Seasonal changes in caddisfly larval assemblages in river-floodplain habitats along a connectivity gradient

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Abstract

In order to assess the impact of connectivity on the ecological values of Lower Rhine river floodplain habitats we studied the seasonal variation in diversity and species assemblages of caddisfly larvae by monthly sampling the littoral zone of four water bodies over a lateral connectivity gradient. Seasonal variation in diversity showed a general pattern in floodplain habitats, which could be related to differences in caddisfly life history and habitat preferences. Highest species numbers of Limnephilidae and Psychomiidae were found in winter and spring, whereas Leptoceridae, Hydroptilidae, Phryganeidae and Polycentropodidae showed highest species richness during summer. Hydropsychidae species richness was very low and did not vary much over the year.

Despite seasonal fluctuations in the occurrence and abundance of individual species, caddisfly species assemblages in the water bodies appeared to be rather stable and could be firmly related to the position of their habitats over the connectivity gradient. The eupotamon (lotic habitat) was clearly separated from the lentic habitats, and the sparsely vegetated plesiopotamon from the well vegetated paleopotamon, indicating the overall importance of connectivity, flow velocity and vegetation development for species assemblages. Hydropsychidae and Psychomiidae have been found in the eupotamon exclusively, whereas Limnephilidae, Phryganeidae, Hydroptilidae and Polycentropodidae have been found predominantly in paleopotamon habitats. Leptoceridae have been found in all habitats, although individual species showed preference for certain habitats. It can be concluded that the impact of connectivity outweighed the impact of season on the caddisfly larvae species assemblages. Hence caddisfly larvae are good indicators which can well be used for ecological quality assessment in hydrological different floodplain habitats. Overall, species richness was highest during summer, however, in order to get a complete species list, caddisfly larvae sampling should be done during spring and summer.

Key-words: biodiversity, seasonality, Trichoptera, connectivity gradient, wetlands, Rhine

Introduction

Trichoptera are a major component of the insect fauna of natural rivers and an essential part of the river food-web (Mackay & Wiggins, 1979). Due to their high species richness and their large variety in species

specific traits they are useful indicators for the ecological monitoring and assessment of river ecosystems (e.g. Chantaramongkol, 1983; Graf et al., 2006). Under natural conditions, floodplain ecosystems frequently harbour numerous water bodies which are characterized by a high spatial and temporal heterogeneity (Amoros et al., 1987), giving rise to a high caddisfly species diversity (Tachet et al., 1994). Over the years, caddisfly species assemblages have been examined for several large European rivers, such as the Rhine, Meuse, Rhone, Danube, Neman, Bug, sometimes as part of monitoring programmes, and mostly concern light trap catches of adults (Chantaramongkol, 1983; Van Urk et al., 1991; Tachet et al., 1994; Czachorowski, 2004; Serafin, 2004; Graf et al., 2006). Surprisingly, studies on the seasonal changes in species composition of caddisfly larvae in riverine floodplain ecosystems are extremely rare. Such information however may be necessary if we wish to conserve or rehabilitate these ecosystems.

In order to assess the impact of connectivity on the ecological integrity of aquatic habitats in the Lower Rhine floodplains, we studied the spatio-temporal variation in species diversity and species assemblages of caddisfly larvae over the whole lateral connectivity gradient. In an earlier study on macroinvertebrate species assemblages in the Lower Rhine river ecosystem (Van den Brink et al., 1994) we found caddisfly species indicative for hydrological different types of floodplain water bodies. In Van den Brink et al. (accepted) we extended the connectivity gradient by including the lotic component of the floodplain ecosystem. Here we test the relative importance of spatial versus seasonal variation in floodplain habitats for the occurrence and abundance of species of caddisfly larvae.

Methods

Study sites

Seasonal fluctuations in occurrence and relative abundance of caddisfly larvae in Lower Rhine floodplain habitats along a lateral hydrological connectivity gradient (eupotamon, plesiopotamon, paleopotamon and paleopotamon-isolated; typology according to Amoros et al., 1987) were studied during 1991 (for situation of sampling sites see Van den Brink et al., 1994). A characterization of the study sites is given in Table 1.

Sampling methods

In the Lower Rhine river channel (eupotamon) artificial substrates were monthly sampled (De Pauw et al., 1994) using standard procedures of the Dutch Institute for Inland Water Management and Waste Water Treatment (Rijkswaterstaat/RIZA, Lelystad, The Netherlands). In three hydrologically different floodplain water bodies (plesiopotamon, paleopotamon and paleopotamon-isolated) the littoral zone was monthly sampled with a dip-net (Van den Brink et al., 1994). In order to analyze the importance of littoral substrate on the occurrence of caddisfly larvae and in order to get a nearly complete picture of caddifly larvae species composition, one site with a sandy-mineral substrate and one site with a clayey-organic substrate was selected in each water body for monthly sampling over one year. The net was quickly pushed through the upper 2 cm of the sediment over a randomly selected surface of approximately 2 m^2. From April to November, during the growth season, when vegetation was present in the selected habitats, sampling occurred between patches of submerged, nymphaeid and marsh vegetation, avoiding sampling of vegetation, although vegetational debris was collected this way. At high water levels sampling was done with the same net by pushing the net through the sediment, using a rubber boat. Wooden fences in the landscape, close to the sampling sites, were used as orientation marks, so that the same areas could be recognized and sampled even in times of floods. All samples were put in plastic bags which were kept cool and transported to the laboratory. After washing over a 500 m mesh sieve the caddisfly larvae were preserved in 70% ethanol, identified and counted.

Environmental parameters

In order to relate the occurrence of caddisfly species to environmental parameters the following data were recorded for each water body: current velocity, water level fluctuation, connectivity duration, relative abundance of aquatic and marsh vegetation and the chlorophyll-a content of the water column. Hydrological parameters were obtained from Rijkswaterstaat/RIZA. The degree of connectivity, here represented by the connectivity duration between the sites and the main channels, was calculated from floodplain elevation maps and long-term (1901-1990) river water level data. The lowest water level of the river at which the floodplain lake becomes connected with the main channel was estimated for each water body. From that the long-term average number of days per year on which the water level in the main channel exceeded the connection level during the year was calculated.

The relative abundance of aquatic and marsh vegetation was recorded via an estimation of the percentage coverage of aquatic macrophytes and helophytes within two representative 3 x 3 m plots per water body.

Data analysis

Caddisfly diversity for each of the river-floodplain habitats was expressed in terms of species diversity (H_q) and species richness (N). Species diversity was calculated according to Shannon, as: $H_q = -n\,p_i*\ln(p_i)$ with p_i as the proportion of species i in the total number of species per sample per habitat type. Species richness was calculated as the total number of observed species during sampling per habitat type, and presented as the total number of observed species per family during sampling per habitat type.

Redundancy analysis (RA), a direct gradient analysis according to a linear response model (as the gradient length was found to be short), was used in order to ordinate the caddisfly species abundances (standardized values) along habitats and season and to analyze the importance of environmental parameters (standardized values) along which the species and habitats were plotted.

Caddisfly species abundances were standardized according to the following scale: 0 = 0, 1 = 1, 2 = 2-3, 3 = 4-8, 4 = 9-17, 5 = 18-34, 6 = 35-67, 7 = 68-132, 8 = 132-261, 9 = > 261 specimens per m^2.

Hydrological parameters were classified as follows: connectivity duration (CONN): 0 = 0 $d.y^{-1}$; 1 = 1-5 $d.y^{-1}$; 2 = 6-20 $d.y^{-1}$; 3 = 21-120 $d.y^{-1}$; 4 = >120 $d.y^{-1}$; and current velocity (CURR): 0 = 0 $m.s^{-1}$; 1 = 0-0.5 $m.s^{-1}$; 2 = 0.5-1.0 $m.s^{-1}$; 3 = 1.0-1.5 $m.s^{-1}$. Water level fluctuation (LEVL) was recorded as the difference between maximum and minimum water level recorded during the sampling year. Water temperature (TEMP) and chlorophyll-a (CHLA) were log-transformed. Microhabitat parameters, such as the vegetational abundance of aquatic macrophytes (AQVE) and helophytes (MAVE) were divided into classes: 0 = absent, 1 = coverage < 10%, 2 = coverage between 10 and 50%, 3 = coverage > 50% within the 3 x 3 m plots.

Results

The diversity of caddisfly larvae in the four Lower Rhine floodplain habitats over a lateral connectivity gradient (Fig. 1) shows large fluctuations during the year. However, certain spatial and seasonal trends

can be distinguished. Generally, highest peaks in diversity occur in the habitats with a low connectivity (paleopotamon and paleopotamon-isolated) and lowest in the habitats with a high degree of connectivity (eupotamon and plesiopotamon). Over the year, highest diversity occurs in the periods March-May and July-October and lowest diversity in the periods June-July and December-January in all four habitats. The fluctuations in species richness roughly follow this diversity pattern (Fig. 2). Moreover, a clear seasonality for most caddisfly families can be observed. In the eupotamon Psychomyiidae, Hydroptilidae and Leptoceridae have been observed during spring only, just as the Limnephilidae in the plesiopotamon, paleopotamon and paleopotamon-isolated habitats. In the latter two habitats Phryganeidae and Hydroptilidae have been collected during summer only. In contrast to this, Leptoceridae have been found during the whole year in all three sampled lentic habitats.

An ordination of seasonal variation in relative abundance of caddisfly species in the four floodplain habitats over a connectivity gradient (Fig. 3) shows that the eupotamon, plesiopotamon, paleopotamon and paleopotamon-isolated habitats are all well separated, indicating that the impact of spatial variation is larger than the impact of temporal variation on the occurrence and abundance of caddisfly species. Characteristic species of the eupotamon are *Hydropsyche contubernalis, Ecnomus tenellus, Ceraclea dissimilis* and *Psychomyia pusilla*, whereas *Oecetis ochracea* can be regarded as a typical species of the plesiopotamon. Species like *Limnephilus decipiens, L. lunatus* and *L. affinus* have been found to occur predominantly in the paleopotamon, whereas *Molanna angustata, Mystacides nigra* and *Anabolia nervosa* have been collected most frequently in the paleopotamon-isolated habitat. Related environmental parameters to these floodplain habitats are current velocity, being highest in the eupotamon; chlorophyll-a and water level fluctuations showing highest levels in the eupotamon and plesiopotamon; and aquatic and marsh vegetation showing highest abundances in the paleopotamon and paleopotamon-isolated habitats (Fig. 3; Table 1).

An ordination of caddisfly larval abundance in three floodplain waters in relation to season and microhabitats (Fig. 4) shows that highest abundances of species of Limnephilidae (*Limnephilus decipiens, L. affinis, L. lunatus* and *Anabolia nervosa*) have been found during late winter and early spring. These species have been found to occur predominantly in the extensive helophyte stands (*Phragmites australis, Typha angustifolia, Scirpus lacustris*) in paleopotamon habitats (see also Table 1). Species belonging to

the Leptoceridae (*Oecetis furva, O. lacustris, Triaenodes bicolor, Athripsodes aterrimus*), Hydroptilidae (*Agraylea sexmaculata, A. multipunctata, Oxyethira flavicornis*) and Polycentropodidae (*Cyrnus crenaticornis, C. flavidus*) showed their highest abundances in late summer and early autumn, and were positively correlated with vegetation coverage (Fig. 4). In contrast to this, *Hydropsyche contubernalis, Oecetis ochracea, Mystracides longicornis* and *M. nigra*, being the most dominant species in the Lower Rhine habitats, were present in the samples during the whole year. Although present in all the three lentic floodplain water bodies, the maximum abundance of *Mystacides longicornis* has been found to decrease with increasing connectivity, and has not been found at all in the main channel.

With respect to microhabitats in the floodplain lakes, species such as *Oecetis ochracea, Mystacides longicornis, M. nigra, Molanna angustata, Limnephilus lunatus* and *Anabolia nervosa* have been found on sandy, mineral (psammon) microhabitats mainly, whereas species such as *Oecetis furva* and *Triaenodes bicolor* have been related to clayey, organic (pelon) microhabitats (Fig. 4).

Discussion

Seasonal variation in caddisfly larvae diversity showed a general pattern, with peaks in March-May and September (Fig. 1), which could be clearly related to the occurrence of Limnephilidae in winter/spring and Leptoceridae, Hydroptilidae, Phryganeidae and Polycentropodidae in summer (Fig. 2). Limnephilidae species appeared some weeks after inundation of the extensive helophyte stands in the paleopotamon habitats during winter and spring floods (Van den Brink et al., 1994). During these floods egg packages of these species came into contact with water, probably giving the trigger for hatching. These helophyte stands in the paleopotamon habitats may be regarded as temporal habitats, since they usually fall dry during the summer months. Limnephilidae are typical inhabitants of such temporal habitats (Otto, 1981; Waringer & Graf, 2002; Serafin, 2004). The occurrence and abundance of Polycentropodidae, Hydroptilidae and Phryganeidae larvae was correlated with the seasonal development of aquatic macrophytes, mainly of the extensive nymphaeid macrophyte stands in the paleopotamon habitats. The most abundant species, i.e. *Cyrnus crenaticornis* and *C. flavidus*, deposit their eggs underneath the floating leaves of nymphaeids (Van der Velde & Bergers, 1987), whereas the observed species of Hydroptilidae and Phryganeidae are related to aquatic vegetation as a habitat for food and/or material for

case building (Higler, 2005; Schmidt-Kloiber & Hering, 2008). The seasonal differences in occurrence are in agreement with earlier observations on life cycles and flight periods of these species (Sommerhäuser et al., 1997; Higler, 2005; Schmidt-Kloiber & Hering, 2008). Moreover, a similar pattern in diversity fluctuations during the summer period has been observed for caddisfly imagines in a Lower Rhine floodplain water body (paleopotamon habitat), which was also related to life cycles and flight periods of several of the same species involved (Van der Velde & Bergers, 1987).

The impact of spatial variation in the distribution of species over the lateral floodplain connectivity gradient outweighed the impact of season on the caddisfly larvae species assemblages (Fig 3). Hence caddisfly larvae appear to be good ecological indicators of hydrologically different floodplain habitats, separating the lotic habitats from the lentic ones and the connected and frequently flooded habitats from the isolated ones. As such they can well be used for ecological quality assessment in hydrologically different floodplain habitats (Tachet et al., 1994; Graf et al., 2006; Van den Brink et al., accepted). Lotic species belonging to the Hydropsychidae and Psychomyiidae have been found in the eupotamon habitats exclusively, with *Hydropsyche contubernalis* being the most dominant species there, a situation which was also observed in the natural Neman river (Czachorowski, 2004) and the Danube river (Chantaramongkol, 1983). Species belonging to Limnephilidae*,* Polycentropodidae, Phryganeidae and Hydroptilidae have been found predominantly in the well vegetated lentic paleopotamon habitats. Their absence in the eupotamon and plesiopotamon habitats of the Lower Rhine may be well explained by the absence of extensive helophyte and nymphaeid macrophyte (*Nuphar lutea, Nymphaea alba)* stands there. Leptoceridae have been found to occur in all habitats, although most species were highly characteristic, e.g. *Ceraclea dissimilis* occured on stones in the eupotamon only, *Oecetis ochracea* was found as a typical inhabitant of the sand flats in the plesiopotamon habitats, whereas *Oecetis furva* and *Triaenodes bicolor* were mainly found on the organic substrates in the well-vegetated paleopotamon habitats (Figs 2, 3), a preference which could be clearly related to the material of the cases of these species.

In the Lower Rhine a total number of 38 caddisfly species has been found as larvae, which is substantial lower as observed in more natural European rivers (Tachet et al., 1994; Czachorowski, 2004; Serafin, 2004; Graf et al., 2006), mainly due to the poor habitat variation in the Lower Rhine main channel (Van

Urk et al., 1991; Van den Brink et al., 1996). Despite this impoverishment, the general pattern of caddisfly family distribution over the lateral connectivity gradient along the Lower Rhine shows much resemblance with those in the Danube, the Rhône, and the Neman (Tachet et al., 1994; Czachorowski, 2004; Graf et al., 2006), with the same or related species occurring in similar habitats (Van den Brink et al., accepted).

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Figure legends

Fig. 1. Seasonal variation in caddisfly larval diversity (Hq= Shannon-index) in four river-floodplain habitats (EU= eupotamon, PLE= plesiopotamon, PAL= paleopotamon, PALi= paleopotamon isolated) over a lateral connectivity gradient along the Lower Rhine.

Fig. 2. Seasonal variation in caddisfly larval species numbers (per family) in four river-floodplain habitats (A: eupotamon, B: plesiopotamon, C: paleopotamon, D: paleopotamon isolated) over a lateral connectivity gradient along the Lower Rhine.

Fig. 3. Ordination of caddisfly larvae (relative abundance data) in four floodplain habitats (EU= eupotamon, PLE= plesiopotamon, PAL= paleopotamon, PALi= paleopotamon isolated) over a lateral connectivity gradient along the Lower Rhine in relation to season and environmental parameters (AQVE= Aquatic vegetation coverage, CHLA= chlorophyll-a concentration, CONN= connectivity duration, CURR= current velocity, LEVL= water level fluctuation, MAVE= marsh vegetation coverage, TEMP= temperature). For explanation of species codes see table 2.

Fig. 4. Ordination of caddisfly larval species abundance in three floodplain lakes along the Lower Rhine (PLE= plesiopotamon, PAL= paleopotamon, PALi= paleopotamon isolated) in relation to season, temperature (TEMP), vegetational coverage (VEG), and pelon and psammon microhabitats. For explanation of species codes see table 2.

Fig. 1.

Fig. 2.

Fig. 3.
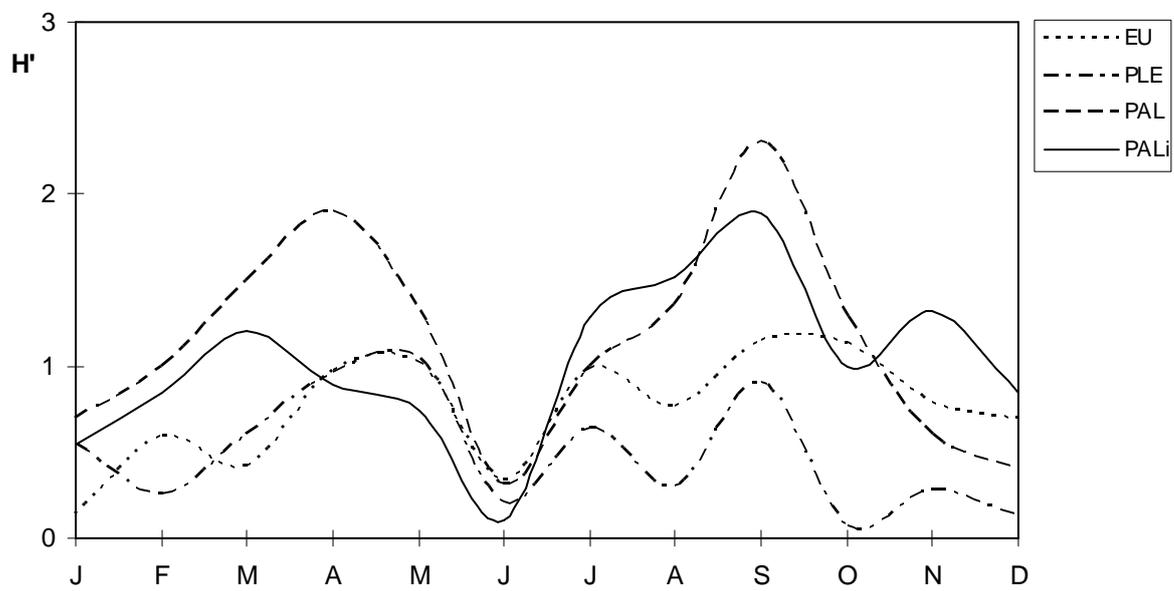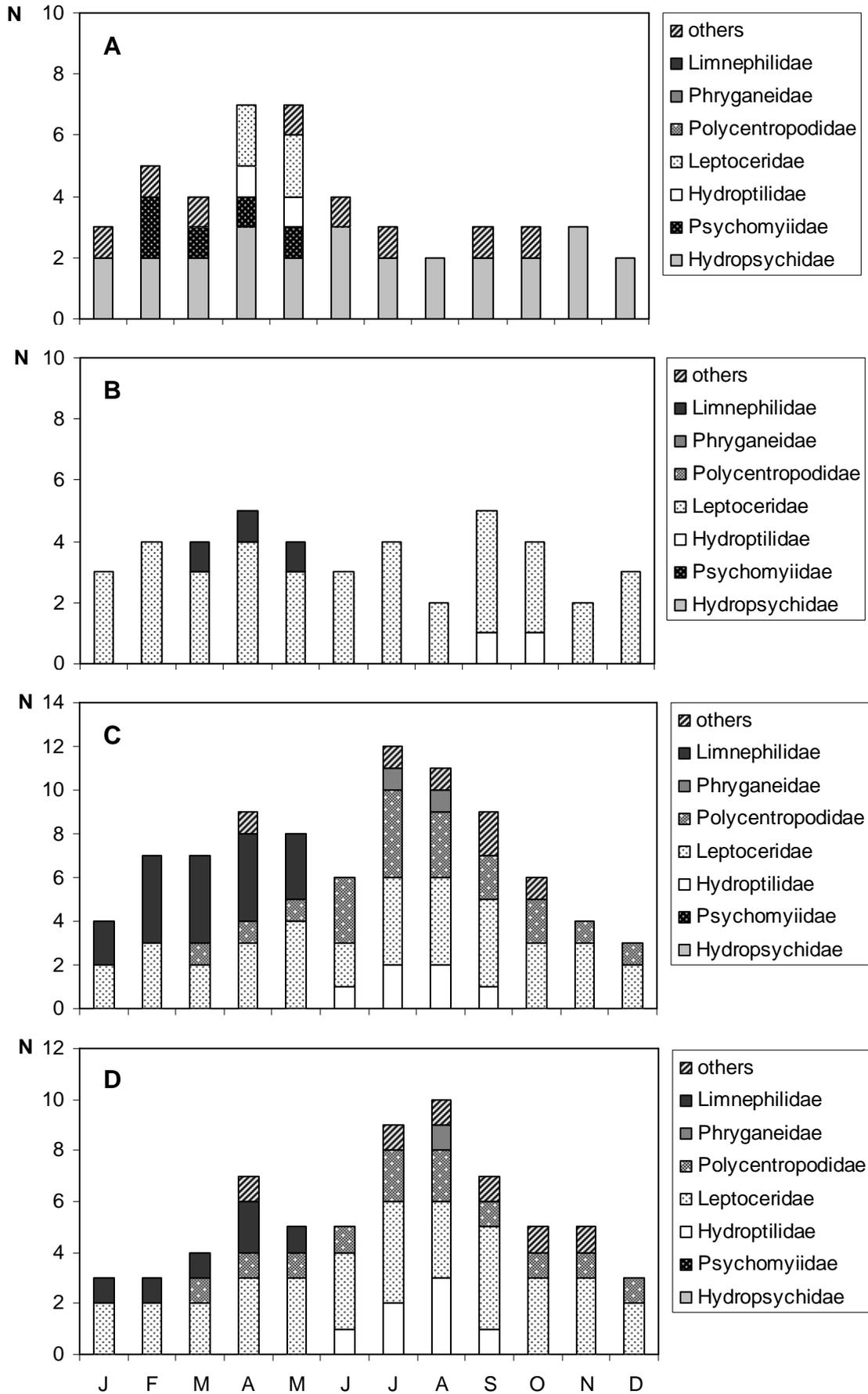
Fig. 4.
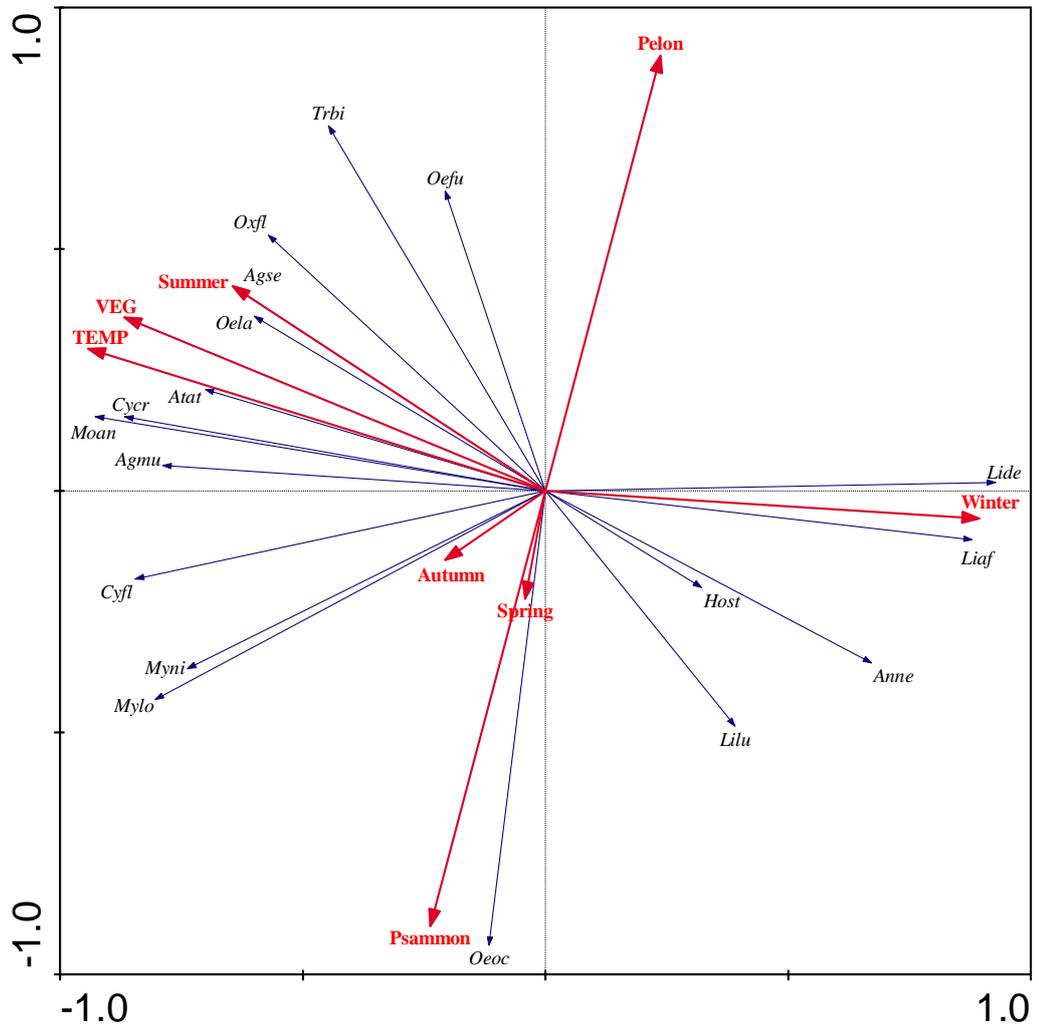
Table 1. Characterization of four Lower Rhine floodplain habitats over a lateral connectivity gradient. For physico-chemical parameters annual mean values (± S.D.) are presented.

Parameter	eupotamon	plesiopotamon	paleopotamon	paleopotamon-isolated
Connectivity duration (day.yr^{-1})	365	90	1	0
Water level fluctuation (m)	5	3	2	1
Current velocity (m.s^{-1})	1.5	0	0	0
pH	7.8 (0.1)	8.1 (0.5)	7.9 (0.2)	8.0 (0.2)
Calcium (mmol.l^{-1})	1.7 (0.2)	1.1 (0.3)	1.4 (0.2)	1.2 (0.4)
HCO_3^- (mmol.l^{-1})	2.2 (0.2)	1.8 (0.3)	2.3 (0.2)	2.8 (0.4)
Cl^- (mmol.l^{-1})	4.4 (1.5)	2.6 (0.5)	2.0 (0.4)	1.7 (0.2)
Total-N (mol.l^{-1})	330 (50)	150 (130)	90 (100)	30 (30)
Dissolved P (mol.l^{-1})	1.4 (0.4)	0.9 (0.7)	0.3 (0.4)	0.1 (0.01)
Chlorophyll-a (g.l^{-1})	20 (10)	50 (40)	10 (5)	5 (5)
Organic matter sediment (%)	1	5	20	10
Major substrate	sand, stones	sand	sand-silt	sand-silt
Coverage aquatic vegetation (%)	0	10-50[1]	> 50[2]	> 50[3]
Coverage marsh vegetation (%)	0	< 10[4]	> 50[5]	> 50[6]

Aquatic vegetation species composition:

[1]: *Nymphoides peltata, Potamogeton pectinatus*

[2]: *Nuphar lutea, Nymphaea alba, Nymphoides peltata, Ranunculus circinatus, Potamogeton lucens, P. pectinatus Fontinalis antipyretica*

[3]: *Nuphar lutea, Nymphaea alba, Elodea nuttalli, Ranunculus circinatus, Potamogeton crispus, P. lucens, P. pectinatus, P. perfoliatus, Chara vulgaris, Ch. globularis, Hippurus vulgaris, Fontinalis antipyretica*

Marsh vegetation species composition:

[4]: *Carex acuta, Phalaris arundinacea*
[5]: *Glyceria maxima, Phragmites australis, Scirpus lacustris, Typha angustifolia*
[6]: *Phragmites australis, Typha latifolia, Hippurus vulgaris*

Table 2. Total species list of caddisfly larvae which have been collected during this study.
*species codes used in figures 3 and 4.

Taxon name	Taxon code*
Hydropsyche contubernalis McLachlan	Hyco
Hydropsyche bulgaromanorum Malicky	
Hydropsyche exocellata Dufour	
Ecnomus tenellus (Rambur)	Ecte
Hydroptila spec.	
Agraylea multipunctata Curtis	Agmu
Agraylea sexmaculata Curtis	Agse
Oxyethira flavicornis (Pictet)	Oxfl
Holocentropus dubius (Rambur)	
Holocentropus picicornis (Stephens)	
Holocentropus stagnalis (Albarda)	Host
Cyrnus crenaticornis (Kolenati)	Cycr
Cyrnus flavidus McLachlan	Cyfl
Cyrnus trimaculatus (Curtis)	
Neureclipsis bimaculata (L.)	
Psychomyia pusilla (Fabricius)	Pspu
Tinodes waeneri (L.)	
Molanna angustata Curtis	Moan
Agrypnia pagetana Curtis	
Phryganea bipunctata Retzius	
Phryganea grandis L.	
Ceraclea annulicornis (Stephens)	
Ceraclea dissimilis (Stephens)	Cedi
Ceraclea senilis Burmeister	
Athripsodes aterrimus (Stephens)	Atat
Mystacides azurea L.	
Mystacides longicornis L.	Mylo
Mystacides nigra (L.)	Myni
Oecetis furva Rambur	Oefu
Oecetis lacustris Pictet	Oela
Oecetis ochracea (Curtis)	Oeoc
Oecetis testacea (Curtis)	
Triaenodes bicolor (Curtis)	Trbi
Anabolia nervosa (Curtis)	Anne
Limnephilus affinis Curtis)	Liaf
Limnephilus decipiens Kolenati	Lide
Limnephilus lunatus Curtis	Lilu
Limnephilus rhombicus (L.)	