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

L. Marziali,[1] B. Rossaro[2]

[1]CNR-IRSA Water Research Institute, U.O.S. Brugherio, Brugherio (MB); [2]Department of Food, Environmental and Nutritional Sciences (DeFENS), University of Milan, Milan, Italy

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.

Correspondence: Laura Marziali, CNR-IRSA Water Research Institute, U.O.S. Brugherio, Via del Mulino 19, 20861 Brugherio (MB), Italy.
Tel.: +39.039.21694207 - Fax: +39.039.2004692.
E-mail: marziali@irsa.cnr.it

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.

Journal of Entomological and Acarological Research 2013; 45:e14
doi:10.4081/jear.2013.e14

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 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 (Lindegaard *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 (Cortelezzi *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; Battegazzore *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=g1) and fourth (kurtosis=g2) 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 *et al.*, 2006b; unpublished data
	Trentino-Alto Adige	Sarca, Adige and Noce rivers	1990, 1996-98, 2005	Boggero *et al.*, 2006; Lencioni *et al.*, 2007
		Lakes Lases, Lamar, Caldonazzo and Tenno (Brenta river)	1996, 2000, 2004-07	Lencioni *et al.*, 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 *et al.*, 1992
		Adda river	1977, 1988-89, 2001-07	Unpublished data
		Ticino river	1979, 1985, 2001-04, 2009-10	Berra *et al.*, 2004
		Lake Garda	1970-71, 1982, 2004, 2007, 2011	Rossaro *et al.*, 2006a, 2011; Bonomi, 1974
		Lakes Viverone and Avigliana	2005-06	Rossaro *et al.*, 2006a, 2011
		Lake Varese	1987, 1994-97, 2002-05	Rossaro *et al.*, 2006a, 2011
		Lake Monate	1977, 2004-05	Rossaro *et al.*, 2006a, 2011; Nocentini, 1979
		Lake Como	1980-84, 2004-05, 2007	Unpublished data
		Lakes Comabbio, Alserio, Pusiano and Annone	1967, 1977, 2004-07	Rossaro *et al.*, 2006a, 2011
		Lake Iseo	1967, 2003-04	Unpublished data
	Piedmont	Lake Mergozzo	1963-64, 1971-72, 1975, 1994, 2010	Rossaro *et al.*, 2006a, 2011; Nocentini, 1979
		Lake Maggiore	1953-54, 1960-61, 1966-67, 1985-88, 1995-96, 2004, 2007, 2009-10	Rossaro *et al.*, 2006a, 2011; Nocentini, 1963
		Ticino river	1985-87, 1991-94, 2000, 2007	Boggero *et al.*, 2006; Unpublished data
		Dora Baltea river	2005	Boggero *et al.*, 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	Rossaro 1987, 1988; Battegazzore *et al.*, 1992
		Taro river	2001-03	Marziali *et al.*, 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 *et al.*, 2006a, 2007a
	Umbria	Tevere river	1977-03	
	Campania	Sele river	2000-01	Marziali *et al.*, 2010a
	Puglia	Ofanto river	1990	Unpublished data
	Sardinia	Cedrino 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 *et al.*, 2006
France		Garonna river	2004	Unpublished data
Germany		Donau river	2006	Free *et al.*, 2009
Austria		Donau river	2006	Free *et al.*, 2009
Algeria		Algerian wadi	2007	Zerguine *et al.*, 2009; Chaib *et al.*, 2011

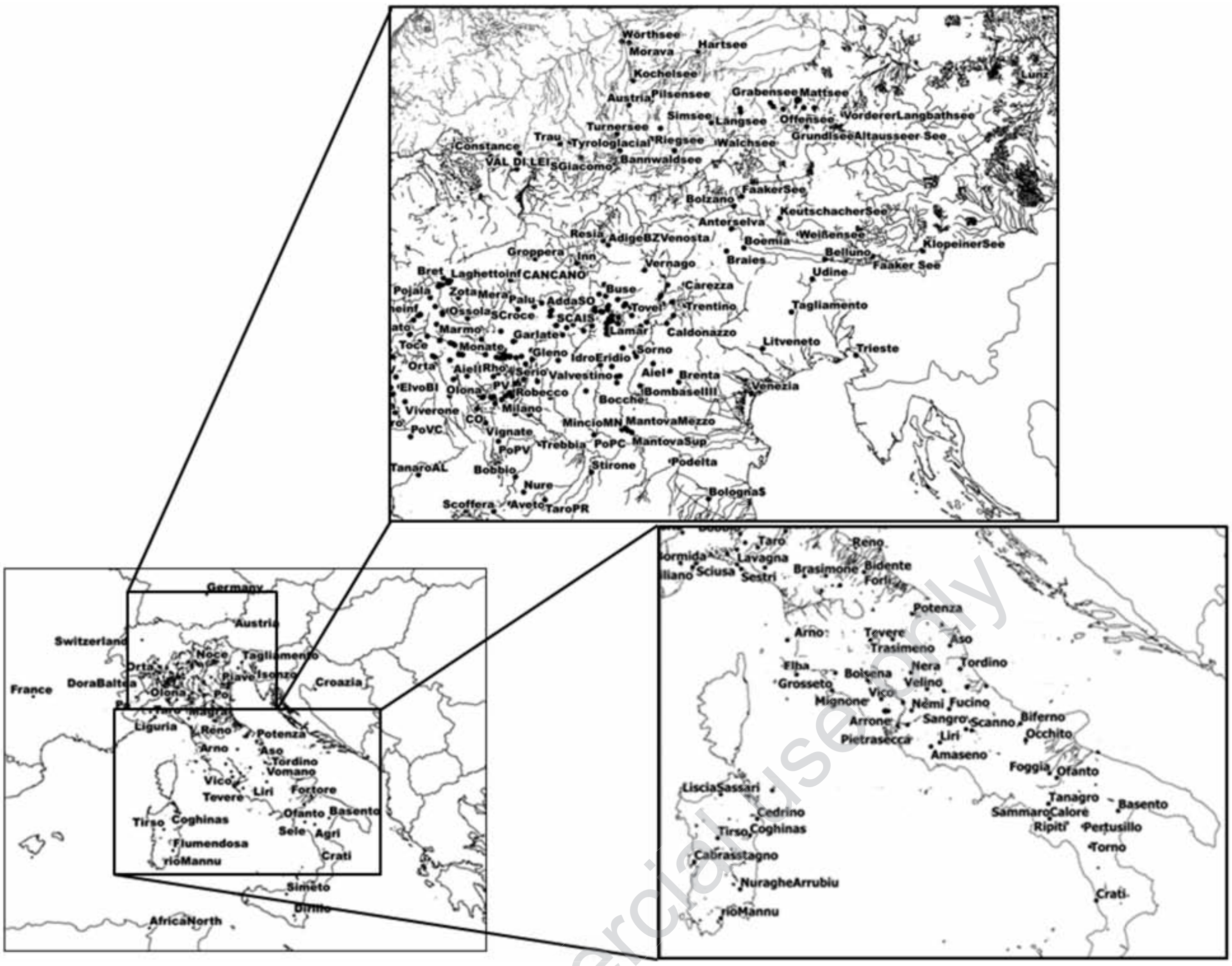

Figure 1. Map of the sampling sites.

Table 2. River catchments with mean latitude and longitude, and number of samples collected in each habitat.

River catchment	lat	long	kn	kr	rh	pt	AL	al	ME	hm	br
Garonna (France)	44°00'00"	02°00'00"	0	0	10	0	0	0	0	0	0
Donau (Germany)	47°41'19"	11°26'16"	0	0	0	0	50	0	0	0	0
Donau (Austria)	47°47'17"	13°20'17"	0	0	0	0	41	0	0	0	0
Dora Baltea	45°37'24"	07°35'14"	7	44	29	1	0	47	0	0	0
Sesia	45°38'00"	07°55'00"	0	0	0	0	1	0	0	0	0
Orta	45°49'00"	08°24'00"	0	0	0	0	1	0	0	0	0
Agogna	45°36'02"	08°28'03"	17	0	107	0	0	0	0	0	0
Ticino (CH)	46°24'33"	08°36'25"	0	0	4	0	0	14	0	0	0
Ticino (NO)	45°37'00"	08°38'00"	0	0	0	9	0	0	0	0	0
Ticino (MI)	45°22'33"	09°24'28"	37	0	0	35	0	0	0	0	0
Toce	46°15'35"	08°16'27"	0	0	11	0	19	0	0	0	0
Maggiore (CH)	46°26'09"	08°48'11"	0	0	0	0	18	0	0	0	0
Maggiore (VB)	45°48'21"	08°34'16"	0	0	0	0	303	0	0	0	0
Maggiore (VA)	45°51'12"	08°40'10"	0	0	0	0	78	0	0	0	0
Mergozzo	45°57'21"	08°27'36"	0	0	0	0	162	0	0	0	0
Varese	45°50'96"	08°43'73"	0	0	1	0	119	0	0	0	0
Lugano	46°28'06"	09°38'12"	0	0	3	0	14	0	0	0	0
Olona	45°30'11"	09°20'52"	0	0	0	43	0	0	0	0	0
Lambro	45°48'37"	09°16'60"	0	0	0	1	163	0	0	0	0
Adda (SO)	46°19'02"	09°43'01"	1	24	0	0	0	0	0	0	0

To be continued on next page

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 g1 means a response curve skewed to the right, *i.e.* the optimum value is closer to the minimum response value. A negative value of g1 means a response curve skewed to the left, *i.e.* optimum water temperature is closer to the maximum response value. A positive value of g2 is a measure of the peakedness of a curve. A curve with a high g2 (>3) is called *leptokurtic* and it has a defined peak, *i.e.* the species has a defined optimum temperature. A negative value of g2 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 g2 suggests a bi- or plurimodal Gaussian distribution (Khurshid, 2007).

Moment calculations were performed converting in Matlab® environment, 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, g1 or g2 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 $_1$ and $_n$ are the peaks to be fitted, a_1 and a_n are the amplitude, m_1 and m_n the centroid (location), s_1 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.

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°C) and skewness (g1) (Table 3) gave an inverse relation (r^2=0.34, 53 df, P<0.01). As well, optimum for water temperature (m°C) and kurtosis (g2) 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°C, with a standard deviation of 5.93°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°C (main peak), 11.39°C and 22.42°C (secondary peaks). Peaks were at 4.93°C (main peak), 7.45°C and 20.77°C considering only samples from Alpine lowland lakes (Figure 2B). Optimum for rhithral samples was 13.9 °C (unimodal response) (Figure 2C, Appendix), while potamal samples gave a trimodal response with peaks at 11.5 °C, 18.64 °C and 23.89 °C (Figure 2D).

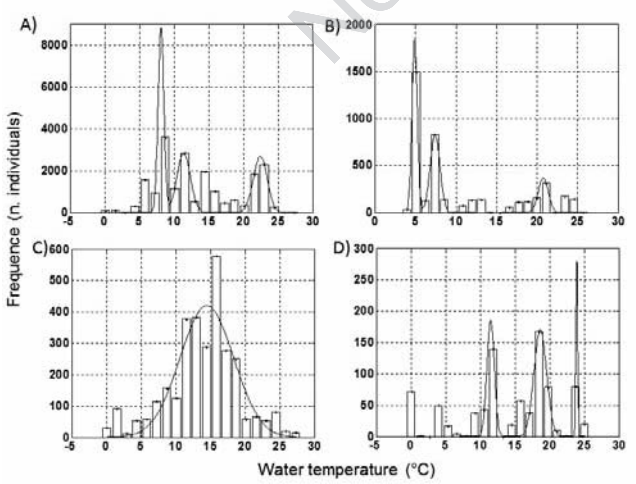

Figure 2. Response of *Conchapelopia pallidula* larvae (number of individuals m^{-2}) to water temperature (°C) in all habitats (A), Alpine ecoregion lowland lakes (B), rhithral (C) and potamal (D).

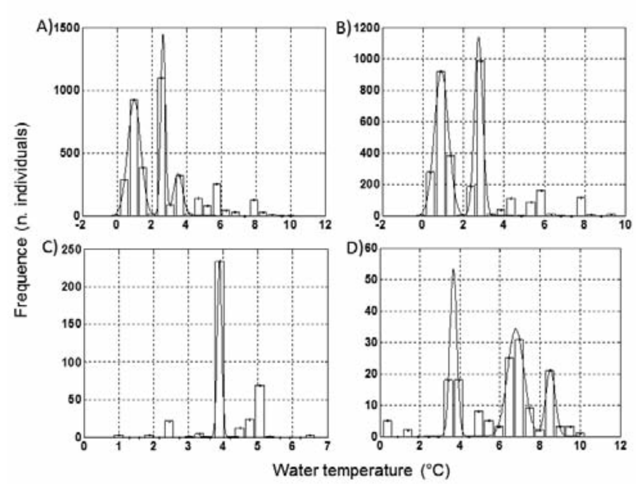

Figure 3. Thermal response of Diamesini larvae. Response of *Diamesa bertrami* (number of individuals m^{-2}) to water temperature (°C) in all habitats (A), kyral (B), krenal (C) and rhithral (D).

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
Procladius choreus	1018	13.39	5.7	0.63	–0.65
Macropelopia nebulosa	127	10.5	5.17	0.47	–0.63
Zavrelimyia barbatipes	128	11.58	4.11	–0.21	0.45
Conchapelopia pallidula	615	13.54	5.93	0.34	–1.03
Rheopelopia ornata	111	14.77	4.3	–0.19	–1.15
Pseudodiamesa branickii	115	5.63	3.08	0.8	0.71
Diamesa steinboecki	106	1.98	1.45	1.06	1.19
Diamesa latitarsis	134	3.43	1.97	0.85	0.27
Diamesa bertrami	200	2.68	1.96	1.16	0.79
Diamesa tonsa	186	7.19	4.66	0.61	–0.18
Diamesa zernyi	215	3.72	2.51	1.62	8.22
Prodiamesa olivacea	246	9.48	4.33	1.79	3.56
Brillia bifida	202	11.38	4.76	0.19	–0.69
Tvetenia calvescens	537	11.08	5.81	0.06	–1.24
Eukiefferiella brevicalcar	133	4.51	1.94	1.66	6.37
Eukiefferiella claripennis	215	14.7	4.41	–0.49	–0.3
Eukiefferiella minor	176	6.8	3.78	0.72	0.41
Psectrocladius (Psectrocladius) oxyura	283	12.17	6.22	0.43	–1.04
Rheocricotopus effusus	124	13.15	5.83	–0.16	–0.49
Rheocricotopus fuscipes	245	16.97	7.97	0.06	–1.49
Synorthocladius semivirens	128	13.38	4.42	–0.16	–0.78
Orthocladius (Euorthocladius) rivicola	366	9.85	4.7	0.52	–0.01
Orthocladius frigidus	261	6.17	3.72	1.25	1.4
Orthocladius oblidens	138	9.18	5.5	1.16	0.21
Orthocladius rhyacobius	212	12.14	4.02	–0.15	–0.24
Orthocladius rubicundus	111	12.45	3.19	0.55	0.91
Paratrichocladius rufiventris	253	17.33	6.32	0.17	–0.82
Cricotopus annulator	161	14.24	4.79	0.09	0.16
Cricotopus bicinctus	276	14.63	5.08	–0.23	–1.04
Cricotopus (Isocladius) sylvestris	183	11.19	5.08	0.82	–0.09
Parametriocnemus stylatus	218	11.14	4.97	0.36	–0.83
Parakiefferiella bathophila	117	5.89	3.69	3.66	12.52
Thienemanniella partita	107	7.73	4.08	0.93	0.3
Corynoneura scutellata	259	11.07	4.06	–0.5	–0.35
Tanytarsus gregarius	421	11.11	6.8	0.72	–1.07
Cladotanytarsus atridorsum	268	14.59	5.11	0.63	–1.05
Paratanytarsus lauterborni	101	10.53	3.01	3.1	9.11
Micropsectra atrofasciata	490	13.79	5.33	0.52	0.88
Micropsectra pallidula	125	6.3	3.58	1.1	0.44
Pagastiella orophila	115	8.12	4.63	1.43	0.75
Pseudochironomus prasinatus	209	13.95	6.56	0.02	–1.37
Paratendipes albimanus	351	12.22	4.43	1.35	0.65
Microtendipes pedellus	394	12.29	2.73	0.6	1.06
Polypedilum convictum	138	15.44	4.07	–0.61	0.44
Polypedilum laetum	112	16.65	5.52	–0.14	–0.38
Polypedilum nubeculosum	566	12.08	4.09	1.26	1.58
Endochironomus tendens	106	12.51	3.91	0.8	0.08
Dicrotendipes nervosus	276	10.08	5.24	0.86	0
Glyptotendipes pallens	154	13.88	7.65	0.08	–1.25
Chironomus anthracinus	525	13.54	6.35	0.5	–1.44
Chironomus plumosus	571	11.19	6.1	0.67	–0.59
Chironomus riparius	333	15.28	4.65	0.32	1.44
Cladopelma viridulum	294	13.63	5.98	0.51	–0.7
Cryptochironomus defectus	473	13.86	5.67	0.43	–0.74
Demicryptochironomus vulneratus	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 g2, *i.e.* leptokurtic response (Table 3, Appendix).

Species with low temperature optimum (cold stenothermal) showed a response curve skewed to the right (g1>0). *Diamesa bertrami* showed a moderately platykurtic response (g2=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 (g1<0). For example, *Cricotopus (Isocladius) sylvestris* in potamal (Figure 4C, Appendix) showed optimum at 17.80°C and g1=2.13; *Paratanytarsus mediterraneus* in potamal (Figure 5D; Appendix) had optimum at 19.42°C and a g1=1.59. *Tanytarsus brundini* in rhithral with optimum at 14.37°C and a negative g1 (g1=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 (g1>0, *i.e.* g1=0.17) (Table 3). A negative value of g2 was an index of a bi- or plurimodal response; *Tanytarsus gregarius* in Alpine ecoregion lakes with a negative g2 (g2=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, *Zavrelimyia 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)	g1	g2
Larvae	Rhythral	363	14.20	6.17	0.42	–0.33
Pupal exuviae	Rhythral	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; g1, skewness; g2, kurtosis; Alpine lakes, Alpine ecoregion lowland lakes.

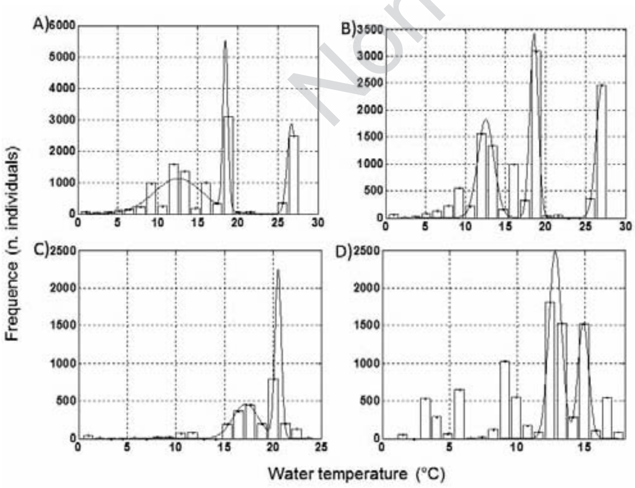

Figure 4. Thermal response of Orthocladiini larvae. Response of *Paratrichocladius rufiventris* (number of individuals m^{-2}) to water temperature (°C) in all habitats (A) and rhithral (B); response of *Cricotopus (Isocladius) sylvestris* in potamal (C); response of *Corynoneura scutellata* in Alpine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

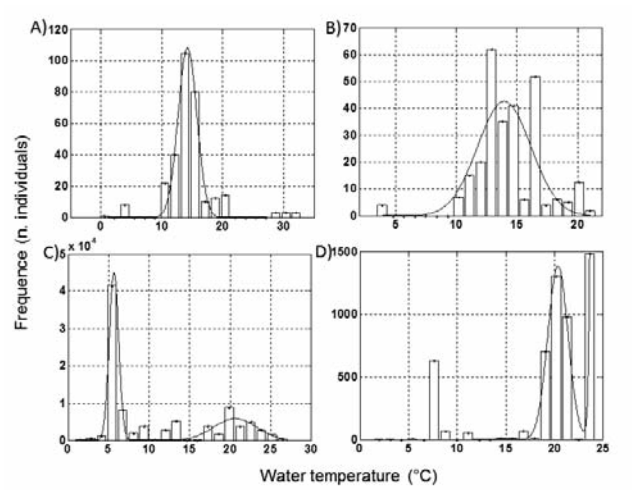

Figure 5. Thermal response of Tanytarsini larvae. Response of *Tanytarsus brundini* (number of individuals m^{-2}) to water temperature (°C) in all habitats (A) and rhithral (B); response of *Tanytarsus gregarius* in Alpine ecoregion lowland lakes (C); response of *Paratanytarsus mediterraneus* in potamal (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
Tanypus punctipennis	118	237	207	2.78	16.96
Procladius choreus	1530	437	303	2.42	7.53
Macropelopia nebulosa	274	1278	524	–0.95	–0.67
Ablabesmyia monilis	143	662	513	1.97	3.43
Zavrelimyia barbatipes	243	1961	540	–2.09	3.16
Conchapelopia pallidula	1005	363	285	3.14	14.63
Rheopelopia ornata	137	177	160	2.22	8.04
Pseudodiamesa branickii	262	1913	611	–1.09	0.11
Diamesa steinboecki	119	2559	221	–2.42	8.87
Diamesa latitarsis	171	2213	572	–1.60	2.59
Diamesa bertrami	277	1933	653	–0.86	0.04
Diamesa tonsa	409	897	654	1.27	0.75
Diamesa zernyi	353	2145	564	–1.14	1.04
Pseudokiefferiella parva	119	2348	475	–1.52	2.49
Prodiamesa olivacea	393	300	421	3.56	12.80
Brillia longifurca	100	458	264	0.87	0.95
Brillia bifida	413	434	298	1.76	6.13
Cardiocladius fuscus	148	677	750	1.60	0.77
Tvetenia calvescens	840	1281	945	0.14	–1.81
Eukiefferiella brevicalcar	162	2013	461	–1.55	2.01
Eukiefferiella claripennis	353	651	691	2.00	2.23
Eukiefferiella minor	324	1489	772	–0.39	–1.52
Psectrocladius (Psectrocladius) oxyura	334	272	373	4.56	20.39
Rheocricotopus chalybeatus	116	342	168	1.50	5.34
Rheocricotopus effusus	205	866	743	1.17	–0.33
Rheocricotopus fuscipes	515	361	242	3.10	17.76
Synorthocladius semivirens	212	451	280	4.10	22.43
Orthocladius (Eudactylocladius) fuscimanus	124	1825	709	–1.25	–0.09
Orthocladius (Euorthocladius) rivicola	618	1052	902	0.66	–1.40
Orthocladius excavatus	141	335	152	1.96	15.17
Orthocladius frigidus	463	1767	743	–0.90	–0.49
Orthocladius oblidens	179	305	188	1.73	2.60
Orthocladius rhyacobius	312	422	228	0.79	1.82
Orthocladius rubicundus	204	409	214	1.19	6.43
Paratrichocladius rufiventris	456	737	610	0.81	–1.18
Paratrichocladius skirwithensis	210	1849	538	–1.57	1.75
Cricotopus annulator	245	412	335	3.81	17.08
Cricotopus bicinctus	422	189	198	1.31	5.93
Cricotopus fuscus	169	1067	624	0.17	–1.18
Cricotopus tremulus	126	968	725	0.75	–0.27
Cricotopus triannulatus	220	220	231	2.56	8.14
Cricotopus (Isocladius) sylvestris	276	322	593	2.89	6.69
Metriocnemus hygropetricus	180	937	685	0.88	–0.59
Chaetocladius laminatus	142	1628	913	–0.44	–1.62
Paratrissocladius excerptus	114	434	242	–0.07	–0.01
Heterotrissocladius marcidus	174	1936	595	–1.45	1.02
Parametriocnemus stylatus	349	1137	878	0.51	–1.19
Parakiefferiella bathophila	165	226	138	4.06	28.87
Thienemanniella partita	173	1141	904	0.19	–1.69
Corynoneura scutellata	395	2130	447	–3.37	11.70
Stempellina bausei	115	426	209	0.00	–1.67
Tanytarsus gregarius	652	561	577	1.21	–0.31
Cladotanytarsus atridorsum	342	406	136	1.92	17.06
Paratanytarsus austriacus	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
Paratanytarsus lauterborni	125	410	549	1.76	1.19
Micropsectra atrofasciata	890	425	361	3.06	10.30
Micropsectra contracta	386	402	114	8.52	93.32
Micropsectra notescens	108	527	313	0.31	1.08
Micropsectra pallidula	166	2184	293	−1.55	3.46
Pagastiella orophila	127	575	245	−0.77	−0.90
Pseudochironomus prasinatus	256	396	202	0.30	−1.74
Paratendipes albimanus	464	308	172	2.83	17.00
Microtendipes pedellus	510	204	213	3.86	18.41
Polypedilum convictum	145	347	167	−0.32	−1.23
Polypedilum laetum	199	340	294	3.06	15.31
Polypedilum cultellatum	100	142	153	1.68	2.34
Polypedilum nubeculosum	812	228	143	5.21	61.77
Phaenopsectra flavipes	149	399	429	2.03	3.05
Endochironomus tendens	140	148	198	6.14	57.78
Stictochironomus pictulus	101	460	443	2.21	2.90
Dicrotendipes nervosus	373	270	104	1.28	1.94
Glyptotendipes pallens	237	241	67	1.56	18.49
Chironomus anthracinus	751	482	356	1.79	3.65
Chironomus plumosus	762	283	132	2.04	7.37
Chironomus riparius	521	229	199	0.93	−0.24
Cladopelma viridulum	390	238	133	6.26	70.75
Parachironomus arcuatus	113	195	98	2.73	16.60
Paracladopelma camptolabis	107	631	546	1.21	0.57
Paracladopelma nigritulum	188	388	55	10.07	221.97
Cryptochironomus defectus	606	305	156	0.93	0.25
Demicryptochironomus vulneratus	163	226	88	3.18	12.09

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

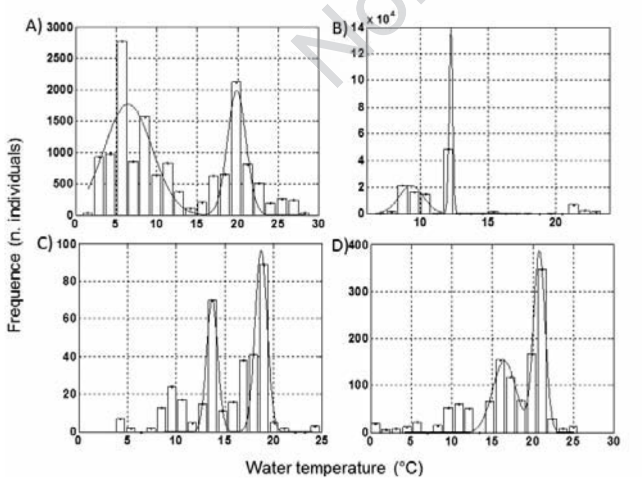

Figure 6. Thermal response of *Polypedilum nubeculosum* larvae (number of individuals m^{-2}) to water temperature (°C) in Alpine ecoregion lowland lakes (A), Mediterranean ecoregion lakes (B), rhithral (C) and potamal (D).

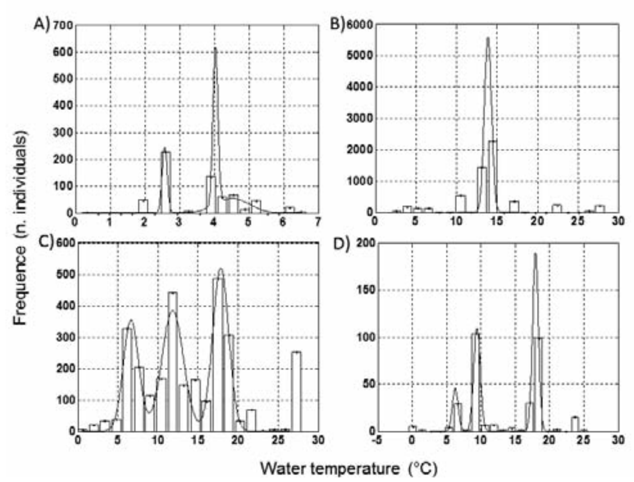

Figure 7. Thermal response of *Micropsectra* spp. larvae. Response of *M. pallidula* (number of individuals m^{-2}) to water temperature (°C) in krenal (A); response of *M. atrofasciata* in Alpine ecoregion lowland lakes (B), rhithral (C) and potamal (D).

lower altitudes, the higher temperature optima were observed for *P. mediterraneus, P. rufiventris* and *Tanypus 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 nigritulum*), 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 steinboecki*, *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
Procladius choreus	1046	21.02	23.02	3.17	23.24
Conchapelopia pallidula	232	4.87	3.34	4.05	31.03
Prodiamesa olivacea	179	21.70	17.71	1.08	1.21
Psectrocladius (Psectrocladius) oxyura	255	4.97	2.39	1.67	4.75
Orthocladius oblidens	110	4.99	2.14	1.97	20.31
Parakiefferiella bathophila	113	5.86	3.27	2.22	5.64
Tanytarsus gregarius	459	10.15	32.08	4.62	23.67
Cladotanytarsus atridorsum	253	3.62	2.38	2.65	17.66
Micropsectra contracta	359	84.91	56.80	1.33	1.62
Pagastiella orophila	116	7.10	2.77	2.69	13.03
Pseudochironomus prasinatus	212	4.26	3.04	6.85	140.29
Paratendipes albimanus	295	4.44	8.81	7.69	152.02
Microtendipes pedellus	228	6.06	4.29	1.54	3.00
Polypedilum nubeculosum	377	3.27	7.90	8.12	126.29
Dicrotendipes nervosus	232	5.70	3.88	2.05	4.46
Chironomus anthracinus	529	13.39	18.62	8.41	113.15
Chironomus plumosus	480	9.73	49.52	7.03	51.04
Cladopelma viridulum	270	8.34	16.38	10.19	163.69
Paracladopelma nigritulum	171	73.31	41.44	0.88	–0.64
Cryptochironomus defectus	423	6.51	4.75	3.70	52.20
Demicryptochironomus vulneratus	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 Doorsalaen *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/steinboecki* (juvenilia), Appendix] and *Tanytarsus* spp.

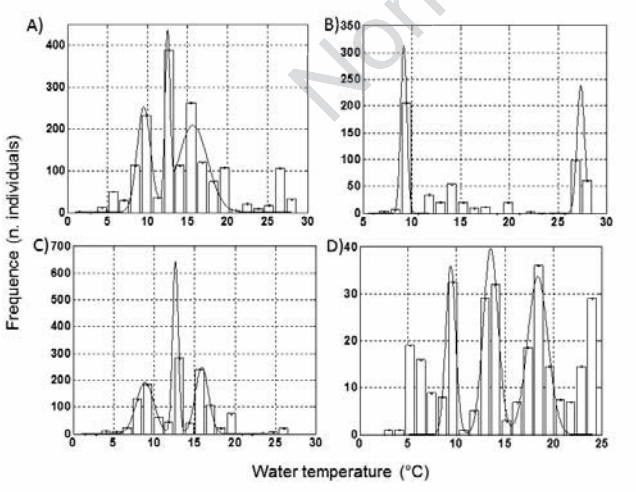

Figure 8. Thermal response of *Micropsectra atrofasciata* pupal exuviae (number of individuals m^{-2}) to water temperature (°C) in all habitats (A), Alpine ecoregion lowland lakes (B), rhithral (C) and potamal (D).

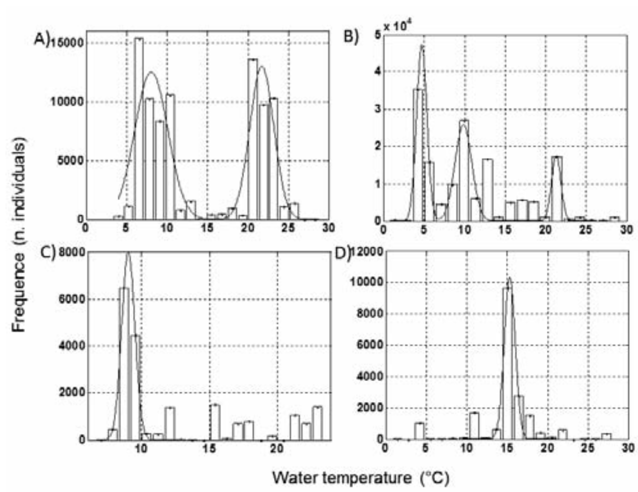

Figure 9. Thermal response of *Chironomus* spp. larvae. Response of *C. anthracinus* (number of individuals m^{-2}) to water temperature (°C) in Alpine ecoregion lowland lakes (A); response of *C. plumosus* in Alpine ecoregion lowland lakes (B), and Mediterranean ecoregion lakes (C); response of *C. 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
Procladius choreus	497	84.56	83.31	1.27	0.06
Zavrelimyia barbatipes	118	3.86	20.05	9.52	123.78
Conchapelopia pallidula	663	81.40	134.03	3.35	10.99
Pseudodiamesa branickii	173	15.96	33.89	2.17	4.00
Diamesa steinboecki	108	0.69	7.32	15.03	226.29
Diamesa latitarsis	123	4.26	13.38	5.16	29.23
Diamesa bertrami	205	2.22	16.28	12.63	218.61
Diamesa tonsa	324	12.20	61.51	23.06	817.69
Diamesa zernyi	229	1.90	10.74	12.79	238.84
Prodiamesa olivacea	207	128.57	96.06	0.14	–1.76
Brillia bifida	302	19.64	31.95	3.35	19.85
Cardiocladius fuscus	115	18.68	79.56	13.42	331.58
Tvetenia calvescens	588	20.91	39.27	4.24	24.07
Eukiefferiella brevicalcar	131	0.81	11.87	20.57	475.86
Eukiefferiella claripennis	243	19.03	32.48	6.56	50.10
Eukiefferiella minor	216	8.79	19.15	4.85	46.65
Psectrocladius (Psectrocladius) oxyura	162	60.00	16.03	0.20	52.13
Rheocricotopus effusus	138	28.92	30.16	0.67	–0.12
Rheocricotopus fuscipes	391	48.28	98.83	5.40	30.02
Synorthocladius semivirens	163	22.23	40.18	3.74	24.97
Orthocladius (Euorthocladius) rivicola	457	28.15	66.53	6.22	42.93
Orthocladius excavatus	109	31.70	87.00	7.89	133.38
Orthocladius frigidus	322	6.39	52.28	33.79	1454.39
Orthocladius oblidens	121	55.14	26.38	0.47	7.27
Orthocladius rhyacobius	215	35.31	89.49	5.16	85.39
Orthocladius rubicundus	106	57.75	43.71	0.40	–0.22
Paratrichocladius rufiventris	317	3.76	35.13	29.05	1517.03
Paratrichocladius skirwithensis	134	14.01	23.29	2.15	3.32
Cricotopus annulator	176	34.10	68.19	7.05	60.01
Cricotopus bicinctus	241	128.77	120.05	1.29	2.98
Cricotopus triannulatus	197	131.92	128.18	1.72	5.47
Cricotopus (Isocladius) sylvestris	150	139.59	119.98	0.02	–0.86
Metriocnemus hygropetricus	132	31.94	50.11	4.62	42.91
Chaetocladius laminatus	117	13.86	30.01	5.65	45.96
Parametriocnemus stylatus	241	16.18	27.90	4.51	33.89
Parakiefferiella bathophila	101	63.12	1.86	–5.20	2484.04
Thienemanniella partita	133	12.60	53.86	9.37	101.81
Corynoneura scutellata	233	12.58	61.42	6.02	39.72
Tanytarsus gregarius	238	67.50	30.09	10.27	181.68
Cladotanytarsus atridorsum	104	57.74	17.82	7.56	111.14
Micropsectra atrofasciata	529	35.41	66.56	8.86	269.38
Micropsectra pallidula	120	1.54	2.29	2.80	15.69
Pseudochironomus prasinatus	119	54.93	5.42	–1.21	11.16
Paratendipes albimanus	130	32.79	28.69	5.33	95.49
Microtendipes pedellus	235	53.65	38.30	2.77	11.10
Polypedilum laetum	164	59.77	73.36	3.91	23.25
Polypedilum nubeculosum	434	90.31	86.70	2.38	9.45
Dicrotendipes nervosus	188	72.25	78.47	6.66	46.00
Glyptotendipes pallens	138	152.20	113.95	0.91	2.80
Chironomus anthracinus	273	57.22	19.98	–1.93	2.80
Chironomus plumosus	282	26.89	44.06	9.88	134.42
Chironomus riparius	227	213.81	69.27	–1.73	2.69
Cladopelma viridulum	131	50.98	23.96	–1.54	0.53
Cryptochironomus defectus	236	84.54	67.67	2.65	9.59
Demicryptochironomus vulneratus	134	53.81	16.62	–2.59	5.90

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

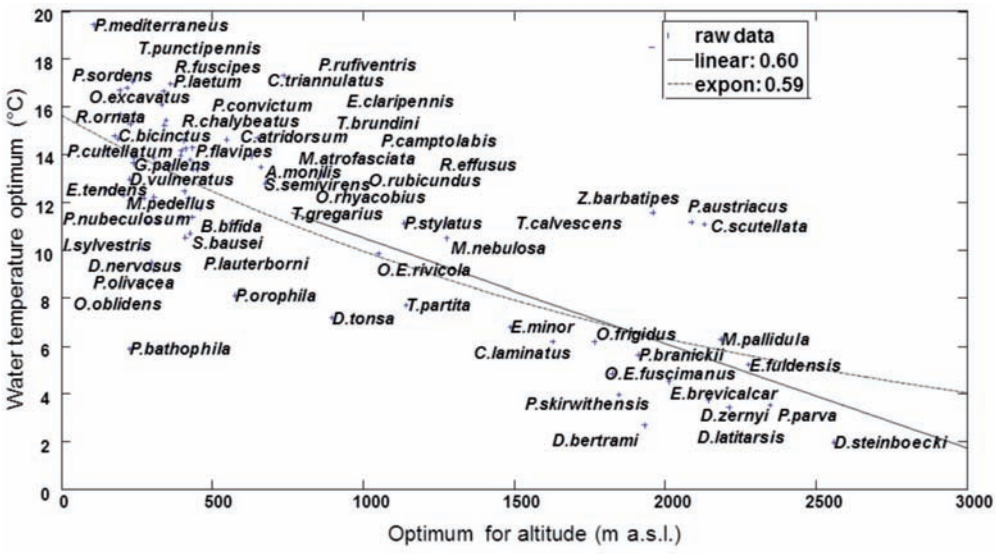

Figure 10. Correlation between species optima for water temperature (°C) *vs* optima for altitude (m a.s.l.).

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

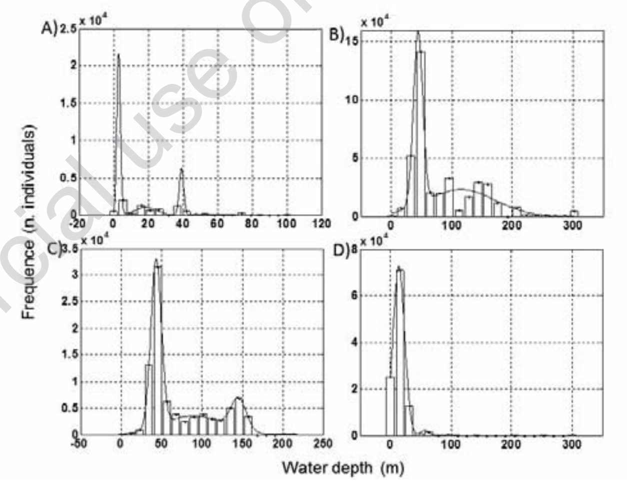

Figure 11. Response of *Prodiamesa olivacea* (A), *Micropsectra contracta* (B), *Paracladopelma nigritulum* (C), *Chironomus anthracinus* (D) larvae (number of individuals m^{-2}) to water depth (m) in Alpine ecoregion lowland lakes.

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

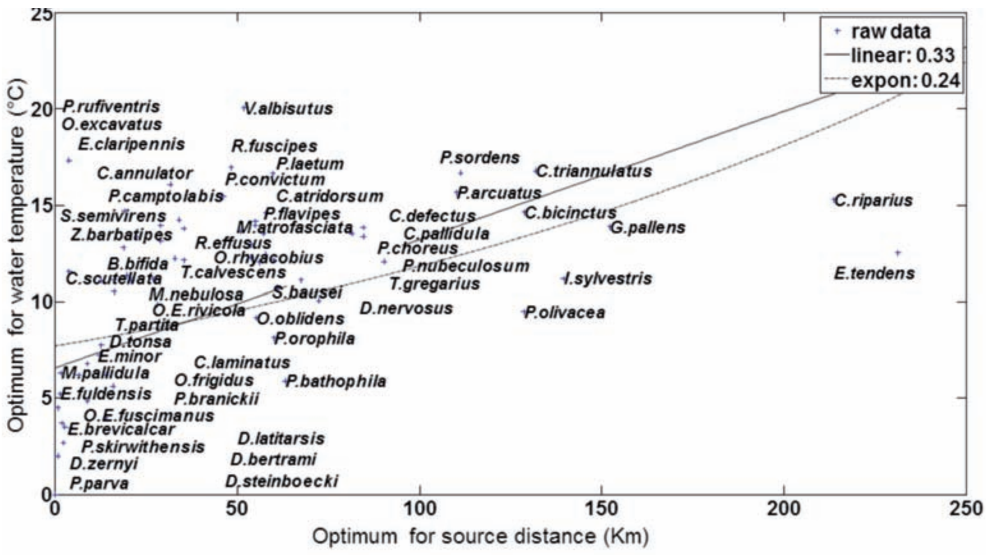

Figure 12. Correlation between species optima for water temperature (°C) *vs* optima for distance from source (km) in running waters.

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 Doorsalaen *et al.*, 2009).

References

BATTEGAZZORE M., PETERSEN R.C., MORETTI G.P., ROSSARO B., 1992 - An evaluation of the environmental quality of the river Po using benthic macroinvertebrates. - Arch. Hydrobiol. 125: 175-206.

BERRA E., FORCELLA M., GIACCHINI R., MARZIALI L., ROSSARO B., PARENTI P., 2004 - Evaluation of enzyme biomarkers in freshwater macroinvertebrates of Taro and Ticino river, Italy. - Int. J. Lim. 40: 169-180.

BOGGERO A., FÜREDER L., LENCIONI V., SIMCIC B., THALER B., FERRARESE U., *et al.*, 2006 - Littoral Chironomid community of Alpine lakes in relation to environmental factors. - Hydrobiologia. 562: 145-165.

BONADA N., DOLÉDEC S., STATZNER B., 2007 - Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. - Glob. Change Biol. 13: 1658-1671.

BONOMI G., 1974 - Benton profondo. Indagini sul lago di Garda. - Quaderni dell'Istituto di Ricerca sulle Acque. 18: 211-223.

BROOKS S.J., BIRKS H.J.B., 2000 - Chironomid-inferred late-glacial and early Holocene mean July air temperature from Kråkanes lake, Western Norway. - J. Paleolimnol. 23: 77-89.

BRUNDIN L., 1966 - Transantarctic relationships and their significance, as evidenced by Chironomid midges, with a monograph of the subfamilies Podonominae and Aphroreniinae and the austral Heptagyiae. - Kungliga Svenska Vetenskapsakadamiens Handlingar, series 4. 11: 1-472.

CASPERS N., 1983 - Chironomiden-Emergenz zweier Lunzer Bäche, 1972. - Arch. Hydrobiol. Suppl. 65: 484-549.

CATALAN J., CURTIS C.J., KERNAN M., 2009 - Remote European mountain lake ecosystems regionalisation and ecological status. - Freshwater Biol. 54: 2419-2432.

CHAIB N., SAMRAOUI B,. MARZIALI L., ROSSARO B., 2011 - Chironomid taxocenosis in a South Mediterranean wadi, the Kebir-East (Algeria). - Studi Trentini di Scienze Naturali. 89: 29-34.

ČIAMPOROVÁ-ZAT'OVIČOVÁ Z., HAMERLÍK L., ŠPORKA F., BITUŠÍK P., 2010 - Littoral benthic macroinvertebrates of alpine lakes (Tatra Mts) along an altitudinal gradient: a basis for climate change assessment. - Hydrobiologia. 648: 19-34.

CORTELEZZI A., PAGGI A.C., RODRIGUEZ M.A., RODRIGUEZ C., 2011 - Taxonomic and non-taxonomic responses to ecological changes in an urban lowland stream through the use of Chironomidae (Diptera) larvae. - Sci. Total Environ. 409: 1344-1350.

CRANSTON P., HARDY N.B., MORSE G., 2012 - A dated molecular phylogeny for the Chironomidae (Diptera). - Syst. Entomol. 37: 172-188.

CRANSTON P.S., OLIVER D.R., 1987 - Problems in Holarctic chironomid biogeography. - Entomol. Scand. 29: 51-56.

DALLAS H.F., RIVERS-MOORE N.A., 2012 - Critical thermal maxima of aquatic macroinvertebrates: towards identifying bioindicators of thermal alteration. - Hydrobiologia. 679: 61-76.

DAVIES R.G., 1971 - Computer programming in quantitative biology. - Academic Press, London: 504 pp.

FERRARESE U., 1983 - Chironomidi, 3 (Diptera: Chironomidae: Tanypodinae). Guide per il riconoscimento delle specie animali delle acque interne italiane. - Consiglio Nazionale delle Ricerche: no. 26. AQ/1/204.

FERRARESE U., ROSSARO B. 1981 - Chironomidi, 1 (Diptera, Chironomidae: Generalità, Diamesinae, Prodiamesinae). Guide per il riconoscimento delle specie animali delle acque interne italiane. - Consiglio Nazionale delle Ricerche: no. 12. AQ/1/129.

FREE G., SOLIMINI A., ROSSARO B., MARZIALI L., GIACCHINI R., PARACCHINI B., *et al.*, 2009 - Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake morphology, aquatic chemistry and sediment composition. - Hydrobiologia. 633: 123-136.

HAMERLIK L., BRODERSEN K.P., 2010 - Non-biting midges (Diptera: Chironomidae) from fountains of two European cities: micro-scale island biogeography. - Aquat. Insect. 32: 67-79.

HAMERLIK L., JACOBSEN D., 2012 - Chironomid (Diptera) distribution and diversity in Tibetan streams with different glacial influence. - Insect. Conserv. Diver. 5: 319-326.

HAMERLIK L., JACOBSEN D., BRODERSEN K.P., 2011 - Low species richness of non-biting midges (Diptera: Chironomidae) in Neotropical artificial urban water bodies. - Urban Ecosyst. 14: 457-468.

HEIRI O., BROOKS S.J., BIRKS H.J B., LOTTER A.F., 2011 - A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. - Quat. Sci. Rev. 30: 3445-3456.

HERING D., MOOG O., SANDIN L., VERDONSCHOT P.F.M., 2004 - Overview and application of the AQEM assessment system. - Hydrobiologia. 516: 1-20.

HESTER E.T., DOYLE M.W., 2011 - Human impacts to river temperature and their effects on biological processes: a quantitative synthesis. - J. Am. Water Resour. As. 47: 571-587.

HOGG I.D., EADIE J.M., DE LAFONTAINE Y., 1998 - Atmospheric change and the diversity of aquatic invertebrates: are we missing the boat? - Environ. Monit. Assess. 49: 291-301.

HUGHES L., 2000 - Biological consequences of global warming: is the signal already apparent? - Trends Ecol. Evol. 15: 56-61.

JACOBSEN D., MILNER A.M., BROWN L.E., DANGLES O., 2012 - Biodiversity under threat in glacier-fed river systems. - Nat. Clim. Change. 2: 361-364.

JACOBSEN D., SCHULTZ R., ENCALADA A., 1997 - Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. - Freshwater Biol. 38: 247-261.

KERNAN M., VENTURA M., BITUŠÍK P., BRANCELJ A., CLARKE G., VELLE G., *et al*., 2009 - Regionalisation of remote European mountain lake ecosystems according to their biota: environmental versus geographical patterns. - Freshwater Biol. 54: 2470-2493.

KHURSHID A., 2007 - A note on finding peakedness in bivariate normal distribution using Mathematica. - Pak. J. Stat. Operat. Res. 3: 75-86.

LANGTON P.H., 1991 - A key to pupal exuviae of West Palaearctic Chironomidae. - Huntingdon, Coleraine: 386 pp.

LANGTON P.H., 1995 - The pupa and events leading to eclosion. In: ARMITAGE P., CRANSTON P.S., PINDER L.C.V. (eds.), The Chironomidae. The biology and ecology of non-biting midges. - Chapman & Hall, London, UK: 169-193.

LAROCQUE I., HALL R.I., GRAHN E., 2001 - Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). - J. Paleolimnol. 26: 307-322.

LAROCQUE-TOBLER I., STEWART M.M., QUINLAN R., TRACHSEL M., KAMENIK C., GROSJEAN M., 2012 - A last millennium temperature reconstruction using chironomids preserved in sediments of anoxic Seebergsee (Switzerland): consensus at local, regional and Central European scales. - Quat. Sci. Rev. 41: 49-56.

LENCIONI V., MAIOLINI B., MARZIALI L., LEK S., ROSSARO B., 2007 - Macroinvertebrate assemblages in glacial stream systems: artificial neural networks. - Ecol. Model. 203: 119-131.

LENCIONI V., MARZIALI L., ROSSARO B., 2006 - Assessment of the ecological status of lakes by macroinvertebrates: a case study. In: Atti del XVI Congresso della Società Italiana di Ecologia, Viterbo-Civitavecchia 9-22 Settembre 2006. Cambiamenti globali, diversità ecologica e sostenibilità. Available from: http://www.ecologia.it/congressi/XVI/articles/

LENCIONI V., MARZIALI L., ROSSARO B., 2012 - Chironomids as bioindicators of environmental quality in mountain springs. - Freshwater Sci. 31: 525-541.

LINDEGAARD C., 1995 - Classification of water bodies and pollution. In: ARMITAGE P., CRANSTON P.S., PINDER L.C.V. (eds.), The Chironomidae. The biology and ecology of non-biting midges. - Chapman & Hall, London, UK: 385-404.

LINDEGAARD C., MORTENSEN E., 1988 - Abundance, life history and production of Chironomidae (Diptera) in a Danish lowland stream. - Arch. Hydrobiol. Suppl. 81: 563-587.

LOTTER A.F., HEIRI O., BROOKS S., VAN LEEUWEN J.F.N., EICHER U., AMMANN B., 2012 - Rapid summer temperature changes during termination 1a: high-resolution multi-proxy climate reconstructions from Gerzensee (Switzerland). - Quat. Sci. Rev. 36: 103-113.

LUOTO T.P., 2012 - Spatial uniformity in depth optima of midges: evidence from sedimentary archives of shallow Alpine and boreal lakes. - J. Limnol. 71: 228-232.

MARZIALI L., ARMANINI D.G., CAZZOLA M., ERBA S., TOPPI E., BUFFAGNI A., *et al*., 2010a - Responses of Chironomid Larvae (Insecta, Diptera) to ecological quality in Mediterranean River Mesohabitats (South Italy). - River Res. Appl. 26: 1036-1051.

MARZIALI L., CASALEGNO C., LENCIONI V., ROSSARO B., 2010b - Definition and Assignment of indicator weights to different Chironomid species. In: FERRINGTON L.C.JR. (ed.), Proceedings of the XV International Symposium on Chironomidae. - Chironomidae Research Group, University of Minnesota, St Paul, MN: 103-108.

MEDEIROS A.S., QUINLAN R., 2011 - The distribution of the Chironomidae (Insecta: Diptera) along multiple environmental gradients in lakes and ponds of the eastern Canadian Arctic. - Can. J. Fish. Aquat. Sci. 68: 1511-1527.

MILNER A.M., PETTS G.E., 1994 - Glacial rivers: physical habitat and ecology. - Freshwater Biol. 32: 295-307.

NOCENTINI A.M., 1963 - Struttura e dinamica della fauna macrobentonica litorale e sublitorale del Lago Maggiore. - Mem. Ist. Ital. Idrobiol. 16: 189-274.

NOCENTINI A.M., 1979 - Variazioni temporali e spaziali della fauna macrobentonica litorale del Lago di Mergozzo. - Mem. Ist. Ital. Idrobiol. 37: 277-327.

NOCENTINI A.M., 1985 - Chironomidi, 4 (Diptera: Chironomidae: Chironominae, larve). Guide per il riconoscimento delle specie animali delle acque interne italiane. - Consiglio Nazionale delle Ricerche: no. 29. AQ/1/233.

NYMAN M., KORHOLA A., BROOKS S.J., 2005 - The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. - Global Ecol. Biogeogr. 14: 137-153.

RAE I.C., 1985 - A multivariate study of resource partitioning in soft bottom lotic Chironomidae. - Hydrobiologia. 126: 275-285.

RAUNIO J., PAAVOLA R., MUOTKA T., 2007 - Effects of emergence phenology, taxa tolerances and taxonomic resolution on the use of the Chironomid pupal exuvial technique in river biomonitoring. - Freshwater Biol. 52: 165-176.

REMPEL R.S., HARRISON A.D., 1987 - Structural and functional composition of the community of Chironomidae (Diptera) in a Canadian Shield stream. - Can. J. Zool. 65: 2545-2554.

ROHLF J., 1987 - BIOM. A package of statistical programs to accompany the text biometry. - Exeter Publ., New York, NY: 238 pp.

ROSSARO B., 1982 - Chironomidi, 2 (Diptera Chironomidae: Orthocladiinae). Guide per il riconoscimento delle specie animali delle acque interne italiane. - Consiglio Nazionale delle Ricerche: no. 16. AQ/1/171.

ROSSARO B., 1987 - Chironomid emergence in the Po river (Italy) near a nuclear power plant. - Entomol. Scand. Suppl. 29: 331-338.

ROSSARO B., 1988 - Mid-Po river zooplankton, a seven years study. - Hydrobiologia. 160: 97-105.

ROSSARO B., 1991a - Chironomids and water temperature. - Aquat. Insect. 13: 87-98.

ROSSARO B., 1991b - Chironomids of stony bottom streams: a detrended correspondence analysis. - Arch. Hydrobiol. 122: 79-93.

ROSSARO B., 1991c - Factors that determine Chironomidae species distribution in freshwaters. - Ital. J. Zool. 58: 281-286.

ROSSARO B., 1992 - Ordination methods and Chironomid species in stony bottom streams. - Neth. J. Aquat. Ecol. 26: 447-456.

ROSSARO B., 1993 - Macroinvertebrate distribution in streams: a comparison of CA ordination with biotic indices. - Hydrobiologia. 263: 109-118.

ROSSARO B., 1995 - The distribution of Palaearctic Diamesinae. - Spixiana. 18: 177-186.

ROSSARO B., BOGGERO A., LENCIONI V., MARZIALI L., SOLIMINI A., 2006a. A Benthic quality index for Italian lakes. - J. Limnol. 65: 41-51.

ROSSARO B., BOGGERO A., LODS CROZET B., FREE G., LENCIONI V., MARZIALI L., 2011 - A comparison of different biotic indices based on benthic macro-invertebrates in Italian lakes. - J. Limnol. 70: 109-122.

ROSSARO B., CARDOSO A.C., SOLIMINI A., FREE G., MARZIALI L., GIACCHINI P., 2007a - A biotic index using benthic macro-invertebrates for Italian lakes. - Ecol. Indic. 7: 412-429.

ROSSARO B., LENCIONI V., BOGGERO A., MARZIALI L., 2006b - Chironomids from southern Alpine running waters: ecology, biogeography. - Hydrobiologia. 562: 231-246.

ROSSARO B., LENCIONI V., MARZIALI L., SOLIMINI A., GIACCHINI R., PARENTI P., 2007b - The relation-ship between body size, pupal thoracic horn development and dissolved oxygen in Chironomini (Diptera: Chironomidae). - Fund. Appl. Limnol. 169: 331-339.

SAUER J., DOMISCH S., NOWAK C., HAASE P., 2011 - Low mountain ranges: summit traps for montane freshwater species under climate change. - Biodivers. Conserv. 20: 3133-3146.

SÆTHER O.A., 1977 - Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. - B. Fish. Res. Board. Can. 197: 1-211.

SÆTHER O.A., 1979 - Chironomid communities as water quality indicators. - Holarctic Ecol. 2: 65-74.

SÆTHER O.A., 2000 - Phylogeny of the subfamilies of Chironomidae (Diptera). - Syst. Entomol. 25: 393-403.

SCHMIDT-KLOIBER A., HERING D., 2012 - The taxa and autecology database for freshwater organisms. Version 5.0. - Availabe from: http://www.freshwaterecology.info/

SERRA-TOSIO B., 1973 - Ecologie et biogéographie des Diamesini d'Europa (Diptera: Chironomi-dae). - Trav. Lab. Hydrobiol. Piscicult. Grenoble 63: 5-175.

SHELDON A.L., 2012 - Possible climate-induced shift of stoneflies in a southern Appalachian catchment. - Freshwater Sci. 3: 765-774.

SOKAL R.R., ROHLF F.J., 1981 - Biometry. - Freeman & Co., San Francisco, CA: 959 pp.

TARTARI G., BURASCHI E., COPETTI D., SALERNO F., MONGUZZI C., PAGNOTTA R., *et al.*, 2006 - Characterization of the Italian laketypes. - Verh. Int. Ver. Theor. Angew. Limnol. 29: 1811-1816.

TER BRAAK C.J.F., PRENTICE I.C., 1988 - A theory of gradient analysis. - Adv. Ecol. Res. 18: 271-317.

TIXIER G., WILSON K.P., WILLIAMS D.D., 2009 - Exploration of the influence of global warming on the chironomid community in a manipulated shallow groundwater system. - Hydrobiologia. 624: 13-27.

TOKESHI M., 1995 - Species interactions and community structure. In: ARMITAGE P., CRANSTON P.S., PINDER L.C.V. (eds.), The Chironomidae. The biology and ecology of non-biting midges. - Chapman & Hall, London: 297-335.

VAN DOORSALAEN W., VANOVERBEKE J., DUVIVIER C., ROUSSEAUX S., JANSEN M., JANSEN B., et al., 2009 - Local adaptation to higher temperatures reduces immigration success of genotypes from a warmer region in the water flea Daphnia. - Glob. Change Biol. 15: 3046-3055.

VANNOTE R.L., MINSHALL G.W., CUMMINS K.W., SEDELL J.R., CUSHING C.E., 1980 - The river continuum concept. - Can. J. Fish. Aquat. Sci. 37: 130-137.

VODOPICH D.S., COWELL B.C., 1984 - Interactions of factors governing the distribution of a predatory aquatic insect. - Ecology. 65: 39-52.

WARD J.V., 1992 - Aquatic insects ecology. - Wiley & Sons, New York, NY: 456 pp.

WARD J.V., STANFORD J.A., 1982 - Thermal responses in the evolutionary ecology of aquatic insects. - Annu. Rev. Entomol. 27: 97-117.

WIEDERHOLM T., 1980 - Use of benthos in lake monitoring. - J. Water Pollut. Control Federat. 52: 537-547.

WIEDERHOLM T., 1983 - Chironomidae of the Holarctic region. Keys and diagnoses. Part I: larvae. - Entomol. Scand. Suppl. 19: 1-457.

WIEDERHOLM T., 1986 - Chironomidae of the Holarctic region. Keys and diagnoses. Part II: pupae. - Entomol. Scand. Suppl. 28: 1-482.

ZERGUINE K., SAMRAOUI B., ROSSARO B., 2009 - A survey of Chironomids from seasonal ponds of Numidia, northeastern Algeria. - Boll. Zool. Agr. Bachicolt. 41: 167-174.