Euro-limpacs

Deliverable No. 332
Habitat preference and current velocity response of six Trichoptera in sandy lowland stream environment: an experimental approach

Habitat preference and current velocity response of six Trichoptera in sandy lowland stream environment: an experimental approach

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Introduction

Climate change and habitat dynamics
There is general agreement on the climate changes expected and the hydrologic consequences in Europe. An increase in temperature, a decrease in summer and an increase in autumn-winter precipitations, and an increase of extreme daily precipitation (especially summer storms), are generally expected. Consequently, discharge will show a more dynamic regime (higher flood frequency and lower flood predictability), due to increases in extreme daily precipitation and in severity of droughts (Arnell 1999). A key concern, especially for stream ecosystems, is how these climate and hydrological regime changes might influence river channel morphology, leading to changes in channel and riparian habitats and species diversity.
In large parts of Europe hydromorphological alterations, such as channel straightening, weir and dam construction, disconnection of the river from its floodplain and alteration of riparian vegetation, are major stressors affecting streams and rivers (Kristensen & Hanson 1994, Armitage & Pardo 1995, Hansen et al. 1998). Under future climate scenarios further stresses will be introduced including the effect of changes in precipitation patterns and intensity on hydrology, and climate induced changes in land-use patterns. The combination of climate change and human disturbances, such as land-use change, is termed global change. Global change will cause changes in catchment hydrology that will affect channel morphology and sediment transport, inundation frequency and extent, and impact aquatic ecosystems from catchment to habitat scale.
The interactions between the natural driver climate and the anthropogenic driver land-use, as well as the response parameters of hydrology and morphology act at large scale (the catchment) and time periods of either season to years (short) or to decades (long). The ultimate response parameter, biology, is driven by hydrology and morphology, and also covers both large and small scales (Verdonschot et al. 1998). In this study we will focus on the small scale, the habitat ands its interaction with current velocity.

Habitat use and dynamics
Habitat structure in sandy, lowland streams is characterised by mosaics of coarse and fine, both organic and mineral materials (Tolkamp 1980). Disturbances and environmental variation are important processes that irregularly in time change this mosaic of habitats (Connell 1978). The patch dynamics concept provides understanding of the mechanisms that control spatial (habitat mosaics) and temporal (habitat dynamics) patterns of species distribution and diversity (Pickett & White 1985, Townsend & Hildrew 1976). The temporal variability of habitats implies the need of movement of organisms between habitats (Lancaster et al. 1991). Movement between habitats includes taking risks being in hostile environments or circumstances, such as predation, drift or mortality (Flecker 1992). The habitat itself provides resources for the organism of which food is the most important, along with shelter, rest, mating, dormancy, egg deposition, and others (Brown 1988). Habitat preference of macroinvertebrates has been the outcome of a number of studies.
Typical uni-modal response curves of species to environmental gradients are long known (Whittaker 1956). Recently, such response curves are described for macroinvertebrates in relation to current velocity (Lancaster 1999). The patchy nature of substrata prevents the description of the same curves in relation to substratum. Substratum is dealt with mostly as a nominal factor with often the numbers of individuals collected representing a quantitative measure of preference (Tolkamp 1982). In general, species with a narrow response curve are defined as specialists and species with a wide amplitude as generalists (Pianka 1978). Substrate is the most important structure component of a macroinvertebrate

habitat. As substratum hardly occurs in a gradient, and one can doubt whether species really treat substratum as such, substrate or habitat specialists prefer a specific habitat and generalists do not. Such grouping would also imply that species respond specifically to a habitat (e.g., as specific food source) and less or not to solely the physical structure. Furthermore, macroinvertebrates are more or less mobile animals, they crawl, burrow, walk, sprawl, swim, drift and thus can move between habitats. Movement implies a more or less continuous redistribution of species patterns over shorter (very mobile) and longer (less mobile) time periods.

Experimental approach
A large number of studies described the habitat preference of macroinvertebrates in streams, based on field observations (Wachs 1967, Tolkamp 1980). Most of these studies provide correlative habitat preference not taking into account the reasons why the species occurred nor the time spend in a habitat (an exception is demonstrated by Townsend & Hildrew 1980). Laboratory experiments in artificial streams using known resources and circumstances permits 1) the controlled manipulation of one or a few variables of interest, and 2) the opportunity to observe a specimens behaviour. The experimental disadvantages are that 1) the habitats are not natural, and b) the substrate or resource quality may not be appropriate.
Trichoptera are common and abundant inhabitants of lowland streams in the Netherlands. Through their taxonomic richness and high abundance the order of Trichoptera is a very suited group to use as both indicator of the stream health (Moor & Ivanov 2008) as well as easy to collect in the field and handle in the laboratory.

Objectives
The three objectives of this study are:
- Do sensitive and ubiquitous trichopteran species show habitat selection in time?
- Do sensitive and ubiquitous trichopteran species respond differently to habitat selection?
- Does current velocity affect these patterns of selection?

Methods / Procedures

Selection and collection of sensitive and ubiquitous trichopterans
The choice of three sensitive and three ubiquitous trichopteran species is based on an extensive analysis of lowland streams in the Netherlands (Verdonschot & Nijboer 2004). A multivariate analysis based on 949 samples taken in heavily degraded to near natural lowland streams showed a gradual distinction between natural lowland streams at one side of the gradient (axis 1) and degraded ones on the other. Along this gradient three trichopteran species projected close to the natural stream sites, the so-called specialists, and three to the degraded sites, the so-called generalists, were selected. The criteria for selection also included that the species needed to be non-predator, case-building and more common. Case-building species are more easy to handle in the laboratory, non-predators show habitat selection and binding amongst others possibly primarily related to food source, and being more common facilitates field collection of large numbers of specimens.
Instar IV and V of the three specialists *Halesus radiatus*, *Micropterna sequax*, and *Chaetopteryx villosa* were collected from the near natural Coldenhoven and Seelbeek stream, situated in the central part of the Netehrlands (Table 1). The generalists *Anabolia nervosa*, *Limnephilus lunatus*, and *Mystacides longicornis* were collected from three different channelized streams/ditches (Table 1). The specimens, 300-400 per species, were kept in the laboratory in an artificial stream with a variety of organic (detritus, leaves, twigs, waterplants) and mineral (fine to coarse mineral sand) materials (v = 5 - 10 cm s^{-1}, 12 $^{\circ}$C, day : night = 16 : 8 hours). Weekly extra food consisting of fresh leaves and detritus, and wheat fragments is added.

Artificial streams
The experiments were conducted in six indoor, re-circulating channels, each channel composed of four parallel gutters, in a temperature and light controlled environment. The flow can be manipulated independently in each channel. Each channel allows six replicate treatments, two in each gutter. Per

gutter each habitat type is replicated two times in a randomised block design. Each gutter is 3.2 m long and 15 cm wide, and divided into 16 compartments of 13.4x14.3 cm each. Each compartment consists of a cover plate with a circular hole of 5.1 cm in diameter. Beneath the cover plate there is a compartment of 5 cm depth almost filled with habitat material (400 cm3). Water level is kept to 3 cm depth above the compartments.

The habitat materials consisted of fresh (dried, frozen) leaves (oak (*Quercus robur*) > 2.0 mm), detritus (mixture of 50% fresh fractionated leaves and 50% 'old' material collected from a stream both in size 0.25-2.0 mm), mineral silt (95% < 0.25 mm), sand (0.25-2.0 mm), and fine gravel (2.0-8.0 mm).

Experimental set-up
For each experiment 20 specimens of one species were released in the most upstream compartment (the compartment without a hole nor substrate) of each of the four gutters within one artificial stream. At a current velocity of 10 cm s^{-1} the position of each specimen was observed after 0.17, 0.33. 0.67, 1, 2, 3, 4, 5, and 6 days. Each time interval referred to a new experiment. At each moment of observation the number of specimens was counted 1) per compartment in a habitat type, 2) walking around outside of the compartments, 3) sitting at the downstream end of the gutter attached to the gauze, 4) having pupated, 5) died. The numbers of catgerory2 and 3 are summed up to the category 'indifferent' that refers to specimens that did not show a habitat preference at the moment of counting. Pupated and death specimens were not included in the analysis. During repeated experiments at current velocities of 30 cm s^{-1} and at 50 cm s^{-1} counts were made only after 2 days. During the experiments the water chemistry (pH, EC, oxygen, and temperature) was measured.

Data analysis
Differences in counts between time intervals were tested by a paired t-test. Habitat preference is defined as a significant positive fraction for a respective habitat in comparison to the fractions of all other habitats, 'indifferent' inclusive, subpreference refers to a significant positive fraction for a respective habitat in comparison to the fraction 'indifferent', and aversion means a significant lower fraction for a respective habitat in comparison to the fraction 'indifferent'. The differences in counts between specialists and generalists were tested with a Fisher's exact test. The Fisher's exact test is used to analyse two categorical variables, in our case specialists and generalists, present in small numbers. It calculates exactly the significance of the deviation from the null hypothesis that there is no difference (Fisher 1954). The differences between up- and downstream compartments were tested with a binomial test. The binomial test is an exact test of the statistical significance of deviations from a theoretically expected distribution of up- versus downstream observations. The pupae were tested according a Poisson distribution. This is a discrete probability distribution that expresses the probability of the number of pupae counted per time interval.

Results

Habitat selection over time
Whether or not trichopteran species selected a specific habitat type was tested for seven time intervals (Figure 1). Based on the fraction indifferent (number of specimen that did not select a habitat type divided by the total number of specimens) a habitat type choice stabilised when no significant differences occurred between consecutive time intervals. For *H. radiatus* the fraction 'indifferent' was significantly lower and stabilised from day 1 on, with on day 6 an even larger significant drop (Figure 1). For *M. sequax* the fraction 'indifferent' was generally low, with a rise on day 1 (outlier?) and a significant drop and stabilisation from day 2 on. For *C. villosa* the fraction 'indifferent' was significantly lower from day 1on, but varied between day 2, 4 and 6. For *A. nervosa* the fraction 'indifferent' was significantly lower and stabilised from day 0.67 on, with on day 6 a significant rise (Figure 1). For *L. lunatus* the fraction 'indifferent' was significantly lower and stabilised from day 1 on, with on day 6 an even larger significant drop, although in general the fraction 'indifferent' was high in comparison to the other species, except for *M. longicornis*. For the latter species the fraction 'indifferent' was significantly lower and stabilised from day 0.67 on, with on day 2 and 6 further

significant drops. Despite a reasonable amount of variation, overall most species show stabilisation in habitat selection from day 1on (Figure 1). In general, the fraction 'indifferent' ranged between about 10% for *M. sequax* up to 50% for both *L. lunatus* and *M. longicornis*. The latter two species thus in half of the experiments did not make a habitat choice.

If all observations from day 1 are considered replicates, fractions 'indifferent' between all species were tested by a Fisher's exact test (Table 1). Two distinct groups occurred, the specialists with lower fractions and the generalists with relative higher fractions 'indifferent'. These two groups mutually exclude each other significantly.

Comparing the fraction upstream in relation to the sum of numbers of specimens up- and downstream only *L. lunatus* did not show any difference while on the contrary *M. longicornis* always occurred significantly more abundant upstream (Table 2). The four other species in about half of the experiments the difference was significant, indicating a more less coincidental movement of specimens. From the results it was concluded that position up- or downstream did not significantly affect the habitat choice.

Habitat preference
The first question was whether the six species showed a significant habitat preference that did not change after that moment in time. Such stabilisation of habitat preference was tested by comparing the observations on one moment in time versus a observations afterwards. The habitat preference did not change anymore for *C. villosa* and *M. sequax* after 0.33 days, for *H. radiatus* this did not change after 0.67 days and for *L. lunatus* after 1 day (Table 3). For *A. nervosa* and *M. longicornis* no stabilisation took place, thus the habitat choice varied continuously in time (Table 3).

Habitat preference, subpreference, and aversion were based on the assumption that habitat selection was stable after day 1, and thus all observation can be seen as replicates independent from duration of the experiment. *H. radiatus, M. sequax,* and *C. villosa* significantly preferred leaves at all time intervals from day 1 (Figure 2). *H. radiatus* showed a slight aversion for sand and silt, *M. sequax* showed a subpreference for detritus, sand and gravel, and *C. villosa* a subpreference for gravel. *A. nervosa* significantly preferred detritus, *L. lunatus* leaves except for detritus on day 6, and *M. longicornis* did not show a preferent nor subpreferent habitat.

Current velocity effects on habitat selection
The habitat choice of *H. radiatus* and *M. sequax* did not change at higher velocities (Figure 3). The habitat choice of both *C. villosa* and *A. nervosa* is increasingly affected by increasing current velocity. At a velocity of 30 cm s^{-1} more specimens, in comparison to the situation of 10 cm s^{-1}, were walking around outside of the habitat materials, and at 50 cm s^{-1} an significantly higher number of specimens was collected at the end gauze. Both *L. lunatus* and *M. longicornis* were affected by higher current velocities, at both 30 and 50 cm s^{-1} significantly more specimens were found at the end gauze.

In general, except for *M. sequax* all other species were hindered by higher current velocities in the habitat choice (Figure 4).

H. radiatus was equally present in habitats up- versus downstream at different current velocities (Table 5). *M. sequax* in all cases quickly and independent from current velocity made its habitat choice. The behaviour of *C. villosa* varies. Both *A. nervosa* and *L. lunatus* at 30 and 50 cm s^{-1} more and more choose the downstream habitats. *M. longicornis* selected upstream habitats at 10 cm s^{-1} but was indifferent at higher velocities (Table 5).

Occurrence of pupae
During the experiments some of the instar V larvae pupated. Of *A. nervosa*, *L. lunatus*, and *M. longicornis* no larvae, and of *H. radiatus* only 5 larvae pupated. These data were not further used. Instar V larvae of both *M. sequax* and *C. villosa* preferred gravel as substrate to pupate (Figure 6).

Discussion

Habitat selection over time

Numerous authors have shown that distinct differences in species composition of macroinvertebrates occur in different substrate types (e.g. Thorup 1966, Mackay 1969, Cummins 1975, Tolkamp 1980). Differences in substrate preference were already half a century ago also shown for different instars or life stages (e.g. Cummins & Lauff 1969, Rees 1972, Otto 1976). A number of these substrate preferences were based on over-representation of specimens of the respective species in field observations. Showing a distinct occurrence in a substrate type does not automatically imply a specific habitat binding or preference. A habitat is not solely the substrate but also includes the current velocity, food, oxygen and other major factors (Tolkamp 1980). Most of these studies did not take into account both time and mobility of macroinvertebrates. Being over-represented in a habitat at a certain moment in time does not tell about the position of a specimen at other moments in time. Being mobile implies also being able to move from habitat to habitat. The experiments on habitat choice showed that between 10 and 50% of the specimens were moving around over the seven time intervals. This is a strong indication that specimens either do not choose a habitat or choose a habitat and after some time leave this habitat and move around. The observations on up- versus downstream distribution strengthen the hypothesis that specimens move, which results in a more even distribution between up- and downstream habitats. The strong, relatively heavy specialist *M. sequax* showed the most explicit habitat choice. Two of the generalists *L. lunatus* and *M. longicornis* more often did not show a clear habitat choice. Natural stream stretches are heterogeneous habitats both in space and time. Such spatiotemporal heterogeneous environment acted as evolutionary force on the organisms and selected for traits that maximize fitness (Frissel et al. 1986, Wilby et al. 2001, Gjerlov et al. 2003). Mobility offers macroinvertebrates the potential to reduce drift distance (Lancaster et al. 1996), to avoid dislodgement, or to move to and from food patches, refugia or shelters. Mobility is an important trait, especially in a heterogeneous environment (Pianka 1970, Mackay 1992, Townsend & Hildrew 1994). The results showed that generalist are more mobile then specialists, a trait gradient that fits the habitat templet for streams (Townsend & Hildrew 1994). The generalist *M. longicornis* furthermore was the smallest of the six species and the specialist *M. sequax* was least mobile but bears the most heavy case. All features fitting in the resilience and resistance traits indicated.

Habitat preference
Except for *A. nervosa* and *M. longicornis,* the other four trichopterans selected a habitat after one day. Despite such habitat stabilisation the habitat specificity or binding was different for different species. Specialists more often significantly preferred leaves, but all also occurred in several other habitats some with a significant subpreference. The generalists did not significantly show a preference, more often they moved around. These results support the hypothesis of the over time moving macroinvertebrates. Preference or subpreference, here with leaves and detritus, most probably is related to food as most other key factors remained constant (like oxygen content, current velocity, temperature) during the experiments. The results also point out that at any moment in time specimens, apart from their favourable habitat, move to all other habitats or can be found in those. Food type is mostly not obligatory (Monakor 2003), the quality of the food can differ strongly between patches, and feeding can probably be limited to certain moments in time. It is therefore an advantage for specimens to move between patches in search for better quality of food (Wilzbach & Cummins 1989) or for shelter. This in its turn is a trait-off against predation risk during movement (e.g. Lancaster 1996, Dahl 1998). Furthermore, the lower the food specialism in combination with a high mobility increases the survival rate in disturbed environments. The generalist showed a lower habitat preference and higher mobility. This confirms the hypothesis of generalist being highly mobile and thus faster colonisers over longer distances, and being food generalists.

Current velocity effects on habitat selection
Stream macroinvertebrates are to some degree adapted to a life in running waters. Various behavioural and morphological adaptations suited to withstand high current velocity and sediment movement are observed (Townsend et al. 1997, Lamouroux et al. 2004, Vieira et al. 2006). Some groups of species are able to withstand stronger currents or a higher degree of sediment movement than others. They possess traits that enable them to survive extreme conditions. Other species, without such traits, disappear when a certain frequency, magnitude, duration, rate of change or timing of extreme events is

exceeded. In theory, sudden changes in the hydrology of a stream, often due to anthropogenic influences, result not only in a change in species composition or abundance, but also cause a shift in the occurrence and abundance of certain species traits (Statzner et al. 2005).Changes in flow rate are mostly related to rate of disturbance. In general, streams with a dynamic flow rate will host less specialists and more generalists (Death 1995, Matthaei et al. 1997). Our results confirm this hypothesis.

Conclusions

Do sensitive and ubiquitous trichopteran species show habitat selection in time?
- Specialist showed a significant preference for leaves, in combination with a subpreference or aversion for other habitat types.
- Generalist sowed a less significant to no preference for leaves, detritus or any habitat type.

Do sensitive and ubiquitous trichopteran species respond differently to habitat selection?
- Specialist showed habitat selection in time, especially after one day but this selection can vary over time. Ten to 20% of all specimens did not select.
- Generalist showed less to no habitat selection over time. Thirty to 50% of all specimens did not select.

Does current velocity affect these patterns of selection?
- Both specialists and generalists are affected by higher current velocities, although generalist respond faster and in higher numbers.

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Figure legends

Figure 1. Fraction indifferent of the six Trichoptera at seven time intervals (0.17, 0.33, 0.67,1, 2, 4, and 6 days).

Figure 2A-F. Average number of individuals of the six Trichoptera collected in each of the five habitat types at 7 time intervals (0.17, 0.33, 0.67,1, 2, 4, and 6 days). A. *Halesus radiatus*, B. *Micropterna sequax*, C. *Chaetopteryx villosa*, D. *Anabolia nervosa*, E. *Limnephilus lunatus*, F. *Mystacides longicornis*.

Figure 3 A-F. Average number of individuals of the six Trichoptera collected at three different current velocities and seven time intervals (0.17, 0.33, 0.67,1, 2, 4, and 6 days). A. *Halesus radiatus*, B. *Micropterna sequax*, C. *Chaetopteryx villosa*, D. *Anabolia nervosa*, E. *Limnephilus lunatus*, F. *Mystacides longicornis*.

Figure 4. Fraction gauze of the six Trichoptera at three different current velocities.

Figure 1
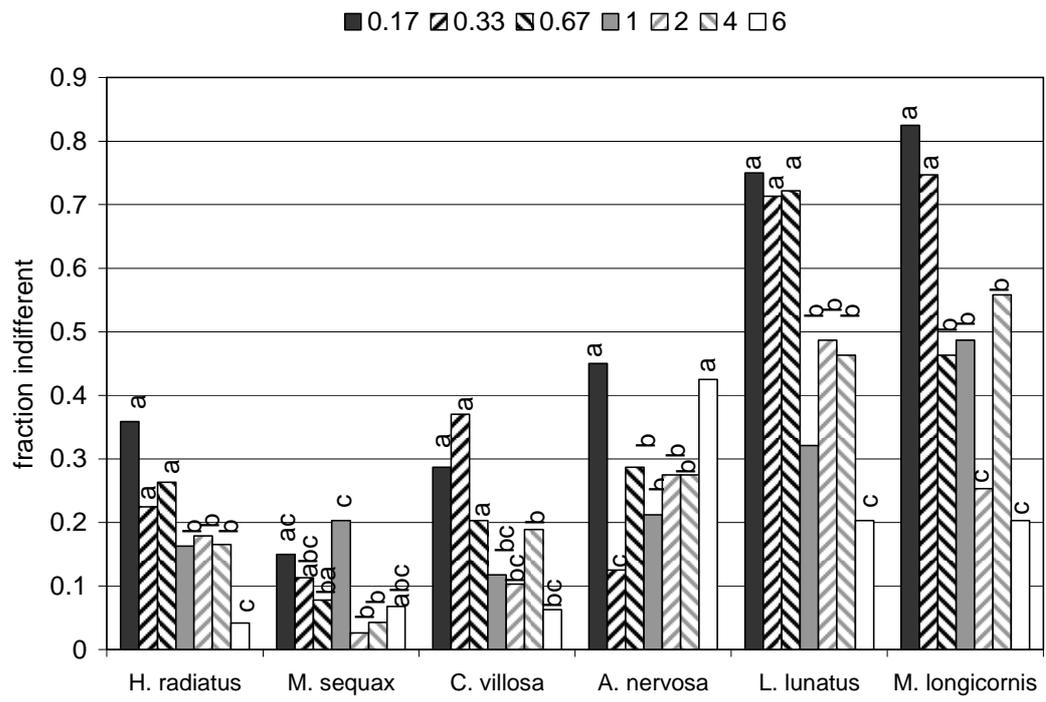
Figure 2 A-C

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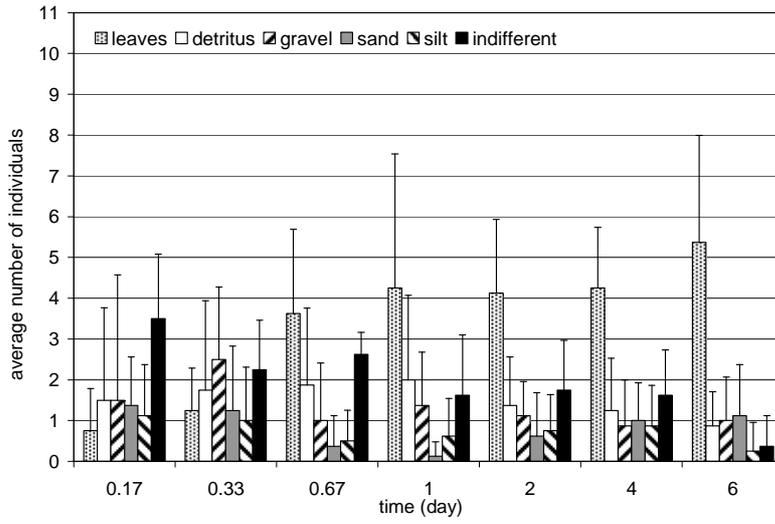
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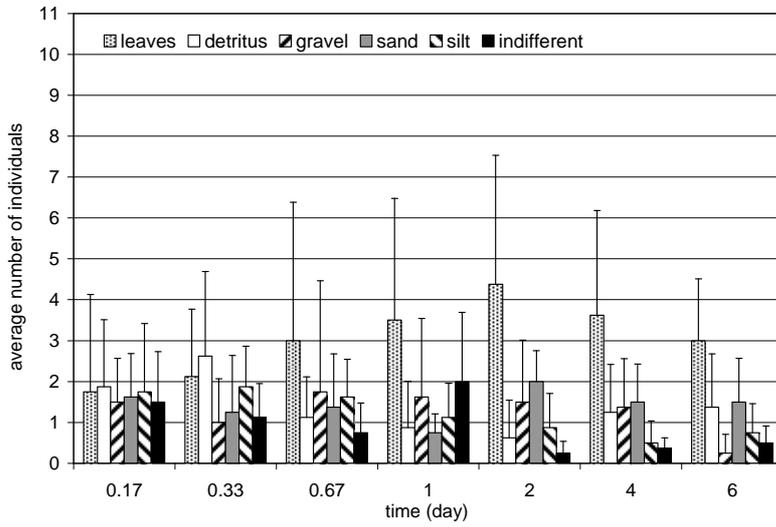
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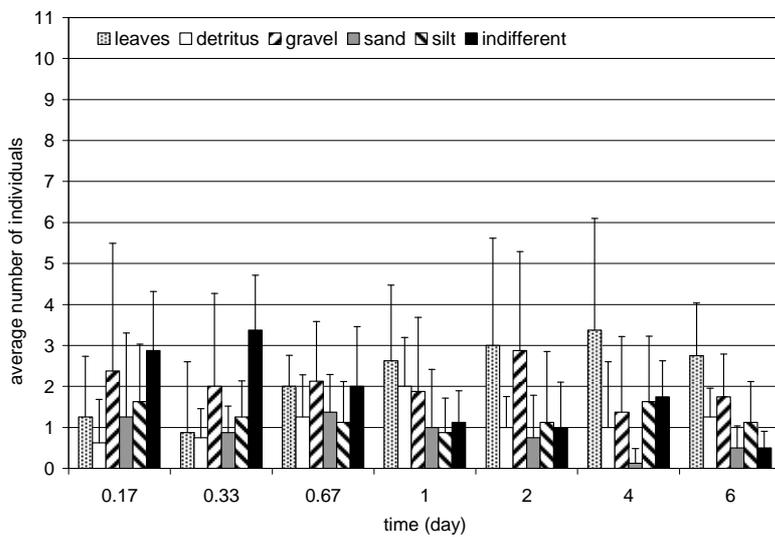
Figure 2 D-F

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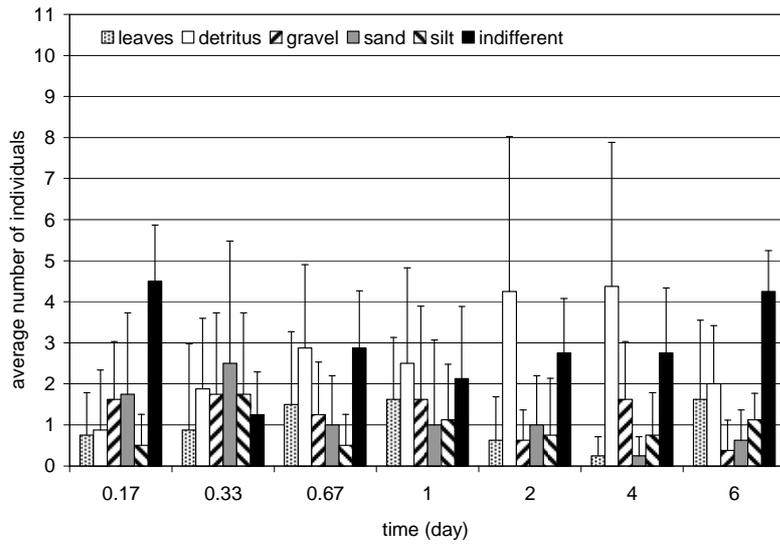
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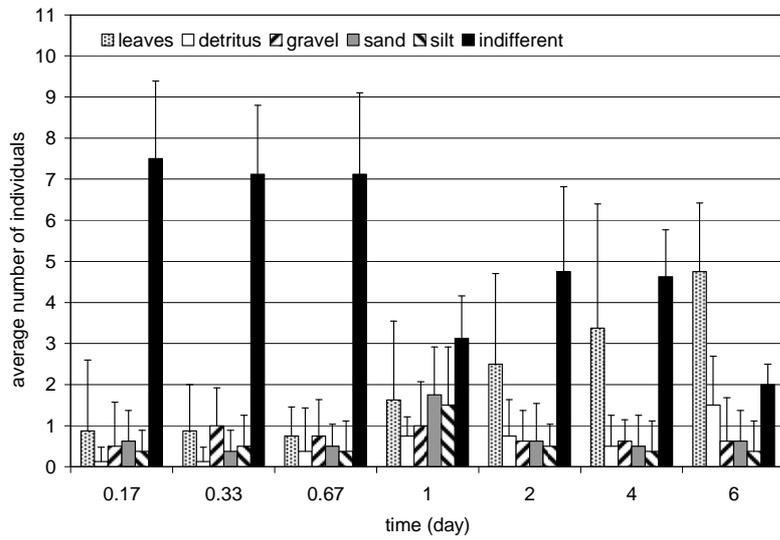
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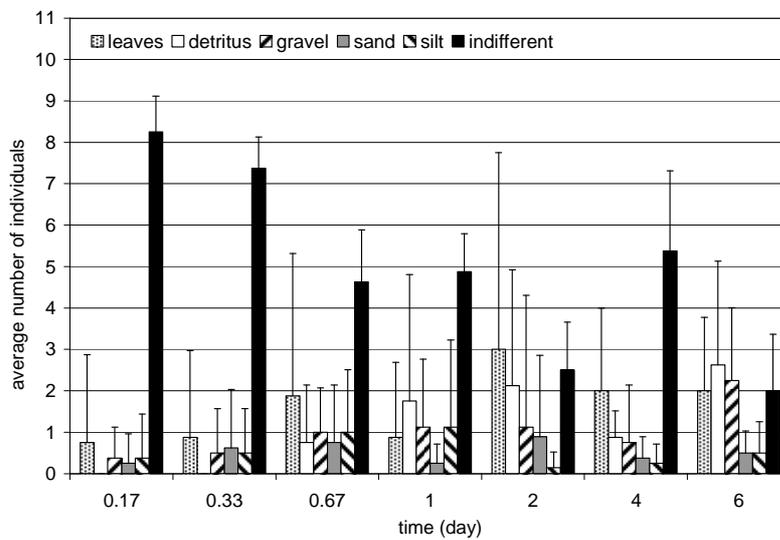
Figure 3 A-C

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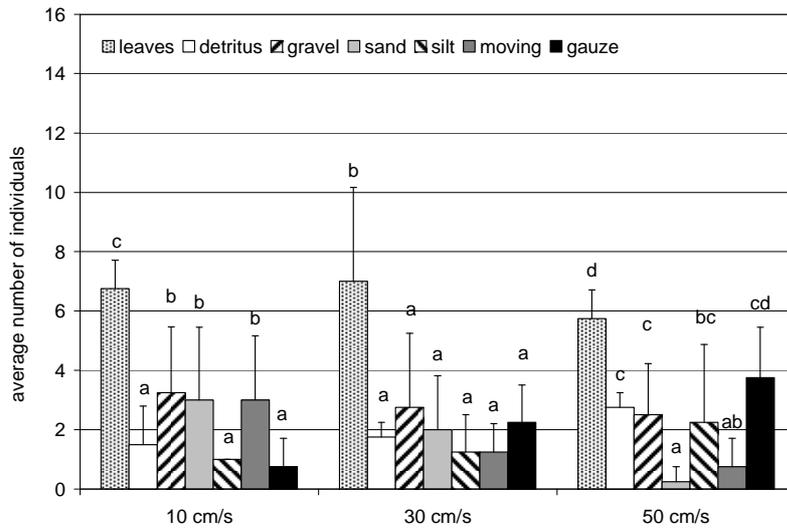
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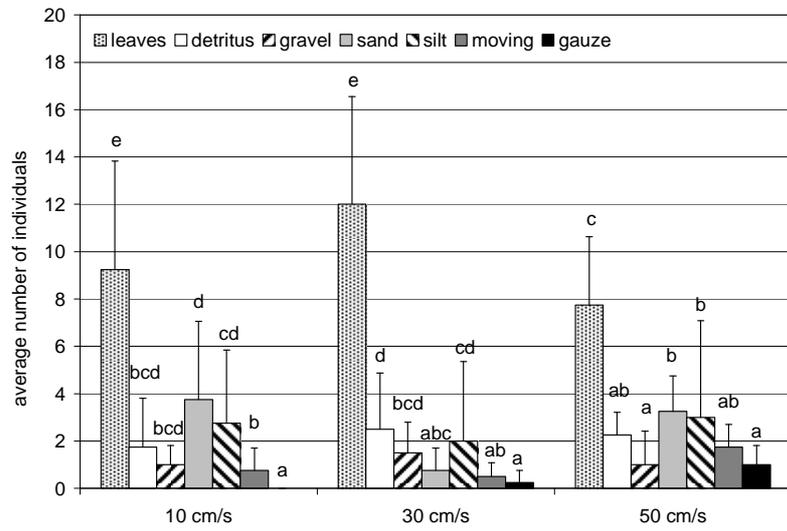
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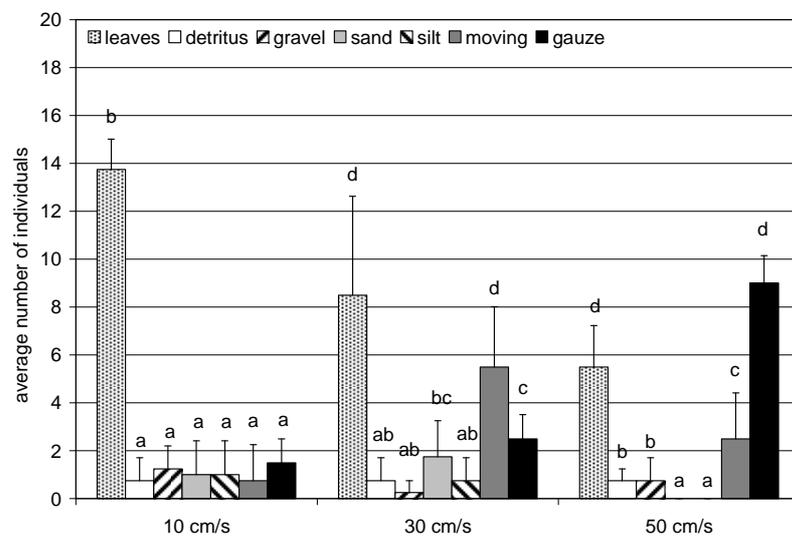
Figure 3 D-F

D
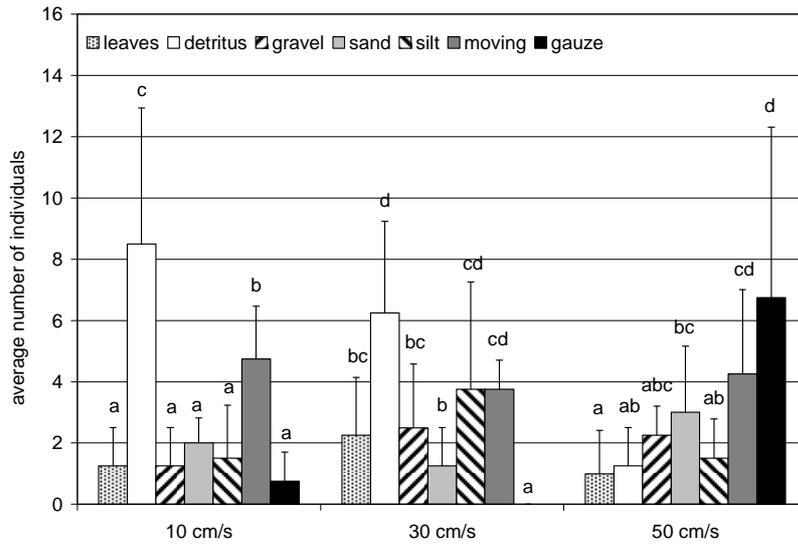
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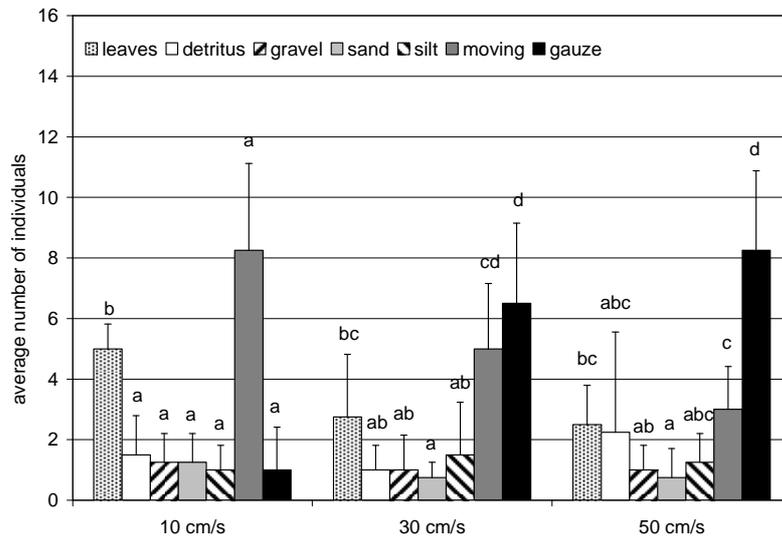
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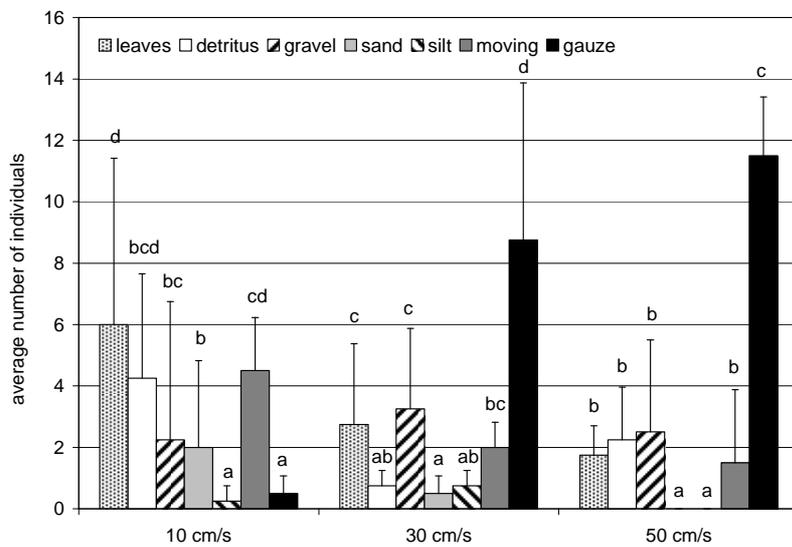
Figure 4
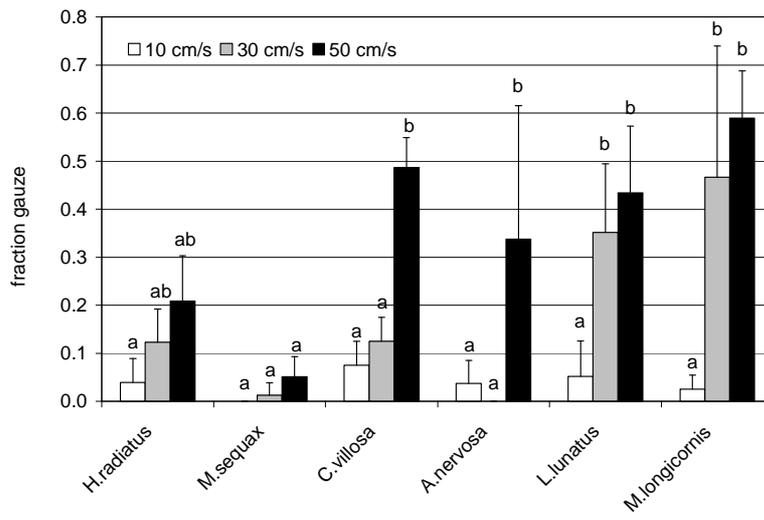
Table 1. Fraction indifferent of and pair wise Fishers exact test (in bold P<0.01) between the six Trichoptera over the total of four time intervals (1, 2, 4, and 6 days).

	fraction 'indifferent'	pair wise test					
H. radiatus	0.137	-					
M. sequax	0.079	**0.008**	-				
C. villosa	0.106	0.179	0.231	-			
A. nervosa	0.297	**0.000**	**0.000**	**0.000**	-		
L. lunatus	0.368	**0.000**	**0.000**	**0.000**	0.068	-	
M. longicornis	0.375	**0.000**	**0.000**	**0.000**	0.046	0.934	-
		Hr	Ms	Cv	An	Ll	Ml

Table 2. Fraction upstream versus downstream and binomial test (in bold P<0.01) of the six Trichoptera over seven time intervals (0.17, 0.33, 0.67,1, 2, 4, and 6 days).

species	time						
	0.17	0.33	0.67	1.00	2.00	4.00	6.00
H. radiatus	0.033	**0.007**	0.018	**0.007**	0.260	0.712	0.470
M. sequax	**0.000**	**0.000**	**0.000**	0.011	0.356	**0.004**	0.788
C. villosa	**0.000**	0.184	0.615	0.027	**0.000**	**0.000**	0.036
A. nervosa	**0.000**	**0.000**	0.033	**0.000**	**0.001**	0.048	0.104
L. lunatus	0.824	1.000	0.134	0.784	0.017	0.761	0.450
M. longicornis	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**

Table 3. Differences in habitat type selection at sequential time intervals (test of a linear position effect, in bold P<0.01).

time	*H. radiatus*	*M. sequax*	*C. villosa*	*A. nervosa*	*L. lunatus*	*M .longicornis*
0.17	**0.000**	**0.000**	**0.000**	**0.000**	0.298	-
0.33	**0.000**	**0.000**	0.012	**0.000**	0.252	**0.000**
0.67	**0.001**	**0.000**	0.133	**0.001**	0.060	**0.000**
1.00	0.022	**0.006**	**0.010**	**0.000**	0.793	**0.000**
2.00	0.127	0.062	**0.000**	**0.000**	0.040	**0.000**
4.00	0.177	0.014	**0.000**	0.011	0.737	**0.000**
6.00	0.255	0.871	0.044	0.291	0.428	**0.000**

Table 4. Fraction upstream versus downstream and T-test (in bold P<0.01)of the six Trichoptera at different current velocities (10, 30 and 50 cm s^{-1}).

current velocity cm s^{-1}	10		30		50	
	fraction	P-value	fraction	P-value	fraction	P-value
H. radiatus	0.484	0.899	0.644	0.036	0.500	1.108
M. sequax	0.757	**0.000**	0.880	**0.000**	0.940	**0.000**
C. villosa	0.592	0.154	0.917	**0.000**	0.536	0.851
A. nervosa	0.724	**0.001**	0.250	**0.000**	0.194	**0.000**
L. lunatus	0.700	0.017	0.250	0.013	0.323	0.071
M .longicornis	0.949	**0.000**	0.562	0.597	0.577	0.557