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Insect emergence in relation to floods in wet meadows and swamps in the River Dalälven floodplain

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Abstract

Annual variation in flood frequency and hydroperiod during the vegetation season has ecological impacts on the floodplain biota. Although many insect groups may have a lower emergence during a flood event, it is poorly known how annual emergence of insects in temporary wetlands is related to the variation in hydrology. Between May and September, we studied the weekly emergence of 18 insect taxa over six consecutive years, 2002–2007, in six temporary flooded wetlands (four wet meadows and two forest swamps) in the River Dalälven floodplains, Central Sweden. We used emergence traps to collect emerging insects from terrestrial and aquatic parts of wet meadows and swamp forests. In all wetlands, the insect fauna was numerically dominated by the orders Diptera, Hymenoptera, Coleoptera and Homoptera. On a weekly basis, 9 out of the 18 insect taxa had lower emergence in weeks with flood than in weeks with no flood, whereas no taxon had a higher emergence in weeks with flood. Over the seasons, we related insect emergence to seasonal flood frequency and length of hydroperiod. The emergence of most studied taxa decreased with increasing hydroperiod, which suggests that emergence after floods do not compensate for the reduced emergence during floods. Only Culicidae and the aquatic Chironomidae sub-families Tanypodinae and Chironominae showed an increase in emergence with increasing hydroperiod, whereas Staphylinidae peaked at intermediate hydroperiod. We conclude that a hydroperiod covering up to 40% of the vegetation season has a significant negative effect on the emergence of most taxa and that only a few taxa occurring in the temporary wetlands are actually favoured by a flood regime with recurrent and unpredictable floods.

Keywords: flood frequency, hydroperiod, insect emergence, temporary wetlands, wetland insects, wetland management, wet meadows

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Introduction

Aquatic and terrestrial insects are in terms of abundance and biomass important parts of the floodplain fauna (Batzer & Wissinger, 1996; Brooks, 2000), and the emergence of insects from the aquatic environment into the terrestrial environment has a large influence on riparian consumer community

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structure and dynamics (Murakami & Nakano, 2002; Paetzold *et al.*, 2005; Gratton *et al.*, 2008; Jonsson & Wardle, 2009). This nutrient flow, between aquatic and terrestrial systems (Polis *et al.*, 1997; Ballinger & Lake, 2006), is especially important in the large and ecologically diverse floodplains of major rivers (Batzer & Wissinger, 1996; Williams *et al.*, 2004; Williams, 2006).

The biological communities in floodplains are structured by flood frequency, flood amplitude and flood predictability (Junk *et al.*, 1989). Moreover, the recurrently inundated floodplain has a major function in organism production and is important for both the primary and the secondary production (Junk *et al.*, 1989; Junk & Wantzen, 2004). The wetland fauna of temporary waters differs over time, following seasonal and hydrological changes (Williams, 1996) and the response of floodplain insect species to floods largely depend on their respective ecological requirements. Floods may be disastrous for truly terrestrial species living in floodplains, and for those taxa fewer floods and shorter hydroperiods are beneficial (Joy & Pullin, 1997). On the other hand, frequent floods and longer hydroperiod in floodplains have been found to be correlated to higher species richness and diversity, mainly due to increased habitat availability for semi-aquatic and aquatic species (Brooks, 2000). Additionally, the recurrent floods may have a positive effect on population growth rates of the wetland lower fauna in a longer term. With each flood the water brings nutrients to the floodplain wetlands which promote the increase in primary production as well as the production of decomposing organisms in the food web (Wiggins *et al.*, 1980; Wissinger, 1999). This potential positive long-term effect of recurrent floods on terrestrial species, and the need of floods for the development of semi-aquatic species, may result in a peak in both productivity and biodiversity at intermediate flood frequencies. Thus, it is likely that both short-term shifts between floods and droughts, and long-term changes in flood frequency and duration, will affect the floodplain insect composition and production.

In spite of the strong structuring force of recurrent floods on the biota, the majority of the previous studies have only investigated the effect of either the aquatic or the terrestrial phases on the insect productivity and emergence in wetlands, and have not included the relative temporal proportion between wet and dry periods in their analyses of temporary wetlands (Wiggins *et al.*, 1980; Gladden & Smock, 1990; Schneider & Frost, 1996; Wissinger, 1999). In a recent study on insect production from temporary flooded wet meadows and swamps in the River Dalälven floodplains, it was indicated that the flooding pattern is a major structuring force for the insect fauna, and that insect production is reduced during floods (Persson Vinnersten *et al.*, 2010).

The objective of the present study was to analyse the temporal emergence of insects from recurrently but irregularly flooded wetlands in relation to floods during vegetation season in the short term and flood regime (frequency and duration) in a longer term. We hypothesise that insect emergence of all taxa other than the aquatic Culicidae, Chironominae and Tanypodinae will be reduced during floods, that the total annual insect emergence will peak at intermediate hydroperiods and flood frequencies, and that the eventual lower insect emergence during floods will be balanced by an (over)compensation with higher insect emergence following floods.

Methods

Study areas

The full season sampling for emerging insects was carried out during 2002–2007 in six temporary flooded wetlands (four wet meadows and two forested swamps) at the edges of Lake Färnebofjärden, in the River Dalälven floodplains of Central Sweden (see Lundström *et al.* (2010*b*)). The River Dalälven catchment upstream the Lake Färnebofjärden is 27,986 km^2 and includes two main branches (River Västerdalälven and River Österdalälven), that join to form main River Dalälven which flows through the floodplains including several lakes before it reaches the Sea of Bothnia. The catchment has a total of 48 water power stations upstream Lake Färnebofjärden, with all the major regulatory dams within the River Österdalälven branch, whereas the River Västerdalälven branch only contains flow-through power stations. The temporal occurrence, the magnitude and the duration of floods in the floodplains around Lake Färnebofjärden are driven by the combined water flow from the relatively unregulated River Västerdalälven branch and from the regulated River Österdalälven branch, but with higher proportion of the water coming from River Västerdalälven during floods.

The irregular but recurrent increases in the water flow of River Dalälven can induce floods up to four times annually during the vegetation season. The last hydro-electrical power plant before Lake Färnebofjärden, Näs Bruk, has a mean average annual discharge of 309 m^3 s^{-1} and occasionally up to 1500 m^3 s^{-1} has been recorded during the vegetation season in the last decades. Vähäkari (2006) constructed a hydrological model of the Lake Färnebofjärden and showed that the water surface area increased from 30 to 110 km^2 during periods of high flood, thus inducing an approximate four-fold increase in the aquatic-terrestrial interface area. The floods may lead to shallow water covering several thousand hectares of terrestrial environments for a few days up to several weeks.

The six wetlands in the present study are included in a long-term general insect monitoring program to study the ecological effects of *Bacillus thuringiensis* var. *israelensis* (Bti) used for floodwater mosquito control (Persson Vinnersten *et al.*, 2009, 2010; Lundström *et al.*, 2010*a*, *b*). Weeks when Bti was applied against mosquito larvae, and the following weeks, were omitted from the emergence analysis for Culicidae, Nematocera and Diptera, because treatment-based reduction in abundance could influence the results.

Insect sampling and identification

Emerging insects were sampled with cone-formed modified Mundie's emergence traps (bottom area 0.31 m^2) (Lundström *et al.*, 2010*b*). These traps float on the water during floods, and settle on the ground during periods without surface water. Emerged insects were caught in a preservative (97% ethylene glycol) and the traps were emptied once a week and collected insects were stored in 70% ethanol until identification.

Four emergence traps were used annually in each of the six wetlands throughout the vegetation season from May (week 19) to September (week 37) during the 6-year study period. Due to occasional extreme floods covering the whole study area, traps could not be sampled all weeks. In total, traps were sampled 103 times. In addition, some traps could not be sampled at some occasions due to local high flood or trap malfunction. On average, each of the 24 traps was sampled 95 times over the 6-year study period ensuring statistical power for at least moderately abundant taxa (see results). No spring flood occurred before trapping started. The 5-month sampling period probably covers most of the season for insect emergence, as observed from previous studies under similar climate conditions (Neckles *et al*., 1990; Salmela *et al*., 2007). The 6-year seasonal insect sampling during both flood and drought conditions provide a suitable material to perform analyses on. However, emergence traps may under-estimate insect taxa with aquatic adult stages (Davies, 1984), and therefore these taxa were excluded from the analyses.

For statistical analyses, numerical abundance data for insect orders, Diptera sub-orders, the six most abundant Diptera families (Chironomidae, Cecidomyiidae, Ceratopogonidae, Sciaridae, Mycetophilidae and Culicidae), the three most abundant Coleoptera families (Chrysomelidae, Scirtidae and Staphylinidae), and the three most abundant Chironomidae sub-families (Chironominae, Orthocladiinae and Tanypodinae) were used.

Hydrological conditions

In the short term analyses, the distinction between floods (water level ≥5 cm) and droughts (water level <1 cm) was made for each individual traps each week. Weeks with water levels between 1 and 4 cm represent ambiguous conditions and were excluded from the analyses.

In the long term analyses, flood frequency is the number of weekly occasions for each summer season with the water level ≥5 cm under the trap. To be judged as a new flood, the water level had to drop below 1 cm between floods. Hydroperiod is the total number of weeks per summer season with the water level ≥5 cm under the trap and weeks with water levels 1–4 cm under the trap included if they were adjoining a week with water levels ≥5 cm, as it by our definition represents the beginning or the end of a hydroperiod.

Statistical analyses

Power analyses were conducted using the binomial distribution to estimate how large the difference in insect emergence between dry and flood conditions needed to be for detect significant differences ($P < 0.05$) for a given total number of individuals collected (n). In total, there were 1888 records during dry conditions and 579 records of flood conditions. That is, for which x number of emergences during dry condition $x/579$ and $(n-x)/1888$ was significantly different with $P < 0.05$ according to a binomial distribution. To study the effect of flood or drought in the sampling week on insect emergence, we compared the insect emergence between traps from flood and drought conditions in the same wetland. We analysed the number of individuals per taxa for each trap and sampling occasion using generalised linear mixed models in SAS 9.2 (SAS, 2004). Data were fitted to a Poisson distribution with 'Year', 'Week'. 'Wetland type', 'Flood/Drought' and the interactions between 'Flood/Drought' × 'Wetland type', 'Flood/Drought' × 'Year', 'Flood/Drought' × 'Week' as fixed factors. If interaction terms were non-significant ($P > 0.1$) or the model could not converge, the interaction terms were removed from the model. For some groups 'Week' also had to be removed for the model to converge. The repeated measures were modelled by assuming 'Wetland' as a random factor with a lag-1 autoregressive structure with trap as a subject factor (this covariance structure generally produced a better fit than if excluding it). Due to over dispersion, data were scaled, and after scaling the 'χ^2/DF' varied between 0.5 and 2 for all groups. The analysis was performed for three orders, sub-orders and some Nematocera and Coleoptera families and Chironomidae sub-families.

To study the effects of flood frequency, number of floods per year and hydroperiod (total number of weeks with flood conditions >5 cm on insect production during a season), we used the total seasonal catch of a given taxa in a trap as dependent variable in a linear mixed models. Although we used count data here, log-transformed counts [ln(count + 1)] with a linear mixed models generally produced a better fit to data than a Poisson-distribution. The repeated measures were modelled by assuming 'Wetland' as a random factor with a lag-1 autoregressive structure and with trap as a subject factor. 'Wetland type', 'Flood Frequency' and 'Hydroperiod' were fixed factors. We also included the quadrate-terms of 'Hydroperiod' and 'Flood Frequency' to test for non-linearity and possible insect production peaks at intermediate flood frequency or hydroperiod levels. Interaction terms between 'Wetland type' and 'Flood Frequency' and 'Hydroperiod', respectively, were also tested. Variables were removed in a backward manner if insignificant ($P > 0.1$) by removing the variable with highest P-value. Sometimes the linear term was excluded with only the quadratic term left, which means the quadratic term had a better fit to the data and that emergence increased or decreased with hydroperiod or flood frequency without any intermediate peak in emergence.

Results

Power analysis

Over the whole study, and for 1000 individuals there was a 95% probability to find a difference in emergence between 41.4% (782 individuals from 1888 samples), and a 37.7% (218 individuals from 579 samples) under dry and flood conditions, respectively, i.e. a 10% difference in emergence rate. However, for some low abundant taxa relative large difference in emergence rate was required to detect significant differences. For Staphylinidae, with 115 total emergences the corresponding difference in emergence rate has to differ 50% for a 95% probability of detecting differences in emergence between dry and flood conditions.

Insect emergence and composition

Over the 6-year study a total of 137,529 insects were collected in the emergence traps. The wetland insect composition comprised 14 insect orders (Diptera, Coleoptera, Hemiptera, Homoptera, Hymenoptera, Dermaptera, Lepidoptera, Mecoptera, Neuroptera, Orthroptera, Plecoptera, Psocoptera, Blattodea and Trichoptera). Diptera dominated the numerical relative abundances (54 families) with 74.3%, followed by Hymenoptera (16 families) with 18.1%, Coleoptera (21 families) with 4.2% and Homoptera (3 families) with 2.4% (table 1). Insects with aquatic, semi-aquatic larvae and terrestrial adults were well represented,

Table 1. Relative abundances of emerged insects identified to insect order, and for the orders Diptera and Coleoptera to family and for the family Chironomidae also to sub-family. The insects were sampled with emergence traps during flood and drought conditions during May–September, 2002–2007, in the River Dalälven floodplains, Sweden.

Taxonomic level of analysis	Taxa analysed	*N*	%
Order	Coleoptera	5762	4.2
	Hymenoptera	24,865	18.1
	Homoptera	3365	2.4
	Diptera	102,193	74.3
	Other	1344	1.0
	Total	137,529	100
Diptera sub-order	Brachycera	29,021	21.1
	Nematocera	73,172	53.2
	Total	102,193	74.3
Nematocera family	Cecidomyiidae	8618	6.3
	Ceratopogonidae	5311	3.9
	Culicidae	1534	1.1
	Mycetophilidae	3006	2.2
	Sciaridae	31,103	22.6
	Chironomidae	21,392	15.6
	Other	2208	1.6
	Total	73,172	53.2
Coleoptera family	Chrysomelidae	402	0.3
	Scirtidae	3839	2.8
	Staphylinidae	362	0.3
	Other	1159	0.8
	Total	5762	4.2
Chirnomidae sub-family	Chironominae	2920	2.1
	Orthocladiinae	17,441	12.7
	Tanypodinae	1031	0.7
	Total	21,392	15.6

whereas insects with aquatic adult stages (e.g. Corixidae and Dytiscidae) were few and therefore excluded from further statistical analyses.

Flood variation

Number of floods during the vegetation season varied among years ($F_{5,127}=3.1$, $P=0.01$, $N=138$), ranging from on average 0.43 floods per trap in 2007 to 1.26 floods per trap in 2002. The number of floods also varied between wetlands ($F_{5,127}=6.0$, $P<0.001$, $N=138$), ranging from on average 0.33 floods per trap and year in swamps to 1.66 floods per trap and year in wet meadows.

Hydroperiod varied among years ($F_{5,127}=8.8$, $P<0.001$, $N=138$), ranging from on average 0.83 weeks in 2007 to 5.43 weeks in 2002. The hydroperiod also varied between wetland types ($F_{5,127}=18$, $P<0.001$, $N=138$), with average 7.5 weeks (range 0–14 weeks) in wet meadows, and average 0.67 weeks (range 0–9 weeks) in swamps. Since the annual study period during the vegetation season was 19 weeks, the average relative flooding was 39.5% of the season for wet meadows and 3.5% of the season for swamps.

Floods and weekly insect emergence

The insect emergence of all orders except Homoptera decreased in weeks with flood (table 2). Also the Diptera sub-orders Brachycera and Nematocera emergence decreased in weeks with flood as well as the emergence of the Nematocera families' Sciaridae, Chironomidae, Cecidomyiidae and Ceratopogonidae. No taxon showed a significant higher emergence during weeks with flood (note that Culicidae had been excluded in weeks with Bti-treatment).

Table 2. Effects of weeks with flood in the River Dalälven floodplains, Central Sweden, on the emergence of insects by taxonomic orders, sub-orders, families and sub-families. Short term (1 week) *F*- and *P*-values from mixed models and *F*-values in bold denote $P<0.05$. Signs within brackets denote the direction of the associations. $N=2264$ except for Diptera, Nematocera and Culicidae where $N=2213$.

Taxonomic level of analysis	Taxa analysed	Flood	
		F	*P*
Order	Coleoptera	**7.6 (−)**	0.006
	Hymenoptera	**26 (−)**	<0.001
	Homoptera	1.3	0.3
	Diptera	**26 (−)**	<0.001
Diptera sub-order	Brachycera	**30 (−)**	<0.001
	Nematocera	**5.3 (−)**	0.02
Nematocera family	Cecidomyiidae	**7.8 (−)**	0.005
	Ceratopogonidae	**5.9 (−)**	0.02
	Culicidae	1.5	0.2
	Mycetophilidae	1.0	0.3
	Sciaridae	**6.2 (−)**	0.003
	Chironomidae	**5.8 (−)**	0.02
Coleoptera family	Chrysomelidae	3.7 (−)	0.06
	Scirtidae	0.1	0.9
	Staphylinidae	1.9	0.16
Chironomidae sub-family	Chironominae	0.1	0.9
	Orthocladiinae	3.2 (−)	0.07
	Tanypodinae	1.2	0.3

Floods and yearly insect emergence

The insect emergence over the study period decreased significantly with increasing hydroperiod for all orders and sub-orders analysed (table 3). Also for the Nematocera families' Cecidomyiidae, Ceratopogonidae, Sciaridae, the Coleoptera families' Chrysomelidae and Scirtidae, and the Chironomidae sub-family Orthocladiinae total emergence over the study period decreased with increasing hydroperiod (table 3, figs 1 and 2). In contrast, the emergence of the families Culicidae, Chironomidae and its sub-families Chironominae and Tanypodinae increased with increasing hydroperiod (table 3, fig. 2). Staphylinidae was the only insect group for which the total emergence over the study period peaked at intermediate hydroperiod (table 3, fig. 1).

Our analysis of insect emergence in relation to flood frequency showed a significant decrease of Diptera emergence with increasing flood frequency (table 3).

There was a significant interaction between wetland type (wet meadows and swamps) and hydroperiod for the emergence of Chironomidae ($F_{1,118}=21$, $P=0.03$). The total annual emergence of Chironomidae in the swamps, but not in the wet meadows, increased with increasing hydroperiod (table 3, fig. 1).

Discussion

Insect emergence in temporary flooded wet meadows and swamps in relation to hydroperiod supported the

Table 3. Long-term effects of hydroperiod and flood frequency in the River Dalälven floodplains, Central Sweden, on the emergence of insects by taxonomic order, sub-order, family and sub-family. *F*- and *P*-values from mixed models and *F*-values in bold $P < 0.05$. Signs within brackets denote the direction of the associations. $N = 138$ except for Culicidae $N = 114$.

Taxonomic level of analysis	Taxa analysed	Hydroperiod		Hydroperiod^2		Flood frequency		Flood frequency^2	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Order	Coleoptera	0	1	**9.2 (–)**	0.05	0.3	0.6	0.4	0.5
	Hymenoptera	**14 (–)**	<0.001	3.5 (+)	0.06	0.1	0.8	0	1
	Homoptera	**5.1 (–)**	0.03	0.8	0.4	0.3	0.6	0.5	0.5
	Diptera	0.1	0.8	**5.2 (–)**	0.03	**4.6 (–)**	0.03	0	1
Diptera sub-order	Brachycera	**33 (–)**	<0.001	1.1	0.3	0.01	0.8	0.1	0.8
	Nematocera	**7.1 (–)**	0.001	0.01	0.9	1.5	0.2	0	1
Nematocera family	Cecidomyiidae	**74 (–)**	<0.001	1.2	0.3	0.01	0.9	1.5	0.2
	Ceratopogonidae	0.1	0.8	**4.6 (–)**	0.03	0.2	0.6	0.4	0.5
	Culicidae	**8.3 (+)**	0.005	3.3 (–)	0.07	0.6	0.4	0.02	0.9
	Mycetophilidae	0	1	**5.6 (–)**	0.03	2.5	0.11	0.6	0.4
	Sciaridae	**18 (–)**	<0.001	2.8 (+)	0.10	0.6	0.4	0	1
	Chironomidae	**6.8**[1] **(+)**	0.01	1.2	0.3	0.5	0.5	0.02	0.9
Coleoptera family	Chrysomelidae	**8.9 (–)**	0.004	3.3 (+)	0.07	0.2	0.6	0.6	0.4
	Scirtidae	0.1	0.7	**8.2 (–)**	0.005	1	0.3	0.2	0.7
	Staphylinidae	**8.3 (+)**	0.005	**9.2 (–)**	0.003	0.6	0.4	0.1	0.8
Chironomidae sub-family	Chironominae	2.0	0.16	**57 (+)**	<0.001	0.03	0.8	1.9	0.2
	Orthocladiinae	0.02	0.9	**5.8 (–)**	0.02	0.2	0.7	0	1
	Tanypodinae	**41 (+)**	<0.001	2.6	0.11	1	0.3	0.03	0.9

[1] There was an interaction between Hydroperiod and Habitat, $F = 4.6$, $P = 0.03$, see fig. 2.

hypothesis that water itself hinders the emergence of many insect taxa, as an increased hydroperiod significantly reduced the emergence of most taxa. Thus, our results do not provide strong support for the often suggested positive effects of recurrent floods on the production of insects (Junk *et al.*, 1989; Poff, 2002), neither in the short term nor in the long term. We found that floods in the River Dalälven floodplains occurred irregular during the vegetation season with alternate wet and dry years. The response of lower insect emergence to flood conditions and increased hydroperiod may be due to the fact that the wet meadows and swamps surrounding the River Dalälven floodplains most of the year are in a terrestrial state, and thus mainly produce insects adapted to terrestrial conditions. Hence, we observed a reduced emergence of mainly terrestrial insect taxa, e.g. Homoptera, Hymenoptera and most Coleoptera families, in relation to floods and hydroperiods. Diptera was the only taxon with lower emergence in relation to both flood frequency and hydroperiod. Several Diptera families that occur frequently in temporary flooded habitats (e.g. Ephydridae, Sphaeroceridae, Sciomyzidae, Syrphidae, Sarcophagidae and Chloropidae) (Wissinger, 1999; Keiper *et al.*, 2002) have evolved physiological or behavioural mechanisms to cope with floods and droughts (Drake, 2001). However, most wetland Diptera, except larvae of truly aquatic Chironomidae, Ceratopogonidae, Chaoboridae and Culicidae species, are restricted to water margins with relatively shallow water due to the need of their larvae to breathe atmospheric oxygen (Drake, 2001). Floodplains are inhabited by a wide range of species adapted to either the aquatic or the terrestrial phases, and whereas the aquatic species colonise the wetlands during floods the terrestrial species inhabit the floodplain during droughts. Consequently, immigrating species from non-flooded uplands may suffer high mortality during unpredictable flood pulses (Adis & Junk, 2002; Rothenbücher & Schaefer, 2006), and the floods may also act as a hinder on the development of species adapted to terrestrial conditions (Junk *et al.*, 1989). Our results are in accordance with Neckles *et al.* (1990), which found that semi-permanent flooding dramatically reduced dominant invertebrate taxa. Thus, the length of hydroperiod in temporary flooded wetlands seems to negatively affect the emergence of both the terrestrial and aquatic wetland insect fauna.

The anticipated peak in insect emergence at intermediate hydroperiods was only found for the Coleoptera family Staphylinidae, and possibly in the flood specialist Culicidae (table 3, figs 1 and 2). There are several possible reasons to why we do not find this pattern among more taxa. Several taxa in the emergence trap material probably consist of truly terrestrial species for which increased flood conditions are unfavourable. On the other hand, the Chironomidae sub-families Chironominae, Tanypodinae together with Culicidae had an overall increase of emergence in relation to hydroperiod. These taxa have aquatic or semi-aquatic larvae, and especially floodwater mosquitoes are well adapted to recurrent floods with short hydroperiods, and they can be extremely abundant in the River Dalälven floodplains (Schäfer & Lundström, 2006; Schäfer *et al.*, 2008). Primary production in floodplains is usually high due to nutrient exchange between the aquatic and terrestrial phases in the moving littoral zone (Junk *et al.*, 1989; Junk & Wantzen, 2004). This may further benefit floodwater mosquito production since their larvae are filter feeders of protozoans in shallow water (Östman *et al.*, 2008). However, mosquitoes may emerge several days after the water has receded (Schäfer & Lundström, 2006), and thus may not be efficiently sampled by emergence traps. It is also important to point out that the Culicidae analyses were based on fewer weeks due to Bti applications, which could have had implications on the result. Moreover, a flood early in the season with a short

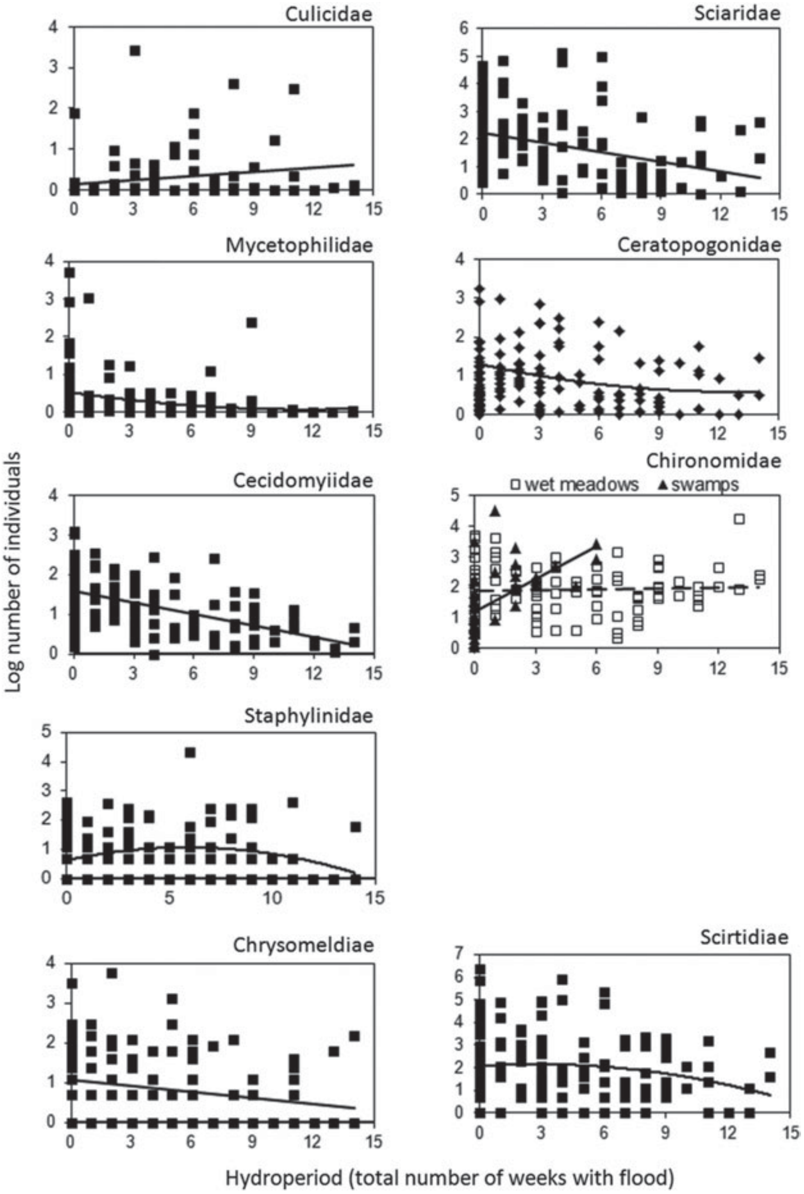

Fig. 1. Insect emergence of Nematocera and Coleoptera families in relation to hydroperiod, based on weekly emergence trap catches May–September 2002–2007. For Chironomidae, we show emergence for wet meadows and forested swamps separately to illustrate the differences in production between wetland types due to significant interactions (open boxes and dashed lines = wet meadows; closed triangles and bold lines = swamps). For the other families there were no interactions and all wetlands are included (closed boxes). Insect numbers in the figure are $\log_n$-transformed.

hydroperiod may be sufficient to trigger insect development and emergence of e.g. Orthocladinae. This Chironomidae subfamily has a large portion of terrestrial and semi-terrestrial species that seems to be favoured by hydroperiods up to 6 weeks, whereas longer hydroperiods may act harmful on their emergence. Another reason why emergence peaks at intermediate hydroperiod were absent, may be a lack of statistical power. Flood and drought conditions are not the only factors trigging insect emergence, since other factors such as temperatures and timing of flood may be of importance, and may mask the relationship between hydroperiod and emergence over the season.

The reduced annual insect emergence in relation to increased hydroperiod provided no evidence for an overcompensation of insect emergence following a flood (table 3, figs 1 and 2).

Diptera and Hymenoptera were the orders with the highest relative abundance (table 1), and both had significant reduced number of emerged insects in relation to hydroperiod. However, within Diptera this reduction was not

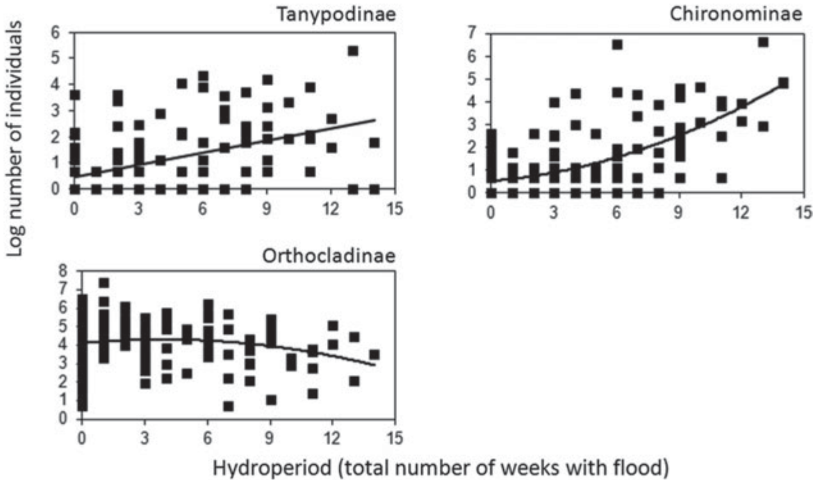

Fig. 2. Insect emergence of three Chironomidae sub-families, Tanypodinae, Chironominae and Orthocladinae, in relation to hydroperiod based on weekly emergence trap catches May–September 2002–2007. Insect numbers in the figure are log$_n$-transformed.

consistent across taxonomic groups. The Diptera sub-order Brachycera and the Nematocera family Cecidomyiidae were both relative abundant (table 1) and had the strongest negative effect of increased hydroperiod. Although the relative less abundant sub-families Chironominae and Tanypodinae of the Chironomidae family were the taxonomic groups that showed the strongest positive effect of increased hydroperiod. In general, when excluding Culicidae it seems that floods have adverse effects on the number of insect emerging of the most abundant taxa occurring in the temporary wetlands of the River Dalälven floodplains, whereas positive effects were only detected for some less abundant taxa. These results contrast with investigations focused on floods as natural disturbances in floodplains, leading to high primary productivity that can be exploited by a wide range of organisms (Junk *et al.*, 1989; Poff, 2002). However, seasonal floods in the River Dalälven occur unpredictably, partly due to the last century's water regulations and it seems that the present flood regime in the River Dalälven favours opportunistic species that cope with these unpredictable flood events (Lundström *et al.*, 2010*a*) while truly flood or drought specialist species are disfavoured.

Using emergence traps to investigate insect composition, emergence and production of insects from aquatic environments is a well-established method (Stagliano *et al.*, 1998; Petersen *et al.*, 1999; Paetzold & Tockner, 2005). However, emergence traps are less suitable for catching insects which spend most of their adult stage in the water or for other explanations avoid the traps (Davies, 1984). As a consequence of this, certain aquatic insect taxa may be underrepresented including dragonflies, diving beetles and scavenger beetles. One reason for the inefficiency to catch these taxa in emergence traps is that they have aquatic larvae that crawl out of the water before reaching imagines. Moreover, there could be specific life history traits explaining why e.g. dragonflies rarely are caught in emergence traps. Northern *Lestes spp*. and *Sympetrum spp*. species, that frequently are found in temporary waters, need more than 6 weeks of uninterrupted hydroperiod to complete their larval stages (Corbet, 1999), and a continuous hydroperiod of such length rarely occur in the River Dalälven floodplains, and not once during the 6 years study period. Aquatic Coleoptera that includes Dytiscidae and Hydrophilidae can reach high abundances during floods in the River Dalälven floodplains (Persson Vinnersten *et al.*, 2009), but are likewise rarely caught in emergence traps. The reason for this could be that most aquatic Coleoptera are good swimmers and their activity makes them difficult to be caught in the traps, either by active avoidance or for other unknown reasons.

In the present study, we observed that emergence of most insect taxa from irregularly and temporary flooded floodplain wetlands are mainly dependent on terrestrial conditions, with the exception of a few flood specialist or aquatic taxa. The findings are important in regard to wetland restoration since one of the main issues in floodplain wetland restoration is the re-establishment of a natural flood pulse (Poff *et al.*, 1997). Our findings indicate that increasing the flood magnitude and hydroperiod will change the insect fauna composition, lead to a decrease of terrestrial insect taxa as the floodplains subsequently may be inhabited by more flood tolerant taxa. Finally, because of mosquito control activity in the area, we omitted any mosquito emergence data from the analysis that could have been affected, reducing the ability to detect a relationship between floods and mosquitoes. However, from other studies (Merdic & Lovakovic, 2001; Schäfer *et al.*, 2008; Balenghien *et al.*, 2010) it is obvious that total annual emergence of nuisance floodwater mosquitoes will increase with increasing number of floods during the vegetation season.

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