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Seasonal changes on two different spatial scales: response of aquatic invertebrates to water body and microhabitat

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Abstract Knowledge about the spatial and temporal scales of both habitat use and the functional significance of different adaptations is essential for an understanding of the population dynamics of invertebrate assemblages. This fundamental knowledge is not only interesting from an academic point of view, but is sorely lacking and needed in the field of restoration ecology. Many species are threatened due to degradation. Knowing what environmental conditions are needed during the life cycle of these species is important in the design of restoration measures which aim to lift existing bottlenecks for threatened species. To assess the relative importance of water type and microhabitat in structuring the invertebrate assemblage during different seasons, invertebrates were sampled in three water bodies differing in trophic level and acidity. Different parts within a water body (microhabitats) were sampled separately and each water body was sampled in all four seasons. Results show that water body is an important factor structuring the invertebrate assemblage early in the season, whereas microhabitat became more important later in the season. Structural complexity of microhabitats was related to the type of locomotion employed by invertebrates. Seasonal differences could be related to population dynamics (reproduction, mortality). Moreover, fluctuations in resource availability were expected to differ between the water bodies, with highest fluctuations in the eutrophic water body and with fluctuations becoming less predictable later in the season. This was confirmed by the data: species synchronization to pulses in food availability was strongest in the eutrophic water body. Moreover, synchronization was strongest in summer, while in autumn waters were invaded by dispersive species. Based on these results a synthesis is presented on the functioning of the different waters during the different seasons.

Key words dispersal, fluctuations in resource availability, food, substrate, synchronization
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Introduction

Freshwater wetlands harbor a high biodiversity. Many wetlands are currently being threatened by habitat reclamation and habitat degradation, including desiccation, eutrophication and acidification. To combat these threats and restore biodiversity, knowledge is necessary on how organisms use their surroundings. In general, individuals of a species need to obtain resources and survive until they have successfully reproduced. To succeed in this task species possess adaptations that increase their chances under specific conditions. In other words when a species is

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present, there is a match between what a species needs and what is supplied by the environment (Verberk & Esselink, 2003). The set of adaptations is called a strategy. According to Southwood (1977) the environment is the template on which these strategies are forged (i.e. the habitat template concept).

Both species' demands and environmental conditions vary in space and time and therefore the match between the two is highly dependent on scale (Levin, 1992). This scale-dependency is one of the main reasons that theoretical predictions based on Southwood's habitat template may fail (Statzner *et al*., 1997). This is especially true for mobile animals, which can use their surroundings on a range of different scales, varying between species and life stages (Beaver, 1977). In addition the relevant scale may be different for an individual compared to a population (Wiens, 1976). Therefore, it is not surprising that incorporating scale has led to improvements in model results and explaining species occurrence. Li *et al.* (2001) showed that linking the occurrence of aquatic invertebrates to environmental factors was scale-dependant. Ritchie and Olff (1999) showed that the relation between productivity and diversity in grazing mammals was predicted more accurately when they incorporated the scale level on which the different species use the landscape. Chase and Leibold (2002) showed that the relation between productivity and diversity in aquatic invertebrates was scale-dependent, having an optimum on the scale of a single catchment, but being linear when different catchments were combined.

To detect the appropriate scale, investigations have to be conducted at different spatial and temporal scales (Sponseller *et al*., 2001, Verberk *et al*., 2002). Research on aquatic invertebrates has strongly focused on the scale of water bodies, describing invertebrate assemblages and creating water typologies (Ranta, 1985; Verdonschot *et al*., 1992). These studies have related presence and abundance of invertebrates to environmental variables that define water bodies as a unit or represent an average value for the whole water body (Fairchild *et al*., 2003). Examples of such variables are site age (Fairchild *et al*. 2000), acidity (Foster, 1995; Verberk *et al*., 2001), surface area (Oertli *et al*., 2002; Ranta, 1985), permanency (Downie *et al*., 1998; Jeffries, 1994; Williams, 1996; Wiggins *et al*., 1980) and salinity (Lancaster & Scudder, 1987). However, water bodies are rarely homogeneous and often consist of different elements. These so-called microhabitats can differ substantially in food availability (Henrikson, 1993), oxygen saturation (Heinis & Crommentuijn, 1992), temperature (Sternberg, 1993), vegetation structure (Henrikson, 1993) and predator and prey abundances. These differences necessitate or enable invertebrates to survive by switching between these microhabitats. Surprisingly little is known about how invertebrates use different microhabitats during their life cycle, as only few studies have focused explicitly on differences between microhabitats (Higler & Verdonschot, 1989; Fairchild *et al*., 2003; Tolkamp, 1980).

Water bodies are not only heterogeneous in space, but also in time. Abiotic conditions fluctuate throughout the season due to litter input and also because temperature fluctuates, influencing for example, mineralization rate, oxygen consumption and primary production. In addition to abiotic fluctuations, shifts occur in biotic interactions as species increase in abundance due to reproduction or change their feeding activity and diet, as they grow larger. To cope with these changes invertebrates can move within a water body (locomotion), move between water bodies (dispersal) and time their lifecycle to coincide with favorable periods (synchronization). Locomotion is expected to be adaptive at the scale of a water body, differentiating between microhabitats. Dispersal and synchronization are strategies, which confer adaptive benefits at larger spatial and temporal scales, respectively. Synchronization is advantageous when it is possible to predict when favorable periods will be present, while dispersal is most advantageous when there are favorable locations present, but it is hard to predict where they will occur (Van Leeuwen, 1966).

The aim of this study was to understand the spatial scale of: (i) habitat use; and (ii) the functional significance of different adaptations; (iii) in relation to seasonal changes. Therefore we investigated invertebrate assemblages on four occasions (every season) in the microhabitats of three water bodies differing in trophic level and acidity. This paper addresses the following questions:

1. What are the differences in invertebrate assemblages between different water bodies?
2. What are the differences in invertebrate assemblages between different microhabitats?
3. Is there a seasonal change in the effect of water body and microhabitat on the invertebrate assemblage?
4. How are these changes related to different adaptations (locomotion, synchronization and mobility)?

Material and methods

Study area and sample locations

All three water bodies sampled were located in the bog remnant Korenburgerveen in the Netherlands (described in detail in Verberk *et al*., 2001). The three sampled water bodies comprised a gradient from acidic-oligotrophic conditions to more alkaline-eutrophic conditions (Table 1). All water bodies had approximately the same age (created

Table 1 Characterization of the aquatic vegetation (on a Tansley scale) and characterization of the physical and chemical conditions of the three sampled water bodies.

Water body		Peat excavation pit	Mesotrophic bombcrater	Eutrophic bombcrater
Trophic status		oligotrophic	mesotrophic	eutrophic
Surface water	Mean alkalinity (mEq) (± S.E.) (*n*=4)	0 ± 0	0.083 ± 0.036	0.540 ± 0.250
	Mean pH (± S.E.) (*n*=7)	3.85 ± 0.13	5.26 ± 0.34	5.84 ± 0.35
Interstitial water	Mean alkalinity (mEq) (± S.E.) (*n*=3)	0.180 ± 0.055	0.350 ± 0.033	0.510 ± 0.068
	Mean pH (± S.E.) (*n*=3)	5.15 ± 0.28	5.84 ± 0.18	5.93 ± 0.35
Area (m^2)		60	80	110
Depth (m)		1−1.5	1−1.5	1−1.5
Vegetation	*Eriophorum angustifolium*	Frequent		
	Sphagnum cuspidatum	Dominant	Occasional	
	Eriophorum vaginatum	Co-dominant	Frequent	Sporadically
	Utricularia minor		Occasional	
	Phragmites australis		Local	Sporadically
	Carex rostrata		Local	Abundant
	Potamogeton natans		Local	Co-dominant
	Typha latifolia			Frequent
	Chara sp.			Frequent
	Juncus effuses			Local

around 1945). The first water body was a former peat excavation pit, with *Sphagnum cuspidatum* and *Molinia caerulea* on the shore (hereafter called oligotrophic). The other two water bodies were bomb craters and at their location, cover sands reach the surface. As a result these water bodies were more alkaline. The meso-eutrophic water body (hereafter called eutrophic) had the highest alkalinity and the water was almost completely covered by floating *Potamogeton natans* with *Typha latifolia* and *Carex rostrata* on the shore. The oligo-mesotrophic water (hereafter called mesotrophic) had a low alkalinity. *Potamogeton natans* occurs locally in the water body and *Eriophorum vaginatum* is abundant on the shores. In both bomb craters *Myrica gale* and *Molinia caerulea* were dominant in the surrounding vegetation.

Invertebrate collection

Invertebrates were collected during four sampling periods, hereafter referred to as winter (February 5, 7 & 12, 2003), spring (April 1−3, 2003), summer (June 25−27, 2003) and autumn (September 12, 15 & 19, 2003). In each water body, different patches were sampled separately. Based on the structure, these samples could be classified into seven different categories of microhabitat (Table 2). Care was taken to sample the vegetation only, without sediment. The shoreline microhabitat is defined as the transition between water and land and was sampled to a maximum depth of 15 cm. The spatial scale characterizing the samples is approximately 1 m^2. Some samples were classified into two different categories of microhabitat, as it was not always possible to classify samples unambiguously. These samples were treated as belonging to both categories for all analyses.

Samples were taken in a semi-quantitive way and were aimed at obtaining a complete list of the invertebrates present. Sample material was collected using a kitchen sieve (mesh size of 1.0 mm) and dip net (mesh size of 0.5 mm). In most categories of microhabitat, both sieve and net were employed, but some microhabitats were always sampled with either the sieve (shoreline) or the net (open water). Samples were sorted in the field using white trays. This enabled the collection of additional material if prior catches had yielded only few animals. Invertebrates smaller than 1 mm are difficult to discern in the field. Therefore differences in species composition as a result of differences in mesh size are expected to be minimal. Sampling effort was kept equal for the different microhabitats at approximately 4 man-hours sorting time, with the exception of open water, for which sampling and sorting took less time (≈ 0.5 h). After this time almost all discernable individuals (> 1 mm) were collected. A full list of the taxa found in this study and their ecology can be found in Appendix 1.

Table 2 Overview of microhabitats sampled in the three water bodies on the four sampling occasions.

		Shoreline	Intricate and complex structure (*Sphagnum*)	Thin emergent vegetation (*Eriophorum*, *Carex*)	Robust emergent vegetation (*Typha*)	Floating vegetation (*Potamogeton*)	Bottom	No structure (open water)	Total
Oligotrophic	Winter	0	1.5	0.5	0	0	1.0	0	3
	Spring	0.5	2.0	0.5	0	0	1.0	1.0	5
	Summer	0.5	2.0	0.5	0	0	1.0†	0	4
	Autumn	0.5	2.0	0.5	0	0	1.0	1.0	5
	Subtotal	1.5	7.5	2.0	0	0	4.0	2.0	17
Mesotrophic	Winter	1.0	0	1.0	0	0	1.0	1.0	4
	Spring	1.0	0.5	1.5	0	1.0	1.0	1.0	6
	Summer	1.0	0	1.0	0	1.0	1.0	1.0	5
	Autumn	1.5	0	0.5	0	1.0	1.0	1.0	5
	Subtotal	4.5	0.5	4.0	0	3.0	4.0	4.0	20
Eutrophic	Winter	1.0	0	1.0	1.0	1.0	1.0	0	5
	Spring	1.0	0	1.0	1.0	1.0	1.0	0	5
	Summer	1.0	0	1.0	1.0	1.0	1.0	0	5
	Autumn	1.5	0	0.5	1.0	1.0	1.0	0	5
	Subtotal	4.5	0	3.5	4.0	4.0	4.0	0	20
	Total	10.5	7.5	9.5	4.0	7.0	12.0	6.5	57

Halves indicate samples were classified in two different types of microhabitat. †no individuals found.

Data analysis

Samples were grouped according to water body and microhabitat. To analyze how well this imposed grouping (either by water body or microhabitat) could discriminate between samples, differing in species composition, we calculated the distance between sample pairs for all possible combinations. Next, the degree of isolation was calculated by dividing the average distance between samples of *different* groups (water body or microhabitat) by the average distance between samples of the *same* group. If the grouping discriminated well between samples, distances between pairs of samples will be smaller when both samples are from the same group compared to the distance when both samples are from a different group, resulting in a high degree of isolation.

To calculate distances between samples reflecting differences in species composition, a correspondence analysis (CA) was performed using Canoco for Windows Version 4.0 (Ter Braak & Smilauer, 1998) on Preston-transformed (Preston, 1962) invertebrate abundance data of all 57 samples. Ordination scores on the first four axes (reflecting the most apparent differences in species composition) were used to calculate the distances using the formula of Pythagoras (eq. 1). Axis scores were multiplied by their eigenvalues to make the axes proportional to the amount of variation explained by that axis.

$$D_{\text{X-Y}} = \text{Square Root } \{[E1*(A1_{\text{X}}-A1_{\text{Y}})]^2+[E2*(A2_{\text{X}}-A2_{\text{Y}})]^2 +[E3*(A3_{\text{X}}-A3_{\text{Y}})]^2+[E4*(A4_{\text{X}}-A4_{\text{Y}})]^2 \}, \qquad (1)$$

with: $D_{\text{X-Y}}$ = Distance between sample X and Y; Ei = Eigenvalue of axis i; Ai_{X} = Score of sample X on axis *i*.

The degree of isolation was calculated for all data combined as well as for each season separately. To assess whether the grouping of samples (according to water body or microhabitat) discriminated well between samples (high degree of isolation), we tested against the null-hypothesis that there was no difference in average distances (within and between groups), using a student *t*-test. The number of possible combinations between sample pairs increases with the number of samples (# pairs = [(#samples) * (#samples - 1)]/2). The calculation of *P*-values was based on a number of degrees of freedom equal to the number of samples minus 1.

Species turnover was investigated by classifying species as new (not found in previous season), lost (found in previous season only) or remaining (found both seasons). Species were thus classified for spring, summer and autumn (but not winter, as no data on the previous season was collected).

To analyze species synchronization, for each season, species were categorized as synchronizing or non-synchronizing. Species were categorized using a range of ecological literature as well as best professional judgment. Larvae and adults were categorized separately for those species of Hemiptera and Coleoptera, which were aquatic both as larvae and adults. Species were categorized as synchronizing species if their occurrence depends on the time of the year (being specifically present or absent in one or two seasons). Species without synchronization or for those where information was lacking were assigned as non-synchronizing, because synchronization is seen as a specialization from the norm.

To analyze the relation between microhabitat use and species locomotion, species were assigned to different types of locomotion (swimmer, clinger, burrower, crawler & skater), using the literature (Verdonschot, 1990) and best professional judgment.

To analyze seasonal changes in dispersing individuals (aerial mobility), species were classified as non-dispersive (0), dispersive (1) or highly dispersive (2) using a range of literature. Species dispersal ability was coded for each season separately, as many species have adult stages (with flight capability) restricted to certain seasons. Species for which data was lacking, but are known to have adults expected to fly (dipterans, aquatic beetles) were coded as dispersive (1). A dispersal index (eq. 2) was calculated, ranging between 0−1, weighted for the different classes (0, 1, 2):

$$\text{Dispersal index} = (N1+N2*2) / (N0+N1+N2*2), \quad (2)$$

with N0 = Number of species classified as non-dispersive (0); N1 = Number of species classified as dispersive (1); N2 = Number of species classified as highly dispersive (2).

The dispersal index reflects the degree of dispersal within the assemblage, with higher values indicating more dispersing individuals (1 & 2) or more highly dispersive individuals (2). The dispersal index was calculated separately for the different species groups (new, lost and remaining) and averaged over the different seasons.

Results

The three different water bodies were clearly separated on the second and third ordination axes (Fig. 1, Table 3).

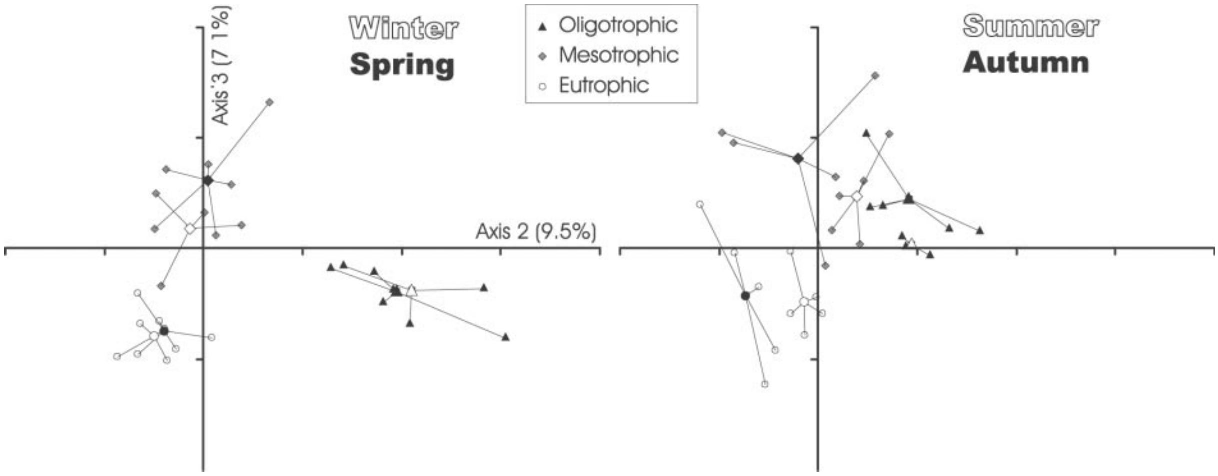

Fig .1 Ordination plot (CA) showing differences in invertebrate assemblages between the different water bodies for the different seasons. Axes 2 and 3 are shown, including the amount of variation explained by them (axis 1 explained 11.4 % of the variation). All samples belonging to the same water body and season are connected to their centroid. Open centroid: winter and summer. Filled centroids: spring and autumn. For reasons of clarity, winter and spring are shown separately (left) from summer and autumn (right).

Table 3 Average distances in the ordination space between samples from the same and from different water bodies and their calculated isolation value.

	Winter	Spring	Summer	Autumn	All seasons
Average distance within the same water body(± S.E.)	0.4950 ± 0.0757 (*n*=12, #pairs=19)	0.5660 ± 0.0979 (*n*=16, #pairs=35)	0.3981 ± 0.0706 (*n*=13, #pairs=23)	0.7691 ± 0.1275 (*n*=15, #pairs=30)	0.6080 ± 0.0473 (*n*=56, #pairs=500)
Average distance between water bodies(± S.E.)	0.9826 ± 0.1253 (*n*=12, #pairs=47)	1.1150 ± 0.1189 (*n*=16, #pairs=85)	0.7493 ± 0.0899 (*n*=13, #pairs=53)	0.9230 ± 0.0976 (*n*=15, #pairs=75)	0.9760 ± 0.0497 (*n*=56, #pairs=1040)
Isolation	1.985***	1.970***	1.882***	1.200	1.606***

Number of samples (n) and the number of possible combinations (#pairs) are indicated between brackets. Significant differences between distances of both groups are indicated as: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; NS, $P > 0.05$.

Isolation values decreased later in the season, becoming non-significant in autumn, indicating that differences between water bodies became less important in structuring the invertebrate assemblage in autumn.

Conversely, the different microhabitats showed high overlap in invertebrate assemblages (Fig. 2, Table 4). Nevertheless, a gradient could be distinguished from structurally complex microhabitats (shore, *Sphagnum*; left) to structurally simple microhabitats (bottom, open water; right). In contrast to the results for the water bodies, isolation values increased in autumn, indicating microhabitat became more important in autumn in structuring the invertebrate assemblage.

Species locomotion was related to microhabitat use (Fig. 3). Species with high-speed locomotion were mainly found in structurally simple microhabitats (e.g. swimmers), whereas species with low speed locomotion (e.g. crawlers) were mainly found in structurally complex microhabitats (*Sphagnum*, thin emergent vegetation). Burrowers reached highest numbers in the bottom samples and *Sphagnum* vegetation. Skaters were always found in low numbers and seemed to be restricted to sheltered/vegetated surface parts of the water body and were rarely found (or observed) at the surface of the open water. Structurally simple habitats (bottom, open water) had lowest numbers of clingers.

Total number of species (Fig. 4) as well as number of

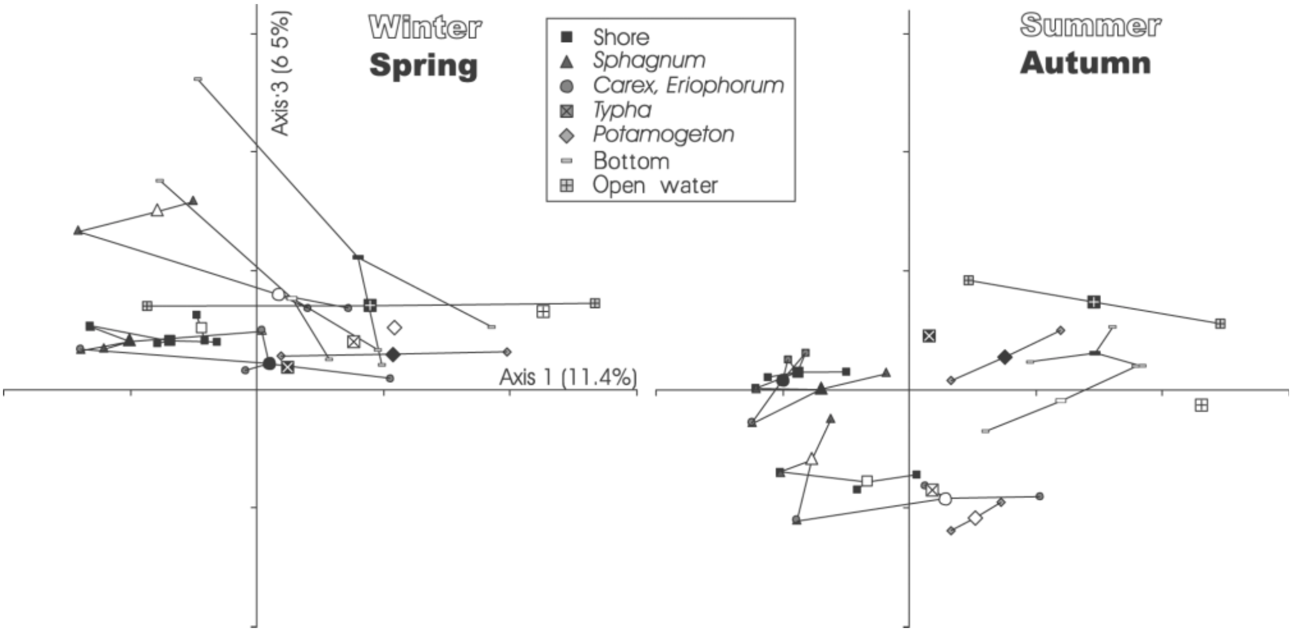

Fig. 2 Ordination plot (CA) showing differences in invertebrate assemblages between microhabitats and seasons. Axes 1 and 3 are shown, including the amount of variation explained by them. All samples belonging to the same microhabitat and season are connected to their centroid. Open centroid: winter and summer. Filled centroids: spring and autumn. For reasons of clarity, winter and spring are shown separately (left) from summer and autumn (right).

Table 4 Average distances in the ordination space between samples from the same and from different microhabitats and their calculated isolation value.

	Winter	Spring	Summer	Autumn	All seasons
Average distance within the same water body(± S.E.)	0.8430 ± 0.01412 (*n*=12, #pairs=8)	0.8630 ± 0.1390 (*n*=16, #pairs=19)	0.4840 ± 0.0730 (*n*=13, #pairs=11)	0.5130 ± 0.0790 (*n*=15, #pairs=20)	0.6660 ± 0.0510 (*n*=56, #pairs=305)
Average distance between water bodies(± S.E.)	0.8420 ± 0.1293 (*n*=12, #pairs=58)	0.9720 ± 0.1330 (*n*=16, #pairs=101)	0.6720 ± 0.0980 (*n*=13, #pairs=67)	0.9650 ± 0.0990 (*n*=15, #pairs=85)	0.9032 ± 0.0530 (*n*=56, #pairs=1235)
Isolation	0.9999	1.1257	1.3887	1.8802***	1.3574***

Number of samples (n) and the number of possible combinations (#pairs) are indicated between brackets. Significant differences between distances of both groups are indicated as: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$; NS, $P > 0.05$.

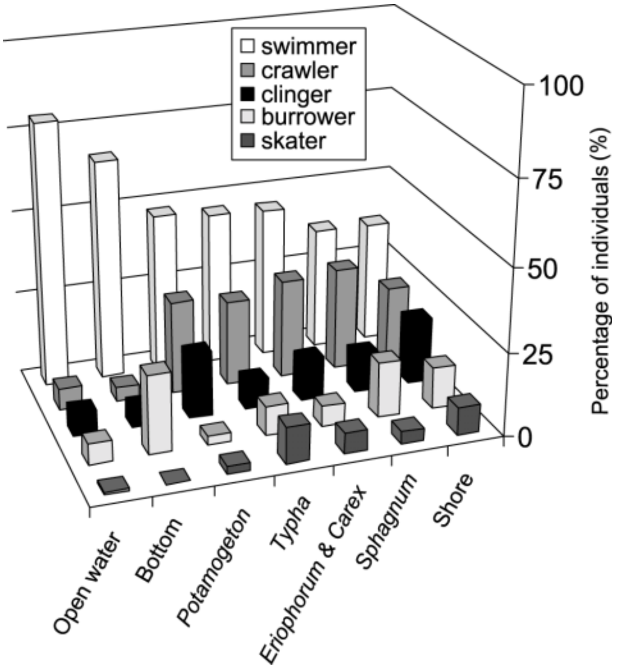

Fig. 3 Percentage of individuals with different types of locomotion in the different microhabitats. Percentages are averaged over the four seasons.

individuals (data not shown) was highest in autumn. Species turnover (lost and new species) was highest and increased strongest during summer and autumn in the mesotrophic and eutrophic water bodies. In contrast, species turnover remained constant in the oligotrophic water body. New species in summer were mainly synchronizing (Fig. 5), and consisted mainly of larval stages of Odonata known to have a synchronized lifecycle (*Lestes* sp, *Sympetrum* sp), nymphs of Hemiptera (Corixidae, Nepidae and several families of Gerromorpha) and larvae of Coleoptera (predominantly Dytiscidae). The increase of new, synchronizing species was strongest in the eutrophic water body, followed by the mesotrophic water body and was lowest in the oligotrophic water body.

Species capable of dispersal increased, being most abundant in summer and autumn and least abundant in winter, as shown by the dispersal index (Fig. 6). When looking at the dispersal capacity of remaining, new and lost species separately, it is clear that many remaining species become mobile in summer and autumn (emergence to adult stage). New species are usually also dispersive species ($\geqslant 50\%$) and this was especially true in autumn, when this group harbored most dispersive species. This indicates that in autumn, there is an invasion of dispersive species, including a number of highly dispersive species, such as *Corixa punctata*, *Hydroporus planus* and *Agabus bipustulatus*.

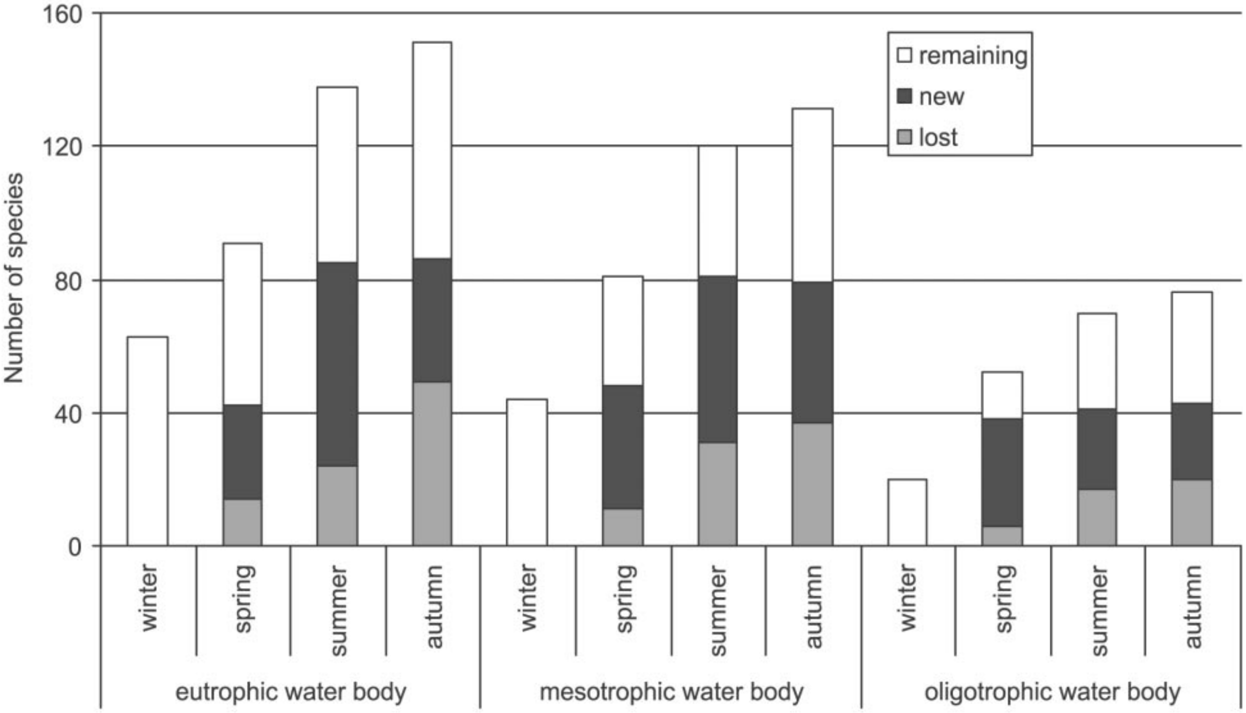

Fig .4 Number of lost (found in previous season only), new (not found in previous season) and remaining species (found in both seasons) in the three water bodies during spring, summer and autumn.

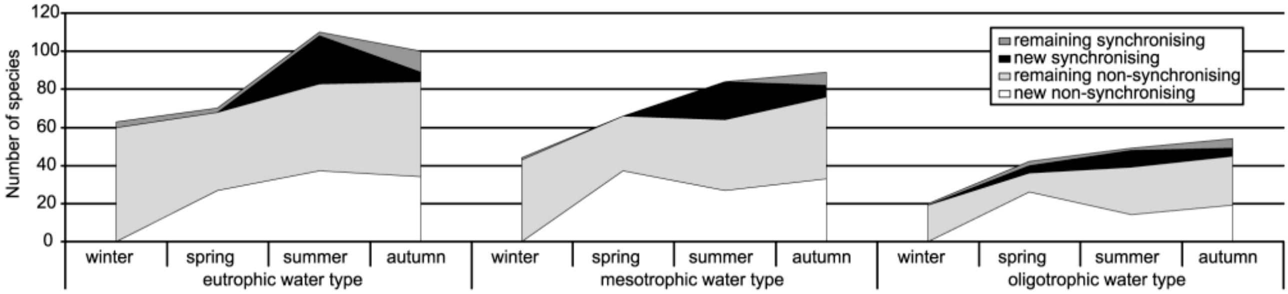

Fig. 5 Number of new (not found in previous season) and remaining (found both seasons) species whose occurrence is either synchronized or non-synchronized.

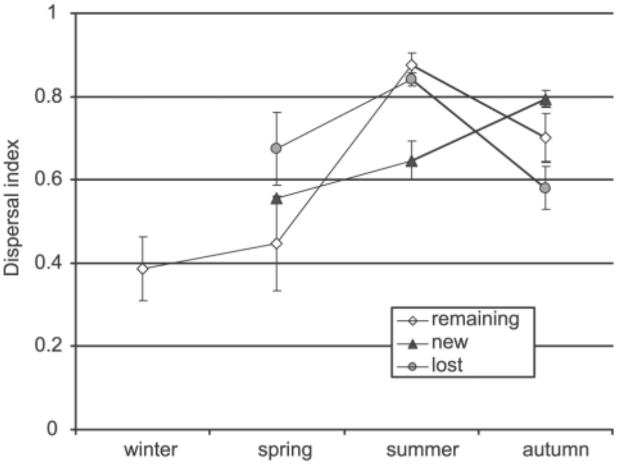

Fig. 6 Dispersal index (± S.E.) of lost (found in previous season only), new (not found in previous season) and remaining species (found in both seasons) during the different seasons (averaged over the different water bodies).

Discussion

Importance of microhabitat and water body in structuring invertebrate assemblages

This study shows that differences in invertebrate assemblages were related to both spatial scales: microhabitat and water body. Invertebrate similarity between microhabitats was higher compared to invertebrate similarity between water bodies. This would indicate that differences between water bodies are more stringent than those between microhabitats. However, four issues need to be considered here: i) There were more categories of microhabitats (seven), compared to water bodies (three), which will inevitably lead to a more gradual description of the variation in species composition; ii) Species exchange between different microhabitats is expected to occur much more frequent than exchange between water bodies; iii) Different types of microhabitat overlapped to some extent, which is partly reflected in samples being categorized in two different types of microhabitat; iv) Different developmental stages were lumped together (except for species with both aquatic larval and adult stages such as species of Hemiptera and Coleoptera). This precludes finding migration to a different microhabitat during the development. For example, final developmental stages of damselflies migrate to the shore for ecdysis (Sternberg, 1999) and evidence for this was also found in this study (data not shown). Also, substrate preference of species may differ seasonally or between different development stages, as was found in lowland streams (Tolkamp, 1980).

Taking the above-mentioned issues into account, differences between microhabitats are expected to be more important than indicated by the results. Furthermore, microhabitats became more important in structuring the invertebrate assemblage later in the season, while differences between the water bodies became less important. Differences between invertebrate assemblages of the different water bodies could be attributed to species known to occur under different environmental conditions such as pH (Verberk *et al*., 2001) and trophic conditions (Verdonschot *et al*., 1992). However, understanding these differences is another matter. The different adaptations (locomotion, synchronization and dispersal) studied here, were related to the differences between water bodies and between microhabitats and seasonal changes therein.

Locomotion

Despite high overlap in invertebrate assemblages between different microhabitats, there was a strong relation between the structural complexity of microhabitats and the locomotion of animals. The locomotion of a species is the combined effect of morphological and behavioral adaptations, which apparently reflects a functional significance on the scale of microhabitats. Assuming a general trade-off between maneuverability and locomotion speed (Ribera & Nilsson, 1995), we can understand species adapted to complex microhabitats will be vulnerable in simple microhabitats (e.g., suffer from predation due to low speed). Conversely, species adapted to high-speed locomotion will be unable to exploit structurally complex microhabitats. This provides an explanation to the distinct invertebrate assemblages in the different microhabitats in autumn: With increasing densities, species interactions are expected to become more intense, thereby increasing the importance of structural differences to evade for example, predators and competitors.

Higler and Verdonschot (1989) also found a relationship between the structural complexity of the microhabitat (termed ‘mesh size’ in their paper) and the species composition. Heino (2000) found habitat structure to be more important than water chemistry in structuring the invertebrate community. In lowland streams, Tolkamp (1980) found invertebrates distinctly preferred a specific substrate and he concluded that the small-scale spatial variation in substrate composition of the streambed is essential for the existence of many stream invertebrate species.

Synchronization

Synchronization is an advantageous adaptation when: (i) there are temporal fluctuations in resource availability (e.g., food); and (ii) these fluctuations are predictable. Food availability was different for the three water bodies as differences in invertebrate assemblages between them could be related to diet (data not shown), with relative carnivore abundance and carnivore species richness decreasing from the oligotrophic to eutrophic water body, which is in agreement with other studies (Leuven *et al*., 1986; Verberk *et al*., 2002).

The number of synchronizing species was low in the oligotrophic water body (Fig. 5). Oligotrophic, acidic conditions present an extreme environment with few possibilities of existence for species. Acidic conditions inhibit decomposition by micro-organisms (Kok & van de Laar, 1991; Leuven & Wolfs, 1988; Roelofs, 1991) and low nutrient conditions inhibit production by algae and higher plants (Lamers *et al*., 1998). Therefore, food availability is low, but constant (Moller Pillot & Buskens, 1990). Under these conditions growth is slow, as species invest much energy in tolerating acidic conditions and in structures hard to decompose; they build to last; for example incorporation of lignin and tannin in plants and mosses or the high abundance of large-bodied species in insects (Leuven *et al*., 1986).

In contrast, under more eutrophic, alkaline conditions, where acid formation due to decomposition is buffered, processes such as decomposition and production can progress much more rapidly. Indeed, as lakes become more eutrophic, the ratio between dissolved organic carbon and particulate organic carbon fluctuated greatly with season (and depth), caused by intensive algal and bacterial growth (Wetzel, 2001). Temporal fluctuations in food availability such as detritus and algae, but also—with some time lag—secondary production are therefore expected to be more pronounced under these conditions. Results show species turnover was higher in the mesotrophic and eutrophic water body compared to the oligotrophic water (Fig. 4). Especially in the (early) summer many species showed synchronization (Fig. 5). In spring and early summer when the temperature rises, decomposition is initiated again after a long and stable period of minimal microbial activity due to low water temperature. This gives rise to a predictable pulse of food availability early in the year, resulting in favorable conditions for growth. Later in the season, however, temporal fluctuations in food availability are expected to become less predictable.

Dispersal

Dispersal is an advantageous adaptation when there are large-scale spatial differences in resource availability. This adaptation holds an advantage over synchronisation when the location of these different places is unpredictable. Under synchronization, it was already argued that fluctuations in food availability would be most predictable early in the year. From the results of this study several other arguments make it likely that autumn poses a less predictable set of environmental circumstances for invertebrates. Environmental circumstances and fluctuations therein are not limited to decomposition and production. Interactions with other invertebrates make up an essential part (Nemjo, 1990).

Highest numbers of invertebrates were found in autumn, following the (synchronized) reproduction of many species in summer. The situation in autumn therefore depends on success and failure of species reproduction, which is very unpredictable, depending on occurrences of summer droughts, temperatures and colonization of competitors and predators (Moller Pillot, 2003).

Lowest numbers of invertebrates were found in winter. One reason for this could be that winter mortality due to for example food shortage, cold and predation is no longer compensated for by reproduction. An alternative explanation for finding low numbers in winter samples could be that many individuals were not recorded. Species can overwinter on land, be present as minute larvae or even eggs, or migrate to deeper parts of the water, burrowing in the sediment. Either one of these explanations (mortality or migration to over-wintering places in deep water or outside the water) or a combination would explain the lower invertebrate numbers during winter. Low invertebrate numbers means empty space and therefore the conditions at the start of the year are comparable, providing all individuals a new opportunity to colonize the vacant microhabitats. As a result, winter may act as a reset-button, with predictable conditions early in the year (low densities of potential competitors, predators, etc.). Autumn is the most unpredictable season, because at this time, the most time has passed since the ecosystem has been reset. Indeed in autumn, dispersive species invaded the sampled water bodies (categorized as new species). Many of these species were dispersive aquatic beetles which accounted for > 75% of the total number of individuals in some microhabitats (Verberk & Esselink, 2005).

Matching organism and environment

For an invertebrate to successfully complete its lifecycle, environmental prerequisites posed at different life stages have to be met at the right time and have to be within reach. To cope with discontinuities in resource availability and inter-specific interactions, species have different adaptations whose function is scale-dependent in space (e.g., small scale: swimming hairs; large scale: flight muscles) and time (e.g., small scale: quiescence; large scale: diapause). Unraveling the function of these adaptations is of vital importance for understanding and predicting effects of environmental changes on invertebrate assemblages. This fundamental knowledge is not only interesting from an academic point of view, but is sorely lacking and needed in the field of restoration ecology (van Duinen *et al*., 2003).

From the results of this study a general pattern of seasonal changes is emerging: Synchronization has adaptive value when there are predictable pulses in resource availability. Pulses occur mainly in more alkaline waters and these pulses are more easily predictable early in the season (spring, summer). In spring, most species migrate to different microhabitats from their over-wintering places to prepare for reproduction (ecdysis, oviposition). During summer, larval offspring is found and growth takes place. Following the reproduction in summer, highest densities of species are found in autumn. As a result, selection for the best structures is most intense and thus the different microhabitats harbor distinct invertebrate assemblages. Autumn is also the most unpredictable season with respect to food availability and the occurrence of predators and competitors, benefiting species adapted to dispersal because they can use the available resources opportunistically. In addition, this will lead to a high mixing of species, decreasing beta-diversity and resulting in an increased overlap of species between the different water bodies (Fig. 1). Winter may act as a reset-button, due to mortality, dispersal to over-wintering places or a combination of both. In a study on dispersing diving beetles (Dytiscidae), Lundkvist *et al*. (2002) observed two peaks in dispersal with females being more common in the first period (April−July) than during the second period (August−October), supporting the idea postulated here of directed migration in spring-summer for reproduction and opportunistic dispersal in autumn.

Knowledge on the function of adaptations is important for identifying bottlenecks in the lifecycle of species: Which different conditions are needed during the lifecycle of a species? What adaptations do species have to cope with the opportunities and restrictions of their environment? If species are no longer able to complete their life cycle, what changes have caused this? This knowledge can be applied in the design of restoration measures in order to lift existing bottlenecks for threatened species.

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Appendix 1 List of all taxa captured. For each taxa information is listed on both their biology (locomotion, synchronization and dispersal capability) and their occurrence (distribution of the individuals over the different water bodies, seasons and microhabitats). Occurence of larvae/nymphs is marked with "lr".

Taxon	Locomotion					Synchronisation					Mobility				Total numbers	Watertype (%)			Season (%)				Microhabitat (%)						
	swimmer	clinger	burrower	crawler	skater	spring	summer	autumn	winter	no/unknown	spring	summer	autumn	winter		oligotrophic	mesotrophic	eutrophic	winter	spring	summer	autumn	shore	intricate and complex structure (*Sphagnum*)	thin emergent vegetation (*eriophorum*, *Carex*)	robust emergent vegetation (*Typha*)	floating vegetation (*potamogeton*)	bottom	no structure (open water)
Hydroida																													
Hydra sp.	0	1	0	0	0	0	0	0	0	1	0	0	0	0	7	0	100	0	0	0	0	100	0	0	0	0	100	0	0
Tricladida																													
Polycelis cf tenuis	0	1	0	0	0	1	0	0	0	0	0	0	0	0	109	90	0	10	11	82	5	3	21	53	5	1	0	0	21
Mollusca	0	0.5	0.5	0	0	0	0	0	0	1	0	0	0	0	912	0	0	100	28	23	26	23	57	0	22	9	8	4	0
Hirudinea																													
Erpobdella sp	0	1	0	0	0	0	0	0	0	1	0	0	0	0	23	0	0	100	13	4	39	43	37	0	15	48	0	0	0
Oligochaeta	0.5	0	0.5	0	0	0	0	0	0	1	0	0	0	0	190	0	89	11	3	34	0	63	13	16	28	7	3	31	1
Aranea																													
Argyroneta aquatica	0	0	0	1	0	0	0	0	0	1	0	0	0	0	254	57	26	17	9	42	35	15	30	42	15	3	6	0	4
Hydrachnellae	1.0	0	0	0	0	0	0	0	0	1	1	1	1	0	502	2	23	75	5	20	34	42	8	1	26	24	37	3	0
Crustacea																													
Asellus aquaticus	0	0	0	1	0	1	1	0	0	0	0	0	0	0	101	0	1	99	36	5	39	21	43	0	28	23	4	1	1
Odonata																													
Zygoptera																													
Lestes sponsa	0.5	0	0	0.5	0	0	1	0	0	0	0	2	0	0	3	0	100	0	0	0	100	0	0	0	100	0	0	0	0
Lestes viridis	0.5	0	0	0.5	0	0	1	0	0	0	0	2	0	0	109	0	80	20	0	0	100	0	6	0	54	4	35	1	0
Ischnura elegans	0	0	0	1	0	0	0	0	0	1	0	2	2	0	3	0	0	100	0	0	100	0	0	0	100	0	0	0	0
Pyrrhosoma nymphula	0	0	0	1	0	0	0	0	0	1	1	2	0	0	59	25	14	61	3	19	14	64	60	12	24	0	0	0	4
Enallagma cyathigerum	0	0	0	1	0	0	0	0	0	1	0	2	2	0	50	0	56	44	0	0	98	2	0	0	4	6	88	0	2
Coenagrion hastulatum	0	0.5	0	0.5	0	0	0	0	0	1	0	1	0	0	49	0	37	63	45	18	0	37	15	0	23	16	45	0	0
Coenagrion lunulatum	0	0.5	0	0.5	0	0	0	0	0	1	0	1	0	0	1	0	0	100	0	0	0	100	0	0	0	0	100	0	0
Coenagrion puella/pulchellum	0	0.5	0	0.5	0	0	0	0	0	1	0	1	0	0	881	1	8	92	30	28	1	41	8	0	29	13	49	1	0
Ceriagrion tenellum	0	0.5	0	0.5	0	0	0	0	0	1	0	1	0	0	84	81	15	4	0	8	37	55	13	43	5	0	15	0	23
Anisoptera																													
Aeshna cyanea	0	0.5	0	0.5	0	0	0	0	0	1	0	2	2	0	2	0	100	0	0	0	100	0	0	0	100	0	0	0	0
Aeshna juncea	0	0.5	0	0.5	0	0	0	0	0	1	0	2	0	0	1	0	100	0	0	0	100	0	0	0	100	0	0	0	0
Cordulia aenea	0	0	0	1	0	0	0	0	0	1	0	2	0	0	15	0	73	27	33	0	53	13	7	0	33	13	7	40	0

(to be continued)

(continued)

Libellula sp	0	0	0.5	0.5	0	0	0	0	0	1	0	2	2	0	22	55	32	14	5	9	73	14	18	39	30	5	0	9	0
Sympetrum sp	0	0	0	1	0	0	1	0	0	0	0	2	2	0	6	33	67	0	0	0	100	0	17	17	50	0	0	17	0
Leucorrhinia dubia	0	0	0	1	0	0	0	0	0	1	1	1	0	0	24	88	8	4	4	13	58	25	4	79	4	4	0	4	4
Leucorrhinia rubicunda	0	0	0	1	0	0	0	0	0	1	1	1	0	0	38	84	11	5	16	21	39	24	14	64	1	3	3	8	7
Ephemeroptera	0.5	0	0	0.5	0	1	1	0	0	0	1	1	1	0	1879	0	2	97	30	18	16	36	4	0	20	34	41	2	0
Plecoptera	0.5	0	0	0.5	0	0	0	0	1	0	0	1	1	0	4	0	0	100	50	50	0	0	25	0	50	25	0	0	0
Hemiptera																													
Nepomorpha																													
Corixa punctata	0.5	0.5	0	0	0	0	0	0	0	1	2	2	2	2	5	60	40	0	0	0	0	100	0	20	0	0	40	0	40
Corixa sp lr	0.5	0.5	0	0	0	0	1	0	0	0	0	0	0	0	1	0	100	0	0	0	100	0	0	0	0	0	100	0	0
Hesperocorixa castanea	0.5	0.5	0	0	0	0	0	0	0	1	2	2	2	2	126	0	69	31	32	23	35	10	54	0	28	0	17	1	0
Hesperocorixa castanea lr	0.5	0.5	0	0	0	0	1	0	0	0	0	0	0	0	139	0	84	16	0	0	100	0	61	0	24	1	14	0	0
Hesperocorixa linnei	0.5	0.5	0	0	0	0	0	0	0	1	2	2	2	2	1	0	0	100	0	0	0	100	0	0	0	100	0	0	0
Hesperocorixa linnei lr	0.5	0.5	0	0	0	1	1	0	0	0	0	0	0	0	7	0	71	29	0	0	100	0	29	0	43	0	29	0	0
Hesperocorixa sahlbergi	0.5	0.5	0	0	0	0	0	0	0	1	2	2	2	2	52	46	21	33	21	6	19	54	5	40	7	17	13	13	4
Hesperocorixa sahlbergi lr	0.5	0.5	0	0	0	1	1	0	0	0	0	0	0	0	6	0	100	0	0	0	100	0	33	0	0	0	0	67	0
Sigara sp	0.5	0.5	0	0	0	0	0	0	0	1	2	2	2	2	5	20	80	0	20	20	60	0	20	20	0	0	20	40	0
Sigara sp lr	0.5	0.5	0	0	0	1	1	0	0	0	0	0	0	0	27	0	78	22	0	0	100	0	48	0	41	0	7	4	0
Ilyocoris cimicoides	1	0	0	0	0	0	0	0	0	1	0	0	0	0	18	39	0	61	0	39	6	56	6	22	3	0	61	0	8
Ilyocoris cimicoides lr	1	0	0	0	0	0	1	0	0	0	0	0	0	0	86	45	10	44	0	0	100	0	16	30	23	9	20	1	0
Nepa cinerea	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3	0	100	0	0	67	0	33	33	33	33	0	0	0	0
Nepa cinerea lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	4	0	50	50	0	0	100	0	100	0	0	0	0	0	0
Ranatra linearis	0	1	0	0	0	0	0	0	0	1	1	1	1	1	3	0	0	100	0	0	100	0	0	0	0	67	0	33	0
Plea minutissima	1	0	0	0	0	0	0	0	0	1	0	0	0	0	19	5	42	53	16	26	21	37	47	3	13	5	32	0	0
Plea minutissima lr	1	0	0	0	0	0	1	0	0	0	0	0	0	0	6	0	67	33	0	0	100	0	0	0	17	0	83	0	0
Notonecta glauca	1	0	0	0	0	0	0	0	0	1	2	2	2	2	22	9	73	18	9	9	0	82	0	5	5	14	64	5	9
Notonecta obliqua	0.5	0.5	0	0	0	0	0	0	0	1	2	2	2	2	12	0	92	8	33	33	8	25	25	0	17	8	25	25	0
Notonecta sp lr	1	0	0	0	0	0	1	0	0	0	0	0	0	0	33	0	48	52	0	0	100	0	18	0	18	30	9	0	24
Gerromorpha																													
Hydrometra gracilenta	0	0	0	0	1	0	0	0	0	1	0	0	0	0	26	4	27	69	0	12	15	73	52	4	29	15	0	0	0
Hydrometra sp lr	0	0	0	0	1	0	1	1	0	0	0	0	0	0	12	0	8	92	0	0	100	0	17	0	58	25	0	0	0
Hebrus pusillus	0	0	0	0	1	0	0	0	0	1	2	2	2	2	1	0	0	100	0	0	0	100	50	0	50	0	0	0	0
Hebrus ruficeps	0	0	0	0	1	0	0	0	0	1	1	1	1	1	3	67	0	33	0	0	33	67	50	33	17	0	0	0	0
Microvelia reticulata	0	0	0	0	1	0	0	0	0	1	1	1	1	1	587	14	41	45	3	21	29	47	41	9	32	13	4	0	1
Microvelia reticulata lr	0	0	0	0	1	0	1	1	0	0	0	0	0	0	203	11	27	63	0	0	88	12	16	7	21	40	14	0	2
Microvelia buenoi	0	0	0	0	1	0	0	0	0	1	0	0	0	0	8	0	0	100	13	88	0	0	100	0	0	0	0	0	0
Microvelia umbricola	0	0	0	0	1	0	0	0	0	1	0	0	0	0	33	9	39	52	0	0	58	42	85	5	11	0	0	0	0
Microvelia umbricola lr	0	0	0	0	1	0	1	1	0	0	0	0	0	0	48	0	6	94	0	0	100	0	88	0	0	13	0	0	0
Gerris argentatus	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	0	0	100	0	0	100	0	0	0	0	100	0	0	0
Gerris lacustris	0	0	0	0	1	0	1	1	0	0	2	1	2	2	1	100	0	0	0	100	0	0	0	100	0	0	0	0	0
Gerris lateralis	0	0	0	0	1	0	1	1	0	0	2	1	2	2	1	0	100	0	100	0	0	0	0	0	100	0	0	0	0

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Gerris odontogaster	0	0	0	0	1	1	1	1	0	0	2	0	2	2	8	75	13	13	0	0	100	0	31	38	6	13	13	0	0
Megaloptera	0	0	0	1	0	0	0	0	0	0	1	1	0	0	23	0	96	4	4	0	65	30	20	0	50	0	0	30	0
Coleoptera																													
Haliplidae																													
Peltodytes caesus	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	100	0	100	0	0	0	0	0	100	0	0	0
Haliplus cf ruficollis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	13	0	31	69	23	15	38	23	35	0	50	8	8	0	0
Haliplus gr ruficollis lr	0	0	0	1	0	0	1	1	0	0	1	1	1	1	1	0	0	100	0	0	0	100	50	0	50	0	0	0	0
Haliplus confines	1	0	0	0	0	0	0	0	0	1	1	1	1	1	7	0	0	100	14	14	43	29	21	0	7	57	0	14	0
Haliplus confines lr	0	0	0	1	0	0	1	1	0	0	1	1	1	1	3	0	0	100	33	0	33	33	17	0	50	0	0	33	0
Noteridae																													
Noterus clavicornis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	21	0	100	0	5	29	14	52	60	10	31	0	0	0	0
Noterus crassicornis	1	0	0	0	0	0	0	0	0	1	0	0	0	0	105	20	5	75	4	35	20	41	40	11	32	4	10	0	3
Dytiscidae																													
Laccophilus minutus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	11	18	36	45	9	0	0	91	68	9	23	0	0	0	0
Hyphydrus ovatus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	0	100	50	25	25	0	0	0	50	25	0	25	0
Hyphydrus ovatus lr	0.5	0	0	0.5	0	0	1	0	0	0	0	0	0	0	33	0	0	100	0	0	100	0	21	0	39	18	18	3	0
Hydroglyphus pusillus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	24	46	21	33	0	0	21	79	35	27	19	8	4	0	6
Bidessus cf grossepunctatus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	3	0	100	0	0	33	33	33	67	17	17	0	0	0	0
Hygrotus impressopunctatus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	4	50	0	50	0	0	50	50	13	25	0	0	50	0	13
Hygrotus decoratus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	214	2	19	79	0	1	3	95	62	1	36	0	0	0	0
Hygrotus decoratus lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	3	67	33	0	0	0	100	0	67	33	0	0	0	0	0
Hygrotus inaequalis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	25	8	60	32	16	12	16	56	56	8	28	4	4	0	0
Hygrotus inaequalis lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	17	76	0	24	0	0	100	0	56	38	0	6	0	0	0
Hydroporus angustatus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	181	1	49	50	3	17	3	77	68	2	29	0	1	0	1
Hydroporus erythrocephalus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	79	57	11	32	9	20	25	46	38	37	12	1	5	0	6
Hydroporus gyllenhalii	1	0	0	0	0	0	0	0	0	1	1	1	1	1	9	33	22	44	44	44	0	11	78	17	6	0	0	0	0
Hydroporus neglectus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	8	75	13	13	25	13	0	63	38	38	13	0	0	0	13
Hydroporus obscurus	1	0	0	0	0	0	0	0	0	1	0	0	0	0	59	58	14	29	0	25	54	20	27	36	25	0	5	0	8
Hydroporus palustris	1	0	0	0	0	0	0	0	0	1	1	1	1	1	6	0	33	67	17	0	0	83	67	0	33	0	0	0	0
Hydroporus planus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	1	100	0	0	0	0	0	100	0	50	50	0	0	0	0
Hydroporus scalesianus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	34	47	35	18	0	0	3	97	43	24	25	0	0	0	9
Hydroporus tristis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	86	48	9	43	9	17	2	71	40	24	23	0	0	0	13
Hydroporus umbrosus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	192	38	42	21	1	34	12	53	54	25	18	1	0	0	2
Hydroporus sp lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	3	100	0	0	0	0	67	33	33	50	0	0	0	0	17
Porhydrus lineatus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	6	0	0	100	50	0	17	33	50	0	0	17	33	0	0
Porhydrus lineatus lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	9	0	0	100	0	0	100	0	78	0	22	0	0	0	0
Graptodytes granularis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	14	0	21	79	0	0	0	100	54	0	46	0	0	0	0
Suphrodytes dorsalis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	30	0	17	83	37	7	7	50	82	2	17	0	0	0	0
Suphrodytes dorsalis lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	3	0	0	100	0	0	100	0	33	0	67	0	0	0	0
Copelatus haemorrhoidalis	1	0	0	0	0	0	0	0	0	1	2	2	2	2	16	6	38	56	6	6	6	81	53	3	34	0	0	6	3
Copelatus haemorrhoidalis lr	0	0	0	1	0	0	1	0	0	0	0	0	0	0	3	0	100	0	0	0	100	0	100	0	0	0	0	0	0

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Agabus affinis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	3	33	67	0	33	67	0	0	50	33	17	0	0	0	0
Agabus bipustulatus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	2	0	0	100	0	0	0	100	75	0	25	0	0	0	0
Agabus bipustulatus lr	0	0	0	1	0	1	1	1	0	0	0	0	0	0	2	0	0	50	100	0	0	0	0	50	0	50	0	0	0
Agabus congener	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	100	0	0	0	100	0	0	50	50	0	0	0	0	0
Agabus sturmii	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	100	0	0	100	0	100	0	0	0	0	0	0
Agabus sturmii lr	0	0	0	1	0	1	1	0	0	0	0	0	0	0	2	0	0	100	0	0	100	0	0	0	100	0	0	0	0
Ilybius aenescens	1	0	0	0	0	0	0	0	0	1	2	2	2	2	12	75	17	8	0	0	58	42	50	38	13	0	0	0	0
Ilybius aenescens lr	0	0	0	1	0	1	0	1	1	0	0	0	0	0	60	98	0	2	57	42	0	2	9	69	0	2	0	5	15
Ilybius ater	1	0	0	0	0	0	0	0	0	1	2	2	2	2	1	0	0	100	0	0	0	100	50	0	50	0	0	0	0
Ilybius ater lr	0	0	0	1	0	1	0	1	1	0	0	0	0	0	12	0	42	58	0	0	0	100	50	0	50	0	0	0	0
Ilybius guttiger	1	0	0	0	0	0	0	0	0	1	2	2	2	2	4	25	25	50	0	50	50	0	75	13	13	0	0	0	0
Ilybius guttiger lr	0	0	0	1	0	1	0	1	1	0	0	0	0	0	7	14	14	71	29	0	0	71	43	7	21	29	0	0	0
Ilybius quadriguttatus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	1	0	0	100	0	100	0	0	100	0	0	0	0	0	0
Rhantus suturalis	1	0	0	0	0	0	0	0	0	1	2	2	2	2	1	0	0	100	0	100	0	0	100	0	0	0	0	0	0
Colymbetes fuscus	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	100	0	0	0	100	0	0	0	100	0	0	0
Colymbetes paykulli	1	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0	0	100	0	0	0	100	75	0	25	0	0	0	0
Nartus grapii	1	0	0	0	0	0	0	0	0	1	1	1	1	1	10	0	30	70	0	30	0	70	70	0	20	10	0	0	0
Nartus grapii lr	0.5	0	0	0.5	0	0	1	0	0	0	0	0	0	0	1	0	0	100	0	0	100	0	100	0	0	0	0	0	0
Hydaticus seminiger	1	0	0	0	0	0	0	0	0	1	1	1	1	1	9	11	0	89	0	44	11	44	72	6	22	0	0	0	0
Acilius canaliculatus	1	0	0	0	0	0	0	0	0	1	2	2	2	2	40	10	65	25	3	3	30	65	5	6	26	15	20	23	5
Dytiscus sp lr	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	100	0	0	0	100	0	0	0	100	0	0	0	0
Hydraenidae																													
Hydraena palustris	0	0	0	1	0	1	0	1	1	0	1	1	1	1	26	0	4	96	0	0	0	100	48	0	48	4	0	0	0
Hydraena testacea	0	0	0	1	0	1	0	1	1	0	1	1	1	1	85	0	61	39	0	0	4	96	60	0	40	0	0	0	0
Ochthebius minimus	0	0	0	1	0	1	0	1	1	0	1	1	1	1	11	0	100	0	0	0	0	100	50	0	50	0	0	0	0
Limnebius aluta	0	0	0	1	0	1	0	1	1	0	1	1	1	1	276	0	41	59	0	0	0	100	56	0	44	0	0	0	0
Hydrochidae																													
Hydrochus brevis	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	0	0	100	0	0	0	100	50	0	50	0	0	0	0
Hydrochus carinatus	0	0	0	1	0	0	0	1	1	0	1	1	1	1	59	3	34	63	0	0	3	97	60	2	38	0	0	0	0
Helophorus brevipalpis	0	0	0	1	0	0	0	1	1	0	1	1	1	1	16	13	13	75	0	0	94	6	16	6	25	13	38	0	3
Helophorus minutus/obscurus	0	0	0	1	0	0	0	1	1	1	2	2	2	2	5	0	40	60	0	0	40	60	50	0	30	0	20	0	0
Helophorus aequalis	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	100	0	0	0	100	0	100	0	0	0	0	0	0
Hydrophilidae																													
Coelostoma orbiculare	0	0	0	1	0	0	0	1	1	0	1	1	1	1	4	0	0	100	0	0	50	50	75	0	25	0	0	0	0
Hydrobius fuscipes	0.5	0	0	0.5	0	0	1	1	0	0	0	0	0	0	19	0	68	32	0	11	11	79	50	5	45	0	0	0	0
Hydrobius fuscipes lr	0.5	0	0	0.5	0	0	0	0	0	1	2	2	2	2	1	0	0	100	0	0	100	0	100	0	0	0	0	0	0
Anacaena globulus	0.5	0	0	0.5	0	0	0	1	1	0	0	0	0	0	6	17	33	50	0	17	67	17	83	8	8	0	0	0	0
Anacaena limbata	0.5	0	0	0.5	0	0	0	1	1	0	1	1	1	1	7	14	0	86	0	0	14	86	57	7	29	0	0	0	7
Anacaena lutescens	0.5	0	0	0.5	0	0	0	1	1	0	1	1	1	1	92	41	12	47	0	2	7	91	39	21	24	1	0	0	15
Laccobius bipunctatus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	3	0	33	67	0	0	0	100	33	0	33	33	0	0	0
Helochares lividus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	1	0	100	0	100	0	0	0	100	0	0	0	0	0	0

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Helochares punctatus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	70	1	71	27	1	6	16	77	61	3	28	7	1	0	0
Helochares sp lr	0	0	0	1	0	0	1	1	0	0	0	0	0	0	28	4	64	32	0	0	82	18	89	2	9	0	0	0	0
Enochrus affinis	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	61	5	59	36	0	8	10	82	45	5	45	3	2	0	0
Enochrus coarctatus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	143	0	42	58	0	3	10	87	59	0	39	2	0	0	0
Enochrus ochropterus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	12	42	8	50	0	25	67	8	25	25	33	17	0	0	0
Enochrus quadripunctatus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	5	0	20	80	0	0	100	0	0	0	20	80	0	0	0
Enochrus testaceus	0.5	0	0	0.5	0	0	0	0	0	1	1	1	1	1	1	0	0	100	0	0	100	0	100	0	0	0	0	0	0
Enochrus sp lr	0	0	0	1	0	0	1	1	0	0	0	0	0	0	37	14	14	73	0	0	97	3	32	8	20	5	32	0	1
Cymbiodyta marginella	0	0	0	1	0	0	0	0	0	1	1	1	1	1	328	0	46	54	0	2	0	98	52	0	48	0	0	0	0
Berosus signaticollis	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	100	0	100	0	0	0	0	0	0	100	0	0
Dryopidae																													
Dryops cf luridus	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	100	0	0	100	0	100	0	0	0	0	0	0
Scirtidae																													
Scirtes sp lr	0	0	0	1	0	0	0	1	1	0	1	1	0	0	2	0	0	100	0	0	100	0	100	0	0	0	0	0	0
Cyphon sp lr	0	0	0	1	0	0	0	1	1	0	1	1	0	0	74	41	28	31	1	1	41	57	59	23	10	0	0	0	8
Microcara testacea lr	0	0	0	1	0	0	0	1	1	0	1	1	0	0	3	0	100	0	0	100	0	0	0	50	50	0	0	0	0
Diptera																													
Tipulidae	0	0	0.5	0.5	0	0	0	0	0	1	1	1	1	0	18	83	0	17	0	28	39	33	17	42	25	17	0	0	0
Cylindrotomidae	0	0	0	1	0	1	0	1	1	0	0	1	0	0	10	100	0	0	0	90	10	0	35	60	5	0	0	0	0
Limoniidae	0	0	0.5	0.5	0	0	0	0	0	1	1	1	1	0	53	0	28	72	17	11	0	72	36	3	31	30	0	0	0
Psychodidae	0	0	0	1	0	0	0	0	0	1	1	1	1	0	16	0	0	100	6	0	0	94	50	0	50	0	0	0	0
Chaoboridae																													
Mochlonyx martinii	1	0	0	0	0	1	1	0	0	0	0	1	0	0	5	100	0	0	0	80	0	20	30	40	10	0	0	0	20
Chaoborus crystallinus	1	0	0	0	0	0	0	0	0	1	0	1	0	0	779	0	73	27	16	26	47	12	1	1	8	10	23	11	46
Chaoborus flavicans	1	0	0	0	0	0	0	0	0	1	0	1	0	0	42	0	100	0	0	38	43	19	0	2	19	0	5	2	71
Chaoborus obscuripes	1	0	0	0	0	0	0	0	0	1	0	1	0	0	303	0	88	12	13	20	17	50	0	0	4	10	11	21	53
Chaoborus pallidus	1	0	0	0	0	0	0	0	0	1	0	1	0	0	354	2	14	85	31	39	21	9	1	1	9	26	12	45	6
Dixidae																													
Dixella aestivalis	0.5	0	0	0.5	0	0	0	0	0	1	1	0	0	0	5	0	20	80	0	0	0	100	40	0	40	20	0	0	0
Dixella amphibia	0.5	0	0	0.5	0	0	0	0	0	1	1	0	0	0	401	0	13	87	32	7	8	53	35	1	55	6	2	0	0
Culicidae	1	0	0	0	0	0	0	0	0	1	0	2	2	0	150	7	3	90	31	7	15	46	18	6	10	5	21	41	0
Chironomidae																													
Ablabesmyia monilis	0.5	0	0	0.5	0	0	0	0	0	1	0	1	1	0	36	33	42	25	0	56	36	8	17	1	35	3	11	0	33
Ablabesmyia phatta	0.5	0	0	0.5	0	0	0	0	0	1	0	1	1	0	17	88	12	0	35	24	29	12	9	79	6	0	0	6	0
Guttipelopia guttipennis	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	100	0	0	100	0	0	0	0	50	50	0	0
Monopelopia tenuicalcar	0.5	0.5	0	0	0	1	1	0	0	0	0	1	1	0	10	50	20	30	0	30	50	20	20	35	5	10	20	0	10
Natarsia sp	1	0	0	0	0	0	0	0	0	1	0	1	1	0	24	0	100	0	13	88	0	0	13	44	44	0	0	0	0
Paramerina cingulata	1	0	0	0	0	0	0	0	0	1	0	1	1	0	10	0	0	100	60	0	10	30	5	0	5	90	0	0	0
Procladius sp	1	0	0	0	0	0	0	0	0	1	0	1	1	0	529	4	83	14	14	19	24	43	18	5	27	12	1	37	0
Psectrotanypus varius	1	0	0	0	0	0	0	0	0	1	0	1	1	0	154	1	99	0	0	10	5	85	3	0	2	0	1	94	0
Telmatopelopia nemorum	0.5	0	0	0.5	0	0	0	0	0	1	0	1	1	0	15	0	100	0	0	93	0	7	17	40	43	0	0	0	0

(to be continued)

(continued)

Xenopelopia sp	0.5	0	0	0.5	0	0	0	0	0	1	0	1	1	0	71	0	3	97	52	15	1	31	11	0	56	31	1	0	0
Acricotopus lucens	1	0	0	0	0	0	0	0	0	1	0	1	1	0	5	0	0	100	0	0	0	100	0	0	0	0	100	0	0
Corynoneura sp	0.5	0.5	0	0	0	0	0	0	0	1	0	1	1	0	7	14	14	71	0	0	14	86	21	7	7	57	0	0	7
Cricotopus sp	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	100	0	0	0	100	0	0	0	0	100	0	0
Limnophyes sp	0	0	0	1	0	0	0	0	0	1	0	1	1	0	9	0	56	44	0	0	22	78	67	0	22	0	0	0	11
Psectrocladius platypus	0.3	0.3	0.3	0	0	0	0	0	0	1	0	1	1	0	551	90	4	5	1	49	13	37	14	58	1	1	4	0	21
Psectrocladius psilopterus	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	3	0	67	33	0	0	100	0	0	0	67	0	33	0	0
Psectrocladius oxyura	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	1	0	0	100	0	100	0	0	0	0	0	0	100	0	0
Psectrocladius psilopterus agg	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	24	25	75	0	0	25	38	38	0	25	8	0	67	0	0
Psectrocladius obvius agg	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	1	0	0	100	0	100	0	0	0	0	0	0	100	0	0
Psectrocladiusgr sordidellus/limbatellus	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	61	8	69	23	41	13	33	13	20	7	26	15	10	21	2
Chironomus sp	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	2042	20	70	10	8	30	11	51	6	16	3	7	1	66	2
Cladopelma gr lateralis	1	0	0	0	0	0	0	0	0	1	0	1	1	0	3	0	100	0	0	100	0	0	0	0	0	0	0	100	0
Dicrotendipes gr lobiger	1	0	0	0	0	0	0	0	0	1	0	1	1	0	9	0	11	89	0	67	33	0	22	0	22	11	22	22	0
Endochironomus tendens	0	1	0	0	0	0	0	0	0	1	0	1	1	0	3	0	67	33	0	100	0	0	0	17	17	33	33	0	0
E. gr dispar	0.5	0.5	0	0	0	0	0	0	0	1	0	1	1	0	566	0	73	27	3	43	47	6	47	8	28	12	4	1	0
Glyptotendipes caulicola	0.3	0.3	0.3	0	0	0	0	0	0	1	0	1	1	0	16	0	13	88	0	25	19	56	13	0	0	31	56	0	0
G. paripes	0.5	0	0.5	0	0	0	0	0	0	1	0	1	1	0	44	0	100	0	0	39	45	16	11	0	14	0	7	68	0
Parachironomus gr arcuatus	0.5	0.5	0	0	0	1	1	0	0	0	0	1	1	0	3	0	67	33	0	0	100	0	67	0	0	33	0	0	0
Polypedilum gr sordens	0	1	0	0	0	0	0	0	0	1	0	1	1	0	15	0	100	0	0	13	53	33	7	0	40	0	53	0	0
P. uncinatum agg	1	0	0	0	0	0	0	0	0	1	0	1	1	0	371	0	55	45	48	27	7	18	15	6	51	6	5	17	0
Paratanytarsus sp	1	0	0	0	0	0	0	0	0	1	0	1	1	0	11	0	0	100	0	55	36	9	9	0	36	55	0	0	0
Tanytarsus sp	1	0	0	0	0	0	0	0	0	1	0	1	1	0	119	0	100	0	0	31	67	2	3	0	74	0	21	3	0
Ceratopogonidae	0.3	0	0.3	0.3	0	0	0	0	0	1	0	1	1	0	342	71	7	22	0	59	15	26	8	56	7	10	10	1	8
Stratiomyidae	0	0	0.5	0.5	0	0	0	0	0	1	0	1	1	0	2	0	0	100	0	0	0	100	50	0	50	0	0	0	0
Tabanidae	0	0	0.5	0.5	0	0	0	0	0	1	0	2	2	0	10	20	40	40	20	10	0	70	35	10	35	20	0	0	0
Syrphidae	0	0	0.5	0.5	0	0	0	0	0	1	0	1	1	0	7	0	100	0	0	0	0	100	21	0	21	0	0	57	0
Ephydridae	0	0.5	0	0.5	0	0	0	0	0	1	0	1	1	0	2	0	0	100	50	0	0	50	75	0	25	0	0	0	0
Other Diptera	0	0	0.5	0.5	0	0	0	0	0	1	1	1	1	0	119	0	3	97	0	21	2	77	17	0	36	45	2	0	1
Trichoptera																													
Triaenodes bicolor	1	0	0	0	0	0	0	0	0	1	0	1	1	0	42	0	2	98	0	0	62	38	32	0	18	26	17	7	0
Limnephilus elegans	0	0	0	1	0	0	0	0	0	1	0	1	1	0	24	100	0	0	58	42	0	0	10	73	4	0	0	4	8
Enoicyla pusilla	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	100	0	100	0	0	100	0	0	0	0	0	0
Agrypnia varia	0	0	0	1	0	0	0	0	0	1	0	1	0	0	3	0	33	67	33	67	0	0	0	0	0	67	33	0	0
Oligotrichia striata	0	0	0	1	0	0	0	0	0	1	0	1	0	0	123	4	24	72	7	11	72	11	60	3	14	14	7	2	0
Holocentropus dubius	0	1	0	0	0	0	0	0	0	1	0	1	0	0	281	0	99	1	10	51	3	37	1	0	15	0	73	11	0
H. stagnalis	0	1	0	0	0	0	0	0	0	1	1	1	0	0	10	40	30	30	70	30	0	0	10	45	15	10	10	10	0
Lepidoptera	0	1	0	0	0	0	0	0	0	1	0	1	0	0	11	18	45	36	0	27	45	27	32	14	9	0	45	0	0