Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany: A multivariate study

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Abstract Benthic insect communities (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) were studied together with water temperature and environmental parameters in streams between June 2000 and June 2001. The sampling area consisted of 20 sites in small and medium-sized streams located in the lower mountainous area of Central Europe. Temperature was recorded nearly continuously and several physicochemical and environmental variables were assessed. Macroinvertebrates were sampled both in spring and summer. Data-sets of species abundance and occurrence were analysed using multivariate techniques and were correlated to the thermal and environmental conditions of the streams. The temperature preferences of the species were compared to published data-sets on their autecological characteristics. Up to 29% of the variability in the Ephemeroptera, Plecoptera, Trichoptera and Coleoptera community was explained by summer temperature variation in the data-sets for both small and medium-sized streams. A smaller, but significant part of the variability in species distribution was explained by conductivity, substratum type, and the percent coverage of local riparian forest. Compared to small streams, temperature was less important for the macroinvertebrate composition in

medium-sized streams. This result is likely due to the more tolerant, eurythermic species composition in larger streams. A total of 33 Ephemeroptera, Plecoptera, Coleoptera and Trichoptera taxa were positively correlated and 28 taxa were negatively correlated to summer temperature patterns. The temperature preferences of taxa considered in this study were related to species traits, such as egg dormancies and life cycle plasticity.

Introduction

The importance of temperature in the evolution, distribution and ecology of stream fauna has long been recognized (Thienemann 1950; Illies 1969; Hynes 1970; Ward and Stanford 1982). Water temperature has been identified as a factor responsible for species distribution and species richness along elevational and altitudinal gradients (Vannote et al. 1980; Ward 1982; Ward 1985; Quinn and Hickey 1990; Brussock and Brown 1991; Reyiol et al. 2001). Stream water temperature is one of the key factors determining life cycle characteristics of stream invertebrates such as embryonic development, nymphal growth, emergence, metabolism and survivorship of many taxa (Hynes

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1970; Sweeney 1984; Lillehammer et al. 1989a; Robinson and Minshall 1998; Watanabe et al. 1999).

Today, the temperature regime in streams has changed considerably through anthropogenic influence. For example, severe temperature changes are caused by deep-water release from impoundments (Webb and Walling 1993; Bergkamp et al. 2000; Jensen 2003) and by discharge of heated industrial water or of cooling water from power stations (Descy and Mouvet 1984; Bunzel-Drüke and Scharf 2004). Furthermore, less drastic influences like climatic change, changes in groundwater level, and land use of the catchment can modify the natural temperature regime of running waters (LeBlanc et al. 1997; Daufresne et al. 2004).

While temperature is generally assumed to have prime importance on the living conditions of aquatic fauna, detailed studies which measure several temperature parameters, such as the rate of temperature change, maxima and minima, and cumulated degree-days are scarce (Hawkins et al. 1997; Vinson and Hawkins 1998). Further, laboratory experiments on detailed temperature preferences have rarely been verified in the field. This discrepancy is evident particularly at the community level, and many basic details of the relationship between temperature and the benthic macroinvertebrate fauna remain hypothetical.

Using extensive field work in 20 German mountain streams, this study aimed at detecting linkages between stream temperature patterns and community composition and the abundance / occurrence of individual taxa with special emphasis on the following questions:
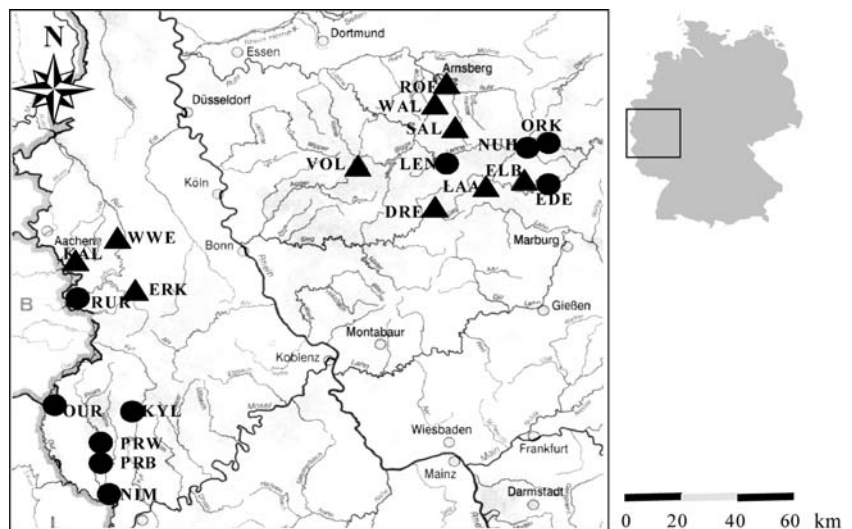
1. Is macroinvertebrate community composition in small and medium-sized streams significantly related to temperature parameters?
2. What is the relative importance of temperature parameters compared to other environmental variables for explaining macroinvertebrate distribution and community composition?
3. Which taxa are positively correlated to temperature patterns? Do results obtained in the field coincide with published results of laboratory studies and do certain species show a thermal preference?

Methods

Study area and study sites

The study area is located in western Germany, in the lower mountainous area of Central Europe (Figure 1), characterized by siliceous, carbonic rocks. Approximately 50% of the area is forested, the remaining parts were covered by pasture, arable land and urban settlements. Study streams were mainly located in floodplain valleys used predominantly for agriculture, and forested areas of the floodplain are mainly restricted to the stream banks.

Fig. 1 Haidekker, Hering. Location of sampling sites in Germany. Triangles: Small streams; circles: Medium-sized streams. Abbreviations for sampling sites see Table 1

Eleven study sites were chosen in the Sauerland and nine sites in the Eifel (Table 1). Two groups of mountain streams were investigated: (1) small streams with a catchment area ranging from 13 to 26 km^2 at altitudes from 280 to 450 m a.s.l., and with a bottom substratum dominated by coarse gravel. Within this group, ten sites in ten different streams were chosen. (2) Medium-sized streams with catchment areas ranging from 143 to 524 km^2 at altitudes between 270 and 400 m a.s.l., and with a substratum of fine to coarse gravel. Ten sites in nine medium-sized streams were selected. Site selection criteria aimed at comparable

Table 1 Study sites. Region: SaLd: Sauerland. Federal states: NRW: Nordrhein-Westfalen (Northrhine-Westphalia), H: Hessen (Hesse), RhP: Rheinland-Pfalz (Rhineland-Palatinate). CA: catchment area. * Stream order designations: Srahler (1957)

Stream	Abbrev.	Site	Region (fed state)	Latitude/longitude	Stream size	Stream order*	CA [km^2]	Altitude [m a.s.l.]
Weiße Wehe	WWE	Hürtgen	Eifel (NRW)	50°42'27'' / 6°20'35''	Small	2	11.2	300
Kall	KAL	Lammersdorf	Eifel (NRW)	50°37'47''/ 6°17'49''	Small	3	17.4	450
Erkensruhr	ERK	Hirschrott	Eifel (NRW)	50°33'44''/ 6°21'24''	Small	3	22.5	400
Volme	VOL	Kierspe	SaLd (NRW)	51°07'41''/ 7°37'06''	Small	3	17.5	345
Waldbach	WAL	Endorf	SaLd (NRW)	51°15'59''/ 8°02'28''	Small	2	9.0	370
Röhr	ROE	Endorf	SaLd (NRW)	51°16'38''/ 8°03'17''	Small	2	4.7	370
Salwey	SAL	Obersalwey	SaLd (NRW)	51°15'01''/ 8°07'22''	Small	2	15.5	340
Elbrighäuser Bach	ELB	Battenberg	SaLd (H)	51°03'01''/ 8°34'53''	Small	2	12.6	380
Laasphe	LAA	Bad Laasphe	SaLd (NRW)	50°57'08''/ 8°23'56''	Small	3	14.8	375
Dreisbach	DRE	Dreis-Tiefenbach	SaLd (NRW)	50°54'58''/ 8°03'00''	Small	3	25.9	270
Rur	RUR	Wiselsley	Eifel (NRW)	50°33'40''/ 6°17'07''	Medium	3	154.0	360
Kyll	KYL	Densborn	Eifel (RhP)	50°06'55''/ 6°36'02''	Medium	3	471.8	305
Prüm W	PRW	Waxweiler	Eifel (RhP)	50°05'18''/ 6°22'08''	Medium	3	286.5	315
Our	OUR	Auel	Eifel (RhP)	50°13'07''/ 6°10'32''	Medium	3	293.6	360
Nims	NIM	Birtlingen	Eifel (RhP)	49°56'52''/ 6°29'04''	Medium	3	222.1	245
Lenne	LEN	Altenhundem	SaLd (NRW)	51°06'31''/ 8°04'35''	Medium	3	190.0	280
Nuhne	NUH	Neukirchen	SaLd (H)	51°07'22''/ 8°44'10''	Medium	3	134.4	310
Eder	EDE	Röddenau	SaLd (H)	51°01'56''/ 8°44'22''	Medium	4	523.7	280
Orke	ORK	Reckenberg	SaLd (H)	51°09'04''/ 8°49'13''	Medium	3	275.0	295
Prüm B	PRB	Beifels	Eifel (RhP)	50°03'00''/ 6°25'23''	Medium	3	327.1	280

altitudes, hydrological, morphological and chemical factors within each group of streams, whereas shading in the floodplain and catchment area should change from site to site, potentially leading to different thermal conditions between streams.

Recording and processing of temperature data

Water temperature was recorded every 30 min for one year starting in June 2000 (Table 1). Temperature in medium-sized streams was recorded three years in total, but the additional recordings were used for interpolation of missing data due to logger failure (see paragraph below). Loggers of the type ''Gemini Data Loggers Tinytag Plus'', with a resolution of ±0.2°C, were used. They were calibrated over 24 hours before installation, and checked and calibrated each time the data were downloaded from the loggers (about every three months depending on the water level). The loggers remained under flowing water at all water levels, they were located above the bottom to avoid being covered by sediments, and were always in the shade to avoid direct solar radiation. Steal stakes were fixed in the stream bottom about 10 to 20 cm above the ground to which the loggers were tied.

Water temperature data from June 2000 to June 2001 were used for analysis. Missing data due to logger-failure were extrapolated using temperature data of the following year for the streams Kyll (Sep to Oct 2000), Nims (Oct to Dec 2000), Eder (Jun to Nov 2000), and Röhr (Jul to Oct 2000). The following temperature parameters were calculated for analysis (Table 2): summer-, spring-, and annual cumulative degree-days; maximum monthly mean temperature, maximum temperature recorded; maximum daily-, monthly mean-, and annual amplitude.The temperature data-sets (yearly mean, maximum and mean daily amplitude, summer maximum and mean) were tested for a normal distribution using the Shapiro-Wilks W Test (Shapiro and Wilk 1965). For all temperature parameters, the W statistic was not significant ($p > 0.2$), indicating data-sets were normally distributed. Statistical tests were conducted using Statistica 6.1 (StatSoft Inc. 2003).

Recording and processing of environmental data

Each study site was characterized using several environmental parameters that were combined into

six groups (Table 2): 1. general parameters and hydrology, 2. water chemistry, 3. microhabitats, 4. land use, 5. other human impacts, and 6. temperature. General parameters such as catchment size and altitude were derived from topographical maps at scales of 1:25,000 and 1:50,000. Water chemistry was sampled parallel to invertebrate sampling. Stream width, depth and current velocity were assessed at each site. The average width was measured from the actual shorelines, mean depth and mean current velocity were calculated from 20 measurements at each site. Land use parameters such as the amount of forest (in 10 % increments) in the catchment area and in the floodplain were taken from the Corine Land Cover System (Statistisches Bundesamt 1997).

For parameter selection, a Pearson correlation matrix of all environmental factors was calculated first to reveal strongly correlated and redundant parameters. For variables that strongly correlated, with $r > 0.7$ and $r < -0.7$, one variable was chosen to avoid redundancy. Some parameters, belonging to the microhabitat, land use and human impact groups, were used to calculate indices (Table 2). The coefficient of variation (CV) was calculated for all environmental and temperature parameters.

Weather data

Daily minimum, maximum and mean air temperature and precipitation from June 2000 to June 2001 were provided by the weather service DWD (Deutscher Wetterdienst, Offenbach). The weather stations are located within 25 km of the study sites.

Invertebrate sampling and processing

Macroinvertebrates were sampled twice, once in spring and once in summer 2000, using a shovel-sampler with a 500μm mesh size and sampler frame size of 0.25×0.25 m. The Multi-Habitat Sampling technique was applied (Hering et al. 2004). A sample consisted of 20 sampling units taken from all microhabitat types with at least 5% coverage at the sampling site. The 20 sampling units were chosen according to the relative share of the microhabitat types. Whenever riffles and pools were distinguishable, the sampling units were distributed among these according to their spatial proportion. The 20 sampling units were pooled, the macroinvertebrates

Table 2 Environmental variables and codes used in the Monte Carlo permutation test for groupwise selection of variables. Chemical and microhabitat parameters were sampled in spring and summer, general parameters, land use and human impact were surveyed once

Group	Parameters / index	Unit / site protocol parameters	Code
General	catchment area	[km^2]	CA
	altitude	[m]	alt
	average stream width	[m]	width
	average stream depth	[cm]	depth
	mean current velocity	[m/s]	currvel
Chemical	pH		pH
	conductivity	[µS/cm]	cond
	total hardness	[mmol/l]	hardtot
	chloride	[mg/l]	cl
	ammonium	[mg/l]	amm
	total phosphate	[µg/l]	p-tot
	nitrate	[mg/l]	na
Microhabitats	akal	[%] gravel > 0.2–2 cm	akal
	psammal	[%] mud and sand	psamm
	habitat diversity-index	% mineral substrata, all size classes-Simpson's index	SubDiv
	organic material-index	% and amount of organic substrata, FPOM, CPOM	OrgMat
Land use	forest in floodplain	% native and non-native forest in floodplain	fp_for
	forest in catchment area	% native and non-native forest in catchment area	ca_for
Other human impacts	shade	width of woody vegetation [m], shoreline covered with woody vegetation [%], shading at zenith (foliage cover) [%]	shade
	dams	number of dams, impoundments, other transverse structures	dams
	channel form	straightening, cut-off meanders, scouring below surface [m]	chann
	removal CWD	removal of Coarse Woody Detritus upstream, downstream, at sampling site	CWD
	bank fixation	stones, plastering with/ without interstices, concrete [%]	fix
Temperature	summer temperature	cumulative degree-days Jun-Aug-00	T Sum
	spring temperature	cumulative degree-days Mar-May-01	T Sp
	winter temperature	cumulative degree days Jan-Feb 01	T Win
	mean temperature Aug-00	warmest monthly mean in study period	MW8_00
	maximum temp. June-00	maximum temperature in study period	Max6_00
	degree-days 1 year	cumulative degree-days Jul-00 to Jun-01	SUMJ
	amplitude 1 year	maximum mean–minimum mean	JAMW
	maximum amplitude	max. daily amplitude in 2001	maxAMAX
	mean amplitude	max. monthly mean of daily amplitude in '01	maxAMW

were sorted out quantitatively, and Ephemeroptera, Plecoptera, Trichoptera and Coleoptera were determined to species level when possible. The identification keys used are listed at http://www.fliessgewaess erbewertung.de/downloads/Operationelle_Taxal-iste_Stand_17Mrz06.zip. The following species, which occurred only in the Eifel, were not included in the analysis: *Rhyacophila dorsalis*; Sauerland: *Rhyacophila nubila*, *Agapetus ochripes*, *Brachycentrus maculatus*, *Micrasema longulum*, *Micrasema minimum*.

Data analysis

For multivariate analysis species abundances were log10(x+1) transformed. Three data-sets were used

for analysis: (1) the complete set, including data-sets on all streams (n = 20); (2) small streams (n = 10); and (3) medium-sized streams (n = 10). For all data-sets, the spring and summer samples were analysed separately. Environmental variables and temperature data-sets were standardized to norm and unit variance (MW = 0; Var = 1) using CANOCO's default setting. Multivariate analysis was performed with CANOCO 4.5 (ter Braak and Šmilauer 2002). Principal Components Analysis (PCA) was performed to describe the Ephemeroptera, Plecoptera, Trichoptera, Coleoptera community structure (EPTC community). To detect possible relationships between species and environmental factors, Redundancy Analysis (RDA) was performed. The RDA value corresponds to regressions with multivariate explanatory variables (= environmental parameters) and response variables (= species). RDA was used in three different ways:

(1) The 31 environmental parameters (including eight temperature parameters, listed in Table 2) were correlated with the change in macroinvertebrate community composition using stepwise forward selection and the Monte Carlo Permutation Test. The correlation and significance of each parameter was calculated in two steps: First, each variable was tested separately to estimate its marginal (independent) effect. Second, each variable was tested in relation to the preceding variables to calculate the conditional (partial) effect; i.e., the effect which the variable explains complimentary to those already selected. For the second step, the significance level is adjusted to account for multiple comparisons (Bonferroni correction). For each parameter group (general, chemical, microhabitat, land use, human impact and temperature) the best correlating parameters were chosen and were jointly tested in a final model.

(2) In order to detect the explanatory power of temperature patterns for species composition, each temperature parameter was tested as an explanatory variable. The first axis was constrained to temperature and the remaining axes were unconstrained (hybrid ordination).

(3) In order to detect how much of the variability in species composition was explained by other environmental factors, a partial RDA was performed in which the effect of temperature was subtracted (as a covariable), and a constrained ordination was performed on the residual variability in species data.

Results

Description of the data-set

The years 2000 and 2001 were on the average warmer compared to long-term records (1961–1990). Spring 2000 was warmer by 2°C and summer by 1 to 1.5°C. The winter 2000/2001 was 1 to 2°C above the long-term average. Precipitation in 2000 to 2001 was higher compared to long-term records: Northrhine-Westphalia had 8%, Hessen 4%, and Rhineland-Palatinate 17% more precipitation, respectively. In the catchment area of the Rhine, precipitation was 12 % higher in the year 2000 and 11% higher in 2001 compared to long-term records.

August 2000 displayed the highest monthly mean water temperature within the recording period. Temperatures of small streams were on average 2.5°C lower than those of medium-sized streams. Within each group of small and medium-sized streams, we observed a significant gradient in *mean temperatures* with the warmest stream being 3°C warmer than the coldest. This variation caused a temperature overlap between the warmest small and the coldest medium-sized streams. *Maximum temperatures* were reached in June 2000. On average, temperature maxima of medium-sized streams were 3°C higher than those in small streams. Maxima varied by 4°C within small streams and by 7°C within medium-sized streams, with an overlap of 2°C between the warmest small and the coldest medium-sized stream.

Variation in winter temperatures was low. Almost all streams reached minimum temperatures of 0°C in January/February 2001, with the exception of one medium-sized stream with a minimum temperature of 2.6°C and three small streams with minimum values between 1 and 2°C. Highest daily temperature fluctuations were recorded in late spring (June 2000 and May, June 2001), with monthly mean amplitudes around 3°C and maximum amplitudes between 3°C and 8°C. Amplitudes did not differ significantly between small and medium-sized streams, but did within each group.

Table 3 Environmental parameters used in the multivariate analysis. For each data-set of small and medium-sized streams in spring and summer n = 10. *: calculated indices from environmental parameters, for details see text. Constant parameters (e.g. size, altitude) are only listed in the spring-data section, but used in both seasons for analysis. s.d.: standard deviation. CV: coefficient of variation

	Small spring					medium-sized spring					small summer					medium-sized summer				
	min	max	mean	s.d.	CV	min	max	mean	s.d.	CV	min	max	mean	s.d.	CV	min	max	mean	s.d.	CV
catchment area [km²]	4.7	25.9	15.1	6.2	41.2	134.4	523.7	287.8	127.6	44.3										
altitude [m]	270	450	360	50.4	14.0	245	360	303	36.07	11.9										
forest in catchm. area*	10	100	72	33	45	30	80	52	17	32										
forest in floodplain*	0	100	49	40	81	0	100	15	34	225										
channel form*	2.0	9.0	5.9	2.3	38.7	2.0	9.0	5.1	2.2	42.8										
transverse structures*	0	12.0	1.7	3.7	218.4	6.0	18.0	9.7	3.4	35.4										
woody material removed*	0	3.0	1.8	1.4	77.7	1.0	3.0	2.3	0.8	35.8										
shade*	0	90	54	32	60	0	85	39	28	71										
rivers banks fixed*	0	85.0	29.5	29.2	99.0	0	100.0	16.5	30.6	185.2										
stream width [m]	3.1	5.0	4.1	0.5	12.7	7.0	20.0	15.8	4.6	29.2	1.8	6.0	3.2	1.3	39.7	6.0	40.0	17.8	9.9	55.8
mean depth [cm]	6.9	38.5	22.7	8.4	36.8	23.5	55.5	44.1	11.0	24.9	3.6	36.2	15.5	9.3	60.3	20.0	47.0	30.2	9.2	30.3
mean current vel. [m/s]	0.1	1.1	0.7	0.3	38.9	0.4	1.0	0.8	0.2	22.4	0.2	1.0	0.4	0.2	63.9	0.3	0.8	0.5	0.2	34.6
PH	6.2	7.7	7.3	0.5	7.3	7.0	8.7	7.5	0.7	8.8	6.1	8.3	7.6	0.6	8.3	7.3	8.4	7.9	0.4	4.5
conductivity [µS/cm]	89.3	255.0	157.7	55.2	35.0	120.8	427.0	206.8	91.3	44.1	93.0	673.0	226.5	163.8	72.3	120.8	440.0	257.5	102.4	39.8
oxygen saturation [%]	93.6	111.0	102.8	6.1	5.9	97.2	110.0	102.3	3.9	3.8	89.0	122.0	102.4	10.1	9.9	91.1	144.0	105.3	15.1	14.4
total hardness [mmol/l]	0.4	0.8	0.6	0.1	23.1	0.3	2.0	0.9	0.5	54.7	0.4	1.4	0.8	0.3	31.8	0.4	1.8	1.0	0.4	42.9
chloride [mg/l]	10.0	36.0	20.6	7.1	34.3	17.0	32.0	23.2	5.1	22.1	12.0	60.0	23.4	13.7	58.7	20.0	30.0	24.9	4.1	16.6
ammonium [mg/l]	0	0.3	0.1	0.1	119.0	0	0.2	0.1	0.1	57.9	0	0.2	0.1	0	59.1	0	0.5	0.2	0.1	89.1
nitrate [mg/l]	2.8	20.1	10.0	5.1	50.8	6.4	21.5	12.3	6.1	49.4	0.7	19.7	9.9	6.4	64.5	3.2	20.7	12.7	6.2	48.6
total phosphate [µg/l]	29.0	1156	185.4	346.6	187.0	38.0	306.0	152.7	82.3	53.9	45.0	1948	410.1	677.6	165.2	85.6	896	341.6	244.2	71.5
akal [%]	0	10.0	4.1	3.8	93.7	0	0	0	0	0	0	5.0	3.1	2.5	79.7	0	1.0	0.1	0.1	316.2
psammal [%]	0	10.0	2.5	3.5	141.4	0	30.0	4.6	9.4	204.2	0	10.0	2.3	3.3	145.0	0	10.0	1.5	3.0	201.8
substrate diversity*	0.2	0.9	0.4	0.2	45.9	0.4	1.0	0.7	0.2	29.0	0.2	0.4	0.3	0.1	19.0	0.4	1.0	0.7	0.2	29.6
organic material*	1.0	20.0	8.1	6.2	76.2	1.0	34.0	9.3	9.8	105.6	1.0	12.0	6.2	3.3	53.7	1.0	38.0	11.2	13.6	121.8

For small and medium-sized streams, most physico-chemical parameters were characterized by CVs ranging between 5 and 50% (Table 4). Hydromorphological parameters were more variable (CVs between 45% and 218%).

A total of 207 EPTC-taxa was recorded, with 160 EPTC-taxa in spring and 159 in summer. Abundance (Ind/m^2) was higher in medium-sized than in small streams, and higher in summer than in spring (Table 5). The number of taxa occurring at the sampling sites was fairly similar for small and medium-sized streams, and for spring and summer

samples. Ephemeroptera contributed over one-third to the total taxa, with *Baetis rhodani*, *Serratella ignita* and *Epeorus sylvicola* dominating in both stream-size classes, and *Torleya major* being most abundant in medium-sized streams. Trichoptera had a share of one-third of the total taxa in small streams, dominated by *Glossosoma conformis*, *Philopotamus ludificatus* and *Hydropsyche instabilis*. In medium-sized streams, between 40 and 50% of the taxa were Trichoptera, mainly *Rhyacophila nubila*, *Brachycentrus maculatus* and *Hydropsyche siltalai*. Coleoptera contributed up to 10% to the EPTC-community with

Table 4 Temperature parameters used in the multivariate analysis for small and medium-sized streams. s.d.: standard deviation; CV: coefficient of variation. Summer: Jun-Aug, winter: Jan/Feb, spring: Mar-May

	small					medium-sized				
	min	max	mean	s.d.	CV	min	max	mean	s.d.	CV
Mean temperature: Aug/00	12.2	15.2	13.4	0.9	7.1	14.6	17.5	15.8	0.9	5.9
Mean temperature: May/01	10.2	12.6	11.0	0.8	7.0	11.8	14.4	13.1	0.8	6.2
Maximum temperature: Jun/00	16.6	20.3	18.1	1.2	6.6	18.3	25.3	21.6	2.1	9.5
Cumulative degree-days: year	3202	4021	3494	282	8	3656	4143	3908	171	4
Cumulative degree-days: summer	1084	1326	1180	81	7	1298	1539	1392	83	6
Cumulative degree-days: winter	884	1285	1068	131	12	943	1223	1070	77	7
Cumulative degree-days: spring	1100	1498	1275	131	10	1266	1515	1422	87	6
Amplitude (year)	7.7	10.9	9.7	1.1	11.2	10.4	14.7	12.6	1.3	10.2
Daily amplitude: max. mean (month)	2.9	4.9	3.8	0.6	15.6	1.5	4.4	3.3	1.0	29.0
Daily amplitude: maximum	4.2	7.7	6.1	1.0	16.5	2.6	7.9	5.8	1.7	29.6
Daily amplitude: mean (year)	1.4	2.2	1.9	0.2	10.5	1.0	2.1	1.7	0.4	23.3
Daily amplitude: mean of max. (year)	2.7	4.0	3.6	0.4	11.2	1.8	4.0	3.3	0.7	21.3

Table 5 Metrics of the Ephemeroptera, Plecoptera, Coleoptera and Trichoptera community of small (n = 10) and medium-sized (n = 10) streams. Small-spring = small streams, spring sample; small-summer = small streams, summer sample; medium-spring = medium-sized streams, spring sample; medium-summer = medium-sized streams, summer sample. The percentage of community is based on the relative abundance of taxa (Ind/m^2)

		small-spring	small-summer	medium-spring	medium-summer
Abundance [Ind./m^2]	mean	359	705	623	1130
	s.d.	207	340	313	900
	CV [%]	58	48	50	80
Number of taxa	total	92	102	123	111
	mean	32	37	38	38
	s.d.	8	13	8	10
	CV [%]	25	33	22	27
Percentage of community	Ephemeroptera [%]	48	31	37	36
	Plecoptera [%]	16	20	3	7
	Coleoptera [%]	10	10	5	10
	Trichoptera [%]	27	39	55	46

Elmis maugetii and *Limnius volckmari* being most frequent in medium-sized streams and *Hydraena gracilis* and *Limnius perrisi* in small streams. Plecoptera had the smallest share of EPTC-taxa in medium-sized streams, and were dominated by *Leuctra geniculata*, while in small streams *Perla marginata*, *Brachyptera risi* and *B. seticornis* were the most frequent species.

Relative importance of thermal parameters compared to other environmental variables

For both, small and medium-sized streams, the first two PCA (Principal Components Analysis) gradients explained about half of the variability in species composition. For the combined data-set, the first ordination axis explained about one third of the variability for both the spring and the summer samples (Table 6). Small and medium-sized streams differed in their community pattern (Figure 2). For the spring data-set, a post-hoc projection of the environmental variables into the ordination space revealed a negative correlation of the parameters catchment area, summer temperatures and conductivity with the first PCA axis. In contrast, higher substratum diversity, share of forest in the catchment area and share of fine-to medium-sized gravel (akal) were positively correlated. The only environmental parameter strongly correlated with the second axis was riverbank fixation (fix). The corresponding diagram for the summer samples revealed similar relationships (Figure 2), but with a better correlation of ammonium concentration with the first axis and a weaker correlation of conductivity.
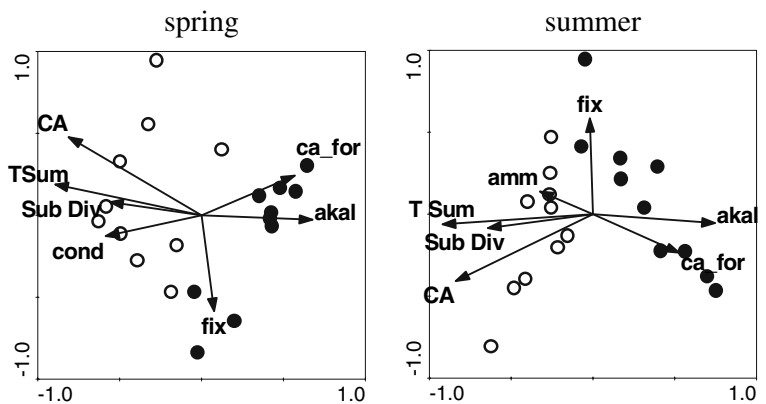
The temperature parameter ''cumulative degree-days for summer (June, July and August: T Sum)''

Table 6 Results of PCA, RDA–Temperature: hybrid RDA (only environmental variable: Temperature, i.e. first axis constrained to temperature, second axis unconstrained) and RDA–Covariable: partial RDA (temperature as covariable). Data-sets centered by species. % ax 1/2: species variability explained by first/second axis. F: F-ratio statistics. p: probability value obtained by Monte Carlo permutation test, 499 permutations (Type I error probability). All axis: Species variability explained by all canonical axes. All SP = all streams, spring; sm SP = small streams, spring; med SP = med-sized streams, spring; All SU = all streams, summer; sm SU = small streams, summer; med SU = med-sized streams, summer

Data-set	PCA		RDA-Temperature					RDA-Covariable		
	% axis 1	% axis 2	% axis 1	r axis 1	% axis 2	F axis 1	P axis 1	% all axis	F all axis	p all axis
all-spring	33.8	14.1	28.3	0.930	15.5	7.089	0.002	19.3	1.847	0.004
small-spring	37.0	15.7	27.7	0.894	17.2	3.070	0.008	25.2	1.431	n.s.
medium-spring	26.7	23.4	20.7	0.963	26.6	2.095	0.010	25.0	1.384	n.s.
all-summer	33.4	11.4	29.1	0.944	11.7	7.378	0.002	24.6	1.860	0.002
small-summer	38.4	15.5	25.8	0.849	19.4	2.769	0.012	23.4	1.567	n.s.
medium-summer	23.6	15.1	16.4	0.947	20.4	1.567	0.020	13.1	1.306	n.s.

Fig. 2 Haidekker, Hering. PCA for spring and summer EPTC species data-sets. Environmental variables have post hoc been projected into the ordination space. Solid circles: small streams; open circles: medium-sized streams; arrows: environmental variables. Abbreviations: see Table 2

was most strongly correlated to species composition in all data-sets. Other parameters concerning summer mean and maximum temperatures like ''monthly means of August and May'' and ''maximum temperature'' (which occurred in June 2000), were also highly correlated to species composition. The correlation with cumulative degree-days for the entire year, and with cumulative degree-days for both winter and spring, was weaker. Parameters concerning daily amplitudes (mean and maxima) were not correlated to community composition.

For further multivariate analysis (''final model''), the summer temperature parameter ''cumulative degree-days for summer (June, July and August: T Sum)'' was selected. In both the entire data-set and small stream data-set, summer temperature alone explained up to almost one-third (26 to 29%, significant at p < 0.05) of the differences in species composition (Table 6, column RDA–Temperature). In medium-sized streams, temperature explained 16

to 20% of the species variability (significant at p < 0.05). The second (unconstrained) ordination axis of the RDA demonstrated less variance in the species community than the axis constrained to temperature. When the variability of the species composition caused by temperature was removed from the model (as a covariable), the remaining factors explained between 13 and 25 % of the differences in species composition (significant only for the data-sets for all streams in spring and summer; Table 6, column RDA-Covariable).

Different temperature parameters had higher explanatory power for the variation in macroinvertebrate distribution compared to all other environmental parameters. Nevertheless, there were several of these variables that correlated with the species distribution: conductivity, fixed stream banks, share of akal (gravel), share of forest in the floodplain and in the catchment area, and the size of the stream (Figure 3, columns ''marginal effects''). Part of the explanatory
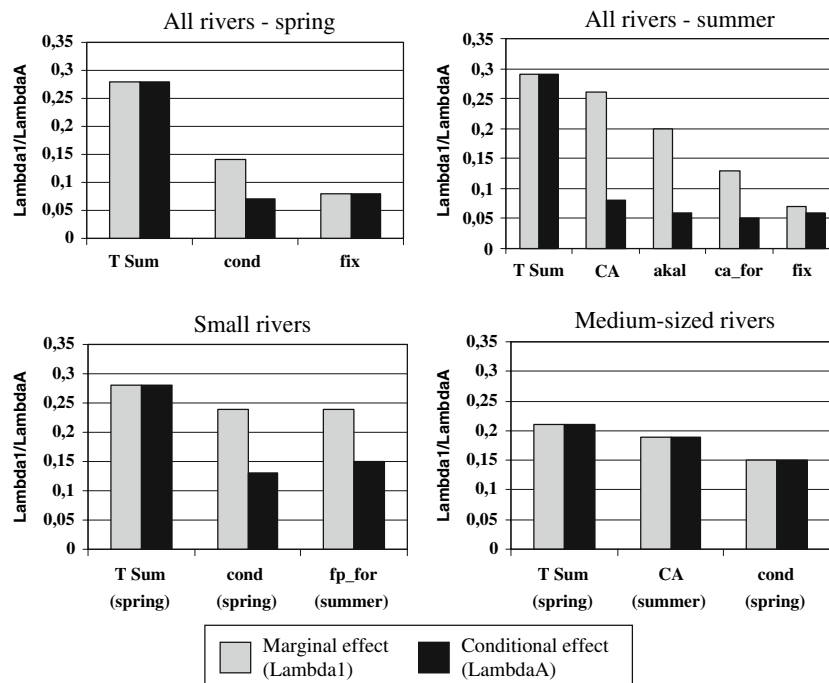

Fig. 3 Haidekker, Hering. Percent species variability (concerning frequency of occurrence) explained by environmental variables. Grey column: Marginal effect, i.e. the amount, the variable explains when correlated with the faunal data (Lambda1). Black column: Conditional effect, i.e. the amount, the variable explains additionally to the already selected, stronger correlated variable (LambdaA). The lower this value

in comparison to the marginal effect, the more is the respective variable correlated with other factors. For small and medium-sized streams results for summer and spring samples are presented in the same diagram, but they were tested separately. All shown variables significant to < 0.05 (Monte Carlo Permutation Test). Spring: Mar-May; Summer: Jun-Aug. For abbreviations of environmental parameters compare Table 2

power of these variables can be attributed to their correlation with temperature parameters. After removing the effects of temperature from the model, the explanatory power of the remaining variables was calculated (Figure 3, columns ''conditional effects''). For the data-set of all streams, the parameters conductivity, share of akal (gravel), share of forest in the catchment area, and the stream-size added < 8% to explaining species variability. Stream bank fixation was not correlated to other environmental factors.

For the data-set of small streams, the conditional effect of conductivity and the share of forest in the floodplain added 13 to 15% to species variability, indicating a greater importance of these parameters compared to the others (Figure 3, columns ''conditional effects''). For medium-sized streams, temperature parameters were much less important for macroinvertebrates, explaining only 20% of the species variability in spring, while, for the summer sample, the explanatory power of temperature parameters was not significant (Figure 3). For this part of the data-sets, stream-size and conductivity explained species variability to a greater extent than in the other data-sets.

Taxa correlating with temperature

The abundance of 28 taxa correlated negatively, while 33 taxa positively, to summer mean temperature (August 2000). Among those species, most Plecoptera preferred colder water temperatures, while the majority of Ephemeroptera, Trichoptera and Coleoptera occurred more frequently at warmer temperatures (Figure 4). Among the group of species negatively correlated to temperature, some taxa occurred exclusively in small streams and occurred in those with a mean temperature below 14°C (warmest month): *Ecdyonurus venosus*, *Dinocras cephalotes*, *Limnius perrisi*, *Rhyacophila obliterata*, and *Glossosoma conformis*. A second group occurred at almost all sampling sites, but the frequency decreased with increasing summer mean temperatures: *Epeorus sylvicola*, *Rhithrogena semicolorata*, *Brachyptera risi*, *Hydropsyche instabilis*, and *Chaetopteryx villosa*. A third group preferred small streams and cold medium-sized streams, but only at sampling sites up to the following summer mean temperatures: *Brachyptera seticornis* (below 15°C), *Perlodes microcephalus* (below 16°C), *Oreodytes sanmarkii* (below 15°C), *Odontocerum albicorne* (up to 16°C).

A similar pattern was observed for species positively correlated with summer mean temperature. Some species were only found in medium-sized streams, and were increasingly abundant in warmer streams: *Baetis lutheri*, *Elmis maugetii*, *Athripsodes cinereus*. Species occurring in either class-size of streams, but increasing in frequency with higher summer mean temperature were *Ecdyonurus dispar*, *Baetis scambus*, and *Limnius volckmari*. Species which occurred more frequently at warmer sampling sites, in both small and medium-sized streams, were *Ecdyonurus torrentis* (T > 14°C), *Leuctra geniculata* (T > 14°C), *Oulimnius tuberculatus* (T > 14°C), *Orectochilus villosus* (T > 12°C), and *Polycentropus flavomaculatus* (> 14°C).

Discussion

Relative importance of thermal parameters for macroinvertebrate community composition

The results of this study indicate that quantitative differences in the aquatic insect community of small and medium-sized streams can be partly explained by water temperature parameters. This finding is in accordance with several studies addressing the longitudinal distribution of individual species and groups of organisms (Ide 1935; Vannote et al. 1980; Roux et al. 1992; Jacobsen et al. 1997). Within the small streams with temperature differences of up to 3°C, changes in the invertebrate composition were predominantly explained by mean summer temperature, supporting Sweeney (1993), who emphasized that small changes in temperature (2 to 5°C) will alter key life-history parameters of many species. In this study, this observation was particularly apparent for the aquatic insect community of small streams, indicating the high thermal sensitivity of the taxa. In medium-sized streams, temperature explained much less of the variability in taxa distribution, though the temperature range was even slightly higher than for small streams. This result may reflect an increased share of more eurythermic and less-specialized invertebrate taxa.

Species distribution was most explained by the summer number of cumulative degree-days (June, July and August) and mean temperatures of the late spring and summer months. Maximum temperatures were correlated with mean temperatures ($r^2 = 0.76$),
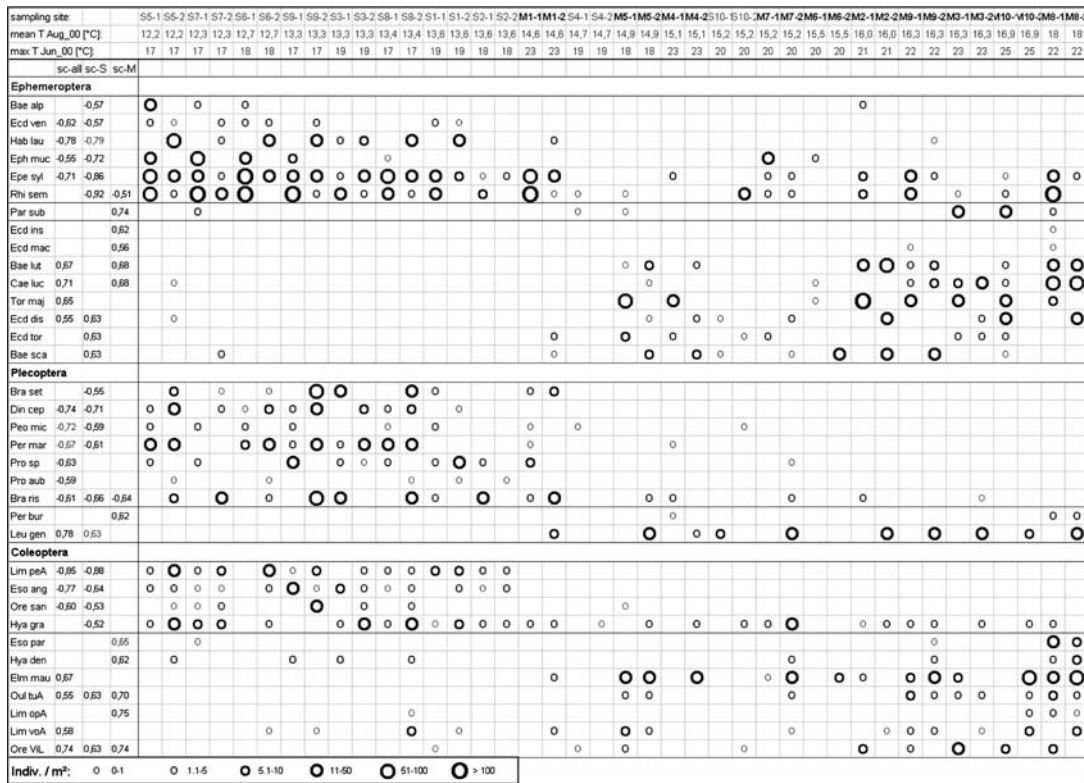
Fig. 4 Haidekker, Hering. Species distribution at the sampling sites (Ind/m^2) in symbols (see legend). Sampling sites are listed according to their summer temperature from left: coldest stream, to right: warmest stream. sc-all/sc-S/sc-M: species scores in RDA of data-sets for all streams, and small and medium-sized streams separately. Negative species scores: Taxon is negatively correlated to temperatures; positive species scores: Taxon positively correlated to temperature. Sampling site abbreviations: S: small streams, M: medium-sized streams. Sampling site numbers: S1: Wwe, S2: Kal, S3: Erk, S4: Vol, S5: Wal, S6: Roe, S7: Sal, S8: Elb, S9: Laa, S10: Dre, M1: Rur, M2: Kyl, M3: PrW, M4: Our, M5: Nim, M6: Len, M7: Nuh, M8: Ede, M9: Ork, M10: PrB. Last numbers: −1: Spring sample, −2: Summer sample

but had less explanatory power. Daily amplitudes and winter temperatures were found to be insignificant for the macroinvertebrate distribution. Thus, the parameters reflecting the thermal demand of the species throughout their development period, such as degree-days and other parameters based on means, seemed to correlate best with the species distribution. Several studies have tested the influence of degree-days on development or distribution of benthic macroinvertebrate species and found strong correlations or directly proportional growth rates (Markarian 1980; Lowe and Hauer 1999; Watanabe et al. 1999; Knispel et al. 2006). Other studies underline the importance of temperature maxima for species growth and distribution (Jacobsen et al. 1997; Lowe and Hauer 1999; Sponseller et al. 2001). Different temperature parameters were found to be important: winter temperatures from December to February correlated best with differences in larval growth and adult size of the stonefly *Soyedina carolinensis* (Sweeney and Vannote 1986), and April temperature was critical for the timing of the emergence of the stonefly *Pteronarcys californica* (Gregory et al. 2000).

The effect of daily amplitudes on benthic macroinvertebrates is still unclear. In some laboratory studies, development rates of Plecoptera and Ephemeroptera correlated with the daily temperature pulse (Sweeney 1978; Humpesch 1982; Wagner 1986; Frutiger 1996), while in other studies daily amplitudes had no influence on development (Brittain 1977; Elliott 1987, 1988, 1991; Marten 1991; Zwick 1996). Vannote et al. (1980) hypothesized greater species richness in habitats with greater thermal variability, since more species find their specific thermal optima. Brussock and Brown (1991) found a negative relationship between invertebrate richness and daily temperature amplitude, while Kamler (1965) found Ephemeroptera richness being positively and Plecoptera richness being negatively correlated with daily variability. In this study, daily temperature amplitudes varied up to 8°C between individual streams, but the magnitude of daily amplitudes did not explain variation in community patterns.

Correlation of taxa distribution and temperature patterns

For many of these species, our field observations are in accordance with the results of experimental

laboratory studies on selected Ephemeroptera, Plecoptera and Trichoptera species (almost no relevant information is available on Coleoptera). The adaptation of benthic macroinvertebrates to water temperature as a selection pressure is especially apparent for Plecoptera and Ephemeroptera. Plecoptera are mostly cool-water species, while mayflies are common in tropical waters. Both orders have developed different strategies to adapt to their environment. The developmental zero and the thermal demand for a successful egg development are often lower at colder temperatures in cold-adapted species (many Plecoptera), since their enzyme function is probably specialized accordingly (Pritchard et al. 1996). Consequently, these species often have a summer diapause to avoid high temperatures. On the other hand, warm adapted species, like many Ephemeroptera, develop faster at higher temperatures and sometimes have a winter quiescence (Brittain 1990; Pritchard et al. 1996).

In this study, several species showed either a significantly positive or negative correlation to the 6°C temperature gradient between the coldest and warmest streams. From our study, it is uncertain whether the life history strategies of the positively and negatively correlated species differ due to this small-scale gradient. Below, we evaluate the possibility for individual species to show such a dependency, with a focus on egg development, emergence timing and voltinism.

Plecoptera

In contrast to the Ephemeroptera and Trichoptera species, more Plecoptera species were negatively correlated than positively correlated with temperature. For four of these species, traits and laboratory studies corroborate these field correlations:

Perlodes microcephalus was present in small and medium-sized streams with mean temperatures below 16°C and its abundance peaked at 12 to 13°C. Its negative correlation with temperature corresponds to the following observations. *P. microcephalus* predominantly occurs in the meta-to hyporhithral with a univoltine life-cycle and it emerges in spring. It has a summer diapause in the egg stage and the main larval growth takes place in autumn; these life-history traits show developmental efficiency at lower temperatures and the avoidance of higher summer temperatures with an egg diapause. Laboratory studies revealed

that this species is especially suited for successful development at lower temperatures because it has a low thermal demand for the egg development and a faster embryonic development at lower temperatures (Marten 1991).

Brachyptera risi was present in small and medium-sized streams up to 16°C, with a maximum abundance at 12 to 13°C. *B. risi* predominantly occurs in the epi-to metarhithral, with a univoltine life-cycle and a summer diapause in the egg stage. The main growth period is directly before the emergence in spring. This demonstrates an avoidance of summer temperatures because it has its highest growth rate in the cooler spring season. According to laboratory studies, the optimum temperature for egg development is 8 to 9°C, and the species has been described as cold-stenothermic (Elliott 1988, 1992). The hatching success and incubation period at a given temperature are stable in British and Norwegian populations in spite of their geographical isolation. No significant intraspecific variation has been observed (Elliott 1988), thus the thermal demands seem to be genetically conservative.

Protonemura auberti and *Brachyptera seticornis* were present only in small streams below 14°C. Their greatest frequency was observed at a temperature of 12 to 13°C. No laboratory studies on the thermal demand of the embryonic development of *B. seticornis* have been performed and there is no information on a summer diapause. Both species occur together in the same habitat and have a similar life-cycle, but *B. seticornis* emerges earlier in spring than *P. auberti* (Illies 1955). However, these species' adaptation to cooler temperatures is evident in their restricted presence to the crenal and epirhithral river habitats in mountainous and sub-mountainous regions. Concerning *Protonemura auberti*, Marten (1990) found interspecific differences in the thermal demand for the embryonic development of five congeners (*P. auberti, P. hrabei, P. meyeri, P. nitida,* and *P. praecox*) to be optimal in respect to resource partitioning, and a temporal displacement of life cycles, which is another aspect of the importance of specific thermal demands in these species.

Two species occurring in the colder small streams could not be characterized as cold-adapted species, according to earlier studies:

Dinocras cephalotes was only present in small streams and up to 14°C. Laboratory studies have revealed that the egg development is highly temperature dependent, with an optimum hatching success at high temperatures between 16 and 20°C. It has a plastic semivoltine life-cycle and emerges in summer. It has a wide temperature range and is a warm-stenothermic of Mediterranean origin (Lillehammer 1987a; Frutiger, 1996; Zwick 1996). *D. cephalotes* occurs in varying local, geographical, and regional populations all showing different genetically determined temperature cues for egg development (Imhof 1994; Elliott 1995; Frutiger 1996; Zwick 1996). Because of plasticity in its life cycle, *D. cephalotes* can reproduce successfully outside its thermal optimum (Lillehammer 1987b). For instance, it can be found from southern Spain to northern Norway, and is the most widespread Perlidae in Europe (Elliott 1989). It is restricted to the crenal and epi - to metarhithral. Consequently, the distribution in this study reflects only the lower part of its distributional range, and so its limitation to stream-size must be interpreted by factors other than temperature. *Perla marginata* was likewise only present in small streams. This species is known to occur mainly in crenal and epirhithral regions, but is a eurythermic, widespread species with a semivoltine life-cycle (2 to 3 years). The temperature dependency of this species is identical to *D. cephalotes*, but it is not genetically as variable as *D. cephalotes* (Frutiger 1996). The distributional pattern is also similar. The life-history traits of *P. marginata*, like *D. cephalotes*, imply that its distribution reflects the preference for small streams of crenal and epirhithral zones with factors other than temperature gradient being important.

Two Plecopteran species were positively correlated with water temperatures in this study. *Perla burmeisteriana* was present only in streams with summer means above 14°C, which seems to be its lower thermal limit. This observation is supported by laboratory experiments from Marten (1991), which indicate a dependency on high temperatures, with the species requiring at least 12°C for successful hatching. *Leuctra geniculata* was present above 13°C, with highest frequencies between 14 and 17°C. This corresponds to the eurythermic nature of *L. geniculata*, even though its egg development is temperature dependent (Elliott 1987). It belongs to the group of warm-adapted Euholognatha. Laboratory studies show that the thermal demand for its embryonic development is low at high temperatures (Elliott

1987). The main growth period of the larvae is in summer (May to August), just before the late summer emergence. It does not have an egg diapause.

Species not correlated with temperature in this study are known to be univoltine, but two have a variable life history, i.e. uni-or semivoltine, depending on the thermal environment (*Leuctra nigra*-a crenal species, and *Nemoura cinerea*). There is no similarity between main growth periods or time of emergence within this group of species. Most have been classified as eury-or warm-stenothermic according to their embryonic development (e.g. *Nemoura cinerea, Protonemura meyeri, Leuctra nigra*) (Elliott 1988). None of the species has an egg diapause in summer, except for *Protonemura intricata*. Dormancy and development of *P. intricata* is dependent on oviposition date and incubation temperature, allowing a synchronised hatch of this species under different thermal conditions (Marten and Zwick 1989).

Ephemeroptera

Most Ephemeropteran species were positively correlated with temperature, which matches assumptions on the evolutionary history of this group. Pritchard et al. (1996) characterizes the evolutionary history of the Ephemeroptera as being unclear, but sharing the tropical origin with their sister-group Odonata. Most temperate-region mayfly species are warm-adapted regarding embryonic development. On the other hand, some mayfly species live in cold environments with a diapause or quiescence in summer. Compared to Plecoptera, less information on the development of Ephemeroptera under different thermal regimes is available for comparison to the results of this study.

Baetis alpinus was negatively correlated with temperature in this study. It was present at sites up to 16°C and had its maximum presence at 12°C. *B. alpinus* is described to have an optimal development between 8 and 11°C, it is known to occur in temperature ranges between 5 and 13°C. *B. alpinus* is a cold stenothermic species (Schmedtje and Kohmann 1992), having a bivoltine life-cycle, but is univoltine at higher altitudes (Ahn 2002).

There is no laboratory data on temperature preferences for *Habrophlebia lauta, Epeorus sylvicola* and *Ephemerella mucronata*, which were found to be negatively correlated with temperature in this study. The latter species might have a summer diapause in the

egg or larval stage (Ahn 2002), and all three species have a univoltine life-cycle with emergence starting mainly in May. This may indicate an avoidance of higher summer temperatures. *Rhithrogena semicolorata* and *Ecdyonurus venosus* were negatively correlated with temperature. But in contrast to this observation, other studies revealed these species developing faster at higher temperatures, and the relationship between hatching time and temperature was described by a power-law between 5.9 and 19.9°C and 2.8 and 18.1°C, respectively (Humpesch and Elliott 1980a, b; Humpesch 1982). Our findings that other Ephemeroptera are positively correlated with temperature agree with results of Humpesch and Elliott (1980a, b) for *Ecdyonurus insignis, E. dispar*, and *E. torrentis*. Their embryonic development is characterized by a lower thermal demand at higher temperatures, and for this reason they are considered to be warm-adapted (Pritchard et al. 1996). Most of the positively correlated species tend to emerge in June to August (*Baetis scambus, Ecdyonurus dispar, Torleya major, Caenis luctuosa, Ecdyonurus insignis*), and several species are bivoltine or variable in their life cycle (e.g. *Baetis lutheri, B. scambus, Caenis luctuosa*). The Ephemeroptera that were found to be negatively correlated with temperature tend to emerge earlier in the year.

Trichoptera

The adult stage of *Chaetopteryx villosa* was found to be temperature dependent (Wagner 2002). It avoids warm temperatures by undergoing larval dormancy during the summer. These observations corroborate with the results of this study showing that the species is negatively correlated with higher temperatures.

Hydropsyche siltalai was present in small and medium-sized streams with a higher abundance in warmer streams. Limiting temperatures were not reached in our study streams. Roux et al. (1992) found this species to be adapted to the temperature regime of the rhithron; its metabolism functioning well at temperatures between 5 and 20°C.

Hydropsyche pellucidula shows a maximum presence at 16°C, declining in numbers above and below these temperatures. *H. pellucidula* is characterized as an ubiquitous species with its metabolism being adapted to temperatures below 20°C, but is also able to tolerate higher temperatures as potamon species (Roux et al. 1992).

Conclusion

Differences in temperature patterns of the investigated streams were a result of floodplain and catchment land uses. Despite a moderate temperature gradient, we observed a significant positive or negative impact of water temperature on 61 Ephemeroptera, Plecoptera, Trichoptera and Coleoptera species (29.5% of the taxa recorded). For many of these species, our field observations are in accordance with the results of experimental laboratory studies. In general, our investigation confirms the crucial role of water temperature for community composition of stream macroinvertebrates and for individual species. In addition, it outlines the indirect impact of riparian and catchment land use on stream biota via changes in water temperatures.

As a result of climate change, pronounced water temperature changes are expected in the next decades, which may have significant effects on benthic stream communities: Increasing temperatures may support eurythermic species and generalists, resulting in less specialized communities among river types. Furthermore, increasing water temperatures may be an ultimate threat to cold stenothermic aquatic insect species. This includes particularly crenal species, which may not find a thermal refuge along the stream continuum. Thermally specialized species, e.g. species with temperature-dependent life cycles for resource partitioning, may also be endangered by changing water temperatures. However, the impacts of climate change might be reduced markedly by alterations in catchment and floodplain land use; at least regionally, riparian forest may contribute to dampen future water temperature increases.

There is a lack of knowledge regarding temperature impact on life cycles of benthic invertebrates. The majority of literature focuses on the impact of temperature changes on egg development and hatching success, or on larval and nymphal growth rates and survival. Regarding the probable effect of climate change on life in running waters, there is still a need for life cycle studies in controlled environments.

Appendix Taxa names and abbreviations

Ephemeroptera		Trichoptera	
Baetidae:		Rhyacophilidae	
Baetis alpinus (PICTET, 1843–1845)	Bae alp	*Rhyacophila obliterata* (McLACHLAN, 1863)	Rhy obl
Baetis lutheri (MÜLLER-LIEBENAU, 1967)	Bae lut	Glossosomatidae	
Baetis scambus (EATON, 1870)	Bae sca	*Glossosoma conformis* (NEBOISS, 1963)	Glo con
Heptageniidae:		Philopotamidae	
Ecdyonurus venosus (FABRICIUS, 1775)	Ecd ven	*Philopotamus ludificatus* (McLACHLAN, 1878)	Phi lud
Ecdyonurus dispar (CURTIS, 1834)	Ecd dis	*Philopotamus montanus* (DONOVAN, 1813)	Phi mon
Ecdyonurus insignis (EATON, 1870)	Ecd ins	Hydropsychidae	
Ecdyonurus macani (THOMAS &SOWA, 1970)	Ecd mac	*Cheumatopsyche lepida* (PICTET, 1834)	Che lep
Ecdyonurus torrentis (KIMMINS, 1942)	Ecd tor	*Hydropsyche incognita* (PITSCH, 1993)	Hyd inc
Epeorus sylvicola (PICTET, 1865)	Epe syl	*Hydropsyche instabilis* (CURTIS, 1834)	Hyd ins
Rhithrogena semicolorata (CURTIS, 1834)	Rhi sem	*Hydropsyche pellucidula* (CURTIS, 1834)	Hyd pel
Leptophlebiidae:		*Hydropsyche siltalai* (DÖHLER, 1963)	Hyd sil
Habrophlebia lauta (EATON, 1884)	Hab lau	Polycentropodidae	
Paraleptophlebia submarginata (STEPHENS, 1835)	Par sub	*Polycentropus flavomaculatus* (PICTET, 1834)	Pol fla
Ephemerellidae:		*Psychomyia pusilla* (FABRICIUS, 1781)	Psy pus
Ephemerella mucronata (BENGTSSON, 1909)	Eph muc	Brachycentridae	
Torleya major (KLAPÁLEK, 1905)	Tor maj	*Brachycentrus subnubilus* (CURTIS, 1834)	Bra sub

Appendix continued

Ephemeroptera		Trichoptera	
Caenidae:		*Micrasema setiferum* (PICTET, 1834)	Mic set
Caenis luctuosa (BURMEISTER, 1839)	Cae luc	Limnephilidae	
		Allogamus auricollis (PICTET, 1834)	All aur
Plecoptera		*Anomalopterygella chauviniana* (STEIN, 1874)	Ano cha
Perlodidae		*Chaetopteryx villosa* (FABRICIUS, 1789)	Cha vil
Perlodes microcephalus (PICTET, 1833)	Peo mic	*Ecclisopteryx dalecarlica* (KOLENATI, 1848)	Ecc dal
Perlidae		Goeridae	
Dinocras cephalotes (CURTIS, 1827)	Din cep	*Goera pilosa* (FABRICIUS, 1775)	Goe pil
Perla burmeisteriana (CLAASSEN, 1936)	Per bur	Lepidostomatidae	
Perla marginata (PANZER, 1799)	Per mar	*Lasiocephala basalis* (KOLENATI, 1848)	Las bas
Taeniopterygidae		*Lepidostoma hirtum* (FABRICIUS, 1775)	Lep hir
Brachyptera risi (MORTON, 1896)	Bra ris	Leptoceridae	
Brachyptera seticornis (KLAPALEK, 1902)	Bra set	*Athripsodes albifrons* (LINNAEUS, 1758)	Ath alb
Nemouridae		*Athripsodes cinereus* (CURTIS, 1834)	Ath cin
Protonemura auberti (ILLIES, 1954)	Pro aub	*Ceraclea annulicornis* (STEPHENS, 1836)	Cer ann
Protonemura sp.	Pro sp	*Mystacides azurea* (LINNAEUS, 1761)	Mys azu
Leuctridae		Odontoceridae	
Leuctra geniculata (STEPHENS, 1836)	Leu gen	*Odontocerum albicorne* (SCOPOLI, 1763)	Odo alb
Coleoptera			
Elmidae			
Elmis maugetii (LATREILLE, 1798)	Elm mau		
Esolus angustatus (MÜLLER, 1821)	Eso ang		
Esolus parallelepipedus (MÜLLER, 1806)	Eso par		
Limnius opacus (MÜLLER, 1806)	Lim opA		
Limnius perrisi(DUFOUR, 1843)	Lim peA		
Limnius volckmari(PANZER, 1793)	Lim voA		
Oulimnius tuberculatus (MÜLLER, 1806)	Oul tuA		
Gyrinidae			
Orectochilus villosus (MÜLLER, 1776)	Ore ViL		
Dytiscidae			
Oreodytes sanmarkii (SAHLBERG, 1834)	Ore san		
Hydraenidae			
*Hydraena dentipes*Ad.(GERMAR, 1844)	Hya den		
Hydraena gracilis(GERMAR, 1824)	Hya gra		

References

Ahn B (2002) Makroinvertebraten im Spiegel der zeitlich-räumlichen Heterogenität von Fließgewässern Nordrhein-Westfalens. Inaugural-Dissertation Universität GH Essen, p 284

Berkamp GM, McCartney P, Dugan J, McNeely, Acreman M (2000) Dams, Ecosystem Function and Environmental Restoration. Thematic Review II.1. Input to the Word Commission on Dams, Cape Town

Brittain JE (1977) The effect of temperature on egg incubation period of Taeniopteryx nebulosa (Plecoptera). Oikos 29:302–305

Brittain JE (1990) Life history strategies in Ephemeroptera and Plecoptera. In: Campbell IC (eds), Mayflies and Stoneflies. Kluwer Academic Publishers, pp 1–12

Brussock PP, Brown AV (1991) Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. Hydrobiologia 220:109–117

Bunzel-Drüke M, Scharf M (2004) Wärmeeinleitung in die Lippe: Auswirkungen auf die Fischfauna. LÖBF-Mitteilungen 3/4:44–51

Daufresne M, Roger MC, Capra H, Lamouroux N (2004) Long-term changes within the invertebrate and fish communities of the upper Rhône river: effects of climatic factors. Glob Change Biol 10:124–140

Descy JP, Mouvet C (1984) Impact of the Tihange nuclear powerplant on the periphyton and the phytoplancton of the Meuse River (Belgium). Hydrobiologia 119:119–128

Elliott JM (1987) Life cycle and growth of Leuctra geniculata (Stephens) (Plecoptera: Leuctridae) in the river Leven. Entomologist's Gazette 38:129–134

Elliott JM (1988) Interspecific and intraspecific variations in egg hatching for British populations of Taeniopteryx nebulosa and Brachyptera risi (Plecoptera: Taeniopterygidae). Holarctic Ecology 11:55–59

Elliott JM (1989) The effect of temperature on egg hatching for three populations of Dinocras cephalotes (Plecoptera: Perlidae). Entomologist's Gazette 40:153–158

Elliott JM (1991) The effect of temperature on egg hatching for three populations of Perla bipunctata (Plecoptera: Perlidae). Entomologist's Gazette 42:61–65

Elliott JM (1992) The effect of temperature on egg hatching for three populations of Perlodes microcephala (Pictet) and three populations of Diura bicaudata (Linnaeus) (Plecoptera: Perlodidae). Entomologist's Gazette 43:115–123

Elliott JM (1995) Egg hatching and ecological partitioning in carnivorous stoneflies (Plecoptera). CR Acad Sci, Paris, 318:237–243

Frutiger A (1996) Embryogenesis of Dinocras cephalotes, Perla grandis and P. marginata (Plecoptera: Perlidae) in different temperature regimes. Freshwater Biology 36:497–508

Gregory JS, Beesley SS, Van Kirk RW (2000) Effect of springtime water temperature in the time of emergence and size of Pteronarcys california in the Henry's Fork catchment. USA. Freshwater Biology 45:75–83

Hawkins CP, Hogue JN, Decker LM, Feminella JW (1997) Channel morphology, water temperature, and assemblage structure of stream insects. J N Am Benthol Soc 16/4:728–749

Hering D, Moog O, Sandin L, Verdonschot PFM (2004) Overview and application of the AQEM assessment system. Hydrobiologia 516:1–20

Humpesch UH (1982) Effect of fluctuating temperature on the duration of embryonic development in two Ecdyonurus spp. and Rhithrogena cf. hybrida (Ephemeroptera) from Austrian streams. Oecologia 55:285–288

Humpesch UH, Elliott JM (1980a) Effect of temperature on the hatching time of eggs of three Rhithrogena spp (Ephemeroptera) from Austrian streams and an English stream and river. Journal of Animal Ecology 49:643–661

Humpesch UH, Elliott JM (1980b) Effect of temperature on the hatching time of parthenogenetic eggs of five Ecdyonurus spp. and two Rhitrogena spp (Ephemeroptera) from Austrian streams and English rivers and lakes. Journal of Animal Ecology 49:927–937

Hynes HBN (1970) The ecology of running waters. University Toronto Press, Toronto, p 555

Ide FP (1935) The effect of temperature on the distribution of the mayfly fauna of a stream. Publ Ont Fish Res Lab 50:1–76

Illies J (1955) Steinfliegen oder Plecoptera. In: Dahl, F. & H. Bischoff (eds.): Die Tierwelt Deutschlands und der angrenzenden Meeresteile. 43.Teil. Gustav Fischer Verlag, Jena

Illies J (1969) Biogeography and ecology of neotropical freshwater insects, especially those from running waters. In: Fittkau E-J, Illies J, Klinge H, Schwabe GH, Sioli H (Hrsg.), Biogeography and Ecology in South America. W. Junk, The Hague: 685-708

Imhof A (1994) Habitatsansprüche und Verhalten von Perla grandis (Rambur) (Plecoptera: Perlidae) und anderen räuberischen Steinfliegenlarven. PhD thesis, ETH,10695

Jacobsen D, Schultz R, Encalada A (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with latitude and altitude. Freshwater Biol 38:247–261

Jensen AJ (2003) Atlantic salmon (Salmo salar) in the regulated River Alta: effects of altered water temperature on parr growth. River Research and Applications 19/7:733–747

Kamler E (1965) Thermal conditions in mountain waters and their influence on distribution of Plecoptera and Ephemeroptera larvae. Ekologia Polska Ser A 13/20:1–38

Knispel S, Sartori M, Brittain JE (2006) Egg development in the mayflies of a Swiss glacial floodplain. Journal of the North American Benthological Society 25/2:430–443

LeBlanc RT, Brown RD, FitzGibbon JE (1997) Modelling the effects of land use change on the water temperature in unregulated urban streams. J of Environmental Management 49:445–469

Lillehammer A (1987a) Intraspecific variation in the biology of eggs and nymphs of Norwegian populations of Leuctra hippopus (Plecoptera). Journal of Natural History 21:29–41

Lillehammer A (1987b) Egg development of the stoneflies Siphonoperla burmeisteri (Chloroperlidae) and Dinocras cephalotes (Perlidae). Freshwater Biology 17:25–39

Lillehammer A, Brittain JE, Saltveit SJ, Nielsen PS (1989) Egg development, nymphal growth and life cycle strategies in Plecoptera. Holarctic Ecology 12/2:173–186

Lowe WH, Hauer FR (1999) Ecology of two large, net-spinning caddisfly species in a mountain stream: distribution, abundance, and metabolic response to a thermal gradient. Can J Zool 77:1673–1644

Markarian RK (1980) A study of the relationship between aquatic insect growth and water temperature in a small stream. Hydrobiologia 75:81-95

Marten M (1990) Interspecific variation in temperature dependence of egg development of five congeneric stonefly species (Protonemura Kempny, 1898, Nemouridae, Plecoptera). Hydrobiologia 199:157–171

Marten M (1991) The effect of temperature on egg incubation period of Perlodes microcephalus, Perlodes dispar (Plecoptera: Perlodidae) and Perla burmeisteriana (Plecoptera: Perlidae). In: Alba-Tercedor, Sanchez-Ortega (eds),

Overview and strategies of Ephemeroptera and Plecoptera. Sandhill Crane Press, Gainesville FL, pp 387–401

Marten M, Zwick P (1989) The temperature dependence of embryonic and larval development in Protonemura intricata (Plecoptera: Nemouridae). Freshwater Biology 22: 1–14

Pritchard G, Harder LD, Mutch RA (1996) Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. Biological Journal of the Linnean Society 58:221–244

Quinn JM, Hickey CW (1990) Characterization and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. New Zealand Journal of Marine and Freshwater Research 24:387–409

Reyjol Y, Lim P, Dauba F, Baran P, Belaud A (2001) Role of temperature and flow regulation on the Salmoniform-Cypriniform transition. Arch Hydrobiol 152/4:567–582

Robinson CT, Minshall GW (1998) Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. Arch Hydrobiol 142/3:257–281

Roux C, Tachet H, Bournaud M, Cellot B (1992) Stream continuum and metabolic rate in the larvae of five species of Hydropsyche (Trichoptera). Ecography 15:70–76

Schmedtje U, Kohmann F (1992) Bestimmungsschlüssel für die Saprobier-DIN-Arten (Makroorganismen). Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft 2/88

Shapiro S, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52/3,4: 591–611

Sponseller RA, Benfield EF, Valett HM (2001) Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biology 46:1409–1424

Statistisches Bundesamt (1997) Daten zur Bodenbedeckung. Wiesbaden

Strahler AN (1957) Quantitative analysis of watershed geomorphology. Trans Amer Geophys Union 38/6:913–920

Sweeney BW (1978) Bioenergetic and developmental response of a mayfly to thermal variation. Limnol Oceanogr 23/ 3:461–477

Sweeney BW (1984) Factors influencing life-history patterns of aquatic insects. In: Resh V, Rosenberg DM (eds) The Ecology of aquatic instects. Praeger Publishers, New York, pp 56–100

Sweeney BW (1993) Effects of Streamside Vegetation on Macroinvertebrate Communities of White Clay Creek in Eastern North America. Proceedings of The Academy of Natural Sciences of Philadelphia 144:291–340

Sweeney BW, Vannote RL (1986) Growth and production of a stream stonefly: Influences of diet and temperature. Ecology 67/5:1396–1410

Ter Braak CJF, Šmilauer P (2002) CANOCO Reference manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power. Ithaca, New York, USA: 500 pp

Thienemann A (1950) Verbreitungsgeschichte des Süßwassertierwelt Europas. Die Binnengewässer 18:1–809

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushiong CE (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137

Vinson MR, Hawkins CP (1998) Biodiversity of stream insects: Variation at local, basin and regional scales. Annu Rev Entomol 43:271–293

Wagner R (1986) Egg development and life cycle of Chaetopteryx villosa (Trichoptera). Holarctic ecology 9: 294–300

Wagner R (2002) The influence of temperature and food on size and weight of adult Chaetopteryx villosa (Fabricius) (Insecta: Trichoptera) along a stream gradient. Arch Hydrobiol 154/3:393–411

Ward JV (1982) Ecological aspects of stream regulation: Responses in downstream lotic reaches. Wat Pollut Management Rev 2, New Delhi: 1–26

Ward JV (1985) Thermal characteristics of running waters. Hydrobiologia 125:31–46

Ward JV, Stanford JA (1982) The serial discontinuity concept of lotic systems. In Fontaine TD, Bartell SM (eds) Dynamics of Lotic Ecosystems. Ann Arbour Sci Publ Ann Arbour, Michigan, pp 29–42

Watanabe NC, Mori I, Yoshitaka I (1999) Effect of water temperature on the mass emergence of the mayfly, Ephoron shigae, in a Japanese river (Ephemeroptera: Polymitaryidae). Freshwater Biology 41:537–541

Webb BW, Walling DE (1993) Spatial variation of water temperature characteristics and behaviour in a Devon river system. Freshwater Biology 16:585-608

Zwick P (1996) Variable egg developement of Dinocras spp (Plecoptera, Perlidae) and the stonefly seed bank theory. Freshwater Biology 35:81–100