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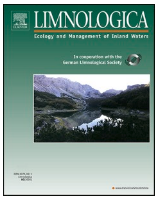

A new index of a water temperature equivalent for summer respiration conditions of benthic invertebrates in rivers as a bio-indicator of global climate change

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ABSTRACT

Detailed information on species temperature preferences are needed to measure the effects of global warming on species and communities in European rivers. However, information currently available in the literature on taxon-specific temperature preferences or temperature tolerances is very heterogeneous and therefore not well suited for forecasting purposes. To close this gap, we derived so-called 'central temperature tendencies' (CTT_t values) for benthic invertebrate species. For this end, 547 species and temperature data from regional monitoring programmes in Germany collected at 4249 sites were analysed. Due to the vulnerability of species to high temperatures, CTT_t values were calculated for mean summer temperatures, following a robust approach of calculating a weighted average based on temperature classes. Derived CTT_t values correspond well to species temperature preferences as reported in literature as long as the latter were homogeneous in terms of how they were derived and which temperature reference was at focus. Based on taxon-specific CTT_t values, a community value, CTT_{Com}, was calculated for each benthic invertebrate sample. CTT_{Com} values were validated by correlation with mean summer water temperatures. As the slope a of the linear regression model between CTT_{Com} values and measured summer temperatures was comparatively low ($a = 0.49$), a correction function was derived in order to optimise the relation between both. This was crucial, because it is assumed that although CTT_t was derived solely from taxa abundances within summer temperature classes, CTT_{Com} not only reflects the effect of (summer) water temperature itself, but also corresponds to a temperature equivalent value, which describes the overall quality of all respiration-relevant aquatic summer habitat conditions that determine the metabolism of respective benthic invertebrates. By comparing this equivalent value with water temperatures measured in the year previous of sampling, statements can be made about the influence of flow conditions and other factors determining oxygen availability.

Thus, CTT_{Com} reflects the mean aerobic scope of the overall benthic invertebrate fauna: the better the respiration conditions for rheophilic species with high oxygen demand, the larger the aerobic scope and the lower CTT_{Com}.

The approach taken in our study is promising and provides a tool to track and even project past, present, and future impacts of global warming on benthic invertebrates in rivers based on measured values of respiratory relevant environmental variables. We encourage all stakeholders in the field of freshwater ecology to test this

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Abbreviations: CTT, central temperature tendency; CTT_t, Taxon-specific central temperature tendency; CTT_{Com}, Community central temperature tendency; KLIWA, Working group on climate change and water management, consisting of the environmental agencies of the German states of Baden-Württemberg, Bavaria and Rhineland-Palatinate in cooperation with the DWD (German Meteorological Service) (www.kliwa.de); $KLIWA\text{-}Index_{MZB}$ or KI_{MZB}, German long and short terms for CTT_{Com} index, as it was developed under a KLIWA contract. MZB is an abbreviation for macrozoobenthos; MMR, maximum metabolic rate; RMR, resting metabolic rate.

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tool, which is already in use in river management practice in Germany and is known under the long or short terms KLIWA-Index$_{MZB}$ or KI$_{MZB.}$

1. Introduction

Ongoing global climate change will lead to an increase of global mean temperatures and to changes in precipitation patterns (Pachauri and Mayer, 2015). In rivers these changes will have a decisive influence on hydrology as well as on other abiotic factors such as water temperature. The latter is crucial since it influences several physicochemical and biological processes such as metabolism rates and therefore has a direct effect on aquatic organisms at all trophic levels (Chuche and Thiéry, 2012 and references therein). Whether species will suffer or benefit from rising temperatures depends on their thermal preferences. Whereas cold stenotherm taxa might be negatively affected by increasing temperatures, eurytherm taxa might benefit from changing thermal conditions (Domisch et al., 2013; Hering et al., 2009; Jyväsjärvi et al., 2015). In any case, long-term rising temperatures will alter both the structure and the composition of benthic invertebrate communities. In order to be able to trace this impact, detailed taxon-specific information on temperature preferences is needed, because many aquatic benthic invertebrates have been classified only into broad categories. For example the European database on freshwater species only distinguishes five categories of species temperature preference (“very cold”, “cold”, “moderate”, “warm” and “eurytherm”) (Schmidt-Kloiber and Hering, 2015).

Ideally, actual numerical values for temperature preferences should be available as opposed to the current descriptive categories used by the traits databases. While this information exists for quite a few benthic invertebrate taxa, it is based on very diverse methodological approaches. Depending on whether species were tested in the laboratory or whether information was derived from field observation, temperature preferences either describe the fundamental or the realised niche (Hutchinson, 1957). Besides, some studies refer to mean annual temperatures (Marziali and Rossaro, 2013), others to high/summer (Wijnhoven, 2003) or lower/winter (Reynoldson et al., 2000) temperature estimates. Therefore, most reported temperature preferences or tolerance values are hardly comparable. As all developmental stages are affected by temperatures (Chuche and Thiéry, 2012) and optima may differ between developmental stages (Bale et al., 2002), comparing reported species-specific temperature preferences without considering the developmental stage is error-prone.

These considerations show the need for a methodological consistent derivation of temperature preferences for a large number of species as a solid basis for studies on climate change impacts on benthic invertebrate communities. One obstacle that has to be overcome is to determine the ’temperature metric’ which is best-suited to trace global warming effects on benthic invertebrates. In temperate and Mediterranean climate zones, summer is an especially critical season for many benthic invertebrates, because high temperature and corresponding low oxygen content in combination with low discharge limit the occurrence of certain species (Hawkins et al., 1997 and references therein). While maximum summer temperatures certainly pose the strictest limits to organisms it is questionable whether they can be detected with sufficient accuracy in water management practice (Babitsch and Sundermann, 2020). With the exception of permanent gauging stations (which are rare and mostly are operated at larger rivers) water temperatures in management practice are only recorded a few times per year, e.g., monthly, at most water courses. As temperature shows distinctive variations on all temporal scales there is a high chance that discrete measurements do not reflect reality sufficiently (Babitsch and Sundermann, 2020). Therefore, focussing on mean summer temperatures calculated from multiple measurements would be more robust than attempts to quantify the maximum and also better reflect the situation in a water body. In consequence it seems appropriate to relate taxon-specific temperature preferences to mean summer temperatures.

As terms like ‘temperature preference’, ‘optimum’ or ‘tolerance value’ are often used interchangeably, but in fact relate to very different aspects of species-specific temperature estimates, it has to be clarified that this study focusses on what (Yuan, 2006) coined ‘central tendency’ of species abundance with regard to water temperature, which he defined as an ‘abundance-weighted average of the relevant environmental variable’.

In order to calculate a more robust indicative value than the arithmetic mean, this study defines the "central tendency temperature" (*CTT*) of a taxon as a mean summer water temperature value at which the taxon’s aggregated relative abundance equals 50%, thus characterising the centre of its ecological distribution, which bears some similarity to the "robust optimum method" (Cristóbal et al., 2014).

As a taxon’s "optimum temperature" describes the temperature value where abundance is at its highest, *CTT* and optimum temperature are equal only if a taxon’s abundance is distributed symmetrically across the observed temperature range. In cases of asymmetrical abundance distributions *CTT* is shifted towards the side of the maximum with the lower slope or decline, respectively. Finally, there might not be a distinguishable maximum at all if a taxon does not show any temperature preference in the observed temperature spectrum. While *CTT* is already meaningful as a single value, which can be used to calculate community indices, inspection of abundance distributions along temperature gradients provides additional insights.

Therefore, we derived taxon-specific *CTT*’s as well as abundance distribution curves of aquatic benthic invertebrates for those temporal water temperature conditions, which are most decisive for the abundance of the species (described as mean summer temperatures). These results then were used as a basis for a community central tendency temperature index CTT_{Com}, which enables reliable detections of temperature related changes in composition and abundance structure of benthic invertebrate communities.

For this purpose, data on water temperature and abundance data on aquatic benthic invertebrate fauna from German states’ Water Framework Directive monitoring programs were processed. A literature search was conducted to validate calculated taxon-specific mean summer temperature preferences with data reported in other studies. Finally, it was evaluated if and how calculated CTT_{Com} values match actual measured mean summer water temperatures.

2. Materials and methods

We focus on 547 river benthic invertebrate species from a nationwide range of locations (Fig. 1). The river sites were located at elevations between 1 and more than 900 m above sea level with catchment areas between approximately 2 and 70,000 km^2. By including the full range of river sizes, a long temperature gradient was covered by our data, to properly describe species’ central tendency temperatures.

2.1. Benthic invertebrate data

A total of 7181 benthic invertebrate samples were available, which were sampled at 4249 sites between 2004 and 2013. The samples originated from routine surface water surveys of German federal state agencies (Haase et al., 2004). The large majority of all samples were collected between February and July (recommended sampling season). Sampling was carried out for microhabitats according to their coverage at the sampling site (multi-habitat sampling), i.e., within a 100 m long stream section, 20 benthic sample units (25 cm^2), proportionally

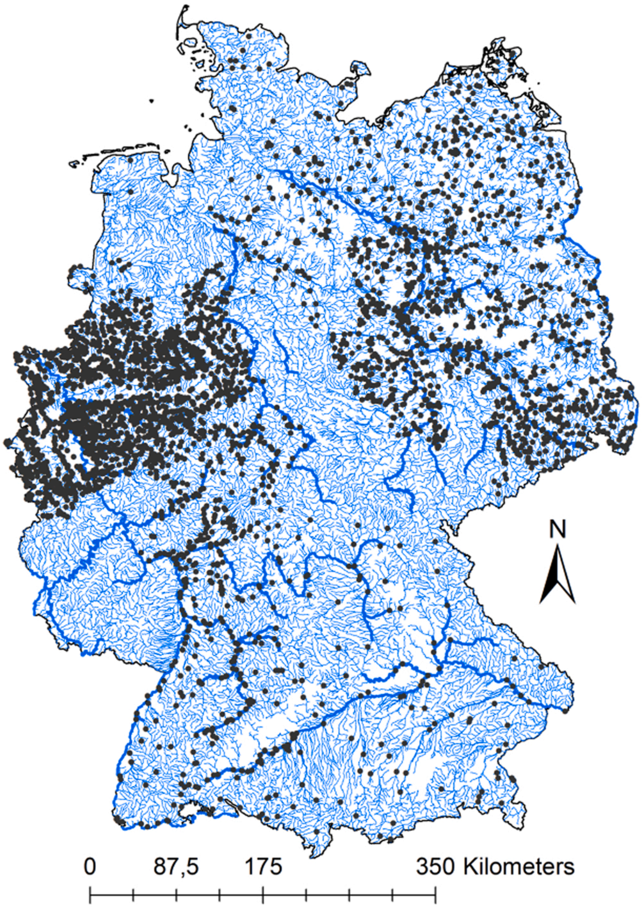

Fig. 1. Location of the analysed sites in Germany.

distributed among microhabitats with a spatial area $\geq 5\%$, were collected, and the material pooled. A kick sampling method according to (Barbour et al., 1999) was applied, and each ‘sampling unit’ (0.0625 m^2) was sampled using a hand net with a 25 × 25 cm opening and a tapering net bag with a mesh size of 0.5 mm. Organisms were separated from sediments, identified in the laboratory and counted. Only taxa identified to the species level were included in our analyses. Higher aggregating taxonomic units such as the genus and family level, with possibly many different species within a group, were not analysed. This should take into account that individual taxa within a genus can have very different temperature requirements. A list with all species analysed in this study and their CTT’s is provided as Supporting information (Appendix A).

2.2. Water temperature data

Information on water temperatures were provided as routine monitoring data by German federal states. Water temperature data were available for all sites where benthic invertebrates were collected. At most sites, the temperature was measured not more than once a month between 2000 and 2013. To characterise mean summer water temperature, recordings from July, August and September were averaged for each sample site and year. In order to generally characterise the benthic invertebrate sampling sites by temperature, a 3-year mean summer temperature was calculated where the mid-years corresponded to benthic invertebrate sampling years. On average, 4 single temperature recordings were available to calculate the 3-year summer temperature mean.

2.3. Calculation of taxon-specific central tendency temperatures

All given samples were ranked in ascending order according to their 3-year mean summer temperature. Percentiles were calculated to define 11 temperature classes (Table 1). The 10th percentile for example corresponds to a mean summer temperature of 13.0 °C and all samples with a mean summer temperature lower than or equal to 13.0 °C fall into this first temperature class. All other classes were defined accordingly (compare Table 1).

Whereas temperature classes one to nine each covered 10% of all sites, temperature classes ten and eleven only covered 7.5% and 2.5% of all sites, respectively. These classes were formed to account for a better differentiation of high extreme (Table 1). The number of temperature classes was set to 11 to ensure a sufficient resolution of species-specific central tendency temperatures and at the same time to ensure a sufficient sample size in each temperature class.

For each temperature class c and each taxon t the sum of the abundances a_{tc} over all P samples in the respective class was calculated according to the following formula:

$$a_{tc} = \sum_{i=1}^{P} a_{itc} \tag{1}$$

Abundance sums a_{tc} were then divided by the number of samples for each temperature class c.

$$\overline{a}_{tc} = \frac{a_{tc}}{n_c} \tag{2}$$

All samples were taken into account, including those in which taxon t did not occur. This “normalisation” minimizes the influence of temperature classes with particularly large numbers of samples (and therefore also taxa, which are found in these samples). Normalised temperature class-related abundance sums of taxa a_{tc} were finally divided by the sum of all normalised abundances A_t.

$$I_{tc} = \frac{\overline{a}_{tc}}{A_t} \tag{3}$$

where I_{tc} is the temperature index value of taxon t in temperature class c. For each species temperature index values I_{tc} can be multiplied by class number c with the product summed for all K classes, resulting in a taxon-specific central tendency temperature index I_t, which is dimensionless.

$$I_t = \sum_{c=1}^{K} c \times I_{tc} \tag{4}$$

I_t indicates the relative preference of a taxon for higher or lower temperatures. However, I_t can approximately be translated into taxa specific temperature values T_t by calculating mean temperatures of each

Table 1
Definition of 11 temperature classes based on the analysed dataset. The upper class limit temperature corresponds to the x^{th} percentile of the analysed dataset.

Temperature class	Percentile	Lower class limit [°C]	Mean class temperature [°C]	Upper class limit [°C]
1	10th	11.65	12.33	≤ 13.00
2	20th	13.00	13.52	≤ 14.03
3	30th	14.03	14.38	≤ 14.73
4	40th	14.73	15.02	≤ 15.32
5	50th	15.32	15.59	≤ 15.85
6	60th	15.85	16.16	≤ 16.47
7	70th	16.47	16.78	≤ 17.10
8	80th	17.10	17.55	≤ 18.00
9	90th	18.00	18.59	≤ 19.19
10	97.5th	19.19	20.04	≤ 20.89
11	100th	20.89	21.93	≤ 22.96 (max. recorded value)

class (Table 1) by polynomial regression (Fig. 2).

Using this polynomial regression function, each temperature index value I_t can be translated to an approximate temperature centroid CTT_t of taxon t (expressed in degree centigrade). This allows for direct comparisons with measured temperature data.

A second important feature is the so-called specificity S_t of the taxon-specific central tendency temperature CTT_t, which is normalised to an interval between 0 and 10.

$$S_t = \frac{K \times \max\,(\overline{a}_{tc})}{K-1} - \frac{\sum_{c=1}^{K} \overline{a}_{tc}}{K} \tag{5}$$

S_t indicates how specific (or how unspecific) a taxon is distributed across K temperature classes. Taxa with a high specificity are (almost) only found in samples of one temperature class, while those with a low specificity react indifferently to temperature and are found in samples of several (or even all) temperature classes.

Community-based central tendency temperature indices I_{Com} can be calculated analogously to the calculation of the saprobic index (Friedrich and Herbst, 2004) as an abundance- and specificity-weighted sum:

$$I_{Com} = \frac{\sum_{t=1}^{T} I_t \times S_t \times a_t}{\sum_{t=1}^{T} S_t \times a_t} \tag{6}$$

Finally, sample-related community central tendency temperature CTT_{Com} can be calculated by using T_t instead of I_t as follows:

$$CTT_{Com} = \frac{\sum_{t=1}^{T} T_t \times S_t \times a_t}{\sum_{t=1}^{T} S_t \times a_t} \tag{7}$$

2.4. Literature search

Information on specific temperature estimates of benthic invertebrate taxa as published in national and international literature was assembled from Web of Science and other databases (e.g. SCOPUS, Google Scholar) by using predefined search terms. The following search terms were used in combination with taxonomic units (e.g. Ephemeroptera, Trichoptera): thermal / temperature preference, thermal / temperature preferendum, thermal / temperature optimum, thermal / temperature tolerance, water temperature, stream temperature. For each identified source the following information was noted: regional reference (country or continent, e.g., Germany, Europe, North America), data origin (field observation or laboratory study), temporal temperature reference (e.g. annual mean, summer maximum, winter minimum), life cycle stage (e.g. egg development, larval growth, non-specified total development). With regard to optimum temperature and temperature tolerance, centre, lower or upper end of a temperature optimum or lower or upper end of a temperature tolerance were distinguished (see Table 2).

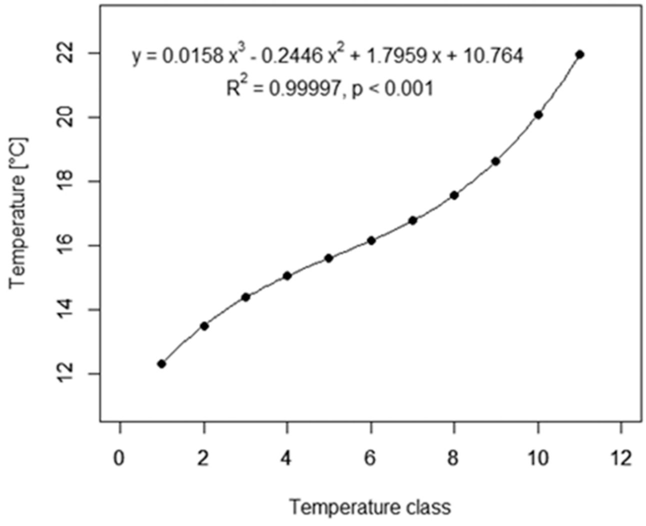

Fig. 2. Polynomial regression model to approximate mean temperature class values.

In order to compare literature data with calculated taxon-specific central tendency temperature CTT_t, it was necessary to build homogeneous data subsets. First, data were divided into three subsets, regarding whether the studies focused on the annual mean temperatures, on summer temperatures or whether this was undefined (Fig. 3, time reference). These subsets were again subdivided with regard to information on the temperature category (mean, upper or lower end of the temperature optimum or temperature tolerance; Fig. 3).

Finally, all of these subsets were subdivided according to their data origin, depending on whether data were collected from laboratory studies or from field observations or whether their origin is undefined. Spearman Rank Correlations were performed to test if and how strong calculated taxon-specific central tendency temperatures (CTT_t) correlate with corresponding information extracted from literature.

2.5. Fine adjustement

Sample-related community central tendency temperatures CTT_{Com} were plotted against measured mean summer water temperatures to test for correlation. For this end, we used the same dataset as described above (i.e. 7181 macroinvertebrate samples at 4249 sites). However, to ensure the causal relationship between water temperature and the index, mean summer temperatures were calculated from only two consecutive years, including the year of the macroinvertebrate sampling and the previous year. In addition, at least one temperature measurement from each of the three summer months had to be available in both years. These criteria were fulfilled for 1811 benthic invertebrate samples at 1297 sites. A linear regression model was calculated to fit community central tendency temperatures CTT_{Com} and measured summer temperature data.

2.6. Evaluation of adjusted CTT_{Com}

An independent dataset that was not included in the derivation of the CTT_t values was used to evaluate the relationship between the adjusted CTT_{Com} and measured mean summer temperatures. For this end, we used a data set, extracted from WFD monitoring data of the German state of Saxonia, covering 13 different stream types according to Pottgiesser and

Table 2
Examples of taxon-specific information on optimum temperature and temperature tolerance as found in literature.

Citation	Temperature category	Temperature value [°C]
"European data suggest that [.] 12–24 °C is required for larval development with 17.3 °C being optimal." (Sprung and Borcherding, 1991) cited in (McMahon, 1996)	mean temperature optimum	17.3
	lower limit of temperature optimum	12.0
	upper limit of temperature optimum	24.0
".it cannot survive water temperatures lower than 2.0 °C" (French and Schloesser, 1991)	lower limit of temperature tolerance	2.0
"The upper lethal threshold temperature lies around 28 °C" (Frutiger, 2003)	upper limit of temperature tolerance	28.0

Time reference	Temperature category	Data origin
1 Annual mean	1.1 TempOpt: mean	1.1.1 Laboratory
		1.1.2 Field data
		1.1.3 Undefined
	1.2 TempOpt: upper end	1.2.1 Laboratory
		1.2.2 Field data
		1.2.3 Undefined
	1.3 TempOpt: lower end	1.3.1 Laboratory
		1.3.2 Field data
		1.3.3 Undefined
2 Summer maximum	2.1 TempOpt: mean	…
	2.2 TempOpt: upper end	…
	2.3 TempOpt: lower end	…
	2.4 TempTol: upper end	…
3 Undefined	3.1 TempOpt: mean	…
	3.2 TempOpt: upper end	…
	3.3 TempOpt: lower end	…
	3.4 TempTol: upper end	…
	3.5 TempTol: lower end	…

Fig. 3. Procedure for building data subsets. TempOpt: optimum temperature, TempTol: temperature tolerance. "…" indicates that subsets were built accordingly.

Sommerhäuser (2014). The macroinvertebrate samples were collected in 2014–2016. Water temperature data were available from two consecutive years, including the year of the macroinvertebrate sampling and the previous year. In this dataset, too, at least one temperature recording had to be available in each of the 6 summer months. These criteria were fulfilled for 129 benthic invertebrate samples and sites. A linear regression model was calculated to fit river type specific transformed community central tendency temperatures CTT_{Com} and measured summer temperature data.

3. Results

3.1. Taxon-specific central tendency temperatures (CTT_t)

Taxon-specific central tendency temperatures CTT_t for 547 freshwater macroinvertebrate species along with information on specificity S_t are given in the Supporting information (S1 Table). Different temperature preference patterns were identified for the analysed macroinvertebrate taxa representing low, medium and high temperature preferences as well as high, medium and low specificities (Fig. 4).

The caddisfly *Chaetopterygopsis maclachlani* (Trichoptera) has a low central tendency temperature and relatively high specificity (CTT_t = 12.76, S_t = 7.50). Mean relative abundances are highest in the lowest temperature classes (Fig. 4a). This shows that this species practically only occurs in rivers and streams with low summer temperatures (Fig. 4b-c). Calculated central tendency temperatures of *Sigara fossarum* and *Baetis vernus* are very similar (16.46 °C and 16.51 °C, respectively). However, while *Sigara fossarum* is found in temperature classes three to nine with a distinguished peak in temperature class six, *Baetis vernus* occurs in all eleven temperature classes with a broad and therefore weak maximum at low relative abundances across temperature classes four to nine. These differences are mirrored by different specificity values S_t: a medium specificity for *Sigara fossarum* (S_t = 2.61) and a very low specificity for *Baetis vernus* (S_t = 0.22). The fourth example shows the results for *Ecnomus tenellus* (Trichoptera) which has a central tendency temperature of 20.92 °C and which is found almost exclusively in the highest temperature classes (S_t = 5.26).

Central tendency temperatures of important taxonomic groups are presented in Fig. 5.

Native and non-native Crustacea showed considerable differences and thus were divided into two groups. Stone flies (Plecoptera) display

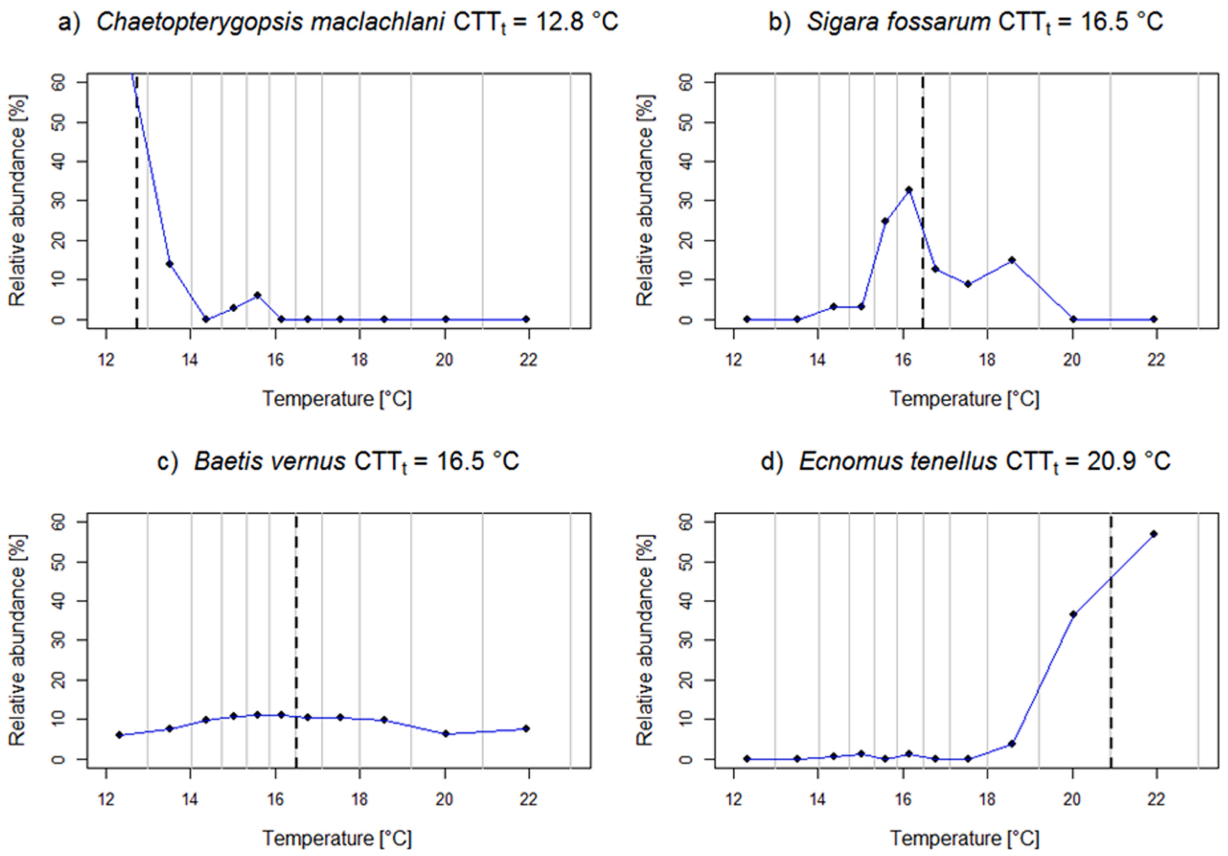

Fig. 4. a-d. Mean relative abundances of four species in each temperature class. Grey vertical lines define the 11 temperature classes. The dashed vertical line represents the calculated species-specific central tendency temperature CTT_t.

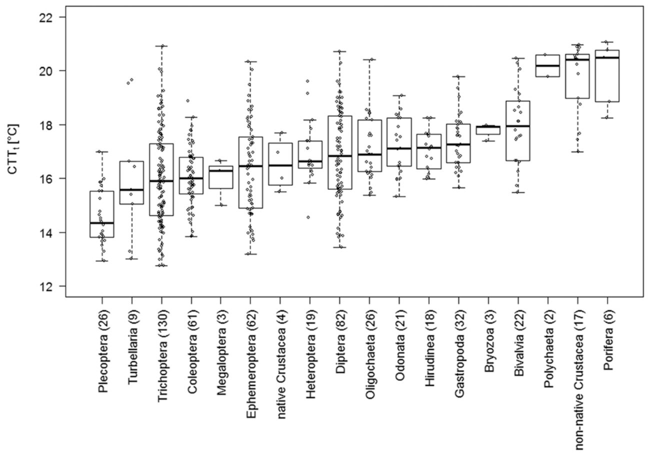

Fig. 5. Taxon-specific central tendency temperature CTT_t in different taxonomic groups. The number of different taxa in each group is given in parenthesis.

particularly low central tendency temperatures, followed by Trichoptera, Coleoptera, Turbellaria, Ephemeroptera and native Crustacea. In contrast, highest central tendency temperatures were calculated for non-native Crustacea as well as for Porifera and Polychaeta. The lowest and highest central tendency temperatures for non-native species were calculated for *Proasellus meridianus* (Crustacea, $CTT_t = 16.99$ °C) and *Echinogammarus trichiatus* (Crustacea, $CTT_t = 20.97$ °C).

3.2. Literature analysis

672 articles, reports and theses were identified as potentially relevant. A total of 181 of these sources contained usable information, i.e. specific temperature data that could be analysed for the compilation. A complete list of the derived species' temperature parameters and their sources is given in the Supplementary material (Appendix B). Overall, 1744 entries (individual information) for 692 taxa were identified from 15 countries, with the largest proportion from Germany (663 recordings), other European countries (607 recordings), and North America (436 recordings). 54% of taxon-specific information was derived from field studies. The majority of information (> 80%) related to the total development of species, and did not distinguish between developmental stages.

Overall, the highest correlation between calculated taxon-specific central tendency temperature CTT_t and corresponding information from literature were calculated for the most homogeneous and therefore smallest data subsets (Table 3). Accordingly, as the number of taxa in these subsets is reduced the more homogeneous the data subset was, rank correlation results were no longer significant in some cases. If annual mean was chosen as a time reference and data on the mean temperature optimum based on field studies was considered, the correlation value was $\varsigma = 0.84$ ($p < 0.001$) (Table 3). Especially in this data subset, calculated central tendency temperatures CTT_t appear to give very good approximations of taxon-specific temperature estimates as described in literature. It is also noteworthy that this data subset is based on one single literature review study (Domisch et al., 2013). In this study, authors calculated occurrence probabilities with regard to annual mean air temperature. Therefore, temperature preferences from (Domisch et al., 2013) are significantly lower than central tendency temperatures calculated in the present project (which refer to mean summer water temperatures). However, both datasets correlate well. Additionally, it becomes clear that the calculated central tendency temperature CTT_t does not correlate well with information reported in laboratory studies (compare results for corresponding subsets, Table 3).

Table 3
Spearman Rank Correlation coefficients between calculated taxon-specific central tendency temperatures and reported information in the literature. Level of significance, *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. x / y: number of taxa in the data subset (e.g. 272) / number of studies in the data subset (e.g. 8). Temp$_{Opt}$: optimum temperature, Temp$_{Tol}$: temperature tolerance. ns: result of the correlation are not significant, the value for ς is not given in these cases. Values for $\varsigma \geq 0.50$ are marked in bold.

Time reference	Temperature category	Data origin:
Annual mean: 0.53 *** 272/8	Temp$_{Opt}$: mean: 0.59 *** 78/5	Laboratory: - ns 0/0 Field: 0.84 *** 35/1 Undefined: - ns 43/1
	Temp$_{Opt}$: upper end: 0.58 *** 107/3	Laboratory: - ns 0/0 Field: 0.59 *** 106/2 Undefined: - ns 1/1
	Temp$_{Opt}$: lower end: 0.63 *** 87/3	Laboratory: - ns 0/0 Field: 0.65 *** 86/2 Undefined: - ns 1/1
Summer maximum: 0.48 *** 216/48	Temp$_{Opt}$: mean: 0.88 *** 11/6	Laboratory: - ns 2/2 Field: 0.89 ** 9/4 Undefined: - ns 0/0
	Temp$_{Opt}$: upper end: 0.43 *** 118/24	Laboratory: - ns 3/3 Field: - ns 62/11 Undefined: 0.53 *** 53/10
	Temp$_{Opt}$: lower end: 0.50 * 23/13	Laboratory: - ns 4/2 Field: - ns 11/6 Undefined: 0.86 ** 8/5
	Temp$_{Tol}$: upper end: 0.62 *** 64/25	Laboratory: - ns 42/17 Field: 0.56 * 17/5 Undefined: - ns 5/3
Undefined: 0.36 *** 274/49	Temp$_{Opt}$: mean: 0.74 *** 39/23	Laboratory: 0.68 *** 35/17 Field: - ns 0/0 Undefined: - ns 4/4
	Temp$_{Opt}$: upper end: 0.30 ** 105/29	Laboratory: 0.30 ** 81/19 Field: - ns 2/1 Undefined: - ns 22/9
	Temp$_{Opt}$: lower end: 0.27 ** 105/27	Laboratory: - ns 67/17 Field: - ns 2/1 Undefined: - ns 36/9
	Temp$_{Tol}$: upper end: - ns 23/10	Laboratory: - ns 23/10 Field: - ns 0/0 Undefined: - ns 0/0
	Temp$_{Tol}$: lower end: - ns 2/2	Laboratory: - ns 2/2 Field: - ns 0/0 Undefined: - ns 0/0

3.3. Fine adjustment of the CTT_{Com}

In watercourses with particularly high summer water temperatures, flow velocities are often particularly low and loads of nutrients and organic substances are significantly increased. In multi-stressor environment like these moderate temperate conditions might already lead to disproportionately poor respiration conditions. In contrast, in near natural streams with very low summer water temperatures species will find disproportionately good respiratory conditions. Thus, the ratio of oxygen demand to oxygen supply relative to the water temperature is disproportionately poor in warm and impacted sites, while the exact opposite holds true in particularly cool and near natural water courses. These correlated respiratory factors can distort the results in such a way that calculated CTT_{Com} values are disproportionately low for cool watercourses and disproportionately high for warm watercourses. This is confirmed when community central tendency temperatures CTT_{Com} are calculated and plotted against mean summer water temperatures from measurements (Fig. 6a).

The linear regression model ($R^2 = 0.603$, $p < 0.001$) results in a relatively low slope ($a = 0.4$), which ideally should be close to 1. Thus,

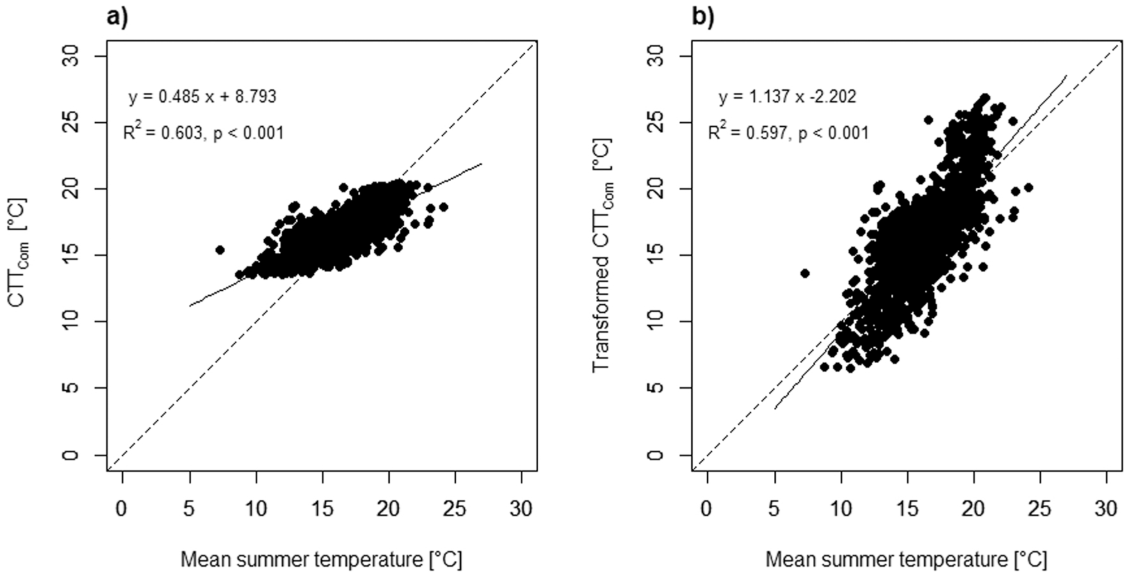

Fig. 6. a-b. Calculated community central tendency temperatures CTT_{Com} (a) and transformed CTT_{Com} (b) plotted against the measured mean summer temperatures for 1811 samples. The solid line represents the result of the linear regression model, the dashed line represents the 1:1 ratio.

communities occurring in streams with rather low mean summer temperatures will indicate comparatively higher temperatures while communities occurring in streams with high mean summer temperatures will indicate comparatively lower temperatures.

In order to optimise the relation between community central tendency temperature CTT_{Com} and measured mean summer water temperature, a correction function was derived by calculating the deviation between CTT_{Com} and measured mean summer temperature for each pair of values. A third order polynomial regression of these deviations against measured mean summer temperature led to a correction function ($y = -0.039x^3 + 2.237x^2 - 44.958x + 308.5$, $R^2 = 0.714$, $p < 0.001$), which was applied to the calculated CTT_{Com} values. Linear regression of transformed CTT_{Com} values and measured mean summer water temperatures resulted in a model with a comparable coefficient of determination ($R^2 = 0.597$) but with a slope much closer to 1 ($a = 1.137$, Fig. 6b). Applying the resulting transformation function to the derived CTT_t and recalculating the CTT_{Com} with these transformed CTT_t yielded a comparable relationship of the thus corrected CTT_{Com} to summer mean water temperatures. As expected, the slope of the linear regression line was close to 1 ($y = 1.2598x - 4.2458$) as for the relationship of the directly transformed CTT_{Com} to summer mean water temperature, and the coefficient of determination was also comparable ($R^2 = 0.597$).

In order to comply with the European Water Framework Directive (European Union, 2000) German authorities distinguish 25 river types (Pottgiesser and Sommerhäuser, 2014), which differ significantly regarding ecoregion, slope, or stream size, which also impact respiratory conditions including temperature. As taxon-specific CTT_t were derived without distinguishing between these river types an additional correction was necessary in order to calculate river type specific community values. Therefore, correction functions were derived for each river type in order to transform CTT_{Com} values of each river type so that the linear regression functions between CTT_{Com} and biennial summer mean temperatures have slopes close to 1 (Appendix C). The derivation method is similar to the one described above.

3.4. Evaluation of the transformed CTT_{Com}

The river type specific transformed community values were plotted against the measured mean water temperatures. In this independent data set, too, the regression line has a slope close to 1 ($a = 1.013$, Fig. 7), which underlines the plausibility of the approach of a river type-specific transformation.

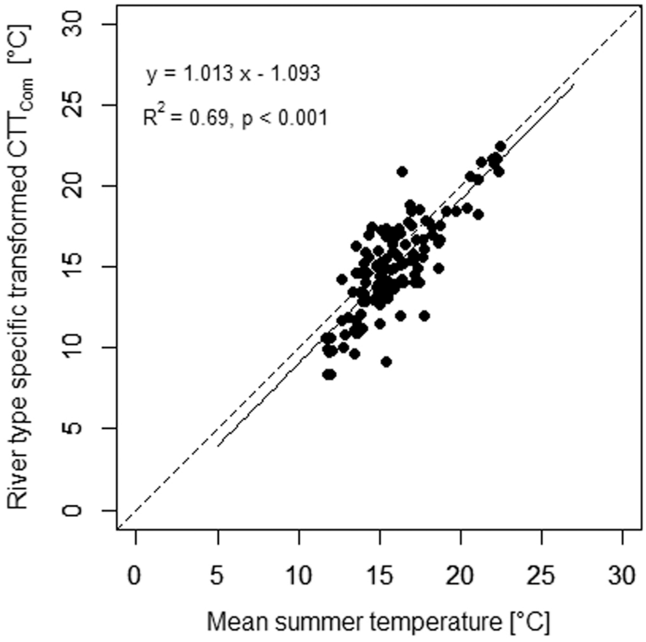

Fig. 7. Calculated river type specific transformed community central tendency temperatures CTT_{Com} plotted against the measured mean summer temperatures for 126 independent samples. The solid line represents the result of the linear regression model, the dashed line represents the 1:1 line.

4. Discussion

The information currently available on taxon-specific temperature preferences or tolerance values is very heterogeneous with regard to data origin and type of temperature reference values. Specifically, taxon-specific temperature values differ depending on whether they were derived in laboratory experiments or from field observations, and with regard to the observed life stages. Therefore, our objective was to derive temperature preferences for a large number of benthic invertebrate taxa based on a consistent method using field data. These should serve as a basis to track effects of global warming on aquatic benthic invertebrate communities in the future.

4.1. Methodological approaches for the derivation of taxon-specific temperature requirements

There are several methodological approaches to derive taxon-specific temperature requirements (Yuan, 2006). One option is to derive tolerance limits, calculated as abundance-weighted standard deviations or as a limit beyond and below which only a defined percentage, e.g. 5%, of individuals occur. Another option is to derive temperature optima, at which taxa show their respective maximum relative abundance. The results of both approaches depend, however, on data distribution (Babitsch and Sundermann, 2020; Schoonjans et al., 2011) and on coincidences, especially if the abundance per area is subject to great variability (Babitsch and Sundermann, 2020; Sundermann et al., 2008). Thus, some temperature parameters relating to maximum abundances of taxa might be more inaccurate than others. Another approach to derive taxon-specific temperature requirements is weighted averaging (WA) to calculate the 'central tendency temperature' (*CTT*) of a taxon, which is defined as mean temperature value of all test sites weighted by the abundances of the taxon (Yuan, 2006). This method is quite popular, often used in ecological studies and a robust approach for estimating the central tendency of a taxon (Braak, ter and Looman, 1986), which makes it meaningful for the application in our study. For the calculation of a comparably robust central value, similar to a median, the mean values of the defined temperature classes were calculated and the taxon abundances of all the sites contained therein were standardised by the number of sites per temperature class. This procedure prevents distortions resulting from an uneven distribution of sites across the temperature gradient and enhances robustness.

4.2. Validity and dependence of CTT_t values derived from field data on thermal and respiratory conditions

The derived taxon-specific central temperature tendencies CTT_t showed highest correlation with literature data when the latter was homogenous regarding time reference, temperature category, and data origin. Deviations between literature data and derived CTT_t values especially occurred when CTT_t values were compared with temperature requirements determined under laboratory conditions. The limited comparability between temperature requirements from laboratory and field studies was also pointed out by (Verberk et al., 2016), where the mayfly *Ephemera danica* endured a higher acute temperature exposure than *Seratella ignita* in the laboratory, but in field studies proved to be more abundant at lower water temperatures as compared to *S. ignita*. Specifically, the abundance-weighted mean water temperature of the evaluated sites of *E. danica* was 10.8 °C and that of *S. ignita* 11.7 °C. The latter temperature values, which relate to mean annual temperatures, fit well in relation to the derived CTT_t values for July, August and September in the present study (CTT_t values for *E. danica*: 15.57 °C and for *S. ignita* 15.97 °C). It can be assumed that results from laboratory and field studies very likely deviated due to a different supply of oxygen to the species under field conditions. Under oxygen saturated conditions some, but not all, species are expected to withstand higher temperatures than under conditions with lower oxygen supply, as given by studies on selected Crustacea (Verberk et al., 2018). Here, *Asellus aquaticus* and *Crangonyx pseudogracilis* showed high temperature limits of 35.6 °C and 36.8 °C under normoxic conditions. Under hypoxic conditions, their temperature limits were almost as high as under normoxic conditions. However, *Gammarus fossarum* and *Dikerogammarus villosus* behaved differently. Their temperature limits under normoxic conditions (32.9 and 32.3 °C) were considerably higher than under hypoxic conditions (30.7 and 30.0 °C) (Verberk et al., 2018). The authors pointed out that the neozoic species *D. villosus* occurs mainly at the shoreline of rivers with riprap that is well ventilated by wave motion, guaranteeing an adequate oxygen supply even at high temperatures. Obviously, this species can benefit from high water temperatures in terms of growth and reproduction without suffering from an undersupply of oxygen. In this respect, the comparatively low temperature limit of *D. villosus* determined in the laboratory is not a sign of a direct sensitivity to heat, but rather an increased need for oxygen. This explains why the CTT_t value for *D. villosus* derived from field data is comparatively high (CTT_t = 20.23 °C), in contrast to the low temperature limit derived in the laboratory (Verberk et al., 2018). However, in the case of native amphipod *G. fossarum*, the temperature limit derived in the laboratory (Verberk et al., 2018) and the CTT_t of 15.43 °C in the present study are both low compared to other species. The difference between *D. villosus* and *G. fossarum* is probably explained by the fact that *G. fossarum* is a common species of small, cool and fast flowing mountain streams. It probably has a similar oxygen demand than *D. villosus* but can benefit significantly less from higher water temperatures.

In their meta-analysis of published original data, Croijmans et al. (2021) could show that the species richness of aquatic macroinvertebrates in relation to the two variables temperature and oxygen is only weakly directly related to temperature but strongly related to oxygen concentration or its availability. Overall, this reveals that oxygen supply significantly influences both acute and chronic effects of water temperature on aquatic invertebrates, which is in concordance to a concept called 'oxygen and capacity limitation of thermal tolerance' (OCLTT) (Pörtner, 2010). After its publication, the validity and applicability to aquatic and terrestrial organisms was widely discussed (Jutfelt et al., 2018, 2014; Lefevre, 2016; Pörtner et al., 2018, 2017; Pörtner, 2014, 2012; Pörtner and Giomi, 2013; Schulte, 2015). One of the central hypotheses of the OCLTT concept relates to the thermal dependence of the 'aerobic scope', which is the difference between the resting metabolic rate (RMR) and the activity-correlated maximum metabolic rate (MMR) and thus a measure of an animal's aerobic energy budget available for growth, reproduction and general fitness functions (Pörtner, 2010). The concept postulates that the balance between oxygen availability and demand deteriorates in proportion to the deviation of water temperature from the species-specific optimum. Oxygen deficiency caused in this way and the associated energy deficit impair the general fitness of individuals with all possible consequences associated with entire populations and biocenoses. This fact must be taken into account when derived taxon-specific and community central tendency temperatures (CTT_t and CTT_{Com} values) are supposed to be used as an indicator of temperature-related changes in ecological communities. In this sense, it is assumed that although the CCT_t of individual taxa were derived solely from their abundances within the different summer temperature classes, CTT_{Com} not only reflects (summer) water temperature itself, but corresponds to a temperature equivalent value for the overall quality of all respiration-relevant summer habitat conditions that determine the metabolism of benthic invertebrates in the respective river. Thus, CTT_{Com} inversely reflects the mean aerobic scope of the overall benthic invertebrate community. The lower CTT_{Com}, the larger the aerobic scope and the better the respiration conditions for rheophilic species with high oxygen demand.

According to Rubalcaba et al. (2020), increasing water temperatures increase RMR more than MMR, reducing the difference between the two and thus the aerobic scope, with all consequences for the species and abundance composition. The higher metabolic rate of MMR already leads to oxygen limitation at lower water temperatures compared to RMR. As a result, MMR is more dependent than RMR on other physical environmental factors that determine oxygen uptake by organisms, such as oxygen concentration and flow velocity. Therefore, at higher water temperatures, CTT_{Com} also should respond less strongly to a further increase in water temperature, but should show a stronger dependence on these environmental factors, which are crucial for oxygen supply in the upper temperature range. Based on experiments with larvae of the stonefly species *Pteronarcys californica* (Frakes et al., 2021) also concluded that the thermal ceilings of aquatic insects are at least partly due to a lack of sufficient oxygen supply. They were able to demonstrate that the animals could tolerate a water temperature about 4 °C higher under flow velocities of 0.1 m s^{-1} than in stagnant water.

4.3. Application of taxon-specific and community central temperature tendencies as an equivalent for the summer respiratory conditions

Lowland rivers are characterised by high temperatures and low flow velocities. Furthermore, these rivers are often organically polluted due to intensive land use in the catchment (Molina-Navarro et al., 2018). This results in disproportionately poor respiratory conditions (Friedrich and Herbst, 2004) compared to a sole impact by increased temperatures. On the other hand, rivers with comparatively low summer water temperatures are predominantly small streams with a high slope and high flow velocities at high altitudes. They are generally less organically polluted than lowland rivers, which adds to their comparatively better respiratory conditions. As a consequence, in lowland streams with suboptimal oxygen conditions, CTT_t and CTT_{Com} index values tend to overestimate the actual temperature conditions. This is due to the fact that species aerobic energy budgets (Pörtner, 2010) in these organically polluted streams are higher than in unpolluted streams with a similar temperature regime. Incidentally, this is also the reason why the slope of the regression line in Fig. 6 is less than one. In contrast, CTT_t and CTT_{Com} index values underestimate field temperatures in fast running streams with good oxygen conditions. Therefore, CTT_{Com} values had to be corrected for each of the 25 stream types in Germany. The correction takes into account that aerobic energy budgets of species not only depend on temperature but also on several other abiotic parameters influencing oxygen conditions in a certain habitat (Verberk et al., 2016).

In summary, tracing effects of global warming by calculating the CTT_{Com} is a promising method. It is comparable to the 'community temperature index' (CTI) originally developed for bird communities to estimate the change in community composition in response to global warming (Devictor et al., 2008). Although it has been claimed that the CTI does not necessarily indicate changes in community composition due to temperature changes but also to other environmental drivers (Bowler and Böhning-Gaese, 2017), the CTI has since been used in many studies, including also with regard to other taxonomic groups (Bowler et al., 2017; Brice et al., 2019; Burrows et al., 2019; Fumy et al., 2020). This shows that these kinds of tools are widely accepted in measuring species as well as community responses to global warming.

The derived CTT_{Com} appears to be a promising tool for assessing the impact of global warming on benthic invertebrate communities in streams and rivers. It is already being applied in water management practice in Germany, which was facilitated by providing a free software tool (available on request). In particular, CTT_{Com} is a suitable indicator due to co-indication of other abiotic factors that influence the aerobic scope of individuals in a community. After all, climate change does not only result in higher summer water temperatures, but also in reduced precipitation and flow velocities during summer times (Pachauri and Mayer, 2015). Both consequences of climate change cause deterioration in the aerobic scope of aquatic taxa that can be indicated with CTT_{Com}. Thus, we encourage all stakeholders in the field of water management practice to evaluate this method in order to understand and to trace the influence of climate change in rivers and streams on a long-term perspective.

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CRediT authorship contribution statement

Andrea Sundermann: Writing – original draft, Visualization, Formal analysis. **Andreas Müller:** Conceptualization, Data curation, Formal analysis, Software, Writing – review & editing. **Martin Halle:** Conceptualization, Formal analysis, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supporting information

Appendix A. Taxon-specific central tendency temperatures (CTT_t) for aquatic benthic invertebrates.

Appendix B. Table. Results of the literature research regarding temperature requirements of aquatic benthic invertebrate species.

Appendix C. Table. Stream type specific correction functions to transform CTT_{Com} values in that way that the linear regression function between CTT_{Com} and biennial summer mean temperatures has a slope close to 1.

Available on request: Software to calculate the community central tendency temperatures (CTT_{Com}).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.limno.2022.125980.

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