activity

Three types of seasonal patterns of flight activity were previously reported in water beetles (Fernando & Galbraith 1973; Landin 1980; Zalom et al. 1979, 1980; Lundkvist et al. 2002) and water bugs (Pajunen & Jansson 1969; Popham 1964; Landin & Vepsäläinen 1977) in the temperate zone of the Northern Hemisphere: a single peak of dispersal in spring, two major peaks in spring and late summer/autumn, or one distinct peak in mid-summer. In the first case it is assumed that this is a pre-breeding dispersal serving to colonize suitable habitats before reproduction. In the second case it is assumed that apart from the spring pre-breeding dispersal, new summer generation migrates in the autumn to water bodies suitable for overwintering (e.g. from temporary to permanent water bodies). In the third case it is assumed that new generation emerging in summer disperses prior to reproduction and after maturation settles permanently at the locality. These interpretations hold in univoltine species and modified dispersal patterns may be expected in species with different life-cycle lengths. Fernando & Galbraith (1973) observed trimodal seasonal flight dynamics with pre-breeding dispersal in spring and two summer peaks in the bivoltine *Helophorus orientalis* (Coleoptera: Helophoridae), corresponding to the emergence of the first generation in early summer and the second generation in late summer, when both old and newly emerged individuals are on the wing. Johnson (1960, 1963) postulated that mostly sexually immature adults should disperse before the onset of reproduction. Data collected so far seem to support this hypothesis (Landin 1980).

Several authors also studied daily changes of flight activity in water insects. According to Csabai et al. (2006), four distinct activity patterns can be recognized: in the morning, in the morning and around sunset, around noon and sunset, and only around sunset. Most water beetles fly preferably around/after sunset and less so before sunrise, but not during the day (Fernando & Galbraith 1973; Zalom et al. 1979, 1980; Csabai et al. 2006). On the other hand, water bugs are known to fly mostly around noon; only some Corixidae and Pleidae continue to fly shortly after sunset (Pajunen & Jansson 1969; Popham 1964; Landin & Vepsäläinen 1977; Csabai et al. 2006). Traditionally, these patterns are explained by daily changes in temperature (e.g. Popham 1964; Pajunen & Jansson 1969; Landin & Vepsäläinen 1977; Zalom et al. 1979, 1980). Recent evidence shows that a polarotactic detection of water surface is the key mechanism used for orientation by migrating water insects (Schwind 1991, 1995; Csabai et al. 2006). Daily changes in polarotactical detectability of water surface are therefore likely to at least partially affect flight activity in water insects (Csabai et al. 2006).

Effects of environmental variables

Several environmental factors have been reported as possible determinants of flight activity in water insects so far. Habitat deterioration (e.g. desiccation, high temperatures, or increased competition) is often considered among the drivers of dispersal, causing e.g. regular late-summer migrations from temporary to permanent waters for overwintering (Popham 1964; Pajunen & Jansson 1969; Fernando & Galbraith 1973; Wiggins et al. 1980; Hutchinson 1993). Temperature is traditionally considered as an important factor; many authors found that water beetles and bugs require temperatures of at least 12-18°C to fly (Popham 1964; Landin & Stark 1973; Landin & Vepsäläinen 1977; Zalom et al. 1979, 1980; Lundkvist et al. 2002). Popham (1964) proposed that in larger species, the temperature threshold is generally higher, because higher temperatures are needed for proper functioning of the flight muscles. Several authors also noticed that the flight activity is generally low in windy weather (Landin & Stark 1973; Zalom et al. 1979, 1980). Lunar phase might affect migrations of some tropical water bugs from the family Belostomatidae flying during the night, as intense moonlight around the full moon may be used for visual orientation (Hutchinson 1993). Most of the results presented in earlier studies concerning the effects of environmental factors on the flight activity of water insects are rather anecdotic; proper statistical data analyses are so far scarce.

Temperature is also often considered as the cause of observed seasonal patterns of flight activity (see references above). However, seasonal patterns are difficult to interpret, because they may depend on additional factors including environmental changes (e.g. fluctuations in water level) and constraints stemming from individual life history and physiological constraints (only some adults can and will fly). All these factors are probably important but their relative contribution to seasonal flight patterns is difficult to elucidate.

Concluding remarks

Dispersal by flight is one of the key features of the life histories of aquatic insects, especially in temporary waters. Several distinct types of the seasonal and daily flight patterns have been repeatedly observed. The interpretation of these patterns by corresponding changes of environmental conditions is still an open question. Nevertheless, hydrology and air temperature seem to be dominant drivers of the flight activity of water insects. New insights stemming from detailed understanding of the ways by which water insects collect information about their environment are still emerging, e.g. interpretation of daily flight patterns by corresponding changes of polarotactical detectability of water surface (Csabai et al. 2006).

3.2 Material and methods

The analysis of the flight activity is based on water beetles collected in the light trap during 2002–2006 (see Chapter 2.2). The raw data used for statistical analyses were the number of specimens of water beetles from cumulative samples collected during 2–3 consecutive nights. Altogether 29,250 individuals of 55 species from six families have been processed (Appendix 1).

Several environmental variables suspected to influence the flight activity of water beetles were measured. Water depth was measured twice a week in the drain next to the light trap at three stations in 2004 and six stations in 2005 and 2006 (maximum depth was used for analyses of flight activity). Data on meteorological variables (air temperature, precipitation, air humidity, air pressure, and cloud coverage) were obtained from the Czech Hydrometeorological Institute in České Budějovice. The meteorological station is located 5.5 km SE of the study site.

Data analyses

The changes of the composition of the assemblages during the season were tested using CCA with year as a categorical covariable in CANOCO 4.5 (ter Braak & Šmilauer 2002). Use of year as a covariable removed any differences in mean relative abundance of species among years. Since the data were found to be autocorrelated in time within years, I used permutations by cyclic shifts in Monte Carlo tests (Lepš & Šmilauer 2003). Monte Carlo test with 9999 replications was used in all analyses in CANOCO.

Seasonal changes of the relative abundance of three dominant groups (Dytiscidae, Hydrophilidae, and Scirtidae) were assessed by generalized additive mixed models with quasibinomial distribution and year taken as a random factor (R 2.6.0 software; R Development Core Team 2007). An autocorrelation function of order one modeled within year which was taken as a random factor to account for the time correlation. Data from years 2002-2006 restricted to the periods from the beginning of May to the end of September were used (flight activity was negligible in early spring and late autumn).

Effects of meteorological variables and water depth on the flight activity were assessed separately on two temporal scales (weeks and days) using additive mixed models with log-transformed number of specimens, $\log_{10}(n+1)$, as a response variable (package mgcv for R; thin plate regression splines were used as smooths; Wood 2006). Only data from years 2004-2006 from early spring to late autumn were used for these analyses (water depth was not measured in 2002 and 2003). Since water depth was measured twice a week and light trap was operating continuously, values of water depth for days when it was not measured were obtained by linear interpolation. In tests of longer temporal scales, mean log-transformed number of specimens aggregated over a week surrounding the sampling date was used as a response variable. Weekly means of predictors were also used; precipitation was log-transformed, $\log_{10}(n+1)$, to lower the extreme right skew of its distribution. Use of data aggregated by weeks removed the short-term changes and allowed me to focus on the seasonal aspects. Tests targeting short-term fluctuations used changes between successive samples as input data. Numbers of specimens were used in the form of log-transformed ratios ($\log_{10}((n_i+1)/(n_{i-1}+1))$), while absolute differences ($n_i – n_{i-1}$) were used for predictors. This corresponds to the hypothesis of a multiplicative response of flight activity to changes in the environment. The data used in the analysis of short-term fluctuations were further restricted to May–September each year and data from the end of August to the end of September 2004 were also excluded, as the wetland dried out.

Temperature thresholds for flight were examined using the full data set from 2002-2006. Mean values for the periods of 2–3 days long sampling periods were used as input data; numbers of specimens (n) were log-transformed as $\log_{10}(n+1)$. To search for the thresholds, a threshold additive model developed by Kung-Sik Chan was used (Stenseth et al. 2004). This method breaks down the predictor between two intervals and fits a smooth function for each interval separately. The optimal value of the threshold is found by an exhaustive search over the range of possible threshold values and selection of the best model by comparing the GCV score for all models (GCV is a criterion for smoothing parameter selection attempting to minimize prediction error; see Wood 2006 for further information). In my case, I assumed no flight activity below the threshold and thus the smooth function was fitted only for values above the threshold.

For analyses of the effects of water depth and meteorological factors on the relative composition of the water beetle assemblages, CCA with year as a covariable was used with the data from years 2004–2006 with the same restrictions as in the case of the additive model analysis of short-term fluctuations; precipitation was log-transformed and other environmental variables were left untransformed.

Sex ratios and proportions of newly emerged immature adults were compared between the light trap and pooled data from other sampling methods that collect beetles in the water. Generalized linear mixed models with species as random factor and quasibinomial distribution were used. Only species with more than 20 specimens in each dataset were included in the analyses. Sex ratios were tested only in the Dytiscidae and the proportion of immatures was tested separately for the Dytiscidae and Hydrophiloidea.

3.3 Results

Water depth and weather conditions

Water depth and air temperature undergo the most considerable seasonal changes among the environmental variables; the magnitude of short-term fluctuations was much larger than any seasonal trend in all other meteorological factors, and only precipitation varied considerably among years (Figs. 7 and 8). The temperature shows strong regular fluctuations over the season with maximum in midsummer. There is no significant difference in mean temperature among the years (F=0.94, p=0.44; year as a fixed factor); short-term fluctuations with relatively large amplitudes were recorded every year. On the other hand, the hydrological regime varied considerably among years. In 2004 the study site completely desiccated in the beginning of August. Only scarce puddles remained in the swamp or in its near environs. In 2005 and 2006 at least parts of the drain remained submerged all season and until mid-October, respectively, despite a few periods of rapid desiccation (Fig. 9). I do not have data for 2002 and 2003, but the year 2002 was very rainy (which was accompanied by two waves of catastrophic floods in summer months) and the alder carr certainly remained flooded throughout the season. The summer in 2003 was very hot and dry and it can be assumed that the alder carr dried out completely.

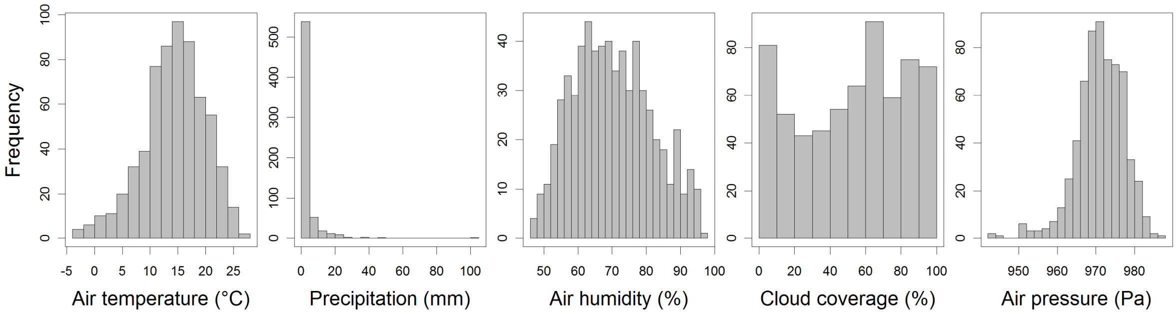

Fig. 7 – Meteorological variables used in the analyses of flight activity, shown as distribution of mean daily values (except a daily sum for precipitation) for 2002–2006 (from March 10 to December 5 every year).

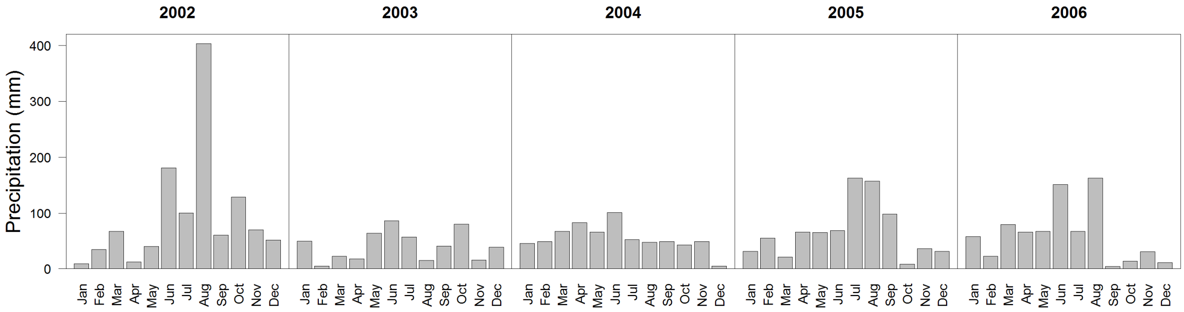

Fig. 8 - Monthly precipitation in 2002–2006.

Seasonal changes in the flight activity

The Dytiscidae (22 species, n=3,759), Hydrophiloidea (Hydrophilidae+Helophoridae, 23 species, n=21,800) and Scirtidae (7 species, n=3642) represent the three most common water beetle families in the light trap samples during 2002–2006 (total n=29,201). Other families were collected rarely (two species of Heteroceridae, n=46; one species of Gyrinidae, n=3) (Appendix 1).

The flight activity is generally highest in summer and major peaks occur during periods of rapid desiccation. The activity was an order of magnitude lower in 2002 than in other years; that year was unusually wet and the alder carr remained flooded. Seasonal changes in the flight activity are fairly similar in the three major groups (Fig. 9) but differ among species; running means and peaks in flight activity of the four most abundant species in each of the three families are shown in Fig. 10.

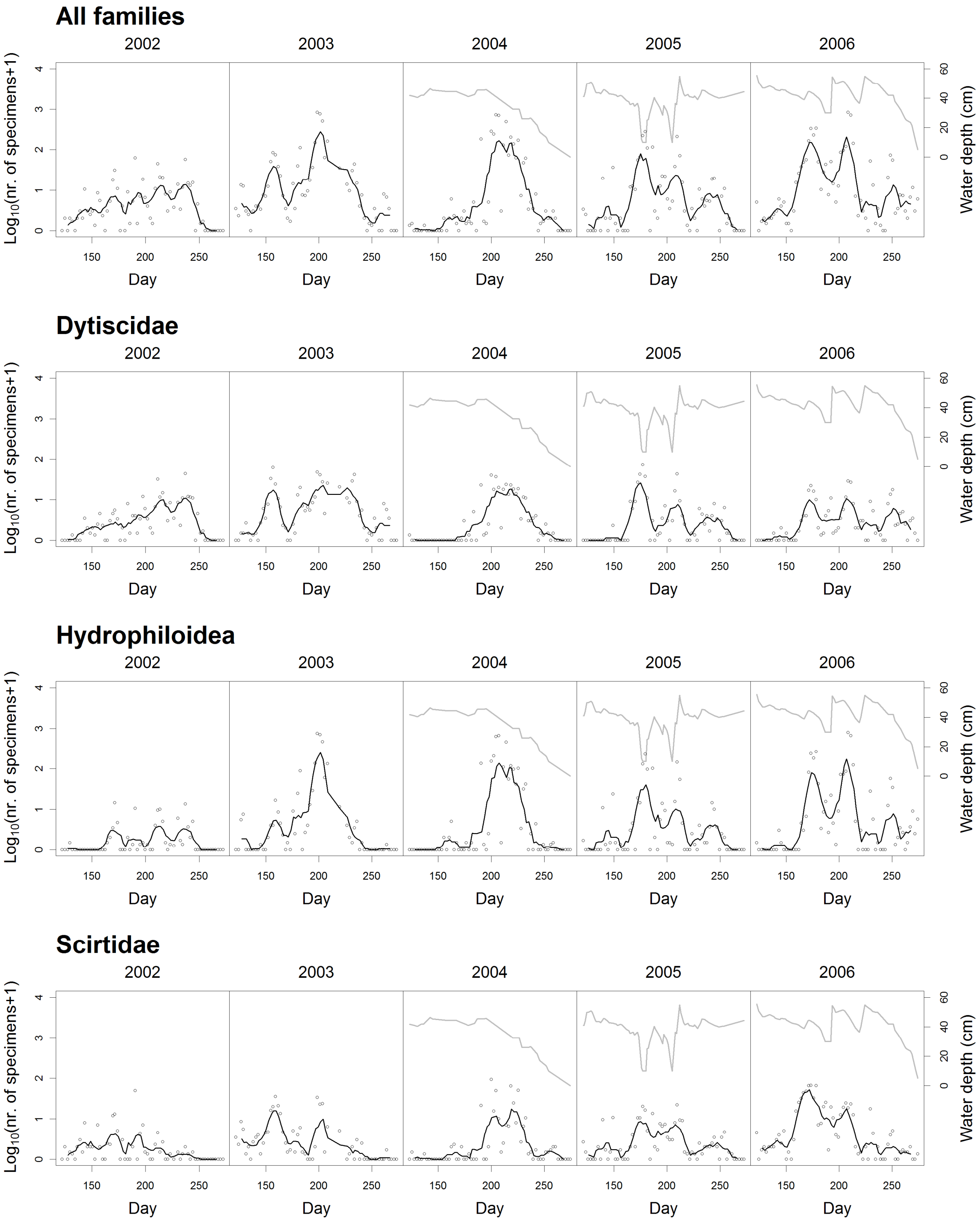

Fig. 9 – Seasonal changes in the flight activity of water beetles in 2002–2006. Running means (for 6 consecutive samples = two weeks interval) are plotted for all families and separately for the Dytiscidae, Hydrophiloidea and Scirtidae (black lines, left y-axis). Circles = numbers of specimens in individual samples per night. Grey line = water depth (right y-axis). Day given as ordinal date.

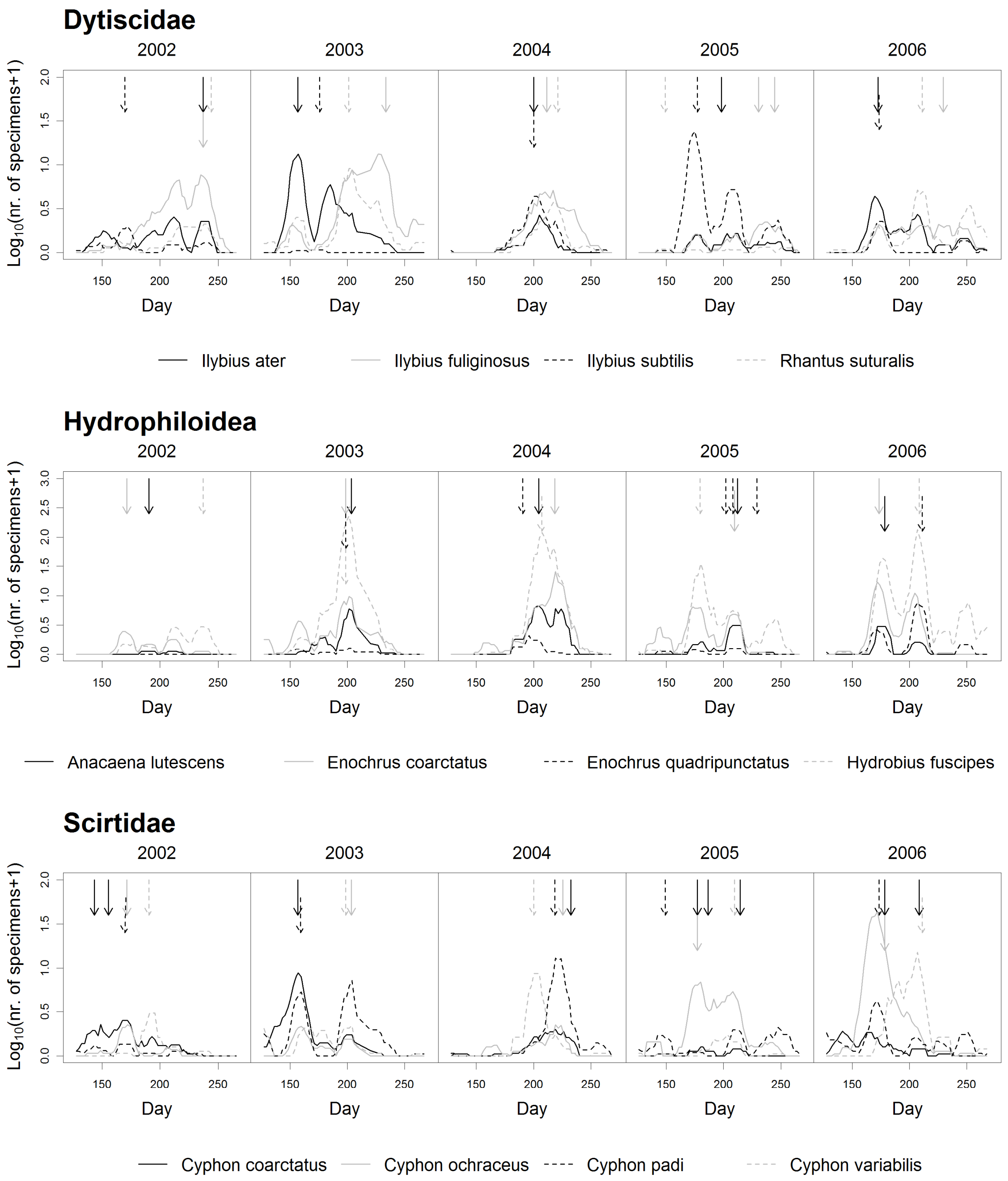

Fig. 10 – Seasonal changes of the flight activity of dominant species of the three main taxonomical groups in 2002–2006. Running daily means (for 6 consecutive samples = two weeks) is plotted for every species. Arrows denote maximum numbers of specimens captured per night. Day given as ordinal date.

Relative species composition undergoes significant changes during the season (Table 3 and Fig. 11). The changes vary significantly among years only when the whole assemblage is considered and remain consistent within the families despite subtle differences apparent in Fig. 10. The Hydrophiloidea clearly dominate in summer, while the Dytiscidae have two separate peaks in late spring and late summer, and the Scirtidae dominate in spring and decline over the season (Fig. 12 and Table 4). The mean relative abundance of individual groups and dominant species also changes among years (Table 5).

Table 3 - Seasonal changes of the relative species composition in the light trap samples (CCA, year taken as a covarible).

	All families		Dytiscidae		Hydrophiloidea		Scirtidae	
	F	P	F	P	F	P	F	P
Day	9.274	**0.0002**	6.969	**0.0005**	4.863	**0.0001**	4.566	0.4120
Day*year [#]	2.474	**0.0378**	1.829	0.1065	1.257	0.3562	-	-
Explained variance	**3.3%[1], 6.7%[2]**		**3.3%[1]**		**2.8%[1]**		**2.1%[1]**	

[#]conditional effect after accounting for day; [1]only day; [2]day+day*year.

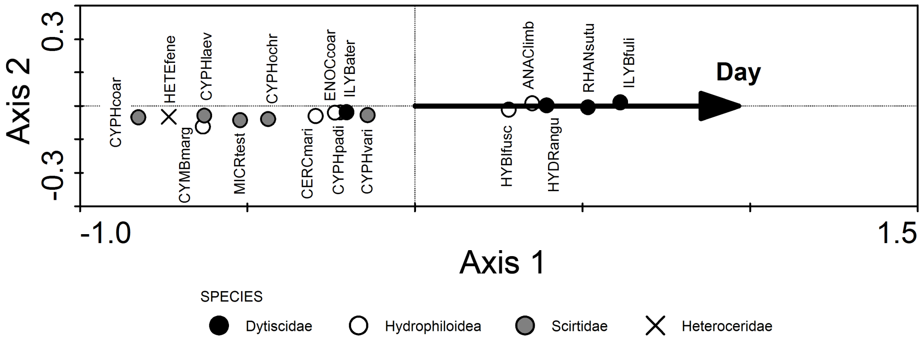

Fig. 11 – Seasonal changes of the relative species composition in the light trap samples. Maxima of the relative abundance of selected species fitted by CCA for the whole assemblage are shown. Species with low frequency or no relation to ordination axes are not displayed. See Appendix 1 for species names.

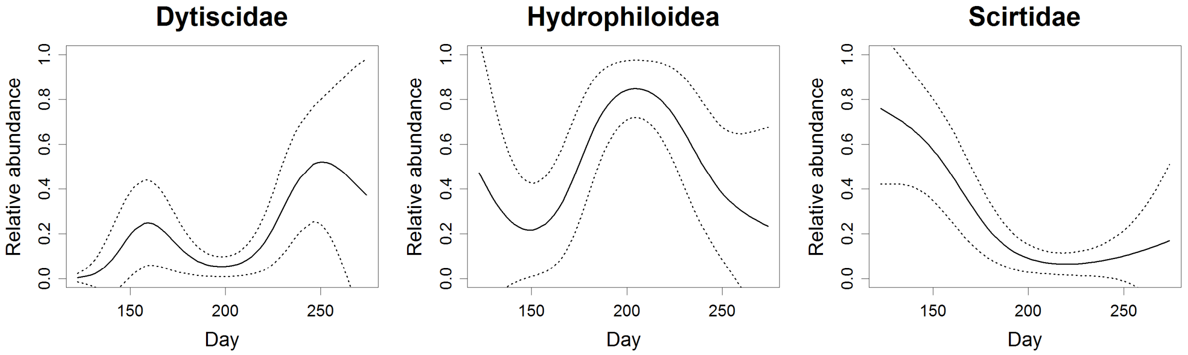

Fig 12 – Seasonal changes in the relative abundance of the three dominant groups fitted by generalized mixed additive models with quasibinomial distribution (fitted values and 95% confidence interval). Fitted values represent the mean of 2002–2006, ignoring the differences in mean relative abundance among years.

Table 4 – Significance of the seasonal changes in the relative abundance of the three dominant groups of water beetles in the light trap catches.

	R^2	F	df (total df = 249)	P
Dytiscidae	0.372	13.66	3.751	**$4.4*10^{-10}$**
Hydrophiloidea	0.980	14.73	3.693	**$8.1*10^{-11}$**
Scirtidae	0.254	14.25	2.900	**$1.7*10^{-10}$**

Table 5 – Relative abundance of the three dominant groups and the most abundant species of water beetles in the light trap samples in 2002–2006.

	2002 (n=1,006)	2003 (n=7,578)	2004 (n=8,713)	2005 (n=3,283)	2006 (n=8,670)
Dytiscidae	**53.42%**	**15.74%**	**8.52%**	**23.03%**	**6.58%**
Ilybius fuliginosus	33.02%	5.52%	2.10%	1.81%	1.07%
Ilybius ater	8.74%	5.02%	0.47%	1.07%	1.37%
Rhantus suturalis	4.63%	3.77%	0.87%	0.27%	2.32%
Ilybius subtilis	3.18%	0.03%	1.50%	18.98%	0.34%
Hydrophiloidea	**18.97%**	**76.56%**	**80.71%**	**62.94%**	**75.99%**
Hydrobius fuscipes	10.61%	68.40%	66.08%	44.53%	62.16%
Enochrus coarctatus	6.37%	5.04%	7.78%	14.14%	6.81%
Anacaena lutescens	0.41%	2.35%	5.64%	3.51%	1.61%
Enochrus quadripunctatus	0.00%	0.13%	0.35%	0.30%	3.91%
Scirtidae	**27.50%**	**7.70%**	**10.52%**	**13.76%**	**17.23%**
Cyphon variabilis	12.36%	1.32%	5.06%	0.73%	4.42%
Cyphon coarctatus	7.85%	2.33%	0.47%	0.27%	0.49%
Cyphon ochraceus	2.89%	0.46%	0.46%	8.41%	9.95%
Cyphon padi	1.81%	3.42%	4.42%	2.89%	1.49%

Effects of weather and water depth on flight activity

The aggregated weekly flight activity (‘seasonal aspect’) is influenced by air temperature and water depth in the wetland (Fig. 13 and Table 6). No significant effect of other variables or seasonal patterns that cannot be explained by temperature and water depth were detected (Table 6). A threshold temperature is apparent in all groups (Fig. 14). The minimum temperatures required for flight, as found by threshold additive models, were 13.5°C (all families), 15.8°C (Dytiscidae), 17.7°C (Hydrophiloidea), and 12.1°C (Scirtidae). Several individuals of all three groups were, however, caught even at temperatures below 10 °C.

Short-term fluctuations of the flight activity can be explained by fluctuations of air temperature (Fig. 15 and Table 7). The effect of cloud coverage in the Hydrophiloidea and Scirtidae was also significant but very weak.

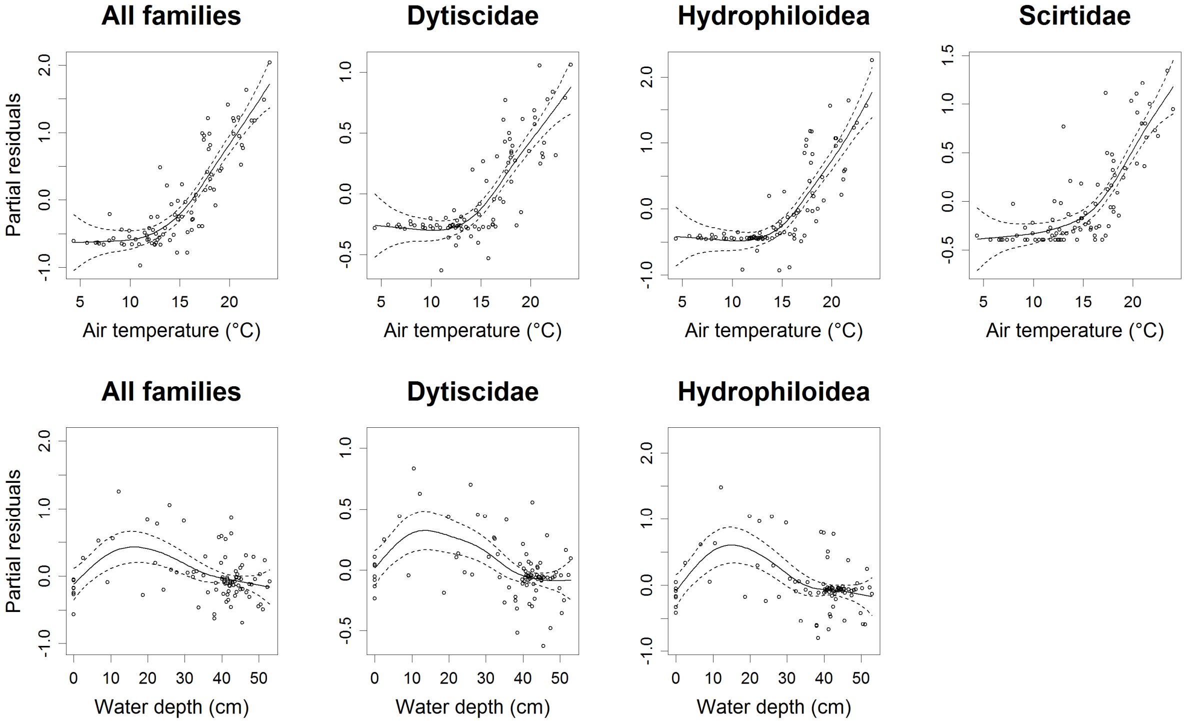

Fig. 13 – The effects of environmental variables on the seasonal aspects of the flight activity of water beetles (fitted values with 95% confidence interval).

Table 6 – Significance of effects of environmental variables on the seasonal aspect of the flight activity of water beetles, tested by additive mixed models.

	F	**df (total df = 86)**	**P**
All families			
Air temperature	33.310	3.518	**$<2*10^{-16}$**
Water depth	3.469	3.426	**0.0027**
Precipitation	0.001	1	0.9829
Air humidity	0.019	1	0.8905
Air pressure	0.022	1	0.8828
Cloud coverage	0.955	1	0.3314
Day	0.531	1	0.4684
R^2 of the final model = 0.80			
Dytiscidae			
Air temperature	22.950	3.521	**$<2*10^{-16}$**
Water depth	5.237	3.723	**$<3*10^{-5}$**
Precipitation	0.829	1	0.3650
Air humidity	0.001	1	0.9760
Air pressure	1.881	1	0.1740
Clouds coverage	0.296	1	0.5880
Day	0.256	1	0.6140
R^2 of the final model = 0.759			
Hydrophiloidea			
Air temperature	25.818	3.692	**$<2*10^{-16}$**
Water depth	4.197	3.919	**0.0003**
Precipitation	1.178	1	0.2810
Air humidity	0.781	1	0.3797
Air pressure	0.924	1	0.3394
Clouds coverage	2.815	1	0.0973
Day	0.112	1	0.7391
R^2 of the final model = 0.766			
Scirtidae			
Air temperature	24.400	3.593	**$<2*10^{-16}$**
Water depth	0.001	1	0.9710
Precipitation	0.229	1	0.6340
Air humidity	1.085	1	0.3010
Air pressure	0.418	1	0.5200
Clouds coverage	0.194	1	0.6610
Day	3.328	1	0.0717
R^2 of the final model = 0.688			

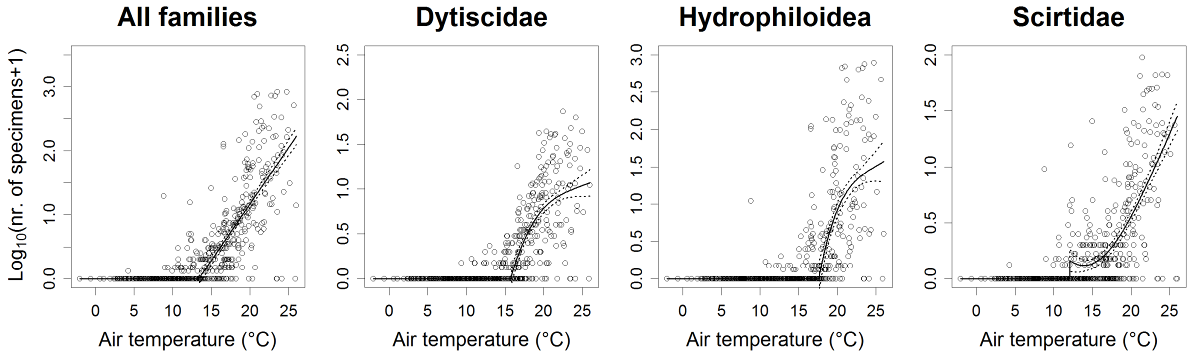

Fig. 14 – The effect of air temperature on the flight activity of water beetles on the level of individual sampling dates tested by threshold additive models (fitted values with 95% confidence interval). Number of specimens = number collected per one night.

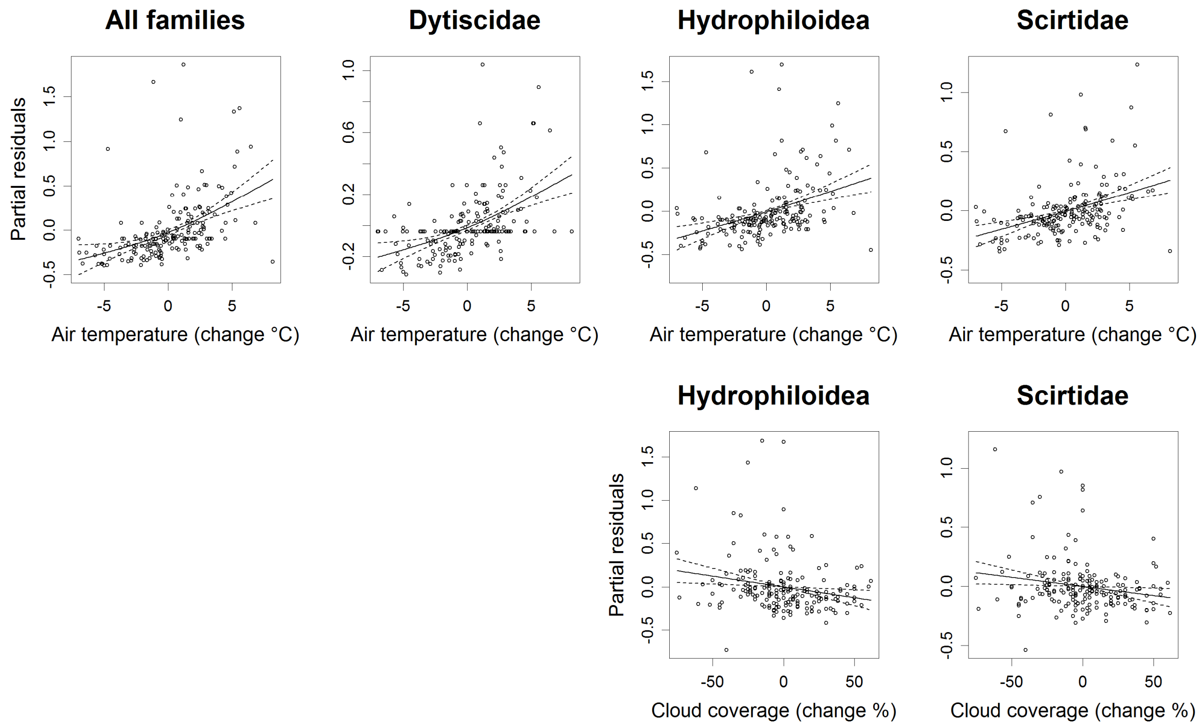

Fig. 15 – Short-term fluctuations of the flight activity in relation to environmental fluctuations. Fitted values with 95% confidence intervals are displayed.

Table 7 – Significance of the impact of short-term environmental fluctuations on short-term fluctuations of the flight activity.

	F	df (total df = 177)	P
All families			
Air temperature	25.060	1.628	**$<3*10^{-10}$**
Water depth	0.333	1	0.5640
Precipitation	0.342	1	0.5590
Air humidity	0.058	1	0.8100
Air pressure	0.038	1	0.8460
Cloud coverage	3.861	1	0.0510
R^2 of the final model = 0.214			
Dytiscidae			
Air temperature	28.220	1.594	**$<3*10^{-11}$**
Water depth	0.949	1	0.3310
Precipitation	2.692	1	0.1030
Air humidity	0.085	1	0.7710
Air pressure	0.108	1	0.7430
Clouds coverage	1.833	1	0.1770
R^2 of the final model = 0.235			
Hydrophiloidea			
Air temperature	14.589	1.130	**$<2*10^{-6}$**
Water depth	2.191	1	0.1406
Precipitation	1.035	1	0.3105
Air humidity	2.000	1.465	0.1656
Air pressure	0.578	1	0.4482
Clouds coverage	7.431	1	**0.0071**
R^2 of the final model = 0.202			
Scirtidae			
Air temperature	14.389	1.103	**$<2*10^{-6}$**
Water depth	0.017	1	0.8970
Precipitation	0.077	1	0.7814
Air humidity	1.741	1.193	0.1785
Air pressure	0.723	1	0.3963
Clouds coverage	6.084	1	**0.0146**
R^2 of the final model = 0.192			

Using CCA, I also identified environmenal variables influencing the relative species composition of the light trap samples, taking into account the seasonality of the data (Table 8 and Fig 16). In all cases but the Scirtidae, the effect of time within season that could not be explained by environmental variables was highly significant. The composition of the whole assemblage is determined by air temperature. There are, however, differences in the effects of tested variables among the three main groups of water beetles. The relative composition is influenced by air temperature and water depth within the Dytiscidae, only by temperature within the Hydrophiloidea, and by none of the tested variables within the Scirtidae (Table 8).

Table 8 – The effects of time and selected environmental variables on the composition of water beetle assemblages collected by the light trap (CCA; partial effects; year taken as a covariable).

	All families		Dytiscidae		Hydrophiloidea		Scirtidae	
	F	P	F	P	F	P	F	P
Day	5.659	**0.0055**	4.487	**0.0011**	4.719	**0.0026**	5.716	0.3952
Temperature	4.178	**0.0003**	4.661	**0.0002**	3.441	**0.0016**	3.530	0.2769
Water depth	2.053	0.0607	2.037	**0.0258**	0.609	0.7352	4.411	0.1337
Air humidity	1.707	0.1792	0.401	0.9422	1.506	0.2292	3.191	0.1304
Air pressure	1.747	0.1486	1.229	0.2289	1.729	0.1860	2.615	0.1704
Cloud coverage	1.304	0.2609	0.827	0.5076	1.722	0.1814	1.260	0.3949
Precipitation	1.079	0.2552	0.923	0.3231	1.330	0.1849	1.200	0.2910
Explained variance	**6.8%^{1}, 3.0%^{2}**		**9.7%^{1}, 6.7%^{2}**		**8.1%^{1}, 3.4%^{2}**		**-**	

^{1} by all significant variables, ^{2} variance explained by environmental predictors after accounting for day.

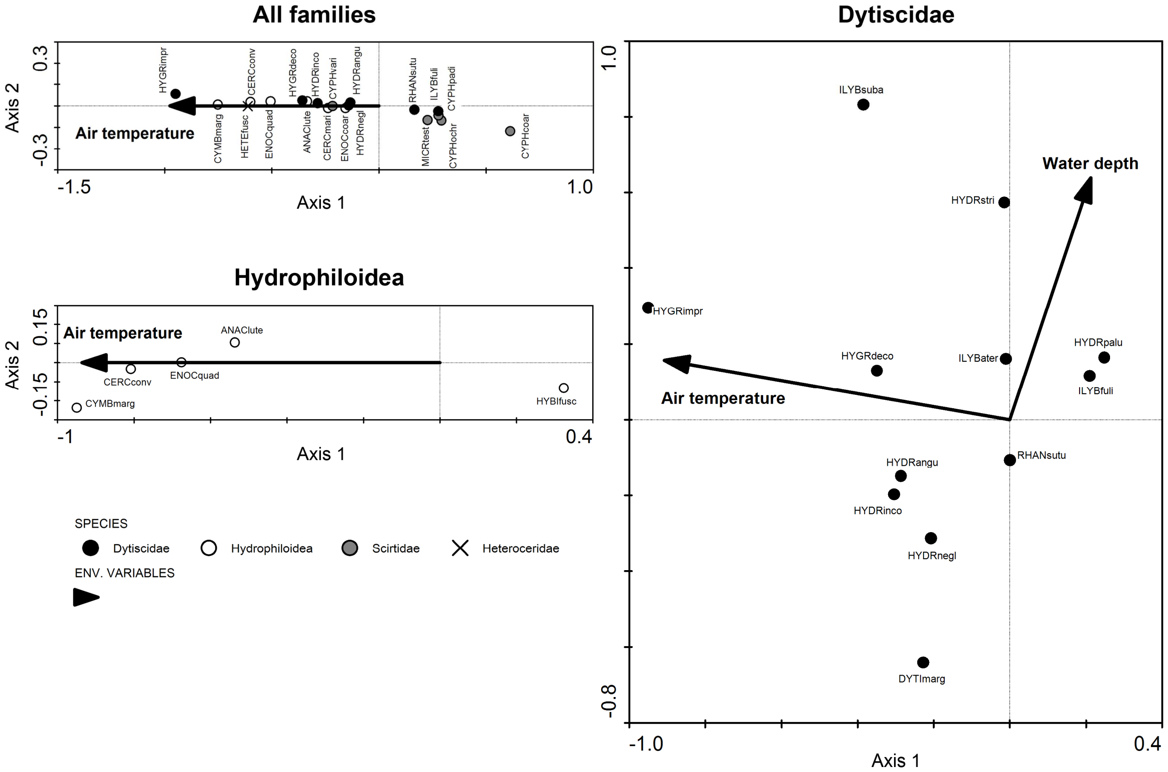

Fig. 16 – The effects of selected environmental variables on the composition of water beetle assemblages collected by the light trap (CCA, year and day taken as covariables). Species with low frequency or no relation to ordination axes are not displayed. See Appendix 1 for species names.

Sex- and age-specificity of the flight activity

The samples of Dytiscidae from the light trap had a higher proportion of females than pooled samples taken by activity traps, box trap and net sampling (generalized linear mixed model; F=64.31, df=1, 6, P=0.0002; Fig. 17). Newly emerged immature adults were also more common in the light trap samples than in samples taken in water (generalized linear mixed model; Dytiscidae – F=33.85, df=1, 8, P=0.0003, Hydrophilidae – F=325.75, df=1, 9, P<0.0001; Fig. 17).

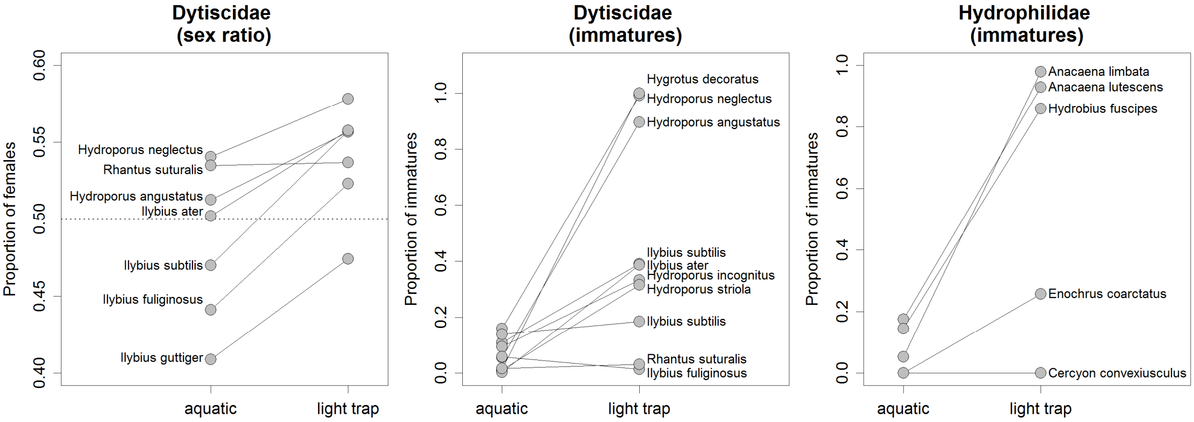

Fig. 17 – The comparison of sex ratios and proportions of immature adults between the light trap and aquatic sampling methods (observed values for pooled data from years 2004-2006; aquatic = pooled data from activity traps, box trap and handnet sampling).

3.4 Discussion

Most central European species of water beetles are univoltine spring breeders with overwintering adults (Hansen 1987; Nilsson 1995). Based on this type of life history, bimodal seasonal flight dynamics with spring pre-breeding dispersal and summer dispersal of new generation are generally expected and were observed several times (Fernando & Galbraith 1973; Landin 1980; Zalom et al. 1979, 1980; Lundkvist et al. 2002). At the study site, spring dispersal was low in most years until the end of May, not supporting the existence of typical spring pre-breeding dispersal. However, in the vicinity of the alder carr, I repeatedly observed dense populations of several species of water beetles in vernal pools filled with smowmelt water as early as in the end of March (e.g. *Helophorus* sp., *Hydroglyphus geminus*, *Hydroporus palustris*). At that time, the alder carr was still at least partly covered by snow and ice, which melted ca. 2–3 weeks later than the exposed pools. Spring dispersal may thus be confined to colonization of shallow exposed puddles with considerably higher temperature and better overall conditions than the shaded alder carr in this area. Alternatively, the spring colonizers might fly during the day and thus cannot be detected by the light trap. However, species found in the vernal pools were rarely caught in the alder carr (Appendix 1) and moreover most of them have been caught by the light trap (in low numbers). The distinct summer peaks of the flight activity and the significantly higher proportion of teneral adults in the light trap data than in water support the widely accepted concept of dispersal of newly emerging adults, which was proposed by Johnson (1960, 1963). In water beetles, only Landin (1980) reported such a pattern in *Helophorus brevipalpis* so far.

The seasonal flight activity of water beetles at the study site seems to be driven primarily by two factors, water depth and air temperature. Dispersal is the main mechanism of coping with drought in water insects, and mass flights during dry-out periods were observed earlier (Wiggins et al. 1980). Surviving a period of drought in a dried-out water body is probably rare but was observed several times. Drought-resistant stages may include adults (Jackson 1952; Wiggins et al. 1980; Davy-Bowker 2002) or eggs (Wiggins et al. 1980; Wissinger & Gallagher 1999). In my case, *Acilius canaliculatus* and *Hydaticus seminiger* showed the least response to drying; it is possible that the adults may bury in wet leaf litter during dry summer months.

The effect of temperature may be twofold: it can put seasonal constraints on flight (low temperatures early and late in the season) and drive the flight patterns on longer timescales together with hydrology, and cause fluctuations in flight activity by short-term fluctuations. Interpreting the general seasonal pattern of flight activity at the community level should be done with caution because the pattern may be determined primarily by the life cycles of dominant species, which may be adapted to the distinctly seasonal environments of the temperate zone.

Most insects need extraneous heat to warm up their flight muscles before flight, and therefore cannot fly at very low temperatures. My study confirmed the presence of temperature thresholds in the dominant groups but also showed subtle differences between groups. The Scirtidae had the lowest temperature threshold. On the other hand, the overall relationship between flight activity and temperature suggests a general pattern in water beetles. Similar values of temperature thresholds are known in several species of water beetles and bugs (Popham 1964; Landin & Stark 1973; Landin & Vepsäläinen 1977; Zalom et al. 1979, 1980; Landin 1980; Lundkvist et al. 2002). In further analyses of the data, I will test the hypothesis of Popham (1964), who proposed that the temperature threshold increases with body mass and demonstrated it in a few species of the Corixidae (Heteroptera). Several authors also found an upper temperature threshold for flight in water beetles (Landin & Stark 1973; Zalom et al. 1979, 1980) or other insects (Taylor 1963). Those studies of water beetles were focused on daily flight periodicity, thus the upper and lower thresholds may arise from the fact that the flight was observed to be most intense around sunset and sunrise. According to Csabai et al (2006), this daily flight pattern is caused by changes in polarotactical detectability of water bodies and not by temperature. The existence of lower temperature threshold is plausible, but the upper threshold may simply arise from the fact that none or very low flight activity was observed around noon. However, in several species of insects, Taylor (1963) found an upper threshold even when the data were restricted to those parts of the day when flight occurs. In water beetles, the upper temperature threshold may occur at higher temperatures than were available in my case.

The Scirtidae have terrestrial adults but aquatic larvae and thus desiccation means loss of habitat for oviposition and larval development. I therefore expected to find some effect of water depth on their flight activity. Although they show a very similar pattern of temperature dependence in flight activity as the Dytiscidae and Hydrophilidae, I could not detect any influence by water depth.

The seasonal differences in the relative species composition in light trap samples are likely to come from differences in life-histories (e.g. the dominance of the Scirtidae in spring, which may represent the pre-breeding dispersal) and different responses to desiccation (clear dominance of the Hydrophiloidea in mid-summer). The responses to temperature and water depth seem to be species specific and may also be a result of differences in life histories. Moreover, as mentioned above, different species may have different temperature thresholds because of physiological constraints. The lack of a significant result in CCA in the Scirtidae may simply come from a low taxonomical and ecological diversity – the family is represented in my data only by six species of *Cyphon* and *Microcara testacea*. The Dytiscidae and Hydrophiloidea in the light trap samples are much more diverse taxonomically as well as ecologically.

Females of the diving seem to disperse more than males, although I also cannot completely rule out methodological artefacts (e.g. sex-specific attractivity of the light trap). A possible explanation of this phenomenon is that females are more sensitive to habitat degradation because they need to oviposit in a safe habitat. The female-biased flight may also be independent of local conditions. Sex-biased dispersal has been observed in birds and mammals, where it is assumed to decrease intrasexual competition and avoid inbreeding (e.g. Greenwood 1980). In insect, sex-biased dispersal is well known e.g. in social Hymenoptera (e.g. Kukuk et al. 2005). No thorough examination of this topic has been carried out in water beetles and most other aquatic insects so far.

4 Topic three

Spatiotemporal dynamics of a water beetle community

4.1 Review of the literature – Spatiotemporal dynamics, habitat associations, biotic and abiotic factors shaping water insect communities of stagnant waters

Habitat associations

Various abiotic and biotic factors are known to influence the composition of insect communities in stagnant water bodies. The current knowledge is taxonomically highly biased towards dragonflies and damselflies (Odonata) but it seems that the structure of communities is shaped by a wide range of both abiotic and biotic factors, the dominant ones generally being habitat permanence and predation (Wellborn et al. 1996; Entrekin et al. 2001; McPeek 1990, 2003a, 2003b). The species composition changes and the diversity generally increases along successional gradients (Fairchild et al. 2000, Suh & Samways 2005). This may be caused by the increase of amount of vegetation, invasion by predators, and other consequent changes. In the following text, I briefly discuss the importance of physicochemical variables, habitat permanence, submerged vegetation, presence of fish predators, and interactions between invertebrate predators.

Abiotic factors

Abiotic factors such as hydrology and water chemistry have been long considered as important determinants of the composition of water insect communities. More recent insights highlight the importance of interspecific interactions on structuring communities (e.g. McPeek 1990; see below), while the significance of individual variables of water chemistry is being disputed. From physico-chemical variables proposed to affect aquatic animals through their impact on physiology, pH is often considered as an important factor determining the composition of water insect communities (e.g. Bendell & McNicol 1995; Johansson & Brodin 2003; Nicolet et al. 2004) but recent results demonstrate that at least some species of water insects have a high tolerance for low pH. Wollmann (2000) collected several species of the Corixidae in lakes with pH<3, and Gorham & Vodopich (1992) found adverse effects of low pH on the predation behavior and physiology of larval Odonata only for pH<4.5. The pH range commonly found in natural conditions is thus probably mostly well tolerated by water insects and possible pH effects may be only indirect, e.g. mediated by the absence of fish in acidic waters (Batzer & Wissinger 1996). The effect of concentration of nutrients on water insects is also unclear. Some authors found a significant effect of the concentration of nitrogen, phosphorus or other determinants of the amount of nutrients on the total abundance and composition of water insect communities (e.g. Kurzatkowska 2003; Michaletz et al. 2005) but others did not (e.g. Johansson & Brodin 2003). The significance of other chemical variables is rarely highlighted.

Habitat permanence plays a key role in the composition of water insect communities (e.g. Schindler et al. 2003; Jeffries 2003, 2005; Whiles & Goldowitz 2005; Tarr et al. 2005). Whiles & Gordowitz (2005) found that the total invertebrate density and biomass increased from emphemeral to permanent water bodies, while species richness and diversity was highest in wetlands experiencing a short period of drought. Water beetles had the highest density and biomass in temporary wetlands. Tarr et al. (2005) reported an increase in species richness and total abundance and changes in the macroinvertebrate community composition with an increasing length of the hydroperiod. Jeffries (2003, 2005) observed species-specific relationships of the probability of incidence at a given locality and the length of dry phase and length of period of flooding in the larvae and adults of the Dytiscidae. Similarly, Eyre et al. (1992) found species-specific dependence of the probability of occurrence on the length of hydroperiod. The changes of species composition along the permanence gradient are to a large extent results of life history trade-offs determining the ability of a given species to persist in a given type of water body. The presence and lengths of dry periods primarily constrain the species pool, and consequent effects of changes in the composition of predator assemblages along hydrological gradient further determine the community composition (reviewed in Wellborn et al. 1996; Stoks & McPeek 2003a).

Biotic factors

The density and character of vegetation also plays an important role in the structuring of water insect communities (Nilsson et al. 1994; de Szalay & Resh 2000; Gibbons 2002; Schindler et al. 2003; Tollonen et al. 2003; Jeffries 2003, 2005). Herbivorous and saprophagous species use vegetation (live, decaying or periphyton) as a food source. Vegetation also provides perching sites and refuges from predators. However, some authors did not consider vegetation as a significant factor (e.g. Johansson & Brodin 2003; Michaletz et al. 2005).

Fish predators are a key factor in shaping the structure of aquatic invertebrate communities (Hrbáček et al. 1961). In water insects, their effect on total abundance, size distribution and composition of communities was repeatedly recognized (Morin 1984; McPeak 1990; Bendell & McNicol 1995; Prejs et al.1997; Johansson & Brodin 2003; Michaletz 2005; Tarr et al. 2005). The difference in foraging behavior and prey size selectivity between fish and invertebrate predators is a key factor determining differences between communities with fish and invertebrate top predators through inducing changes in antipredator behavior and life-histories (reviewed in Wellborn et al. 1996; Stoks & McPeek 2003a, 2003b).

The interactions among dominant groups of predaceous insects in stagnant waters (Coleoptera, Odonata and Heteroptera) and their differential impact on community structure are insufficiently known (Larsson 1990; McPeek 1998). A number of studies have recently highlighted the importance of competition and intraguild predation on the structure of aquatic insect communities. For example, McPeek (1990) evaluated the effect of a broad spectrum of environmental variables on the composition of *Enallagma* (Odonata: Coenagrionidae) communities and found no effect of chemical variables at all, but highlighted the importance of interspecific competition and the impact of predaceous fish. Unlike in herbivores and sediment feeders (e.g. Chironomidae; Entrekin et al. 2001) the effect of prey availability on predaceous water insects is virtually unknown. Juliano & Lawton (1990) found no food limitation in *Hyphydrus ovatus* (Coleoptera, Dytiscidae), which suggests that rather intraguild predation and presence of vertebrate predators than food availability may shape the community structure of predaceous water insects. The presence of both vertebrate and invertebrate predators also affects the colonization of water bodies in insects which actively avoid waters with predators as oviposition sites (Resetarits 2001; Binckley & Resetarits 2005; Brodin et al. 2006).

Most species of aquatic insects have a distinct pattern of microhabitat occupation and can be roughly classified as shore dwellers, bottom dwellers, phytophilous and free swimming species. Among water beetles, the Hydrophiloidea usually occupy the shoreline and crawl in litter and mats of vegetation, whereas most Dytiscidae are freely swimming in the littoral zone. Microhabitat occupation may be strongly altered by the presence of predators or competitors through a growth-predation/competition trade-off; individuals may choose microhabitats where they suffer lower risk of predation although they may not be profitable for foraging (Sih 1981; Wellborn & Robinson 1987; Suutari et al. 2004).

Spatial structure

Spatial structure can be studied on a number of spatial scales, ranging from the microhabitat choice across patterns within a given water body to continental scales. Distribution of water insects within a water body was rarely studied in stagnant waters unlike in rivers and streams, where significant changes in community composition were observed along and across the stream caused by spatial distribution of microhabitats and current speed (e.g. Dudgeon 1995). In stagnant waters, a number of studies examined the changes in invertebrate communities along environmental gradients on the level of among-localities/habitats differences but the importance of such gradients within a single wetland was rarely assessed. In terrestrial wetland insects, a few authors examined the compositional changes along the edge-centre gradient in peatbogs, where substantial changes from generalist dominance in the edge areas to specialist tyrphobiont species in the centre was detected (e.g. Bezděk et al. 2006). Spatial distribution of phytophilous aquatic invetebrates is determined by spatial changes of vegetation density (de Szalay & Resh 2000; Tolonen et al. 2003). Hydrological gradients within a single wetland area can also play an important role in the spatial structuring of water insect communities (see above). On regional scales (tens of kilometers), differences in the proportion of permanent and temporary water bodies and the forest cover may affect the abundance and diversity of water insect communities (Schäfer et al 2006). On even larger scales, climatic gradients come to the question (Eyre et al. 2006).

Seasonal dynamics

Life-histories and life-cycles of many central European species of water insects are reasonably well known. Most central European water beetles are univoltine. Among the Hydrophiloidea, only the Sphaeridiinae are bivoltine. The Hydrophiloidea usually lay eggs in late spring, the larvae undergo rapid development during early summer, and adults of a new generation emerge in summer, and almost all species overwinter as adults (Hansen 1987). The Dytiscidae are also mostly univoltine but the life cycles are more variable. Most central European species breed in the spring, have summer larvae, and overwinter as adults. Other univoltine species breed from summer to autumn and overwinter as eggs. Some semivoltine species and species with flexible life cycles are known in the Agabini (Nillson & Holmen 1995). The Scirtidae, which have aquatic larvae and terrestrial adults, are also mainly univoltine.

Seasonal dynamics of invertebrate communities in permanent water bodies can be characterized by unimodal dynamics with a spring maximum (de Szalay et al 2003). In temporary water bodies, the dynamics are primarily driven by the timing of desiccation and filling with water and the duration of hydroperiod (Wiggins et al. 1980). In water beetles, studies focused on the seasonal dynamics of the whole community are scarce. Key factors driving the dynamics of adult populations are the appearance of overwintering adults and spring immigrants, causing the spring peak of abundance, and the emergence of a new generation, causing the summer peak. Such bimodality was observed by Bosi (2001), Dettner (1976) and Valladares (1994) also in permanent wetlands.

Concluding remarks

The seasonal dynamics of communities of aquatic insects seems to be driven by life cycles and seasonal changes of hydrological conditions. The second factor is especially important in temporary water bodies. Spatial distribution and habitat associations of aquatic insects are studied mostly on the scale among localities within a small region. Both the large scale and small scale patterns are poorly known. The composition of aquatic insect communities is probably driven by hydrology and interspecific interactions – predation and competition.

4.2 Material and methods

The analysis of spatiotemporal dynamics presented here is based on data from activity traps – 2,261 samples in 2004-2006; 62 species of adults (n=23,018) and 25 species of larvae (n=1763); box trap – 51 samples in 2004; 41 species of adults (n=1238) and 12 species of larvae (n=432) and handnet sampling – 46 samples in 2006; 32 species of adults (n=407) and 27 species of larvae (n=805).

Analyses of selected physicochemical variables were carried out in 2006. Temperature, pH, conductivity and concentration of dissolved oxygen were measured in the field using a WTW multimeter at four regularly spread sites in the drain. Water samples for laboratory analyses were taken at the same sites four times per season (one mixed sample from two subsamples per site). Concentration of nitrates+nitrites, amonium ions and phosphorous ions was analyzed using a FIA spectrophotometer in the laboratory. Vegetation density was visually estimated as a cover of emergent macrophytes on an ordinal scale (three levels).

The drain and wetland interior were compared using the box trap data. Generalized linear mixed models with quasipoisson distribution were used to deal with the non-normal distribution of the response variable (number of specimens and species) and spatiotemporal structure of the data. The sampling date and spatial location of paired samples (drain+wetland interior) were used as random factors, the latter being nested within the former. I also tested the difference in relative species composition between the drain and the wetland interior using box trap data in CANOCO. CCA was fitted with the paired sample ID used as a qualitative covariable.

I further studied the spatiotemporal distribution of water beetles using additive mixed models fitted separately to data from activity traps. Log-transformed numbers of specimens and species, $\log_{10}(n+1)$, were used as a response variable. Predictors were time in days and distance from the wetland edge. Spatial autocorrelation of order one discovered during data exploration was modeled within sampling date. The effect of location variables (drain width, water depth and vegetation density) on the log-transformed total number of specimens and species was tested by additive mixed models with sampling date as a random factor and spatial autocorrelation of order one modeled within sampling date. These analyses were performed under the assumption that possible spatial trend in the distribution of water beetles along the drain can be explained by the tested variables, as water depth and drain width change along the drain (Fig. 18) and the measured physicochemical variables do not show any consistent spatial pattern (Fig. 19).

The spatiotemporal changes in species composition were tested using CCA with year as a covariable and day and distance from the edge of the wetland as predictors. Unlike in additive models, it was not possible to account for autocorrelation because of the restricted possibility to design a proper permutation scheme. The effect of location variables on the relative species composition in activity traps was tested in CCA with the sampling date taken as a qualitative covariable and supposed spatial autocorrelation was accounted for using permutations by cyclic shifts within the sampling date (Lepš & Šmilauer 2003). All analyses were performed separately for adults and larvae. For testing significance, Monte Carlo test with 9999 permutations was used.

4.3 Results

Patterns of seasonal and spatial community variation

The spatial structure of the habitat can be classified at two local scales: first, the difference between the drains, which are most of the season full of water, and the temporarily flooded rest of the wetland area and second, a gradient along the intersection through the wetland from the southern edge with adjacent meadows and fields and the northern margin forming a southern shore of a large fish pond.

The number of specimens as well as the number of species of adult water beetles is significantly higher in the drain than in the surrounding parts of the wetland interior, based on box trap data. On the other hand, no such difference was detected in larvae (Table 9). In the adults, a significant difference in the species composition was detected between the drain and the wetland interior (F = 1.985, P = 0.0012, explained variance = 9.9%, Fig. 18) but not in the larvae (F = 1.188, P = 0.1490, explained variance = 9.7%). Species with a higher relative abundance both in the drain and in the interior can be found in the Hydrophiloidea as well as in the Dytiscidae (Fig. 18).

The adults as well the larvae occasionally reached very high densities of several hundred individuals/m^2 but the mean density was much lower (Table 10). The larvae of the Scirtidae reached an order of magnitude higher density than the larvae of the Dytiscidae and Hydrophiloidea in the drain. The densities of both adults and larvae of the Dytiscidae and Hydrophiloidea were fairly similar (Table 10). All these patterns were consistent between the box trap and handnet sampling.

Table 9 – Differences between the drain and wetland interior in the number of specimens and species per box trap sample for adults and larvae (GLMM).

	Adults			**Larvae**		
	Effect[#]	**F1,18**	**P**	**Effect**[#]	**F1,18**	**P**
Number of specimens						
wetland interior vs. drain	0.390	35.351	**<0.0001**	1.254	0.760	0.3949
Number of species						
wetland interior vs. drain	0.722	8.550	**0.0091**	1.085	0.127	0.7263

[#] fitted value for the ratio of numbers in wetland interior over numbers in the drain

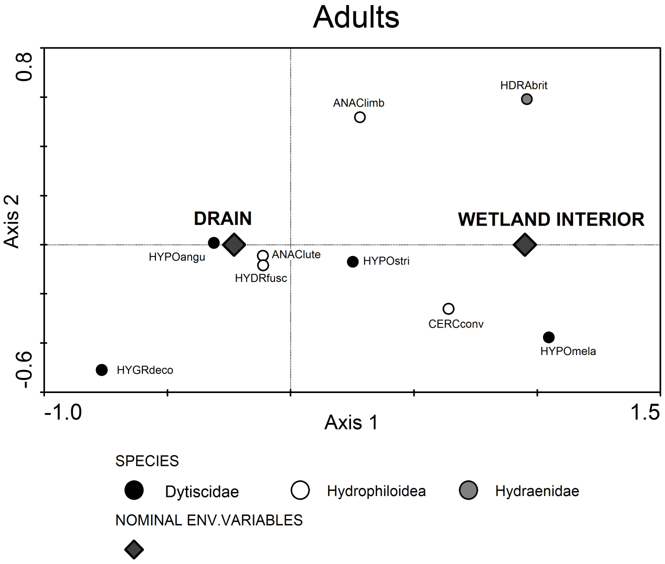

Fig. 18 – Differences between the drain and wetland interior in the relative species composition of adults sampled by the box trap (CCA; ca. 12% of species with best fit and highest total abundance are displayed). See Appendix 1 for species names.

Table 10 – Estimated population densities of water beetles (individuals/m^2) in the wetland. Mean and maximum values (in parentheses) are given.

	Adults		Larvae	
	Drain	Wetland interior	drain	Wetland interior
Box trap 2004				
All families	135.50 (1052)	32.42 (80)	46.88 (448)	12.00 (48)
Dytiscidae	64.38 (512)	6.53 (48)	1.63 (12)	1.68 (8)
Hydrophiloidea	66.25 (540)	20.21 (64)	1.13 (8)	3.37 (16)
Scirtidae			44.13 (448)	6.95 (40)
Handnet sampling 2006				
All families	35.39 (112)		70.00 (924)	
Dytiscidae	15.65 (96)		11.39 (60)	
Hydrophiloidea	18.78 (96)		1.91 (24)	
Scirtidae			56.70 (916)	

The gradient across the wetland is characterized by changes in water depth and drain width (Fig. 19) and consequently local permanence. No consistent spatiotemporal patterns were detected in the physicochemical variables (Fig. 20). Water depth varies considerably during each season (Fig. 21). Water temperature, pH, conductivity, concentration of dissolved oxygen as well as concentration of nutrients also undergo more or less distinct seasonal changes (Fig. 20).

The number of adults and larvae (both specimens and species) in activity traps vary in time and space (Figs. 21–23 and Table 11). Most specimens and species per trap were found in the central part of the wetland. During desiccation periods, adult beetles densities greatly increase, especially in the central part of the wetland as the drain dries out from both ends. Both the spatial and the seasonal component of variation in community composition was highly significant, as well as their interaction.

The seasonal dynamics differs considerably among years, and the overall pattern of seasonal dynamics is superimposed by marked short-term fluctuations (Fig. 21). The highest total abundance of adults coincides with periods of rapid desiccation of the wetland, the highest number of species is usually found during late spring and early summer. Seasonal changes in the community composition may be attributed to life-cycle differences. *Agabus affinis*, *A. uliginosus*, *A. unguicularis* and *Rhantus exsoletus* in adults create the typical spring aspect. In larvae, the composition shifts from overwintering larvae of *Ilybius* spp. with the highest relative abundance in the spring to *Dytiscus* spp., *Acilius canaliculatus* and *Hydaticus seminiger* and to *Hydrochara caraboides* prevailing in late summer.

The spatiotemporal patterns of total abundance and species richness are much more similar in the larvae than in the adults (Fig. 23). The spatial distribution undergoes considerable changes during the season, and the interaction of the two predictors, date and distance from wetland edge, is in general highly significant. This may be linked to seasonal changes of water depth (compare Fig. 21). Finally, significant spatiotemporal changes in the species composition of assemblages of adults as well as larvae were detected (Fig. 24 and Table 12).

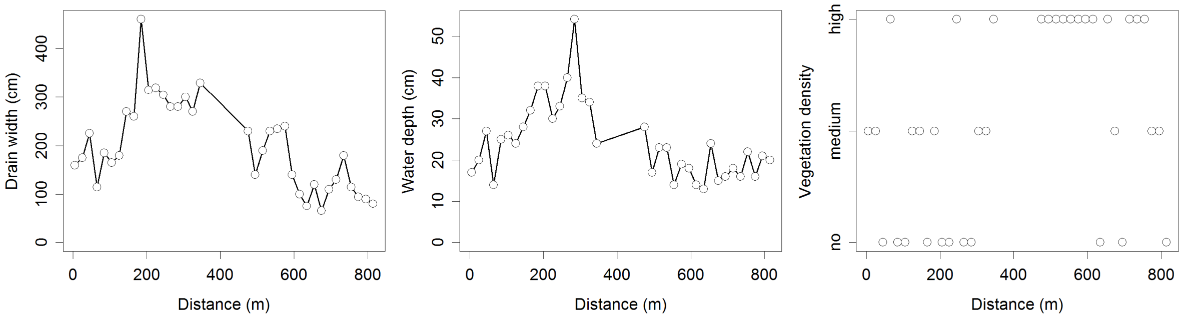

Fig. 19 – Spatial changes in drain width, water depth (representing ca. medium seasonal values) and density of vegetation on September 13, 2006. Distance measured from south to north.

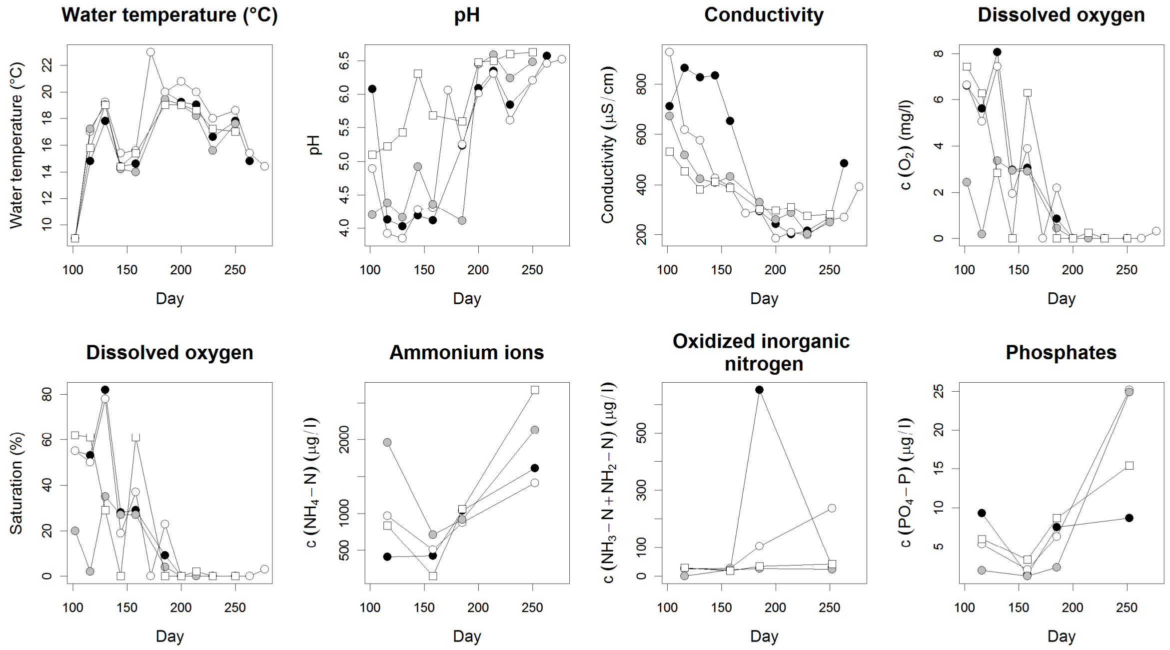

Fig. 20 – Seasonal changes of measured physico-chemical variables at four sites within the drain in 2006 (black circles = site 1, 115 m away from the wetland's edge; empty circles = site 2, 235 m away; gray circles = site 3, 585 m away; squares = site 4, 705 m away). Day given as ordinal date.

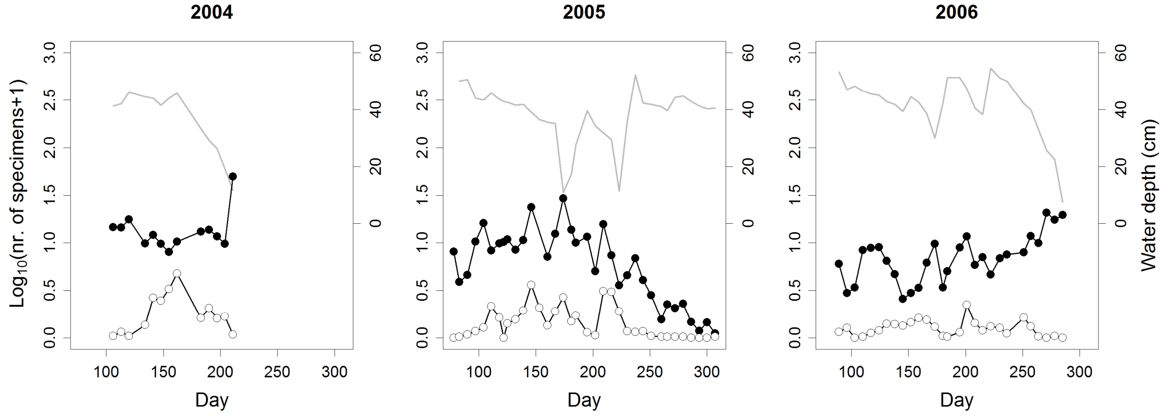

Fig. 21 – Seasonal dynamics of water beetles sampled by activity traps in 2004–2006. Mean number of specimens per trap is given for all sampling dates. Adults as full circles, larvae as empty circles (left y-axis) and water depth as a gray line (right y-axis). Day given as ordinal date.

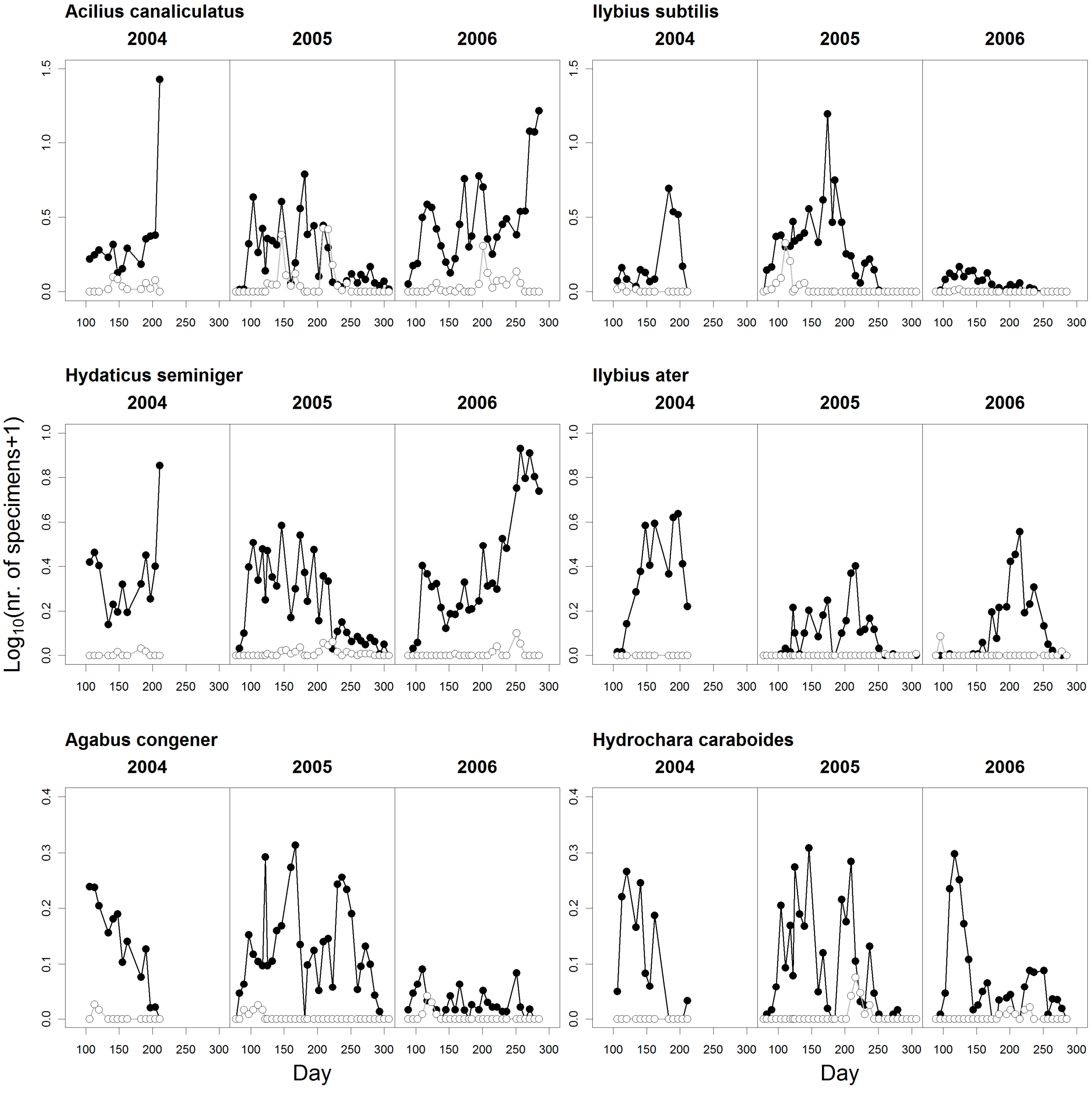

Fig. 22 – Seasonal dynamics of the six most abundant species in activity traps, shown as mean number of specimens per trap and sampling date. Adults as full black circles, larvae as empty circles. Day given as ordinal date. Note the different scales for abundance in each row.

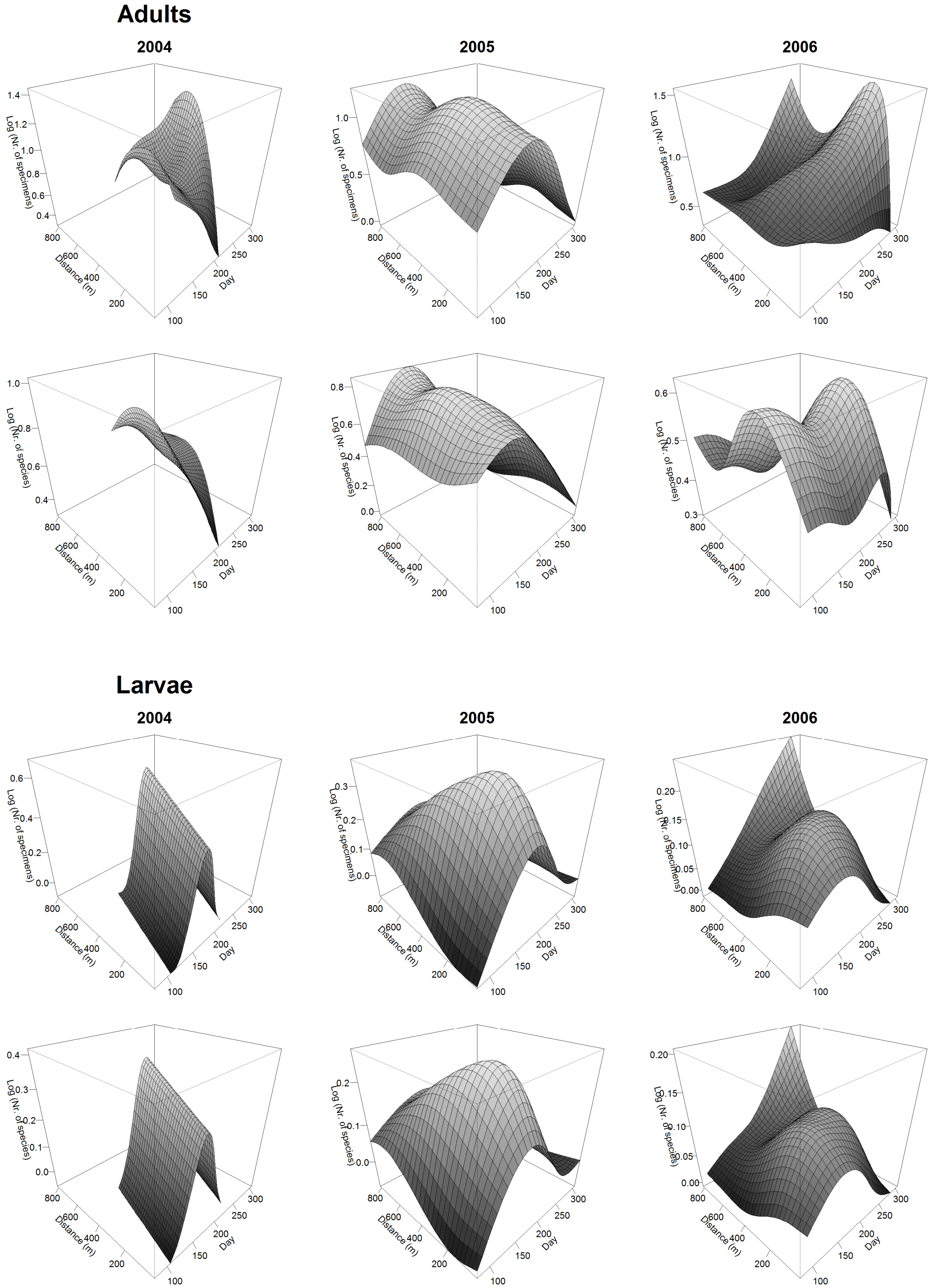

Fig. 23 – Spatiotemporal dynamics of the total number of specimens and species of adults and larvae of water beetles per activity trap. Every plot is based on a separately fitted generalized additive model and only predicted values are displayed. Distance is measured from the southern end of the sampled drain; day given as ordinal date.

Table 11 – The significance of spatiotemporal changes of the total number of specimens and species of adult and larval water beetles per activity trap, tested by generalized additive models.

	2004			**2005**			**2006**		
	F	**df (total df = 215)**	**P**	**F**	**df (total df = 1114)**	**P**	**F**	**df (total df = 893)**	**P**
Adults – Number of specimens									
Day	3.193	2.317	**0.0143**	148.317	3.719	**$<2*10^{-16}$**	9.978	2.089	**$<7*10^{-8}$**
Distance	9.108	1	**0.0029**	5.982	3.550	**$<1*10^{-6}$**	14.825	3.612	**$<1*10^{-13}$**
	L-ratio	**df**	**P**	**L-ratio**	**df**	**P**	**L-ratio**	**df**	**P**
Day*distance	13.824		**0.0002**	0.499		0.4799	30.368		**<0.0001**
R2 of the final model		**0.211**			**0.486**			**0.215**	
	F	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**
Adults – Number of species									
Day	9.281	1.597	**$<7*10^{-7}$**	170.723	3.706	**$<2*10^{-16}$**	3.953	3.464	**0.0035**
Distance	8.646	1	**0.0036**	5.622	3.464	**0.0002**	11.037	3.480	**$<1*10^{-10}$**
	L-ratio	**df**	**P**	**L-ratio**	**df**	**P**	**L-ratio**	**df**	**P**
Day*distance	6.665		**0.0098**	5.209		**0.0225**	11.220		**0.0008**
R2 of the final model		**0.221**			**0.493**			**0.086**	
	F	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**
Larvae – Number of specimens									
Day	29.820	3.792	**$<2*10^{-16}$**	21.023	3.484	**$<2*10^{-16}$**	5.610	2.797	**0.0002**
Distance	16.070	1	**$<9*10^{-5}$**	1.765	1.810	0.134	4.504	3.123	**0.0013**
	L-ratio	**df**	**P**	**L-ratio**	**df**	**P**	**L-ratio**	**df**	**P**
Day*distance	**Significantly worse fit**			10.549		**0.0012**	11.988		**0.0005**
R2 of the final model		**0.364**			**0.203**			**0.066**	
	F	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**
Larvae – Number of species									
Day	25.470	3.614	**$<2*10^{-16}$**	31.670	3.640	**$<2*10^{-16}$**	7.532	3.509	**$<6*10^{-6}$**
Distance	10.860	1	**0.0012**	2.582	2.468	**0.0358**	5.976	3.235	**$<1*10^{-6}$**
	L-ratio	**df**	**P**	**L-ratio**	**df**	**P**	**L-ratio**	**df**	**P**
Day*distance	**Significantly worse fit**			15.466		**0.0001**	11.727		**0.0006**
R2 of the final model		**0.345**			**0.242**			**0.076**	

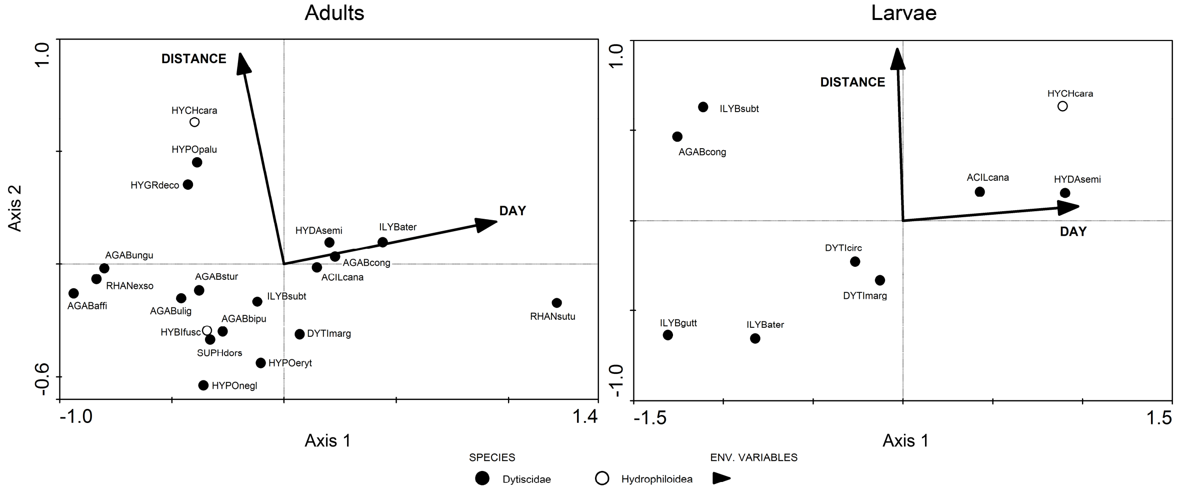

Fig. 24 – Spatiotemporal changes in the relative species composition of samples from activity traps tested separately for adults and larvae (CCA). Species with low frequency or no relation to the ordination axes are not displayed. See Appendix 1 for species names.

Table 12 – Spatiotemporal changes in the relative species composition of samples from activity traps tested by CCA. Distance is measured from the southern end of the drain; day coded as ordinal date.

	adults		**larvae**	
	F	**P**	**F**	**P**
Day	15.157	**<0.0001**	19.158	**<0.0001**
Distance	8.728	**<0.0001**	7.371	**<0.0001**
Day*distance #	1.843	**0.0081**	7.444	**<0.0001**
Total explained variance	**1.4%**		**5.2%**	

conditional effect after accounting for main effects

Location effects

I have also examined the influence of local drain depth and width and the character of vegetation on the results in the drain. The highest number of specimens and species per activity trap was found in the deep and wide parts of the drain (Fig. 25). Vegetation density had a slightly significant effect only on the total abundance of adults (Table 13). Water depth and drain width are tightly correlated (Pearson's correlation coefficient r = 0.73, t = 6.2908, df = 34, p-value = $3.62 \cdot 10^{-7}$). Consequently, after one of them as the superior predictor was included into the additive model, the other one had a small or insignificant effect. Marginal effects of both water depth and drain width were highly significant for the total abundance as well as the number of species per trap ($p<10^{-4}$ in all cases). Water depth is a better predictor in the adults whereas drain width is superior in the larvae (Table 13). Water depth, drain width and vegetation density all had a significant effect on the composition of assemblages of adult beetles, whereas only water depth and vegetation density had a significant effect on the larvae (CCA; Table 14 and Fig. 26). The effect of drain width in the larvae was just above the p=0.05 level of significance, but its marginal effect was very strong (F = 3.813, P=0.0007).

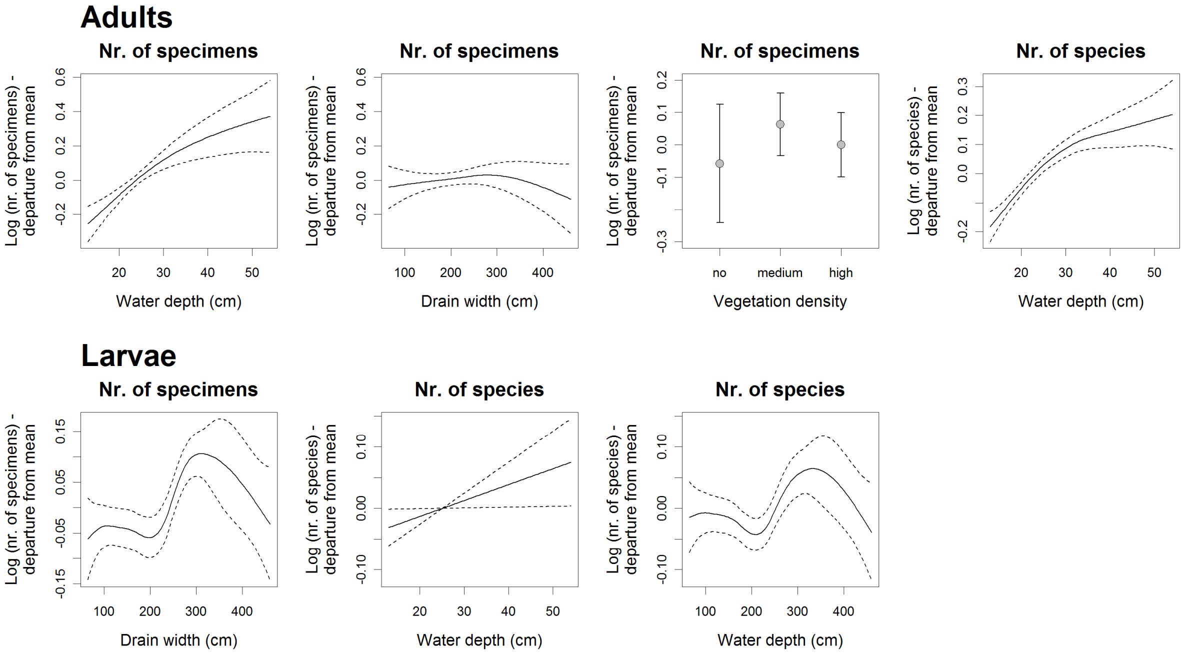

Fig. 25 – The effects of location parameters on the total abundance and number of species of adults and larvae of water beetles per activity trap (fitted values with 95% confidence interval).

Table 13 – The effects of location variables on the number of specimens and the number of species per activity trap in adults and larvae of water beetles.

	Adults			**Larvae**		
	F	**df (total df = 2090)**	**p**	**F**	**df (total df = 2090)**	**p**
Number of specimens						
Water depth	7.268	1.984	**$<9*10^{-6}$**	1.726	1.361	0.1595
Drain width	2.339	2.066	**0.0396**	5.243	4.710	**$<5*10^{-7}$**
Vegetation density	3.176	2	**0.0419**	0.796	2	0.4510
R2 of the final model		**0.036**			**0.018**	
Number of species						
Water depth	13.110	2.508	**$<2*10^{-14}$**	4.744	1	**0.0295**
Drain width	1.543	1.763	0.1870	4.091	4.577	**$<4*10^{-5}$**
Vegetation density	1.456	2	0.2330	0.328	2	0.7200
R2 of the final model		**0.033**			**0.024**	

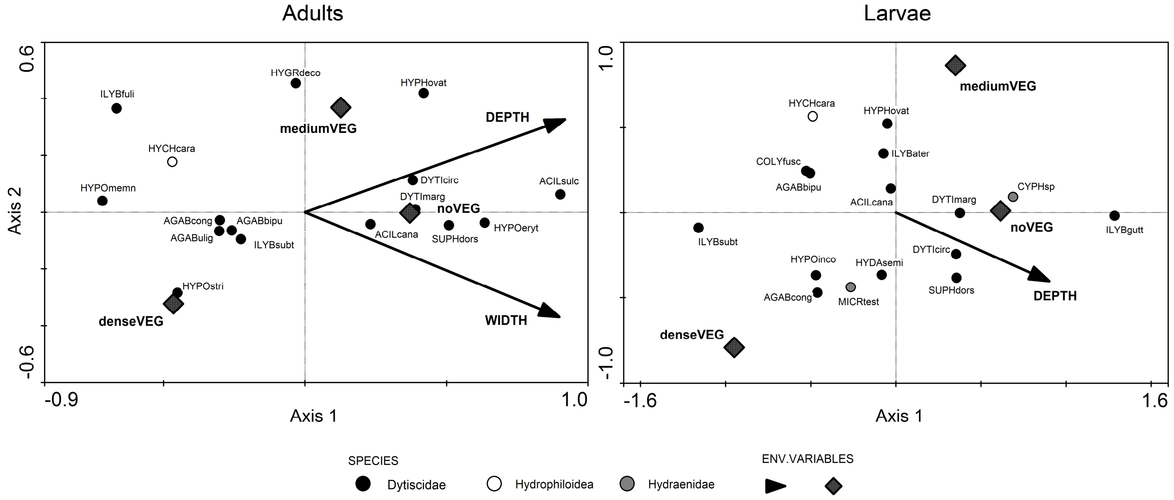

Fig. 26 – The effects of location variables on the relative species composition in activity traps, tested separately in adults and larvae using CCA. See Appendix 1 for species names.

Tab. 14 – The effects of microhabitat variables on the composition of water beetle assemblages tested by CCA.

	adults		**larvae**	
	F	**P**	**F**	**P**
Water depth	3.388	**0.0037**	2.588	**0.0076**
Drain width	3.705	**<0.0001**	1.829	0.0508
Vegetation density	1.549	**0.0169**	1.352	**0.0403**
Total explained variance#	**1.0%**		**1.1%**	

#only by variables with significant effect.

4.4 Discussion

In this part of the thesis, I have examined patterns in the spatiotemporal dynamics of water beetles at the study site in an alder carr. The dynamics are clearly affected by the phenology the individual species that constitute the local aquatic insect community as well as changes in the environment, especially the water level.

Changes in the environmental variables and the density and composition of water beetle community seem to be closely linked. The higher abundance and species richness of adult water beetles in the drain compared to a nearby wetland interior may result from the temporary nature of the latter mesohabitat. Increasing abundance and species richness at different localities were repeatedly observed along the permanence gradient (e.g. Tarr et al. 2005), and this relationship may be repeated within a single wetland. The apparently more even distribution of the larvae in the wetland may be explained by their seasonal dynamics. The highest larval densities were found in late spring, while the study site usually dries out in mid-summer. Associated mortality risks are thus low for larvae and they do not need to concentrate in the drains and avoid the wetland interior. Shallow warm water full of leaf litter may moreover provide ideal conditions for development of detritivorous and saprophagous larvae and larvae feeding on small prey (citace Batzer et al. 2004). Spring oviposition in the flooded wetland interior followed by the retreat of the adults to the drain may therefore be advantageous for reproduction and also decrease competition, cannibalism and intraguild predation between the larvae and adults.

Spatiotemporal variation in the abundance of adult and larval beetles in the drain is likely to be a result of life-cycle constraints and varying hydrological conditions. Most central European species are univoltine with reproduction in the spring (Hansen 1987; Nilsson & Holmen 1995). Seasonal dynamics of larval assemblages with the maximum number of specimens and species in late spring and early summer corresponds well to this observation. The very similar patterns in seasonal changes of species richness and total abundance are a simple consequence of the positive relationship between the number of specimens and species and the similarity in life cycles. The seasonal dynamics of adult assemblages can be clearly linked to hydrological changes. Peaks in the abundance correspond to periods of desiccation and most likely result from the concentration of adults in a small volume of remaining habitable pools. However, I observed remarkably different seasonal patterns of species richness, which gradually decreased while abundance increased in 2004; in 2005 and 2006, species richness peaked distinctly before the peak in abundance. The decline in species richness well before the wetland (almost) desiccates may be explained by species-specific responses to desiccation. Sensitive species are likely to leave the locality well before it dries out completely, while several resistant species remain at the locality until it completely desiccates and perhaps even stay afterwards buried in wet bottom substrate. Davy-Bowker (2002) and Jackson (1952) observed this behavior in *Agabus bipustulatus*.

The relative species composition of both adults and larvae also changes in space and time. As noted above, water depth, drain width and consequently permanence are the main factors creating the gradient from the edges to the centre of the wetland. Several species clearly increase in abundance towards the end of the drain connected to the Černis pond, most notably *Hydrochara caraboides* (Hydrophilidae). In this species the pattern is consistent in both adults and larvae. The proximity of the pond may result in changes in chemistry (however only higher pH was observed in the spring of 2006), impact of fish, and prey availability; the latter was not evaluated in detail during this study. The plausibility of fish predation as the underlying cause of the observed pattern is unlikely. Only a few small specimens of fish were collected by activity traps and only several times other fish were observed in the drain (especially in the part adjacent to the Černiš pond) during the three years of the research. The connection of the drain and the pond is very shallow, which probably limits the possibility for fish to enter the drain for most of the year.

Seasonal changes in the relative community composition may be attributed to life-cycle differences. Adults of *Agabus affinis*, *A. uliginosus*, *A. unguiculais* and *Rhantus exsoletus* create the typical spring aspect. In larvae, the composition during the season shifts from overwintering larvae of *Ilybius* spp. to *Dytiscus* spp., *Acilius canaliculatus* and *Hydaticus seminiger* and finally to *Hydrochara caraboides* in late summer. These changes are consistent with data on the life cycles of these species (Hansen 1987; Nilsson & Holmen 1995).

The effect of water depth and drain width on abundance as well as species richness along the drain in 2004–2006 can be easily explained by the preference of water beetles for stable conditions in the centre of the wetland and the lack of water in the shallowest parts of the drain every summer. Surprisingly, vegetation density had only a slightly significant effect on the total abundance of adult beetles and no effect at all on the number of species of adults and on the number of specimens and species of larvae. Increasing abundance and species richness with increasing vegetation density may be expected and was repeatedly documented (Nilsson et al. 1994; de Szalay & Resh 2000; Gibbons 2002; Schindler et al. 2003; Tollonen et al. 2003) as most water insects use vegetation as a refuge, perching site or food source. In my case, these services might have been provided by a thick layer of leaf litter and small branches covering the bottom of the drain. The importance of leaf litter for the structure and richness of aquatic invertebrate communities was recently highlighted by Batzer et al (2004). Substitution of the various functions of vegetation by leaf litter and other biotic structures may have obscured the effect of vegetation in some earlier studies which did not found much support for the importance of vegetation density for aquatic invertebrate communities (e.g. Johansson & Brodin 2003; Michaletz et al. 2005). Vegetation density together with water depth and drain width still had a significant effect on the relative species composition of both adults and larvae, suggesting some interspecific differences in microhabitat use, although the amount of explained variance is very low.

5 Conclusions

In my project, I focused on several questions concerning the structure and dynamics of a water beetle community in a semipermanent wetland. Using a combination of methods, I demonstrated that the studied community is highly dynamic and to a large extent driven by seasonal and spatial changes of a few key environmental factors. As expected, seasonal hydrological variation has a major impact on the community.

The tests of selectivity of four standard sampling methods demonstrated that their choice should be carefully evaluated and their selectivity should not be overlooked. The combination of two or three qualitatively different methods can yield the most complete information about the community composition and species richness.

The seasonal flight activity appears to be driven by the desiccation of the wetland and temperature thresholds. Short-term fluctuations of the flight activity were linked to similar fluctuations of temperature. Other meteorological variables were not important, but this may be caused by the resolution of the data and the impossibility to measure these variables locally. The samples consisted of catches during two or three nights, but e.g. changes in air pressure or precipitation levels may influence the flight activity on a much finer scale. Importance of short showers, drops of air pressure before a storm, and other similarly fast short-term events could not be evaluated in this study.

The observed spatiotemporal dynamics of the water beetle community seem to be a combination of general life-cycle driven seasonal dynamics and changes induced by variable water levels in time and space. Vegetation seems to play only minor role in the stucturing of the water beetle community at the study site, but its role might have been obscured by the rich leaf litter deposits in the wetland. One potentially important aspect of the spatiotemporal dynamics, which I did not thoroughly test yet, is interspecific interactions. Examining this topic may bring new insights and new complexity to my present interpretations of the processes in the studied community.

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Appendix – The list of species recorded at the study site; numbers of specimens are given.

A. Adults

Species	Activity Traps 2004-2006	Light Trap 2002-2006	Box trap 2004	Net sampling 2006	Species code
Gyrinidae					
Gyrinus substriatus Stephens, 1828	-	3	-	-	GYRIsubs
Haliplidae					
Haliplus heydeni Wehncke, 1875 [1]	-	-	-	-	
Haliplus ruficollis (De Geer, 1774)	2	-	-	-	HALIrufi
Noteridae					
Noterus crassicornis (O. F. Müller, 1776)	5	-	1	2	NOTEcras
Dytiscidae					
Acilius canaliculatus (Nicolai, 1822)	6806	-	15	42	ACILcana
Acilius sulcatus (Linné, 1758)	116	-	-	-	ACILsulc
Agabus affinis (Paykull, 1798)	73	-	-	-	AGABaffi
Agabus bipustulatus (Linné, 1767)	363	-	5	-	AGABbipu
Agabus congener (Thunberg, 1794)	1050	-	2	1	AGABcong
Agabus sturmi (Gyllenhål, 1808)	172	-	2	-	AGABstur
Agabus uliginosus (Linné, 1761)	385	-	3	-	AGABulig
Agabus undulatus (Schrank, 1776)	16	-	-	-	AGABundu
Agabus unguicularis (Thomson, 1867)	280	-	-	1	AGABungu
Colymbetes fuscus (Linné, 1758)	398	-	-	2	COLYfusc
Dytiscus cimcumcinctus Ahrens, 1811	222	-	-	1	DYTIcirc
Dytiscus marginalis Linné, 1758	544	10	-	-	DYTImarg
Graphoderus cinereus (Linné, 1758)	18	-	-	-	GRAPcine
Graptodytes granularis (Linné, 1767)[1]	-	-	-	-	
Graptodytes pictus (Fabricius, 1787)	4	2	3	-	GRPTpict
Hydaticus continentalis J. Balfour-Browne, 1944	4	-	-	-	HYDAcont
Hydaticus seminiger (De Geer, 1774)	4352	-	3	20	HYDAsemi
Hydaticus transversalis (Pontoppidan, 1763)	1	-	-	-	HYDAtran
Hydroglyphus geminus (Fabricius, 1792)	1	12	-	-	HYGLgemi
Hydroporus angustatus Sturm, 1835	121	221	37	2	HYPOangu
Hydroporus erythrocephalus (Linné, 1758)	82	1	5	-	HYPOeryt
Hydroporus incognitus Sharp, 1869	91	45	18	7	HYPOinco
Hydroporus melanarius Sturm, 1835	14	-	7	-	HYPOmela
Hydroporus memnonius Nicolai, 1822	86	1	64	16	HYPOmemn
Hydroporus neglectus Schaum, 1845	198	128	174	24	HYPOnegl
Hydroporus nigrita (Fabricius, 1792)[1]	-	-	-	-	
Hydroporus palustris (Linné, 1761)	99	6	6	6	HYPOpalu
Hydroporus planus (Fabricius, 1781)	14	-	1	1	HYPOplan
Hydroporus rufifrons (Duftschmid, 1805)	1	-	-	-	HYPOrufi
Hydroprorus scalesianus Stephens, 1828	2	-	1	-	HYPOscal
Hydroporus striola Gyllenhål, 1827	230	19	27	4	HYPOstri
Hydroporus tristis (Paykull, 1798)	5	1	4	-	HYPOtris
Hydroporus umbrosus (Gyllenhål, 1808)	6	-	-	-	HYPOumbr
Hydrovatus cuspidatus (Kunze, 1818)[1]	-	-	-	-	
Hygrotus decoratus (Gyllenhål, 1810)	215	21	78	24	HYGRdeco

Species	Activity Traps 2004-2006	Light Trap 2002-2006	Box trap 2004	Net sampling 2006	Species code
Hygrotus impressopunctatus (Schaller, 1783)	8	13	1	-	HYGRimpr
Hygrotus inequalis (Fabricius, 1777)	3	2	-	-	HYGRineq
Hyphydrus ovatus (Linné, 1761)	103	-	-	-	HYPHovat
Ilybius ater (De Geer, 1774)	1429	651	7	4	ILYBater
Ilybius chalconatus (Panzer, 1796)	4	-	-	-	ILYBchal
Ilybius fuliginosus (Fabricius, 1792)	30	1061	3	1	ILYBfuli
Ilybius guttiger (Gyllenhål, 1808)	1103	97	3	7	ILYBgutt
Ilybius quadriguttatus (Boisduval et Lacordaire, 1835)	5	1	-	-	ILYBquad
Ilybius subaeneus Erichson, 1837	1	10	-	-	ILYBsuba
Ilybius subtilis (Erichson, 1837)	2504	827	65	5	ILYBsubt
Ilybius wasastjernai (C. R. Sahlberg, 1824)[2]	-	-	-	-	
Laccophilus hyalinus (De Geer, 1774)[1]	-	-	-	-	
Laccornis oblongus (Stephens, 1835)	2	-	-	-	LACCoblo
Liopterus haemorrhoidalis (Fabricius, 1787)	16	4	2	-	LIOPhaem
Nartus grapi (Gyllenhål, 1808)	7	-	-	-	NARTgrap
Rhantus exsoletus (Forster, 1771)	71	-	-	-	RHANexso
Rhantus frontalis (Marsham, 1802)	1	-	-	-	RHANfron
Rhantus suturalis (MacLeay, 1825)	37	626	-	6	RHANsutu
Suphrodytes dorsalis (Fabricius, 1787)	267	-	10	6	SUPHdors
Helophoridae					
Helophorus aequalis Thomson, 1868	-	-	3	3	HELOaequ
Helophorus aquaticus (Linné, 1758)	4	-	4	-	HELOaqua
Helophorus flavipes Fabricius, 1792[2]	-	-	-	-	
Helophorus granularis (Linné, 1761)	2	1	4	2	HELOgran
Helophorus griseus Herbst, 1793	-	8	-	1	HELOgris
Helophorus minutus Fabricius, 1775[1]	-	-	-	-	

Species	Activity Traps 2004-2006	Light Trap 2002-2006	Box trap 2004	Net sampling 2006	Species code
Helophorus obscurus Mulsant, 1844[1]	-	1	-	-	HELOobsc
Helophorus strigifrons Thomson, 1868[1]	-	-	-	-	
Hydrochidae					
Hydrochus crenatus (Fabricius, 1792)	-	-	-	1	HYCHcari
Hydrochus megaphallus Berge Henegouwen, 1988	7	-	40	8	HYCHmega
Hydrophilidae					
Anacaena limbata (Fabricius, 1792)	16	47	37	4	ANAClimb
Anacaena lutescens (Stephens, 1829)	134	881	461	129	ANAClute
Berosus frontifoveatus Kuwert, 1888	-	9	-	-	BEROfron
Cercyon bifenestratus Küster, 1851	-	1	-	-	CERCbife
Cercyon convexiusculus Stephens, 1829	11	42	34	6	CERCconv
Cercyon laminatus Sharp, 1873	-	11	-	-	CERClami
Cercyon lateralis (Marsham, 1802)	-	16	-	-	CERClate
Cercyon marinus Thomson, 1853	-	61	-	-	CERCmari
Cercyon quisquilius (Linné, 1761)	-	6	-	-	CERCquis
Cercyon sternalis Sharp, 1918	2	1	1	-	CERCster
Cercyon unipunctatus (Linné, 1758)	-	8	-	-	CERCunip
Coelostoma orbiculare (Fabricius, 1775)	1	4	-	-	COELorbi
Cryptopleurum minutum (Fabricius, 1775)	-	1	-	-	CRYPminu
Cryptopleurum subtile Sharp, 1873 [2]	-	-	-	-	
Cymbiodyta marginella (Fabricius, 1792)	-	38	-	-	CYMBmarg
Enochrus coarctatus (Gredler, 1863)	3	2112	5	-	ENOCcoar
Enochrus quadripunctatus (Herbst, 1797)	-	402	-	1	ENOCquad
Enochrus testaceus (Fabricius, 1801)	-	10	-	-	ENOCtest
Helochares obscurus (O. F. Müller, 1776)	-	1	1	-	HECHobsc

Species	Activity Traps 2004-2006	Light Trap 2002-2006	Box trap 2004	Net sampling 2006	Species code
Hydrobius fuscipes (Linné, 1758)	225	18135	75	67	HYBIfusc
Hydrochara caraboides (Linné, 1758)	1046	4	1	3	HCHAcara
Laccobius bipunctatus (Fabricius, 1775)[1]	-	-	-	-	
Laccobius minutus (Linné, 1758)[1]	-	-	-	-	
Laccobius striatulus (Fabricius, 1801)[1]	-	-	-	-	
Megasternum concinnum (Marsham, 1802)[2]	-	-	-	-	
Hydraenidae					
Hydraena britteni Joy, 1907	-	-	23	-	HDRAbritt
Hydraena melas Dalla Torre, 1877 [1]	-	-	-	-	
Limnebius cf. *truncatellus* (Thunberg, 1794) [2]	-	-	-	-	
Limnebius crinifer Rey, 1885 [1]	-	-	-	-	
Limnebius parvulus (Herbst, 1797) [1]	-	-	-	-	
Ochthebius alpinus (Ienistea, 1979)	-	-	2	-	OCHTalpi
Ochthebius pusillus Stephens, 1835 [1]	-	-	-	-	
Scirtidae					
Cyphon coarctatus Paykull, 1799	-	338	-	-	CYPHcoar
Cyphon laevipennis Tournier, 1868	-	9	-	-	CYPHlaev
Cyphon ochraceus Stephens, 1830	-	1214	-	-	CYPHochr
Cyphon padi (Linné, 1758)	-	858	-	-	CYPHpadi
Cyphon pubescens (Fabricius, 1792)	-	25	-	-	CYPHpube
Cyphon variabilis (Thunberg, 1787)	-	1061	-	-	CYPHvari
Microcara testacea (Linné, 1767)	-	137	-	-	MICRtest
Heteroceridae					
Heterocerus fenestratus (Thunberg, 1784)	-	34	-	-	HETEfene
Heterocerus fusculus Kiesenwetter, 1843	-	12	-	-	HETEfusc
Total number of species	62	55	41	32	
Total number of specimens	23018	29250	1238	407	

[1] species found only by individual collecting in the alder carr or in its near surroundings,

[2] species not collected during my study, but recorded by ČÍŽEK (1999), his record of *Hydroporus brevis* was excluded due to misidentification (Boukal et al. 2007).

B. Larvae

Species	Activity Traps 2004-2006	Box trap 2004	Net sampling 2006	Species code
Dytiscidae				
Acilius canaliculatus (Nicolai, 1822)	629	3	28	ACILcana
Acilius sulcatus (Linné, 1758)	3	-	1	ACILsulc
Agabus affinis (Paykull, 1798)	-	-	1	AGABaffi
Agabus bipustulatus (Linné, 1767)	10	4	-	AGABbipu
Agabus congener (Thunberg, 1794)	25	1	10	AGABcong
Agabus sp.	2	-	-	AGABsp
Agabus sturmi (Gyllenhål, 1808)	-	-	1	AGABstur
Agabus uliginosus (Linné, 1761)	1	3	2	AGABulig
Agabus undulatus (Schrank, 1776)	-	-	1	AGABundu
Agabus unguicularis (Thomson, 1867)	2	4	3	AGABungu
Colymbetes fuscus (Linné, 1758)	5	-	-	COLYfusc
Dytiscus cimcumcinctus Ahrens, 1811	141	-	-	DYTIcirc
Dytiscus marginalis Linné, 1758	560	-	-	DYTImarg
Hydaticus seminiger (De Geer, 1774)	75	-	5	HYDAsemi
Hydroporus incognitus Sharp, 1869	5	3	5	HYPOinco
Hydroporus rufifrons (Duftschmid, 1805)	-	-	1	HYPOrufi
Hydroporus striola Gyllenhål, 1827	-	-	16	HYPOstri
Hydroporus sp.	1	-	4	HYPOsp
Hygrotus decoratus (Gyllenhål, 1810)	-	-	12	HYGRdeco
Hyphydrus ovatus (Linné, 1761)	5	-	1	HYPHovat
Ilybius ater (De Geer, 1774)	19	-	15	ILYBater
Ilybius fuliginosus (Fabricius, 1792)	-	-	5	ILYBfuli
Ilybius guttiger (Gyllenhål, 1808)	6	-	8	ILYBgutt
Ilybius subtilis (Erichson, 1837)	177	2	1	ILYBsubt
Liopterus haemorrhoidalis (Fabricius, 1787)	1	-	-	LIOPhaem
Rhantus exsoletus (Forster, 1771)	-	-	2	RHANexso
Rhantus suturalis (MacLeay, 1825)	1	-	2	RHANsutu
Suphrodytes dorsalis (Fabricius, 1787)	9	1	7	SUPHdors
Hydrophilidae				
Anacaena sp.	-	-	2	ANACsp
Enochrus sp.	-	1	-	ENOCsp
Hydrobius fuscipes (Linné, 1758)	2	24	9	HYBIfusc
Hydrochara caraboides (Linné, 1758)	37	-	-	HCHAcara
Sphaeridiinae gen. sp.	-	-	11	SPHAsp
Scirtidae				
Cyphon sp.	22	338	593	CYPHsp
Microcara testacea (Linné, 1767)	25	48	59	MICRtest
Total number of species	25	12	27	
Total number of specimens	1763	432	805	