

Response of chironomid species (Diptera, Chironomidae) to water temperature: effects on species distribution in specific habitats

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Abstract

The response of 443 chironomid species to water temperature was analyzed, with the aim of defining their thermal optimum, tolerance limits and thermal habitat. The database included 4442 samples mainly from Italian river catchments collected from the 1950s up to date. Thermal preferences were calculated separately for larval and pupal specimens and for different habitats: high altitude and lowland lakes in the Alpine ecoregion; lowland lakes in the Mediterranean ecoregion; heavily modified water bodies; kryal, krenal, rhithral and potamal in running waters. Optimum response was calculated as mean water temperature, weighted by species abundances; tolerance as weighted standard deviation; skewness and kurtosis as 3rd and 4th moment statistics. The responses were fitted to normal uni- or plurimodal Gaussian models. Cold stenothermal species showed: i) unimodal response, ii) tolerance for a narrow temperature range, iii) optima closed to their minimum temperature values, iv) leptokurtic response. Thermophilous species showed: i) optima at different temperature values, ii) wider tolerance, iii) optima near their maximum temperature values, iv) platikurtic response, often fitting a plurimodal model. As expected, lower optima values and narrower tolerance were obtained for kryal and krenal, than for rhithral, potamal and lakes. Thermal

response curves were produced for each species and were discussed according to species distribution (*i.e.* altitudinal range in running water and water depth in lakes), voltinism and phylogeny. Thermal optimum and tolerance limits and the definition of the thermal habitat of species can help predicting the impact of global warming on freshwater ecosystems.

Introduction

Global warming is affecting freshwater macroinvertebrate communities with alteration of species distribution and phenology. In particular, increased water temperature will induce a change in distribution of species, which will react following their thermal optimum along an altitudinal and/or latitudinal gradient (Hughes, 2000; Nyman *et al.*, 2005; Bonada *et al.*, 2007; Sheldon, 2012).

According to species adaptations, each habitat will show different sensibility: in Southern Europe, kryal, krenal, high altitude lakes and ponds are supposed to be sensitive habitats, being characterized by stenotopic taxa directly influenced by water temperature (Boggero *et al.*, 2006; Rossaro *et al.*, 2006a; Tixier *et al.*, 2009; Jacobsen *et al.*, 2012; Lencioni *et al.*, 2012). A lot of species won't probably survive global warming, since spatial isolation may give little opportunity to migrate elsewhere.

On the contrary, the response of habitats at lower altitude is poorly understood, as species thermal optimum and tolerance are less known and other factors generally contribute in structuring biotic communities (Jacobsen *et al.*, 1997). Moreover, some studies showed that local adaptations may induce different thermal sensibility of single species at different sites and habitats. In particular, acclimation temperature during lifetime was proved to affect tolerance of populations (Dallas & Rivers-Moore, 2012). Besides, microevolutionary dynamics at local scale may separate the response of populations, and consequently their fitness (Hogg *et al.*, 1998; Van Doorsalaen *et al.*, 2009). Therefore it is necessary to determine the extent to which thermal response of species varies among habitats, to determine which communities are more menaced by global warming.

Studies on aquatic organisms based on lethal or sub-lethal endpoints (*e.g.* death, ability to escape unfavourable conditions, growth, reproduction, etc.) were carried out in experimental mesocosms or lab tests to derive thermal performance curves that relate species response to water temperature (Hester & Doyle, 2011; Dallas & Rivers-Moore, 2012), with definition of critical thermal maxima or minima. This approach may be successful to detect biological or physiological processes mostly affected by altered temperature. Nonetheless thermal history, acclimation, rate of temperature change, test duration, life stage have been shown to affect results. Moreover, the difficulty of taxa identification may hinder test application at species level, and many

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Key words: Chironomidae, thermal tolerance, ecological traits, global warming.

Acknowledgements: data stored in the CHIRDB were collected within sampling surveys supported by different grants. Details about the projects are in the publications of the first Author quoted in the reference paragraph.

Received for publication: 4 April 2013.

Revision received: 29 April 2013.

Accepted for publication: 30 May 2013.

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Journal of Entomological and Acarological Research 2013; 45:e14

doi:10.4081/jea.2013.e14

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studies considered genera, families or even orders (Dallas & Rivers-Moore, 2012).

More realism could be achieved determining the temperature range that organisms experience in the field (Rossaro, 1991a, 1991b, 1991c). Data from different ecological surveys in freshwater ecosystems could be gained and specimens collected can be identified at species level. In this way a large amount of data for each species can be gathered. This approach could be successful to determine species thermal preferences and tolerance limits (*i.e.* temperature beyond which organisms avoid) in different habitats, seasons and life stages. In fact, empirical data may allow going beyond local adaptations of taxa and drawbacks of manipulation tests. This approach was recently adopted at European scale (AQEM project) (Hering *et al.*, 2004) for many macroinvertebrate groups collecting published data to derive species' ecological preferences (Schmidt-Kloiber & Hering, 2012). Nonetheless species responses have been expressed as qualitative rather than quantitative features, because most publications do not provide raw data. Therefore much work is still needed to better quantify the response to natural and anthropogenic factors, as a valuable tool for biomonitoring.

For what concerns water temperature, among macroinvertebrate taxa, insects were shown to be mainly responsive to this pressure (Bonada *et al.*, 2007; Čiamporová-Zat'ovičová *et al.*, 2010; Dallas & Rivers-Moore, 2012). In particular, chironomids are a suitable indicator group, being characterized by a large number of species with a wide range of responses to environmental factors (Lindgaard *et al.*, 1995). Fossil remains of these dipterans in lake sediments have been used as proxy to reconstruct shifts in air and water temperature, since many species were shown to respond rapidly to climatic fluctuations (Larocque *et al.*, 2001; Lotter *et al.*, 2012). Moreover, they have been used as indicators of oxygen concentration (Rossaro *et al.*, 2007b) and trophic levels in lakes (Sæther 1979, Rossaro *et al.*, 2011) and as indicators of organic (Raunio *et al.*, 2007) and toxic (Cortezezz *et al.*, 2011) pollution in rivers. Nonetheless many studies showed that water temperature is one of the main factors determining taxa assemblages and species distribution (Rossaro, 1991a, 1991b, 1991c; Brooks & Birks, 2000; Medeiros & Quinlan, 2011). Lack of information could be possibly filled by biogeographic studies considering ecological equivalents in different regions (Jacobsen *et al.*, 1997, 2012; Hamerlik & Brodersen 2010; Hamerlik *et al.*, 2011), but species names are often not corresponding in different areas, since at large spatial scale biogeographic gradients may be present (Catalan *et al.*, 2009) or, at smaller scale, taxonomic determination by different experts often affects data comparability (Kernan *et al.*, 2009; Heiri *et al.*, 2011). Therefore at present only data at regional scale can be likely compared.

The present research aims at quantitatively determine the thermal response of chironomid species in different freshwater habitats in Southern Europe, following the empirical approach. At this purpose, chironomid samples collected in many surveys mostly from Italy but also from other Alpine and Mediterranean countries are considered. Species response to altitude, source distance in rivers and water depth in lakes is also determined. Different life stages are analyzed.

Materials and methods

To investigate the thermal response of chironomid species the CHIRDB database (Rossaro *et al.*, 2006b) was used. This database contains records about chironomid samples collected in freshwater ecosystems mainly in Italy, but also in Algeria, Austria, France, Switzerland and Germany from the 1950s up to date (Table 1). Other data were derived from published papers (Table 1).

A map of the sampling sites is shown in Figure 1.

Sampling sites were grouped into different habitats:

- kryal=glacial streams above the tree line (Rossaro *et al.*, 2006b);

note that this definition of kryal is more extended than the one given by Milner & Petts (1994) and water temperature can be much higher than 2°C

- krenal=springs (Vannote *et al.*, 1980)
- rhithral=mountain reach of rivers below the tree line (Vannote *et al.*, 1980)
- potamal=lowland reach of rivers (Vannote *et al.*, 1980)
- Alpine lowland lakes=natural lakes within the Alpine ecoregion (with latitude >44° 00') with altitude below 800 m a.s.l. (Tartari *et al.*, 2006)
- Alpine high altitude lakes=natural lakes within the Alpine ecoregion (with latitude >44° 00') with altitude above 800 m a.s.l. (Tartari *et al.*, 2006)
- Mediterranean lakes=natural lowland lakes within the Mediterranean ecoregion (with latitude <44° 00'), with altitude below 800 m a.s.l. (Tartari *et al.*, 2006)
- heavily modified water bodies=reservoirs and artificial lakes
- brackish ponds=ponds with high salinity (water conductivity >2500 µS cm⁻¹ at 20°C) (Tartari *et al.*, 2006)

Sampling sites are summarized in Table 2. Samples are grouped into river catchments and the number of samples collected in each habitat is reported.

The same site was generally sampled covering all seasons. Chironomid samples were collected using different tools, according to the habitat: i) pond net collections of larvae from small water bodies (krenal, kryal, high altitude Alpine lakes) (Rossaro *et al.*, 2006b); ii) surber net collections of larvae in stony bottom streams (rhithral) (Rossaro, 1991b, 1991c, 1992, 1993; Marziali *et al.*, 2010a, 2010b); iii) Ekman, Petersen, Ponar dredge samples of larvae from natural lowland lakes and heavily modified water bodies, brackish ponds and from large rivers (potamal) (Rossaro, 1988; Batteggazzore *et al.*, 1992; Rossaro *et al.*, 2006a, 2011); iv) drift samples of pupal exuviae using a Brundin net (lakes, kryal, krenal, rhithral, potamal) (Rossaro, 1991b, 1991c); v) adult captures collected with hand nets, emergence traps or Malaise traps (Rossaro, 1987); imagines were used for confirming species identifications, but were not considered for data analysis.

For each sampling site latitude, longitude, altitude (m a.s.l.), distance from source (km) in running waters and sampling depth (m) in lakes were recorded in the field or were derived using geographic information system-based cartographic data (<http://www.sinanet.isprambiente.it>). Water temperature (°C) was measured with a field multiprobe during the samplings.

Chironomid samples were slide mounted and identified to species using specialized keys (Wiederholm 1980, 1983, 1986; Ferrarese & Rossaro, 1981; Ferrarese, 1983; Rossaro, 1982; Nocentini, 1985; Langton, 1991) and comparing different life stages (*e.g.* larval exuviae with pupae; pupal exuviae with imagines). In the present work, the abundances of 309 species as larvae (18,886 records) and 325 species as pupal exuviae (7619 records) from 4442 samples were considered.

Chironomid species nomenclature and systematics follow Sæther (1977), Rossaro (1991c), Sæther (2000), Cranston *et al.* (2012).

Data analysis

Data were stored in a Microsoft Access database (CHIRDB) (Rossaro *et al.*, 2006b). Data on larval samples were expressed as specimens per square meter when collected with Surber (rhithral) and dredge samples (lowland lakes, heavily modified water bodies, potamal, brackish ponds); and as number of specimens for unit of effort (about 15 min sampling) when collected with pond nets (high altitude lakes, kryal, krenal). Data on pupal exuviae samples collected with a Brundin net in all habitats were expressed as number of specimens per unit of effort (about 15 min sampling).

Records of species abundances matching water temperature measures were selected using MS-Access queries and were imported into

Matlab environment for statistical analyses. The moment statistics, used for describing probability distributions, were then calculated. The expected value of a random variable (the mean) is derived by the first moment, the variance by the second moment, the skewness (*i.e.* the asymmetry of the probability distribution) by the third moment, the kurtosis (*i.e.* the peakedness of the probability distribution) by the fourth moment (Khurshid, 2007).

The water temperature range experienced by each species was divided into 20 equally-ranged classes and the frequency of the species in each of the 20 classes was calculated. A thermal response curve was then produced for each species relating species abundance to water temperature.

The formulae used to calculate the first (weighted average), second (weighted standard deviation), third (skewness= g_1) and fourth (kurtosis= g_2) central moments can be found in Sokal & Rohlf (1981).

Table 1. Data stored in the CHIRDB database are derived from different surveys here summarized.

Country	Region	River catchment	Sampling years	References
Italy	Aosta Valley	Dora Baltea river	1995-98	Rossaro <i>et al.</i> , 2006b; unpublished data
	Trentino-Alto Adige	Sarca, Adige and Noce rivers	1990, 1996-98, 2005	Boggero <i>et al.</i> , 2006; Lencioni <i>et al.</i> , 2007
		Lakes Lases, Lamar, Caldonazzo and Tenno (Brenta river)	1996, 2000, 2004-07	Lencioni <i>et al.</i> , 2006
	Lombardy	Oglio and Mincio rivers	1978-83, 2006	Rossaro, 1991c
		Lambro and Olona rivers	1977-78, 1986-87, 2003	Unpublished data
		Brembo and Serio rivers	1980-81, 2003	
		Po river	1977-93	Rossaro 1987, 1988; Battegazzorre <i>et al.</i> , 1992
		Adda river	1977, 1988-89, 2001-07	Unpublished data
		Ticino river	1979, 1985, 2001-04, 2009-10	Berra <i>et al.</i> , 2004
		Lake Garda	1970-71, 1982, 2004, 2007, 2011	Rossaro <i>et al.</i> , 2006a, 2011; Bonomi, 1974
		Lakes Viverone and Avigliana	2005-06	Rossaro <i>et al.</i> , 2006a, 2011
		Lake Varese	1987, 1994-97, 2002-05	Rossaro <i>et al.</i> , 2006a, 2011
		Lake Monate	1977, 2004-05	Rossaro <i>et al.</i> , 2006a, 2011; Nocentini, 1979
		Lake Como	1980-84, 2004-05, 2007	Unpublished data
		Lakes Comabbio, Alserio, Pusiano and Annone	1967, 1977, 2004-07	Rossaro <i>et al.</i> , 2006a, 2011
		Lake Iseo	1967, 2003-04	Unpublished data
	Piedmont	Lake Mergozzo	1963-64, 1971-72, 1975, 1994, 2010	Rossaro <i>et al.</i> , 2006a, 2011; Nocentini, 1979
		Lake Maggiore	1953-54, 1960-61, 1966-67, 1985-88, 1995-96, 2004, 2007, 2009-10	Rossaro <i>et al.</i> , 2006a, 2011; Nocentini, 1963
		Ticino river	1985-87, 1991-94, 2000, 2007	Boggero <i>et al.</i> , 2006; Unpublished data
		Dora Baltea river	2005	Boggero <i>et al.</i> , 2006
		Agogna river	1976-77, 1981-82	Rossaro, 1991c
		Toce river	1991-94, 2000	Unpublished data
		Sesia river	1987	Unpublished data
		Lake Lugano	2004-04	Unpublished data
		Po and Tanaro rivers	1989-90	Unpublished data
		Lake Orta	1976	Unpublished data
		Emilia Romagna	Po and Trebbia river	1977-83
Taro river	2001-03		Marziali <i>et al.</i> , 2010b	
Liguria	Danè river	1998-99	Unpublished data	
Toscana	Magra river	2001	Unpublished data	
Marche	Potenza river	1986	Rossaro, 1988	
Abruzzo	Tordino, Vomano and Aterno rivers	1978, 1986-92, 1995, 2010	Unpublished data	
Lazio	Tevere and Nera rivers	1989-90	Unpublished data	
	Trasimeno river	2003	Unpublished data	
	Lakes Bolsena, Bracciano and Vico	1970-73	Rossaro <i>et al.</i> , 2006a, 2007a	
Umbria	Tevere river	1977-03		
Campania	Sele river	2000-01	Marziali <i>et al.</i> , 2010a	
Puglia	Ofanto river	1990	Unpublished data	
Sardinia	Cedrina and Rio Mannu rivers	1978, 1986	Unpublished data	
Lazio, Abruzzo, Basilicata, Puglia, Sicily	Heavily modified water bodies (Fibreno, Brasimone, Scontrone, Pertusillo, Occhito, Dirillo)	1976-77, 1934-85, 1989, 1991	Unpublished data	
Switzerland	Ticino river	2005	Boggero <i>et al.</i> , 2006	
France	Garonna river	2004	Unpublished data	
Germany	Donau river	2006	Free <i>et al.</i> , 2009	
Austria	Donau river	2006	Free <i>et al.</i> , 2009	
Algeria	Algerian wadi	2007	Zerguine <i>et al.</i> , 2009; Chaib <i>et al.</i> , 2011	

Table 2. Continued from previous page.

River catchment	lat	long	kn	kr	rh	pt	AL	al	ME	hm	br
Adda (LC)	45°48'16"	09°23'27"	0	0	3	0	21	0	0	0	0
Adda (MI)	45°37'00"	09°29'97"	0	0	0	17	0	0	0	0	0
Adda (LO)	45°16'02"	09°37'00"	0	0	1	19	4	0	0	0	0
Adda (CR)	45°28'00"	09°31'00"	0	0	0	18	0	0	0	0	0
Adda (BG)	46°07'00"	09°53'00"	13	0	0	1	0	0	0	0	0
Sarca	46°08'02"	10°37'32"	87	206	115	0	0	15	0	0	0
Noce	46°17'00"	10°40'00"	0	3	0	0	1	0	0	0	0
Adige (BZ)	46°02'41"	11°15'33"	0	0	0	0	4	0	0	0	0
Adige (TN)	46°20'25"	10°29'21"	0	0	1	0	114	38	0	0	0
Brenta	46°01'34"	11°19'39"	0	0	0	0	78	0	0	0	0
Como	45°40'01"	09°17'02"	0	0	0	0	107	0	0	0	0
Brembo	45°42'46"	09°38'39"	1	0	56	0	0	0	0	1	0
Serio	45°30'10"	09°44'12"	1	0	36	0	0	0	0	0	0
Iseo	45°40'24"	09°35'38"	0	0	0	0	28	0	0	0	0
Oglio	45°35'17"	09°45'14"	2	4	25	2	51	0	0	0	0
Mincio (MN)	45°33'32"	10°39'45"	0	0	0	0	6	0	0	0	0
Garda (VR)	45°41'00"	10°41'01"	0	0	0	0	353	0	0	0	0
Po (MI and PV)	45°41'05"	09°16'02"	0	0	216	103	46	0	0	0	0
Po (PC)	45°07'00"	10°25'06"	0	0	0	427	0	0	0	0	0
Po (FE)	44°10'00"	12°00'00"	0	0	0	1	0	0	0	0	0
Tanaro	44°21'00"	08°11'04"	0	0	85	27	0	0	0	0	0
Danè	44°16'00"	08°25'00"	0	0	95	0	0	0	0	0	0
Trebbia	44°29'16"	09°21'18"	4	0	11	0	5	0	0	0	0
Taro	44°35'30"	09°33'21"	2	0	31	28	0	0	0	0	0
Magra	44°22'00"	09°53'00"	0	0	1	0	0	0	0	0	0
Reno (Brasimone)	44°08'00"	11°08'00"	0	0	0	0	0	0	0	1	0
Potenza	43°19'00"	13°24'00"	0	0	10	10	0	0	0	0	0
Tevere (PG)	43°18'00"	12°18'00"	0	0	0	3	0	0	0	0	0
Trasimeno	43°10'00"	12°00'00"	0	0	0	0	0	0	2	0	0
Bolsena	42°35'00"	11°55'00"	0	0	0	0	0	0	102	0	0
Bracciano	42°07'00"	12°14'00"	0	0	0	0	0	0	59	0	0
Vico	42°18'00"	12°10'00"	0	0	0	0	0	0	40	0	0
Tordino-Vomano	42°36'00"	13°38'00"	0	0	2	3	0	0	0	1	0
Nera	42°25'00"	13°05'00"	0	0	2	0	0	0	0	0	0
Aterno-Pescara	42°26'00"	13°22'00"	12	0	4	0	0	0	0	1	0
Sangro (Scontrone)	41°34'00"	13°38'00"	1	0	2	1	2	0	0	4	0
Fortore (Occhito)	41°35'00"	14°57'00"	0	0	0	0	0	0	0	14	0
Liri (Fibreno)	41°38'00"	13°22'00"	0	0	0	0	0	0	1	0	0
Ofanto	40°52'00"	15°05'00"	0	0	1	0	0	0	0	0	0
Cedrino	40°35'00"	09°42'00"	1	0	0	0	0	0	0	0	0
Sele	40°33'00"	15°19'00"	0	0	33	0	0	0	0	0	0
Agri (Pertusillo)	40°16'00"	15°56'00"	0	0	0	0	0	0	0	103	0
rio Mannu	39°18'00"	09°08'00"	0	0	2	0	0	0	0	0	3
Dirillo	37°08'00"	14°45'00"	0	0	0	0	0	0	0	4	0
Kebir (Algeria)	36°46'38"	08°19'31"	0	0	90	0	0	0	0	0	0

lat, latitude; long, longitude; kn, krenal; kr, kryal; rh, rhithral; pt, potamal; AL, Alpine ecoregion lowland lakes; al, Alpine ecoregion high altitude lakes; ME, Mediterranean ecoregion lakes; hm, heavily modified water bodies; br, brackish ponds. Abbreviations in brackets are Italian provinces.

The first central moment has the meaning of optimum response value, the second moment can be interpreted as a measure of tolerance (Ter Braak & Prentice, 1988). A positive value of g_1 means a response curve skewed to the right, *i.e.* the optimum value is closer to the minimum response value. A negative value of g_1 means a response curve skewed to the left, *i.e.* optimum water temperature is closer to the maximum response value. A positive value of g_2 is a measure of the peaked-

ness of a curve. A curve with a high g_2 (>3) is called *leptokurtic* and it has a defined peak, *i.e.* the species has a defined optimum temperature. A negative value of g_2 means a *platykurtic* response or flat response, *i.e.* the species is present over a wide range of water temperature values. In general, a negative value of g_2 suggests a bi- or plurimodal Gaussian distribution (Khurshid, 2007).

Moment calculations were performed converting in Matlab® envi-

ronment, version R2012a, some FORTRAN programs, program 9 (Davies, 1971) and program STATFD (Rohlf, 1987).

The central moment calculation formulae were used also to analyze the response of species to altitude, water depth (for lacustrine species) and distance from source (for lotic species). Regression between species optima for water temperature and standard deviation, g_1 or g_2 was also calculated to relate species optimum and tolerance characters.

To represent graphically species response to water temperature the Curve-Fitting Matlab® toolbox was used, fitting species abundances against water temperature values; the toolbox allows to fit many different models, in particular the one-, two- or n-term Gaussian library model:

$$y = a_1 * e^{-((x-m_1)/s_1)^2} + \dots + a_n * e^{-((x-m_n)/s_n)^2}$$

where i and n are the peaks to be fitted, a_i and a_n are the amplitude, m_i and m_n the centroid (location), s_i and s_n are coefficients related to the peak width. Separate models were tested for each species collected as larvae and pupal exuviae in the different habitats.

The fitted curves given in Figures 2-11 are the ones giving the best fit (*i.e.* the lowest mean square error). Models with more than three terms (see formula) were not considered to avoid overfitting.

Regression curves between optima for water temperature (as dependent variable) and optima for altitude, water depth, distance from source (as independent variables) were calculated.

Results

Of all available data, 281 samples were from kryal, 186 from krenal, 987 from rhithral, 749 from potamal, 1903 from lakes in the Alpine ecoregion (*i.e.* 114 from high altitude lakes and 1789 from lowland lakes), 204 from natural lakes in the Mediterranean ecoregion, 129 from heavily modified water bodies, 3 from brackish ponds (Table 2). A total of 443 chironomid species were present in the sampling sites.

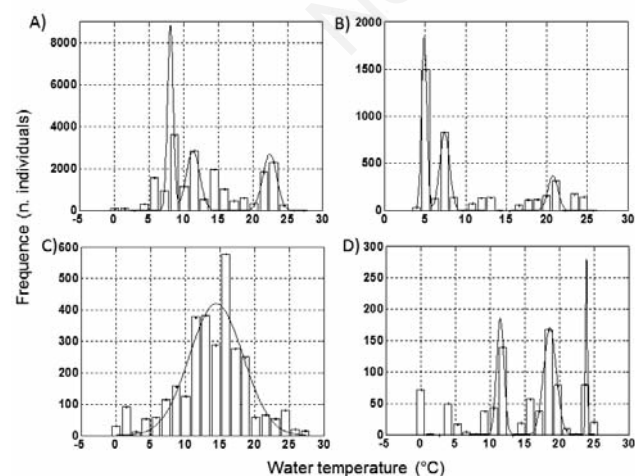


Figure 2. Response of *Conchapelopia pallidula* larvae (number of individuals m^{-2}) to water temperature ($^{\circ}C$) in all habitats (A), Alpine ecoregion lowland lakes (B), rhithral (C) and potamal (D).

Water temperature

Thermal response was first calculated considering all data on larvae (*i.e.* joining all habitats) to generally characterize each species' preferences for water temperature. Results for the 55 species present in ≥ 100 records are given in Table 3. For each species the number of samples used to calculate the weighted mean, standard deviation, skewness and kurtosis are reported. In general, species with preference for low temperature had a lower standard deviation than species with optima in warm waters. For this reason the former can be defined as cold stenothermal, the latter as warm eurithermal. In fact, the r^2 value obtained regressing optimum water temperature of each species with its standard deviation was significant [$r^2=0.48$, 53 degree of freedom (df), $P<0.01$].

The regression between optimum for water temperature ($m^{\circ}C$) and skewness (g_1) (Table 3) gave an inverse relation ($r^2=0.34$, 53 df, $P<0.01$). As well, optimum for water temperature ($m^{\circ}C$) and kurtosis (g_2) were inversely related ($r^2=0.22$, 53 df, $P<0.01$). These relations suggest that cold stenothermal species generally show a response curve skewed to the right, with optimum value closed to minimum values, and leptokurtic (*i.e.* unimodal trend); whereas thermophilous species generally show a curve skewed to the left, with optimum value closed to maximum values, and platykurtic (*i.e.* bi- or plurimodal trend).

Thermal response was then calculated for each separate habitat to better characterize each species' preferences (*i.e.* using data on larvae collected with the same sampling method) (Appendix).

The thermal response of some species is represented in Figures 2-9. For example, thermal curves for *Conchapelopia pallidula* are shown in Figure 2. Optimum response calculated from 615 records (all habitats pooled, Figure 2A) was $13.54^{\circ}C$, with a standard deviation of $5.93^{\circ}C$, a small positive skewness of 0.34 and a negative kurtosis of 1.03 (Table 3). The negative kurtosis suggested a trimodal response with three peaks at $8.13^{\circ}C$ (main peak), $11.39^{\circ}C$ and $22.42^{\circ}C$ (secondary peaks). Peaks were at $4.93^{\circ}C$ (main peak), $7.45^{\circ}C$ and $20.77^{\circ}C$ considering only samples from Alpine lowland lakes (Figure 2B). Optimum for rhithral samples was $13.9^{\circ}C$ (unimodal response) (Figure 2C, Appendix), while potamal samples gave a trimodal response with peaks at $11.5^{\circ}C$, $18.64^{\circ}C$ and $23.89^{\circ}C$ (Figure 2D).

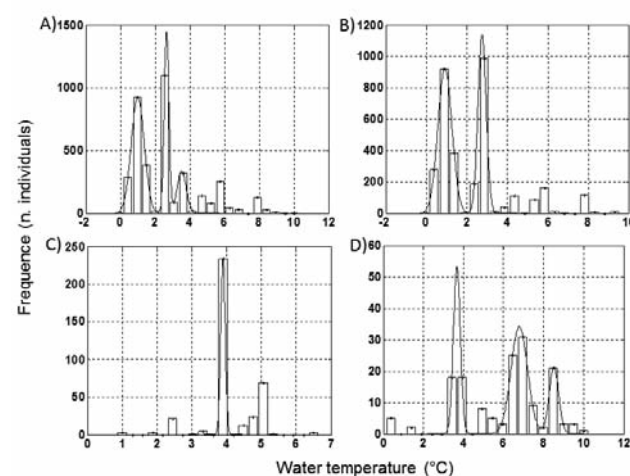


Figure 3. Thermal response of *Diamesa bertrami* larvae. Response of *Diamesa bertrami* (number of individuals m^{-2}) to water temperature ($^{\circ}C$) in all habitats (A), kryal (B), krenal (C) and rhithral (D).

Table 3. Thermal response (°C) of species (larvae) in all habitats: number of samples, weighted mean, standard deviation, skewness and kurtosis of species abundance vs water temperature values. Only the species with ≥100 records in the dataset are reported. Species are in phylogenetic order.

Species	n	m (°C)	SD (°C)	g1	g2
<i>Procladius choreus</i>	1018	13.39	5.7	0.63	-0.65
<i>Macropelopia nebulosa</i>	127	10.5	5.17	0.47	-0.63
<i>Zavrelimyia barbatipes</i>	128	11.58	4.11	-0.21	0.45
<i>Conchapelopia pallidula</i>	615	13.54	5.93	0.34	-1.03
<i>Rheopelopia ornata</i>	111	14.77	4.3	-0.19	-1.15
<i>Pseudodiamesa branickii</i>	115	5.63	3.08	0.8	0.71
<i>Diamesa steinboeckii</i>	106	1.98	1.45	1.06	1.19
<i>Diamesa latitarsis</i>	134	3.43	1.97	0.85	0.27
<i>Diamesa bertrami</i>	200	2.68	1.96	1.16	0.79
<i>Diamesa tonsa</i>	186	7.19	4.66	0.61	-0.18
<i>Diamesa zernyi</i>	215	3.72	2.51	1.62	8.22
<i>Prodiamesa olivacea</i>	246	9.48	4.33	1.79	3.56
<i>Brillia bifida</i>	202	11.38	4.76	0.19	-0.69
<i>Tvetenia calvescens</i>	537	11.08	5.81	0.06	-1.24
<i>Eukiefferiella brevicar</i>	133	4.51	1.94	1.66	6.37
<i>Eukiefferiella claripennis</i>	215	14.7	4.41	-0.49	-0.3
<i>Eukiefferiella minor</i>	176	6.8	3.78	0.72	0.41
<i>Psectrocladius (Psectrocladius) oxyura</i>	283	12.17	6.22	0.43	-1.04
<i>Rheocricotopus effusus</i>	124	13.15	5.83	-0.16	-0.49
<i>Rheocricotopus fuscipes</i>	245	16.97	7.97	0.06	-1.49
<i>Synorthocladius semivirens</i>	128	13.38	4.42	-0.16	-0.78
<i>Orthocladius (Euorthocladius) rivicola</i>	366	9.85	4.7	0.52	-0.01
<i>Orthocladius frigidus</i>	261	6.17	3.72	1.25	1.4
<i>Orthocladius oblidens</i>	138	9.18	5.5	1.16	0.21
<i>Orthocladius rhyacobius</i>	212	12.14	4.02	-0.15	-0.24
<i>Orthocladius rubicundus</i>	111	12.45	3.19	0.55	0.91
<i>Paratrachocladius rufiventris</i>	253	17.33	6.32	0.17	-0.82
<i>Cricotopus annularis</i>	161	14.24	4.79	0.09	0.16
<i>Cricotopus bicinctus</i>	276	14.63	5.08	-0.23	-1.04
<i>Cricotopus (Isocladius) sylvestris</i>	183	11.19	5.08	0.82	-0.09
<i>Parametriocnemus stylatus</i>	218	11.14	4.97	0.36	-0.83
<i>Parakiefferiella bathophila</i>	117	5.89	3.69	3.66	12.52
<i>Thienemanniella partita</i>	107	7.73	4.08	0.93	0.3
<i>Corynoneura scutellata</i>	259	11.07	4.06	-0.5	-0.35
<i>Tanytarsus gregarius</i>	421	11.11	6.8	0.72	-1.07
<i>Cladotanytarsus atridorsum</i>	268	14.59	5.11	0.63	-1.05
<i>Paratanytarsus lauterborni</i>	101	10.53	3.01	3.1	9.11
<i>Micropsectra atrofasciata</i>	490	13.79	5.33	0.52	0.88
<i>Micropsectra pallidula</i>	125	6.3	3.58	1.1	0.44
<i>Pagastiella orophila</i>	115	8.12	4.63	1.43	0.75
<i>Pseudochironomus prasinatus</i>	209	13.95	6.56	0.02	-1.37
<i>Paratendipes albimanus</i>	351	12.22	4.43	1.35	0.65
<i>Microtendipes pedellus</i>	394	12.29	2.73	0.6	1.06
<i>Polypedilum convictum</i>	138	15.44	4.07	-0.61	0.44
<i>Polypedilum laetum</i>	112	16.65	5.52	-0.14	-0.38
<i>Polypedilum nubeculosum</i>	566	12.08	4.09	1.26	1.58
<i>Endochironomus tendens</i>	106	12.51	3.91	0.8	0.08
<i>Dicrotendipes nervosus</i>	276	10.08	5.24	0.86	0
<i>Glyptotendipes pallens</i>	154	13.88	7.65	0.08	-1.25
<i>Chironomus anthracinus</i>	525	13.54	6.35	0.5	-1.44
<i>Chironomus plumosus</i>	571	11.19	6.1	0.67	-0.59
<i>Chironomus riparius</i>	333	15.28	4.65	0.32	1.44
<i>Cladopelma viridulum</i>	294	13.63	5.98	0.51	-0.7
<i>Cryptochironomus defectus</i>	473	13.86	5.67	0.43	-0.74
<i>Demicryptochironomus vulneratus</i>	143	12.96	7.28	0.44	-1.36

n, number of samples; m, weighted mean; SD, standard deviation; g1, skewness; g2, kurtosis.

Many cold stenothermal species such as *Diamesa zernyi* and *Pseudokiefferiella parva* showed only one maximum, with a high g_2 , i.e. leptokurtic response (Table 3, Appendix).

Species with low temperature optimum (cold stenothermal) showed a response curve skewed to the right ($g_1 > 0$). *Diamesa bertrami* showed a moderately platykurtic response ($g_2 = 0.79$), with a trimodal curve considering all habitats (Figure 3A), a bimodal curve with main peak at 2.76°C in kryal samples (with a second peak at 0.93°C) (Figure 3B), a unimodal response in krenal with peak at 3.90°C (Figure 3C), a trimodal response in rhithral with peaks at 3.67°C, 6.79°C and 8.52°C (Figure 3D).

Species with optimum at high temperatures (thermophilous species) showed a response curve skewed to the left ($g_1 < 0$). For example, *Cricotopus (Isocladius) sylvestris* in potamal (Figure 4C, Appendix) showed optimum at 17.80°C and $g_1 = 2.13$; *Paratanytarsus mediterraneus* in potamal (Figure 5D; Appendix) had optimum at 19.42°C and a $g_1 = 1.59$. *Tanytarsus brundini* in rhithral with optimum at 14.37°C and a negative g_1 ($g_1 = 0.29$) is an example of a curve moderately skewed to the left (Figure 5B; Appendix).

Some exceptions were shown: *Paratrichocladius rufiventris* (Figure 4A) had optimum temperature value of 17.33°C and a response curve skewed to the right ($g_1 > 0$, i.e. $g_1 = 0.17$) (Table 3). A negative value of g_2 was an index of a bi- or plurimodal response; *Tanytarsus gregarius* in Alpine ecoregion lakes with a negative g_2 ($g_2 = 1.09$; Appendix) had a bimodal response with two peaks at 5.68°C and 20.66°C (Figure 5C); the very different optima suggest the presence of two populations, the former inhabiting high depth habitats (down to 350 m depth) characterized by low temperatures.

Similarly, it was possible to compare the response of *Polypedilum nubeculosum* larvae in different habitats (Figure 8). A plurimodal response was evident, with different peaks in different habitats.

The response of the larval and pupal stages was compared in different habitats (Figures 6-7, Table 4). For example, larvae of *Micropsectra atrofasciata* in rhithral showed peaks at 6.63°C, 11.83°C and 17.84°C (Figure 6C), while pupal exuviae at 8.91°C, 12.65°C and 15.92°C (Figure 7C); in potamal larvae had peaks at 6.26°C, 9.43°C and 17.95°C (Figure 6D), while pupal exuviae at 9.40°C, 13.53°C and 18.39°C (Figure 7D).

The response of species belonging to the same genus was also analyzed (Figures 7 and 9). *Chironomus anthracinus* showed a bimodal

response in Alpine lowland lakes (Figure 9A). *Chironomus plumosus* had a trimodal response in Alpine lowland lakes, and the main peak was at the lowest temperature (Figure 9B); a similar response was observed in Mediterranean lakes (Figure 9C). *Chironomus riparius* showed a unimodal response in the rhithral habitat (optimum at 15°C) (Figure 9D, Appendix).

Altitude

The response to altitude for the most frequently captured species is reported in Table 5. All data on larvae were used (i.e. all habitats). The regression between optima for altitude and for water temperature was calculated selecting 78 species present in at least 66 samples, for which both altitude and water temperature values were available. This selection gave the highest r^2 . Regression coefficient was negative ($r^2 = 0.60$, 76 df, $P < 0.01$, Figure 10). At high altitudes, *Zarelimyia barbatipes*, *Corynoneura scutellata*, *Paratanytarsus austriacus* showed an optimum water temperature higher than predicted by altitude, whereas *D. bertrami*, *Paratrichocladius skirwithensis*, *Orthocladius (Eudactylocladius) fuscimanus* had temperature optima lower than expected by altitude; at

Table 4. Thermal response (°C) of *Micropsectra atrofasciata* (Chironominae) in specific habitats at different life stages: number of samples, weighted mean, standard deviation, skewness and kurtosis of species abundance vs water temperature values.

Life stage	Habitat	n	m (°C)	SD (°C)	g_1	g_2
Larvae	Rhithral	363	14.20	6.17	0.42	-0.33
Pupal exuviae	Rhithral	89	13.24	4.11	0.45	0.50
Larvae	Potamal	37	13.50	5.48	-0.03	-1.02
Pupal exuviae	Potamal	79	14.86	5.87	-0.06	-1.09
Larvae	Alpine lakes	48	14.05	4.62	0.67	2.47
Pupal exuviae	Alpine lakes	56	16.31	7.54	0.58	-1.38

n, number of samples; m, weighted mean; SD, standard deviation; g_1 , skewness; g_2 , kurtosis; Alpine lakes, Alpine ecoregion lowland lakes.

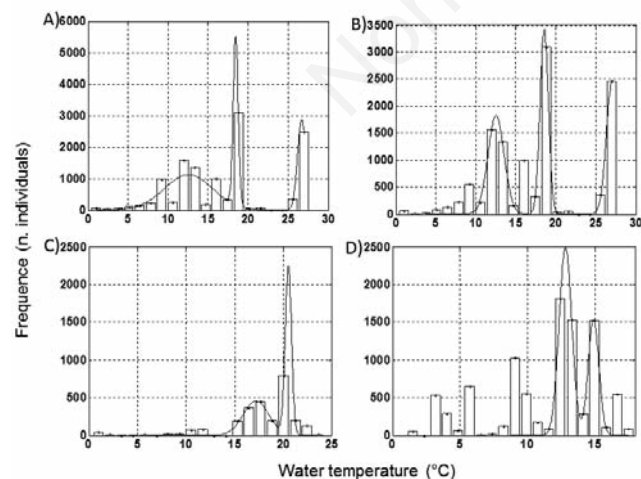


Figure 4. Thermal response of Orthoclaudiini larvae. Response of *Paratrichocladius rufiventris* (number of individuals m^{-2}) to water temperature (°C) in all habitats (A) and rhithral (B); response of *Cricotopus (Isocladius) sylvestris* in potamal (C); response of *Corynoneura scutellata* in Alpine ecoregion high altitude lakes (D).

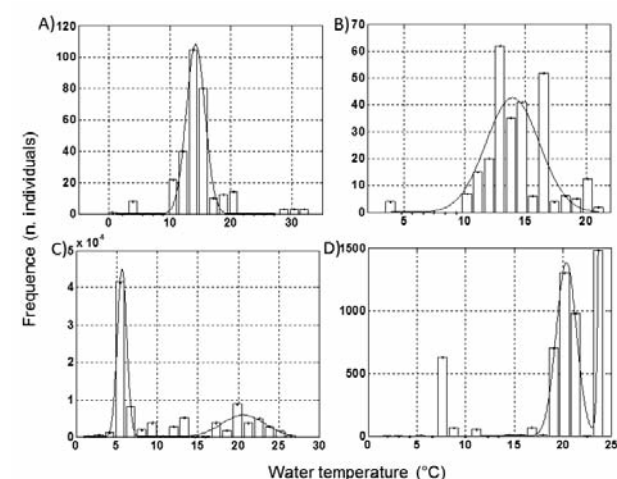


Figure 5. Thermal response of Tanytarsini larvae. Response of *Tanytarsus brundini* (number of individuals m^{-2}) to water temperature (°C) in all habitats (A) and rhithral (B); response of *Tanytarsus gregarius* in Alpine ecoregion lowland lakes (C); response of *Paratanytarsus mediterraneus* in potamal (D).

Table 5. Response of species (larvae) to altitude (m a.s.l.) in all habitats: number of samples, weighted mean, standard deviation, skewness and kurtosis of species abundance vs site altitude values. Only the species with ≥ 100 records in the dataset are reported. Species are in phylogenetic order.

Species	n	m (m a.s.l.)	SD (m a.s.l.)	g1	g2
<i>Tanytus punctipennis</i>	118	237	207	2.78	16.96
<i>Procladius choreus</i>	1530	437	303	2.42	7.53
<i>Macropelopia nebulosa</i>	274	1278	524	-0.95	-0.67
<i>Ablabesmyia monilis</i>	143	662	513	1.97	3.43
<i>Zavrelimyia barbatipes</i>	243	1961	540	-2.09	3.16
<i>Conchapelopia pallidula</i>	1005	363	285	3.14	14.63
<i>Rheopelopia ornata</i>	137	177	160	2.22	8.04
<i>Pseudodiamesa branickii</i>	262	1913	611	-1.09	0.11
<i>Diamesa steinboeckii</i>	119	2559	221	-2.42	8.87
<i>Diamesa latitarsis</i>	171	2213	572	-1.60	2.59
<i>Diamesa bertrami</i>	277	1933	653	-0.86	0.04
<i>Diamesa tonsa</i>	409	897	654	1.27	0.75
<i>Diamesa zernyi</i>	353	2145	564	-1.14	1.04
<i>Pseudokiefferiella parva</i>	119	2348	475	-1.52	2.49
<i>Prodiamesa olivacea</i>	393	300	421	3.56	12.80
<i>Brillia longifurca</i>	100	458	264	0.87	0.95
<i>Brillia bifida</i>	413	434	298	1.76	6.13
<i>Cardiocladius fuscus</i>	148	677	750	1.60	0.77
<i>Tvetenia calvescens</i>	840	1281	945	0.14	-1.81
<i>Eukiefferiella brevicar</i>	162	2013	461	-1.55	2.01
<i>Eukiefferiella claripennis</i>	353	651	691	2.00	2.23
<i>Eukiefferiella minor</i>	324	1489	772	-0.39	-1.52
<i>Psectrocladius (Psectrocladius) oxyura</i>	334	272	373	4.56	20.39
<i>Rheocricotopus chalybeatus</i>	116	342	168	1.50	5.34
<i>Rheocricotopus effusus</i>	205	866	743	1.17	-0.33
<i>Rheocricotopus fuscipes</i>	515	361	242	3.10	17.76
<i>Synorthocladius semivirens</i>	212	451	280	4.10	22.43
<i>Orthocladius (Eudactylocladius) fuscimanus</i>	124	1825	709	-1.25	-0.09
<i>Orthocladius (Euorthocladius) rivicola</i>	618	1052	902	0.66	-1.40
<i>Orthocladius excavatus</i>	141	335	152	1.96	15.17
<i>Orthocladius frigidus</i>	463	1767	743	-0.90	-0.49
<i>Orthocladius oblidens</i>	179	305	188	1.73	2.60
<i>Orthocladius rhyacobius</i>	312	422	228	0.79	1.82
<i>Orthocladius rubicundus</i>	204	409	214	1.19	6.43
<i>Paratrithocladius rufiventris</i>	456	737	610	0.81	-1.18
<i>Paratrithocladius skirwithensis</i>	210	1849	538	-1.57	1.75
<i>Cricotopus annulator</i>	245	412	335	3.81	17.08
<i>Cricotopus bicinctus</i>	422	189	198	1.31	5.93
<i>Cricotopus fuscus</i>	169	1067	624	0.17	-1.18
<i>Cricotopus tremulus</i>	126	968	725	0.75	-0.27
<i>Cricotopus triannulatus</i>	220	220	231	2.56	8.14
<i>Cricotopus (Isocladius) sylvestris</i>	276	322	593	2.89	6.69
<i>Metriocnemus hydropetricus</i>	180	937	685	0.88	-0.59
<i>Chaetocladius laminatus</i>	142	1628	913	-0.44	-1.62
<i>Paratrithocladius excerptus</i>	114	434	242	-0.07	-0.01
<i>Heterotrithocladius marcidus</i>	174	1936	595	-1.45	1.02
<i>Parametriocnemus stylatus</i>	349	1137	878	0.51	-1.19
<i>Parakiefferiella bathophila</i>	165	226	138	4.06	28.87
<i>Thienemanniella partita</i>	173	1141	904	0.19	-1.69
<i>Corynoneura scutellata</i>	395	2130	447	-3.37	11.70
<i>Stempellina bausei</i>	115	426	209	0.00	-1.67
<i>Tanytarsus gregarius</i>	652	561	577	1.21	-0.31
<i>Cladotanytarsus atridorsum</i>	342	406	136	1.92	17.06
<i>Paratanytarsus austriacus</i>	135	2087	311	-2.58	8.72

To be continued on next page

Table 5. Continued from previous page.

Species	n	m (m a.s.l.)	SD (m a.s.l.)	g1	g2
<i>Paratanytarsus lauterborni</i>	125	410	549	1.76	1.19
<i>Micropsectra atrofasciata</i>	890	425	361	3.06	10.30
<i>Micropsectra contracta</i>	386	402	114	8.52	93.32
<i>Micropsectra notescens</i>	108	527	313	0.31	1.08
<i>Micropsectra pallidula</i>	166	2184	293	-1.55	3.46
<i>Pagastiella orophila</i>	127	575	245	-0.77	-0.90
<i>Pseudochironomus prasinatus</i>	256	396	202	0.30	-1.74
<i>Paratendipes albimanus</i>	464	308	172	2.83	17.00
<i>Microtendipes pedellus</i>	510	204	213	3.86	18.41
<i>Polypedilum convictum</i>	145	347	167	-0.32	-1.23
<i>Polypedilum laetum</i>	199	340	294	3.06	15.31
<i>Polypedilum cultellatum</i>	100	142	153	1.68	2.34
<i>Polypedilum nubeculosum</i>	812	228	143	5.21	61.77
<i>Phaenopsectra flavipes</i>	149	399	429	2.03	3.05
<i>Endochironomus tendens</i>	140	148	198	6.14	57.78
<i>Stictochironomus pictulus</i>	101	460	443	2.21	2.90
<i>Dicrotendipes nervosus</i>	373	270	104	1.28	1.94
<i>Glyptotendipes pallens</i>	237	241	67	1.56	18.49
<i>Chironomus anthracinus</i>	751	482	356	1.79	3.65
<i>Chironomus plumosus</i>	762	283	132	2.04	7.37
<i>Chironomus riparius</i>	521	229	199	0.93	-0.24
<i>Cladopelma viridulum</i>	390	238	133	6.26	70.75
<i>Parachironomus arcuatus</i>	113	195	98	2.73	16.60
<i>Paracladopelma camptolabis</i>	107	631	546	1.21	0.57
<i>Paracladopelma nigrifulum</i>	188	388	55	10.07	221.97
<i>Cryptochironomus defectus</i>	606	305	156	0.93	0.25
<i>Demicryptochironomus vulneratus</i>	163	226	88	3.18	12.09

n, number of samples; m, weighted mean; SD, standard deviation; g1, skewness; g2, kurtosis.

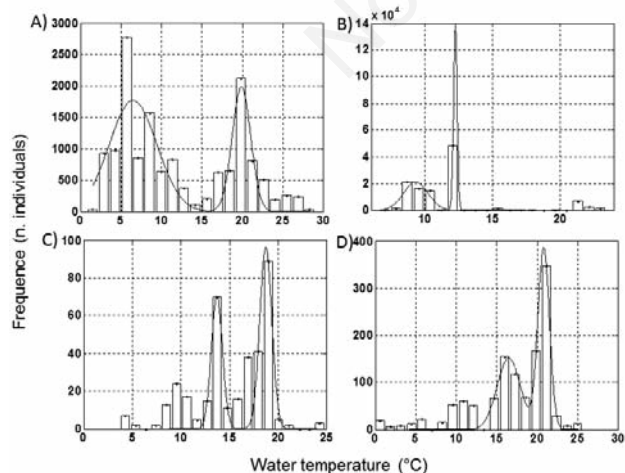


Figure 6. Thermal response of *Polypedilum nubeculosum* larvae (number of individuals m^{-2}) to water temperature ($^{\circ}C$) in Alpine ecoregion lowland lakes (A), Mediterranean ecoregion lakes (B), rhithral (C) and potamal (D).

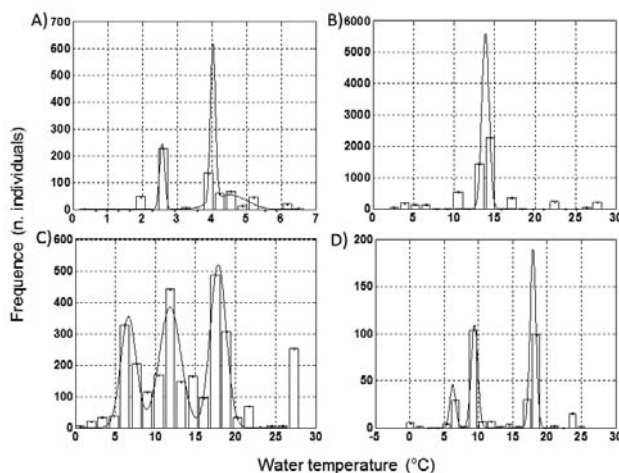


Figure 7. Thermal response of *Micropsectra* spp. larvae. Response of *M. pallidula* (number of individuals m^{-2}) to water temperature ($^{\circ}C$) in krenal (A); response of *M. atrofasciata* in Alpine ecoregion lowland lakes (B), rhithral (C) and potamal (D).

lower altitudes, the higher temperature optima were observed for *P. mediterraneus*, *P. rufiventris* and *Tanytus punctipennis* and the lower for *Orthocladius oblidens*, *Pagastiella orophila*, *Parakiefferiella bathophila*, *Prodiamesa olivacea*, *Diamesa tonsa*.

Depth

Response of lacustrine species (*i.e.* larvae in Alpine ecoregion lowland lakes) to depth is summarized in Table 6. Only few species showed optimum at >40 m depth (*Micropsectra contracta*, *Paracladopelma nigrifulum*), others had maxima at lower depth (*e.g.* at 20-25 m, *Procladius choreus*, *Prodiamesa olivacea*). Response curves of some species are shown in Figure 11. *C. plumosus*, *C. anthracinus*, *Demicryptochironomus vulneratus* and *T. gregarius* showed a wide range of depth tolerance (Table 6).

Source distance

The optimum values for source distance were calculated for species (*i.e.* larvae in running water habitats) for which at least 100 samples were available (Table 7). A relation between optimum for water temperature and for source distance was calculated for the 75 species present in ≥ 81 samples. The relation is shown in Figure 12, with $r^2=0.33$ (73 df, $P<0.01$) fitting a linear model. As expected, cold stenothermal species had optimum near the stream source (*e.g.* *Diamesa* species) while eurithermal ones (*Endochironomus tendens*, *C. riparius*, *Glyptotendipes pallens*, *C. I. sylvestris*, *Cricotopus triannulatus*, *Cricotopus bicinctus*) showed optimum at high distance from source.

Discussion

Notwithstanding the approximation of joining data collected with different sampling methods in different habitats, some generalizations could be argued by the analysis of the dataset on larvae collections. Thermophilous species often showed platikurtic responses, fitting plurimodal Gaussian models, with: i) optima closed to their maximum temperature values, ii) wide tolerance, iii) negative skewness and negative kurtosis (Rossaro, 1991a, 1991c). On the contrary, species restricted to few habitats, such as kryal (*e.g.* *Diamesa steinboeckii*, *Diamesa latitarsis*) or krenal (*e.g.* *Chaetocladius laminatus*, *Micropsectra pallidula*), showed low optima for water temperature (cold stenothermal) and low tolerance (stenoecious). These species often showed: i) optima closed to their minimum temperature values, ii) tolerance for a narrow temperature range, iii) positive skewness and positive kurtosis (Rossaro, 1991c). Even if a bimodal response can be fitted, the two maxima are generally rather closed to each other (Figure 3). These species could be thus more sensitive to an increasing trend of temperature (Hester & Doyle, 2011).

For a better approximation of species preferences and tolerance, optima for water temperature were calculated for each species in different habitats, thus considering data collected with the same sampling strategy (Appendix). As expected, lower values were obtained for kryal and krenal, and higher values for rhithral, potamal and lakes. Most taxa showed different responses according to the habitat. When data are

Table 6. Response of lacustrine species (larvae) to water depth (m depth) in Alpine ecoregion lowland lakes: number of samples, weighted mean, standard deviation, skewness and kurtosis of species abundance vs sampling depth values Only the species with ≥ 100 records in the dataset are reported. Species are in phylogenetic order.

Species	n	m (m depth)	SD (m depth)	g1	g2
<i>Procladius choreus</i>	1046	21.02	23.02	3.17	23.24
<i>Conchapelopia pallidula</i>	232	4.87	3.34	4.05	31.03
<i>Prodiamesa olivacea</i>	179	21.70	17.71	1.08	1.21
<i>Psectrocladius (Psectrocladius) oxyura</i>	255	4.97	2.39	1.67	4.75
<i>Orthocladius oblidens</i>	110	4.99	2.14	1.97	20.31
<i>Parakiefferiella bathophila</i>	113	5.86	3.27	2.22	5.64
<i>Tanytarsus gregarius</i>	459	10.15	32.08	4.62	23.67
<i>Cladotanytarsus atridorsum</i>	253	3.62	2.38	2.65	17.66
<i>Micropsectra contracta</i>	359	84.91	56.80	1.33	1.62
<i>Pagastiella orophila</i>	116	7.10	2.77	2.69	13.03
<i>Pseudochironomus prasinatus</i>	212	4.26	3.04	6.85	140.29
<i>Paratendipes albimanus</i>	295	4.44	8.81	7.69	152.02
<i>Microtendipes pedellus</i>	228	6.06	4.29	1.54	3.00
<i>Polypedilum nubeculosum</i>	377	3.27	7.90	8.12	126.29
<i>Dicrotendipes nervosus</i>	232	5.70	3.88	2.05	4.46
<i>Chironomus anthracinus</i>	529	13.39	18.62	8.41	113.15
<i>Chironomus plumosus</i>	480	9.73	49.52	7.03	51.04
<i>Cladopelma viridulum</i>	270	8.34	16.38	10.19	163.69
<i>Paracladopelma nigrifulum</i>	171	73.31	41.44	0.88	-0.64
<i>Cryptochironomus defectus</i>	423	6.51	4.75	3.70	52.20
<i>Demicryptochironomus vulneratus</i>	144	4.06	24.24	11.46	138.48

n, number of samples; m, weighted mean; SD, standard deviation; g1, skewness; g2, kurtosis.

available for the same species in different habitats, as for *Orthocladius* (*Euorthocladius*) *rivicola*, optimum values are lower in krenal (2.83°C) and kryal (5.23°C) than in rhithral (11.98°C), potamal or lakes. Other species (e.g. *M. atrofasciata*) did not show significant differences between optima values in different habitats, but the response curves were very different (Figures 7-8). These species are euryecious and eurythermal with more than one generation per year with different water temperature optimum for the different populations developing during the year.

Among stenothermal taxa, some species at lower altitude habitats (rhithral, potamal) showed restricted tolerance to temperature, being potentially good indicators of climate change. For example, *Microtendipes pedellus* showed optimum for warm temperature (12.29°C), but a narrow range of tolerance (SD=2.73°C).

For these taxa, the increasing temperature trend may induce a migration toward higher elevations, changing in some years the response curve to altitude (Nyman *et al.*, 2005; Bonada *et al.*, 2007) and increasing species diversity at high elevation sites (Čiamporová-Zat'ovičová *et al.*, 2010; Jacobsen *et al.*, 2012). Alternatively, species may adapt to higher temperature, showing altered thermal curves in some years (Hogg *et al.*, 1998; Van Doorslaen *et al.*, 2009). In the case of cold stenothermal or stenotopic species, a probable loss is expected (Jacobsen *et al.*, 2012), as was observed in some localities in the Apennines for some species, such as *Diamesa insignipes* (Rossaro *et al.*, 2006b).

Even if species response to altitude is surely influenced by water temperature, high elevations also imply different habitats and different ecological conditions. Therefore species distribution could be constrained by other factors. For example, the CHIDB data showed that some species colonizing high altitude lakes such as *Zavrelimyia* spp., *Heterotrissoclaius marcidus*, *C. scutellata* and *P. austriacus* are more warm stenothermal than predicted by altitude, while species living in kryal, krenal or rhithral habitats such as *Diamesa* spp., *Pseudodiamesa branickii* and *P. parva* (Rossaro, 2006b) are more cold stenothermal than expected.

Likewise, at lower altitude species living in the profundal zone of lakes, such as *P. olivacea*, *P. bathophila*, *Micropsectra radialis* and *C.*

plumosus as well as species living in lowland springs such as *Brillia bifida*, *Chaetocladius perennis* or in the interstitial habitats as *Hydrobaenus distylus* are cold stenothermal.

For what concerns lacustrine species, distribution could be affected by water depth beside water temperature (Rossaro *et al.*, 2006a; Luoto, 2012). Only few species showed an optimum depth below 20 m (e.g. *M. contracta*, *P. nigritulum*). Their distribution plotted against depth showed that they have more than one maximum, often with the main peak at lower depth than the other peaks (Figure 11). Results suggest that possibly depth does not influence species distribution directly, but indirectly through temperature, dissolved oxygen or competition.

Different thermal optimum values were derived for different life stages (*i.e.* larvae *vs* pupal exuviae), probably due to species phenology. In particular, pupation in chironomids has a short duration, lasting at most 72 h (Langton, 1995). Therefore pupal exuviae are found in specific seasons and times. On the contrary, larval stage has a long duration, lasting most lifetime.

According to species voltinism, more than one generation per year was often observed. This occurs both in lacustrine and in lotic species. This could explain bimodal or trimodal responses of species. Lindegaard & Mortensen (1988) observed that chironomids generally do not have more than four generations per year, but some species (e.g. *C. riparius*) have surely more than four generation per year in Southern Europe areas. Thus, a plurimodal response could also be expected, but more data are needed to fit plurimodal models with a higher number of parameters.

Likewise, plurimodal response could be due to spatial distribution of species, which may show preferences for more than one specific habitat; local adaptations of single populations may as well be responsible for plurimodal trends of some species (Dallas & Rivers-Moore, 2012). In fact, such curves were mostly achieved for eurythermal and euryecious species. Sometimes curves with two peaks might suggest the presence of more than one species instead of more than one population. This is the case of taxa belonging to genera rich in species, which are not easily separated at the larval stage, such as *Diamesa* [e.g. *D. latitarsis/steinboeckii* (juvenilia), Appendix] and *Tanytarsus* spp.

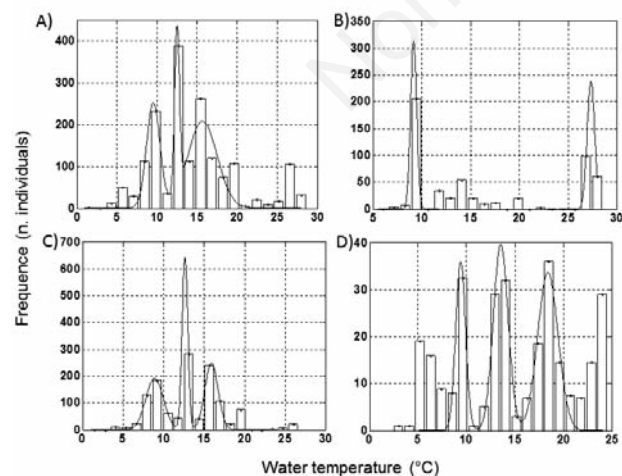


Figure 8. Thermal response of *Micropsectra atrofasciata* pupal exuviae (number of individuals m⁻²) to water temperature (°C) in all habitats (A), Alpine ecoregion lowland lakes (B), rhithral (C) and potamal (D).

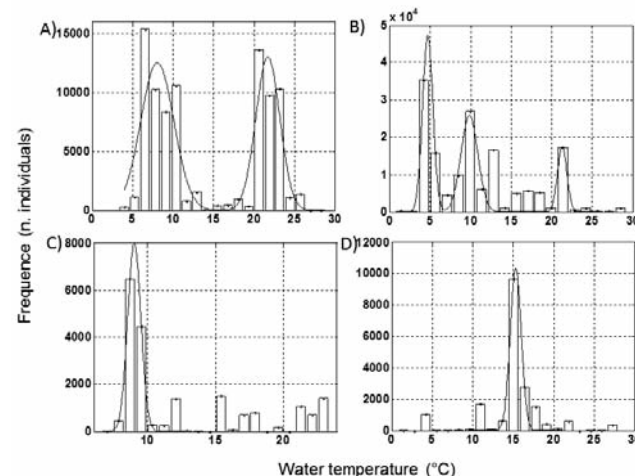


Figure 9. Thermal response of *Chironomus* spp. larvae. Response of *C. anthracinus* (number of individuals m⁻²) to water temperature (°C) in Alpine ecoregion lowland lakes (A); response of *C. plumosus* in Alpine ecoregion lowland lakes (B), and Mediterranean ecoregion lakes (C); response of *C. riparius* in rhithral (D).

Table 7. Response of lotic species (larvae) to distance from source in all riverine habitats: number of samples, weighted mean, standard deviation, skewness and kurtosis of species abundance vs distance from source values. Only the species with ≥ 100 records in the dataset are reported. Species are in phylogenetic order.

Species	n	m (km)	SD (km)	g1	g2
<i>Procladius choreus</i>	497	84.56	83.31	1.27	0.06
<i>Zavrelimyia barbatipes</i>	118	3.86	20.05	9.52	123.78
<i>Conchapelopia pallidula</i>	663	81.40	134.03	3.35	10.99
<i>Pseudodiamesa branickii</i>	173	15.96	33.89	2.17	4.00
<i>Diamesa steinboeckii</i>	108	0.69	7.32	15.03	226.29
<i>Diamesa latitarsis</i>	123	4.26	13.38	5.16	29.23
<i>Diamesa bertrami</i>	205	2.22	16.28	12.63	218.61
<i>Diamesa tonsa</i>	324	12.20	61.51	23.06	817.69
<i>Diamesa zernyi</i>	229	1.90	10.74	12.79	238.84
<i>Prodiamesa olivacea</i>	207	128.57	96.06	0.14	-1.76
<i>Brillia bifida</i>	302	19.64	31.95	3.35	19.85
<i>Cardiocladius fuscus</i>	115	18.68	79.56	13.42	331.58
<i>Tvetenia calvescens</i>	588	20.91	39.27	4.24	24.07
<i>Eukiefferiella breviculcar</i>	131	0.81	11.87	20.57	475.86
<i>Eukiefferiella claripennis</i>	243	19.03	32.48	6.56	50.10
<i>Eukiefferiella minor</i>	216	8.79	19.15	4.85	46.65
<i>Psectrocladius (Psectrocladius) oxyura</i>	162	60.00	16.03	0.20	52.13
<i>Rheocricotopus effusus</i>	138	28.92	30.16	0.67	-0.12
<i>Rheocricotopus fuscipes</i>	391	48.28	98.83	5.40	30.02
<i>Synorthocladius semivirens</i>	163	22.23	40.18	3.74	24.97
<i>Orthocladius (Euorthocladius) rivicola</i>	457	28.15	66.53	6.22	42.93
<i>Orthocladius excavatus</i>	109	31.70	87.00	7.89	133.38
<i>Orthocladius frigidus</i>	322	6.39	52.28	33.79	1454.39
<i>Orthocladius oblidens</i>	121	55.14	26.38	0.47	7.27
<i>Orthocladius rhyacobius</i>	215	35.31	89.49	5.16	85.39
<i>Orthocladius rubicundus</i>	106	57.75	43.71	0.40	-0.22
<i>Paratrachocladius rufiventris</i>	317	3.76	35.13	29.05	1517.03
<i>Paratrachocladius skirwithensis</i>	134	14.01	23.29	2.15	3.32
<i>Cricotopus annulator</i>	176	34.10	68.19	7.05	60.01
<i>Cricotopus bicinctus</i>	241	128.77	120.05	1.29	2.98
<i>Cricotopus triannulatus</i>	197	131.92	128.18	1.72	5.47
<i>Cricotopus (Isocladius) sylvestris</i>	150	139.59	119.98	0.02	-0.86
<i>Metriocnemus hydropetricus</i>	132	31.94	50.11	4.62	42.91
<i>Chaetocladius laminatus</i>	117	13.86	30.01	5.65	45.96
<i>Parametriocnemus stylatus</i>	241	16.18	27.90	4.51	33.89
<i>Parakiefferiella bathophila</i>	101	63.12	1.86	-5.20	2484.04
<i>Thienemanniella partita</i>	133	12.60	53.86	9.37	101.81
<i>Corynoneura scutellata</i>	233	12.58	61.42	6.02	39.72
<i>Tanytarsus gregarius</i>	238	67.50	30.09	10.27	181.68
<i>Cladotanytarsus atridorsum</i>	104	57.74	17.82	7.56	111.14
<i>Micropsectra atrofasciata</i>	529	35.41	66.56	8.86	269.38
<i>Micropsectra pallidula</i>	120	1.54	2.29	2.80	15.69
<i>Pseudochironomus prasinatus</i>	119	54.93	5.42	-1.21	11.16
<i>Paratendipes albimanus</i>	130	32.79	28.69	5.33	95.49
<i>Microtendipes pedellus</i>	235	53.65	38.30	2.77	11.10
<i>Polypedilum laetum</i>	164	59.77	73.36	3.91	23.25
<i>Polypedilum nubeculosum</i>	434	90.31	86.70	2.38	9.45
<i>Dicrotendipes nervosus</i>	188	72.25	78.47	6.66	46.00
<i>Glyptotendipes pallens</i>	138	152.20	113.95	0.91	2.80
<i>Chironomus anthracinus</i>	273	57.22	19.98	-1.93	2.80
<i>Chironomus plumosus</i>	282	26.89	44.06	9.88	134.42
<i>Chironomus riparius</i>	227	213.81	69.27	-1.73	2.69
<i>Cladopelma viridulum</i>	131	50.98	23.96	-1.54	0.53
<i>Cryptochironomus defectus</i>	236	84.54	67.67	2.65	9.59
<i>Demicryptochironomus vulneratus</i>	134	53.81	16.62	-2.59	5.90

n, number of samples; m, weighted mean; SD, standard deviation; g1, skewness; g2, kurtosis.

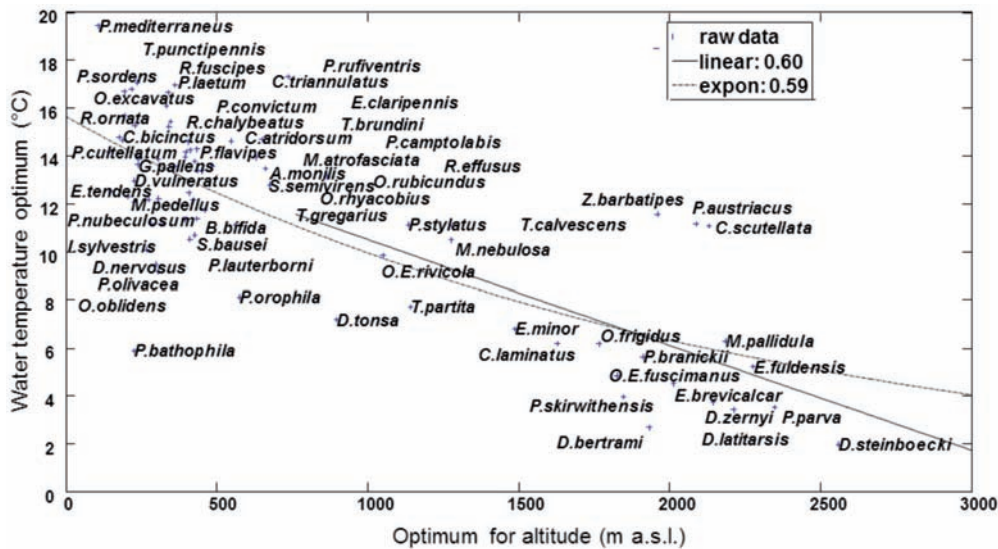


Figure 10. Correlation between species optima for water temperature (°C) vs optima for altitude (m a.s.l.).

Conclusions

Chironomids are considered generalist, opportunistic, r-strategy organisms and their distribution is driven by environmental variables, such as water temperature (Rempel & Harrison, 1987), substrate composition (Rae, 1985), current velocity (Caspers, 1983) and other variables such as competition, parasitism, predation and other biological constraints (Tokeshi, 1995; Vodopich & Cowell, 1984). Water temperature has been often recognized as the factor that accounts for the largest percentage of variation in community composition (Heiri *et al.*, 2011). Beyond direct effects caused by increased water temperature, such as distribution, phenology and adaptation, also indirect effects are expected, such as different balance of inter- and intra-specific relation, *i.e.* competition, predation and parasitism (Tixier *et al.*, 2009). These latter aspects still need to be investigated.

Some chironomid species showed unimodal response to water temperature (Larocque *et al.*, 2001), but bimodal and trimodal responses were also frequently found. The present data emphasized that standard deviation generally increased with optimum temperature, meaning that eurythermal species are often warm-water adapted, while cold-water dwellers are mostly stenothermal. Nonetheless some warm stenothermal species were also found, being possibly good indicators of water temperature in lowland habitats (*e.g.* *M. pedellus*).

Aquatic insect ecology can be interpreted by an evolutionary perspective. Entire orders of aquatic insects probably evolved in cool habitats. Thus, groups inhabiting warmer waters are considered later descendants of cool-adapted ancestral lines (Ward & Stanford, 1982; Ward, 1992). It is supposed that plesiomorphic species are cold stenothermal while apomorphic species are warm stenothermal or eurythermal. The chironomid ancestral habitat is supposed to be cool head-waters (Brundin, 1966; Cranston & Oliver, 1987; Cranston *et al.*, 2012) and ecology and biogeography of Diamesinae gives support to this statement (Serra-Tosio, 1973; Rossaro, 1995). A phylogenetic trend from plesiomorphic cold-stenothermal species to apomorphic warm adapted species was then hypothesized (Rossaro, 1991c), since a general trend toward increasing adaptation to warm habitats was observed from cold stenothermal Diamesini to warm eurythermal Chironomini (Rossaro *et al.*, 2007b). This was confirmed only in part, likely because: i) ecological data on species are incomplete, ii) the evolutionary tree of chironomids is not completely known (Cranston *et al.*, 2012), iii) the relation

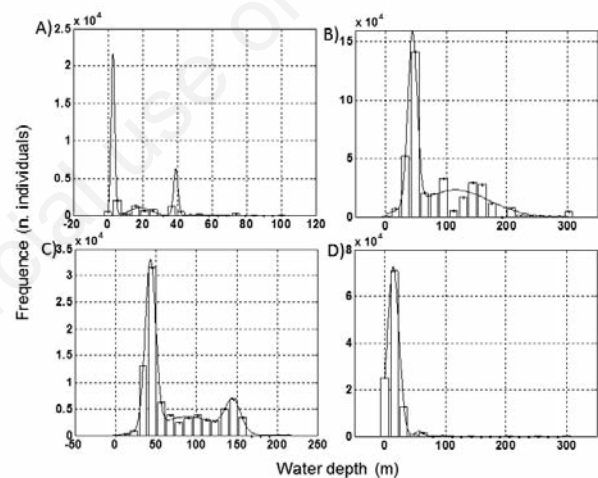


Figure 11. Response of *Prodiamesa olivacea* (A), *Micropsectra contracta* (B), *Paracladopelma nigrifulum* (C), *Chironomus anthracinus* (D) larvae (number of individuals m^{-2}) to water depth (m) in Alpine ecoregion lowland lakes.

between thermal response and the position of a taxon in the phylogenetic tree may be observed at different taxonomic hierarchy, *i.e.* at the level of populations within the same species, of species within the same genus or of genus within the same tribe.

In this paper emphasis is given to water temperature, with the aim of quantifying the responses of single species in different habitats and to describe the detailed pattern of response. The authors acknowledge that results may be biased, being a different number of data available for each species, with a different spatial and temporal resolution in different sites, and thus optimum values must be interpreted with caution. Nevertheless it must be considered the difficulty of selecting a balanced database for a large number of species, some of which rare, living in specialized habitats, others common and widespread, living in different habitats. The data considered in the present paper are still fragmentary and will be revised in the future, as soon as new information will become available. At present, a comparison of quantitative results with other published papers is

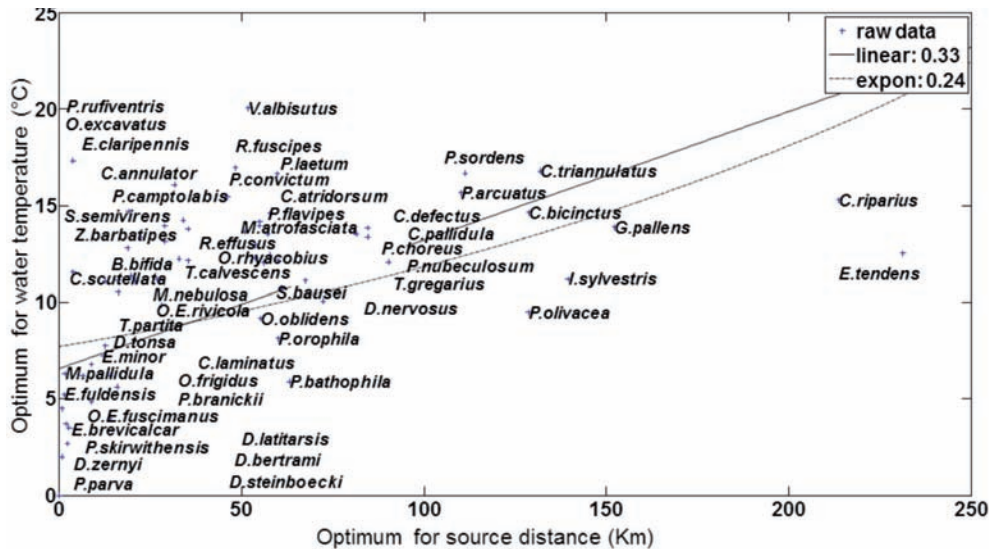


Figure 12. Correlation between species optima for water temperature ($^{\circ}\text{C}$) vs optima for distance from source (km) in running waters.

recommended. For example, a comparison could be achieved with estimated tolerance and optima for lacustrine species used as climate proxy in palaeolimnological studies (Larocque *et al.*, 2001; Larocque-Tobler *et al.*, 2012), even if available data are mainly from Northern areas. Otherwise, a comparison could be carried out with sensitivity derived from specific studies on existing chironomid communities (Tixier *et al.*, 2009; Čiamporová-Zat'ovičová *et al.*, 2010; Hamerlik & Jacobsen, 2012).

Knowledge on thermal tolerance of species is important for a long-term management and monitoring of aquatic ecosystems exposed to the effects of climate change. In fact, thermal curves can help anticipate impacts of climate change to various species by quantifying their thermal habitat (Hester & Doyle, 2011). Species response under different global change scenarios can thus be predicted (Bonada *et al.*, 2007; Sauer *et al.*, 2011). To this purpose, more understanding into species adaptations by acclimation and genetics is also needed (Hogg *et al.*, 1998; Van Doorslaen *et al.*, 2009).

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Appendix

Thermal response (°C) of species (larvae) in different habitats: number of samples (n), weighted mean (m), standard deviation (SD), skewness (g1) and kurtosis (g2) of species abundance vs water temperature values. Species with ≥ 30 records in the dataset are reported. Species are in phylogenetic order.

Krenal	n	m (°C)	SD (°C)	g1	g2
<i>Pseudodiamesa branickii</i>	48	3.84	1.57	1.20	15.76
<i>Diamesa bertrami</i>	33	4.07	0.75	-0.63	2.72
<i>Diamesa zernyi</i>	47	4.34	1.12	-0.83	1.10
<i>Tvetenia calvescens</i>	69	4.57	2.41	1.91	6.19
<i>Eukiefferiella brevicar</i>	47	3.98	1.00	0.23	0.31
<i>Eukiefferiella minor</i>	43	4.39	1.23	-0.15	0.42
<i>Orthocladius (Euorthocladius) rivicola</i>	50	2.83	1.77	0.49	2.95
<i>Orthocladius frigidus</i>	63	3.56	1.40	0.85	1.29
<i>Chaetocladius laminatus</i>	34	3.94	1.61	0.48	-1.23
<i>Micropsectra pallidula</i>	46	3.59	1.14	0.28	-0.40

Kryal	n	m (°C)	SD (°C)	g1	g2
<i>Diamesa latitarsis/steinboecki</i> (juvenilia)	34	2.60	1.44	0.58	-0.24
<i>Diamesa steinboecki</i>	94	1.98	1.39	1.08	1.27
<i>Diamesa latitarsis</i>	93	3.24	1.72	0.55	-0.04
<i>Diamesa bertrami</i>	121	2.41	1.86	1.33	1.47
<i>Diamesa tonsa</i>	43	2.67	1.55	1.20	2.74
<i>Diamesa zernyi</i>	117	3.54	2.18	0.17	-0.78
<i>Pseudokiefferiella parva</i>	49	3.36	1.41	1.40	4.06
<i>Tvetenia calvescens</i>	62	4.87	1.74	0.08	0.48
<i>Eukiefferiella brevicar</i>	35	4.25	1.30	-0.49	3.72
<i>Eukiefferiella minor</i>	32	3.53	2.61	0.25	-1.11
<i>Orthocladius (Euorthocladius) rivicola</i>	48	5.23	1.95	-0.23	-0.37
<i>Orthocladius frigidus</i>	53	4.82	1.40	0.06	3.41
<i>Paratrichocladius skirwithensis</i>	37	4.99	1.13	-0.22	1.97

Rhithral	n	m (°C)	SD (°C)	g1	g2
<i>Procladius choreus</i>	38	16.04	3.09	-2.25	10.16
<i>Macropelopia nebulosa</i>	82	12.06	4.86	0.00	-0.93
<i>Macropelopia notata</i>	35	17.34	2.20	-1.87	2.17
<i>Zavreliomyia melanura</i>	38	14.75	2.21	-1.01	1.61
<i>Zavreliomyia barbatipes</i>	64	10.20	5.05	-0.52	-0.31
<i>Conchapelopia pallidula</i>	322	13.94	5.09	-0.32	0.52
<i>Rheopelopia ornata</i>	94	13.49	3.35	0.20	-0.54
<i>Pseudodiamesa branickii</i>	33	7.37	1.95	-1.44	2.42
<i>Diamesa bertrami</i>	46	6.01	2.11	-0.65	0.02
<i>Diamesa tonsa</i>	113	7.84	4.64	0.26	-0.49
<i>Diamesa zernyi</i>	45	5.22	2.64	-0.41	-0.72
<i>Diamesa insignipes</i>	58	10.67	2.95	0.82	2.36
<i>Potthastia longimanus</i>	32	11.59	6.09	0.26	-1.57
<i>Prodiamesa olivacea</i>	69	12.97	4.65	-0.95	1.72
<i>Brillia bifida</i>	185	11.49	4.77	0.18	-0.70
<i>Brillia longifurca</i>	54	12.39	4.83	-0.50	-0.47
<i>Cardiocladius fuscus</i>	67	16.14	5.32	-1.26	0.70
<i>Tvetenia calvescens</i>	375	12.92	5.18	-0.42	-0.89
<i>Eukiefferiella brevicar</i>	50	4.71	2.29	1.58	4.46
<i>Eukiefferiella claripennis</i>	187	14.79	4.33	-0.48	-0.25
<i>Eukiefferiella minor</i>	90	8.74	3.90	0.26	0.24
<i>Rhecticotopus chalybeatus</i>	58	14.31	5.57	-0.09	0.17
<i>Rhecticotopus effusus</i>	102	12.59	5.39	-0.35	-0.66
<i>Rhecticotopus fuscipes</i>	206	17.54	7.80	0.03	-1.56
<i>Paracricotopus niger</i>	53	16.67	3.95	-0.60	0.25
<i>Nanocladius bicolor</i>	38	17.74	6.51	-0.20	-0.76
<i>Synorthocladius semivirens</i>	113	13.49	4.40	-0.18	-0.75
<i>Orthocladius (Euorthocladius) rivicola</i>	242	11.98	5.19	-0.03	-0.84
<i>Orthocladius (Eudactylocladius) fuscimanus</i>	44	6.69	4.39	1.70	2.47
<i>Orthocladius excavatus</i>	73	16.10	3.70	-0.96	-0.62

<i>Orthocladius frigidus</i>	115	8.11	3.78	0.53	-0.34
<i>Orthocladius rhyacobi</i>	183	11.94	3.85	-0.14	-0.28
<i>Orthocladius rubicundus</i>	102	12.26	2.98	0.42	1.08
<i>Paratrichocladius rufiventris</i>	221	17.72	6.17	0.16	-0.80
<i>Cricotopus annulator</i>	110	15.00	4.66	-0.32	0.99
<i>Cricotopus bicinctus</i>	205	12.76	4.63	0.26	-0.48
<i>Cricotopus (Isocladius) intersectus</i>	37	14.60	3.80	0.88	-0.48
<i>Cricotopus Isocladius sylvestris</i>	50	14.63	5.60	-0.20	-1.45
<i>Metriocnemus fuscipes</i>	71	11.37	3.91	0.06	0.03
<i>Parametriocnemus stylatus</i>	168	11.51	5.11	0.25	-1.01
<i>Chaetocladius laminatus</i>	31	7.42	3.48	1.05	2.01
<i>Paratrissocladius excerptus</i>	84	15.07	2.67	-0.47	-0.41
<i>Epoicocladius flavens</i>	40	13.00	2.43	-0.24	1.69
<i>Thienemanniella partita</i>	68	9.11	4.30	0.14	-0.68
<i>Corynoneura scutellata</i>	126	7.71	3.25	0.55	1.54
<i>Tanytarsus brundini</i>	63	14.37	2.70	-0.29	2.34
<i>Virgatanytarsus albisutus</i>	41	19.10	3.52	-0.25	1.17
<i>Micropsectra atrofasciata</i>	363	14.20	6.17	0.42	-0.33
<i>Micropsectra pallidula</i>	36	5.37	1.76	0.65	-1.16
<i>Micropsectra recurvata</i>	51	14.41	3.54	-0.08	-1.55
<i>Paratendipes albimanus</i>	36	16.90	1.93	-3.59	17.80
<i>Microtendipes pedellus</i>	111	12.22	4.93	0.12	-0.98
<i>Microtendipes rydalensis</i>	45	13.30	2.59	0.17	1.01
<i>Polypedilum albicorne</i>	34	13.63	3.42	0.03	-0.42
<i>Polypedilum convictum</i>	108	15.43	3.51	-0.35	-1.08
<i>Polypedilum laetum</i>	70	17.43	4.19	0.05	0.87
<i>Polypedilum cultellatum</i>	45	13.13	3.68	0.06	-1.10
<i>Polypedilum nubeculosum</i>	80	15.27	3.85	-0.69	0.01
<i>Phaenopsectra flavipes</i>	37	14.23	3.89	-1.60	4.54
<i>Chironomus riparius</i>	230	14.99	3.69	-0.54	3.68

Potamal	n	m (°C)	SD (°C)	g1	g2
<i>Conchapelopia pallidula</i>	69	14.21	6.87	-0.57	-0.50
<i>Cricotopus bicinctus</i>	63	19.59	3.32	-2.40	6.11
<i>Cricotopus triannulatus</i>	65	17.02	4.12	-1.79	4.45
<i>Cricotopus Isocladius sylvestris</i>	76	17.80	3.82	-2.13	6.02
<i>Paratanytarsus mediterraneus</i>	73	19.43	4.97	-1.59	1.31
<i>Micropsectra atrofasciata</i>	37	13.50	5.48	-0.03	-1.02
<i>Microtendipes pedellus</i>	50	14.22	5.95	-0.59	-0.74
<i>Polypedilum laetum</i>	36	15.96	6.63	-0.02	-1.13
<i>Polypedilum cultellatum</i>	33	16.74	4.96	-0.72	0.22
<i>Polypedilum nubeculosum</i>	72	16.98	5.04	-1.27	1.25
<i>Polypedilum (Pentapedilum) sordens</i>	53	16.85	4.84	-1.09	0.70
<i>Endochironomus tendens</i>	50	15.72	4.43	-0.93	1.02
<i>Dicrotendipes nervosus</i>	32	16.29	3.65	-0.72	3.40
<i>Glyptotendipes pallens</i>	67	15.15	6.10	-0.55	-0.72
<i>Glyptotendipes paripes</i>	33	16.90	4.65	-0.82	-0.80
<i>Chironomus riparius</i>	64	18.42	5.83	-0.32	-1.05
<i>Parachironomus arcuatus</i>	36	17.27	4.99	-1.40	1.88

Alpine ecoregion lowland lakes	n	m (°C)	SD (°C)	g1	g2
<i>Tanypus punctipennis</i>	48	17.13	6.02	-0.18	-1.28
<i>Procladius choreus</i>	722	14.43	6.60	0.12	-1.29
<i>Macropelopia nebulosa</i>	36	8.74	3.93	0.22	-0.87
<i>Ablabesmyia monilis</i>	59	13.61	7.09	0.53	-1.08
<i>Conchapelopia pallidula</i>	117	10.53	6.64	0.94	-0.73
<i>Prodiamesa olivacea</i>	158	9.08	4.50	1.89	4.07
<i>Psectrocladius (Psectrocladius) oxyura</i>	153	11.08	7.05	0.58	-1.42
<i>Orthocladius oblidens</i>	83	8.13	5.82	1.66	1.10
<i>Parakiefferiella bathophila</i>	114	6.11	3.61	3.70	12.83

<i>Stempellina bausei</i>	87	10.69	6.62	0.91	-0.75
<i>Tanytarsus gregarius</i>	331	10.98	6.93	0.74	-1.09
<i>Cladotanytarsus atridorsum</i>	203	15.22	5.32	0.19	-1.11
<i>Micropsectra atrofasciata</i>	48	14.05	4.62	0.67	2.48
<i>Pseudochironomus prasinatus</i>	174	14.12	7.66	-0.13	-1.73
<i>Pagastiella orophila</i>	115	8.12	4.63	1.44	0.75
<i>Paratendipes albimanus</i>	151	12.11	4.28	1.25	0.58
<i>Microtendipes pedellus</i>	163	13.88	4.74	-0.46	-0.54
<i>Polypedilum nubeculosum</i>	257	12.22	7.05	0.39	-1.27
<i>Endochironomus tendens</i>	31	15.48	5.26	-0.53	-0.95
<i>Dicrotendipes nervosus</i>	181	8.63	5.74	1.45	0.87
<i>Cryptochironomus defectus</i>	333	14.74	6.85	0.01	-1.35
<i>Cladopelma viridulum</i>	224	13.21	7.02	0.57	-1.16
<i>Paracladopelma camptolabis</i>	68	13.97	7.30	0.61	-1.37
<i>Paracladopelma nigrifulum</i>	32	11.89	5.37	0.81	-1.14
<i>Paralauterborniella nigrohalteralis</i>	59	13.34	3.83	-0.47	-0.99
<i>Demicryptochironomus vulneratus</i>	142	12.96	7.28	0.44	-1.36
<i>Glyptotendipes pallens</i>	77	13.77	7.80	0.15	-1.27
<i>Chironomus anthracinus</i>	431	14.28	6.88	0.20	-1.73
<i>Chironomus plumosus</i>	350	10.81	6.00	0.72	-0.47

Alpine ecoregion high altitude lakes	n	m (°C)	SD (°C)	g1	g2
<i>Zavrelimyia barbatipes</i>	56	11.79	3.79	-0.02	0.52
<i>Heterotrissocladius marcidus</i>	31	11.06	2.67	-1.28	1.51
<i>Parakiefferiella bathophila</i>	114	6.11	3.61	3.70	12.83
<i>Corynoneura scutellata</i>	66	11.40	3.82	-0.80	-0.29
<i>Paratanytarsus austriacus</i>	52	11.63	3.79	-0.30	-0.42

Mediterranean ecoregion lakes	n	m (°C)	SD (°C)	g1	g2
<i>Procladius choreus</i>	161	12.26	3.29	1.58	2.05
<i>Conchapelopia pallidula</i>	89	14.33	5.47	0.40	-1.38
<i>Psectrocladius (Psectrocladius) oxyura</i>	104	13.62	4.54	0.96	-0.37
<i>Tanytarsus gregarius</i>	80	12.57	4.95	0.90	-0.57
<i>Cladotanytarsus atridorsum</i>	48	13.83	4.87	1.01	-0.79
<i>Paratanytarsus lauterborni</i>	44	10.14	3.16	2.94	7.61
<i>Pseudochironomus prasinatus</i>	35	13.52	3.80	1.37	0.28
<i>Paratendipes albimanus</i>	140	11.94	4.47	1.45	0.81
<i>Microtendipes pedellus</i>	61	12.23	1.92	0.74	0.86
<i>Polypedilum nubeculosum</i>	104	11.78	3.55	1.94	3.15
<i>Dicrotendipes nervosus</i>	42	11.96	2.27	2.80	10.90
<i>Cryptochironomus defectus</i>	94	12.26	3.15	1.57	2.64
<i>Cladopelma viridulum</i>	69	14.61	3.07	1.03	1.46
<i>Stictochironomus pictulus</i>	41	11.46	3.54	2.23	3.84
<i>Chironomus anthracinus</i>	69	11.43	3.88	1.83	2.28
<i>Chironomus plumosus</i>	97	12.64	5.08	0.99	-0.58

Heavily modified water bodies	n	m (°C)	SD (°C)	g1	g2
<i>Procladius choreus</i>	86	7.71	3.77	3.35	9.46
<i>Polypedilum nubeculosum</i>	43	8.93	2.64	0.87	1.46
<i>Chironomus plumosus</i>	88	13.86	6.99	0.14	-1.85