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

L. Marziali,1 B. Rossaro2

1CNR-IRSA Water Research Institute, U.O.S. Brugherio, Brugherio (MB); 2Department 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 specimens 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 unimodal or multimodal Gaussian models. Cold stenothermal species showed: i) unimodal response, ii) tolerance for a narrow temperature range, iii) optima close to their maximum 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. 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 Doorslaer 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 causes and biological factors are as 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; Žižková and Žižková 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 response 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 (Larouche et al., 2001; Lotter et al., 2012). Moreover, they have been used as indicators of oxygen concentration (Rossaro et al., 2006b) and trophic levels in lakes (Sæther 1979, Rossaro et al., 2011) and as indicators of organic (Raunio et al., 2007) and toxic (Corte-Lezzi 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; Herit 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 chironomids 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:
- krenal=glacial streams above the tree line (Rossaro et al., 2006b);
- kryal=lakes and heavily modified water bodies=reservoirs and artificial lakes;
- potamal=lowland reach of rivers (Vannote et al., 1980);
- rhithral=mountain reach of rivers below the tree line (Vannote et al., 1980);
- polimial=high altitude lakes=natural lakes within the Alpine ecoregion (with altitude >4° 00’), with altitude above 800 m a.s.l. (Tartari et al., 2006);
- polimial=high altitude lakes=natural lakes within the Alpine ecoregion (with altitude >4° 00’), with altitude above 800 m a.s.l. (Tartari et al., 2006);
- Mediterranean lakes=natural lowland lakes within the Mediterranean ecoregion (with altitude <4° 00’), with altitude below 800 m a.s.l. (Tartari et al., 2006);
- heavily modified water bodies=reservoirs and artificial lakes;
- brackish ponds=pools 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, Pond nursery collections of larvae from natural lowland (krenal, kryal, high altitude Alpine lakes) (Rossaro, 1991b, 1991c, 1992, 1993; Marziali et al., 2010a, 2010b); 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 measurements were selected using MS-Access queries and were imported into
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 (variance = g2), third (skewness = g1) and fourth (kurtosis = g2) central moments can be found in Sokal & Rohlf (1981).

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).

### 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 | 1990, 1996-98, 2005 | Rossaro et al., 2006; Lencioni et al., 2007 |
|         | 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, 2000-04 | Lencioni et al., 2006 |
|         |         | Lombardy Oglio and Mincio rivers | 1977-78, 1986-87, 2003 | Rossaro, 1991c |
|         |         | Po river | 1995-96, 2004-07 | Unpublished data |
|         |         | Adida river | 1979, 1985, 2001-04, 2009-10 | Rossaro, 2006a, 2011; Bonomi, 1974 |
|         |         | Ticino river | 1970-71, 1982, 2004, 2007, 2011 | Rossaro, 2006a, 2011 |
|         |         | Lake Garda | 2005-06 | Unpublished data |
|         |         | Lakes Viverone and Aigligiana | 1987, 1994-97, 2002-05 | Rossaro et al., 2006a, 2011 |
|         |         | Lake Varese | 1997, 2004-05 | Rossaro et al., 2006a, 2011 |
|         |         | Lake Monate | 1980-84, 2004-06, 2007 | Unpublished data |
|         |         | Lake Como | 1997, 2004-05 | Rossaro et al., 2006a, 2011 |
|         |         | Lakes Comabbio, Alerio, Pusiano and Annone | 1967, 1977, 2004-07 | Unpublished data |
|         |         | Lake Iseo | 1967, 2003-04 | Unpublished data |
|         | Piedmont | Lake Mergozzo | 1973-72, 1975, 1984, 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; Baggiozaro et al., 1992 |
|         | Taro river | 2001-03 | Marziali et al., 2010b |
|         | Liguria | Dané 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 | 1997-03 | Unpublished data |
| 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" | 02'00" | 0  | 0  | 10 | 0  | 0  | 0  | 0  | 0  | 0  |
| Donau (Germany)          | 47'11" | 11'28" | 0  | 0  | 0  | 0  | 50 | 0  | 0  | 0  | 0  |
| Donau (Austria)          | 47'47" | 13'20" | 0  | 0  | 0  | 0  | 41 | 0  | 0  | 0  | 0  |
| Dora Baltea              | 45'37" | 07'35" | 7  | 44 | 29 | 1  | 0  | 47 | 0  | 0  | 0  |
| Sesia                    | 45'38" | 07'55" | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  |
| Orta                     | 45'49" | 08'24" | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  |
| Agogna                   | 45'36" | 08'28" | 17 | 107| 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| Ticino (CH)              | 46'24" | 08'36" | 0  | 0  | 4  | 0  | 0  | 14 | 0  | 0  | 0  |
| Ticino (NO)              | 45'37" | 08'38" | 0  | 0  | 9  | 0  | 0  | 0  | 0  | 0  | 0  |
| Ticino (MI)              | 45'22" | 09'24" | 37 | 0  | 35 | 0  | 0  | 0  | 0  | 0  | 0  |
| Toce                     | 46'15" | 08'16" | 0  | 0  | 11 | 0  | 19 | 0  | 0  | 0  | 0  |
| Maggiore (CH)            | 46'26" | 08'48" | 0  | 0  | 0  | 0  | 18 | 0  | 0  | 0  | 0  |
| Maggiore (VR)            | 45'48" | 08'34" | 0  | 0  | 0  | 0  | 303| 0  | 0  | 0  | 0  |
| Maggiore (VA)            | 45'51" | 08'40" | 0  | 0  | 0  | 0  | 78 | 0  | 0  | 0  | 0  |
| Mergozzo                 | 45'57" | 08'27" | 0  | 0  | 0  | 0  | 162| 0  | 0  | 0  | 0  |
| Varese                   | 45'50" | 08'43" | 0  | 0  | 1  | 0  | 119| 0  | 0  | 0  | 0  |
| Lugano                   | 46'28" | 09'38" | 0  | 0  | 3  | 0  | 14 | 0  | 0  | 0  | 0  |
| Olona                    | 45'39" | 09'20" | 0  | 0  | 0  | 0  | 43 | 0  | 0  | 0  | 0  |
| Lambro                   | 45'48" | 09'16" | 0  | 0  | 0  | 0  | 163| 0  | 0  | 0  | 0  |
| Adda (SO)                | 46'19" | 09'43" | 1  | 24 | 0  | 0  | 0  | 0  | 0  | 0  | 0  |

To be continued on next page
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 peakedness 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 unimodal Gaussian distribution (Khurshid, 2007).

Moment calculations were performed converting in Matlab® envi-
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 characteristics.

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:

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

where $a_1$, ..., $a_n$ are the peaks to be fitted, $a_0$ and $a_1$ 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 euthermal. 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 (°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 (°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 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 joined all habitats) to generally characterize each species’ prefer-

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 joined all habitats) to generally characterize each species’ prefer-

Figure 3. Thermal response of Diamesini larvae. Response of Diamesa bertramii (number of individuals m⁻²) to water temperature (°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    |
|--------------------------------------|-----|--------|---------|-------|-------|
| Procladius choreus                   | 1018| 13.39  | 5.7     | 0.63  | −0.65 |
| Macropleopia nebulosa                | 127 | 10.5   | 5.17    | 0.47  | −0.63 |
| Zarellimyia barbatipes               | 128 | 11.58  | 4.11    | −0.21 | 0.45  |
| Conchapelopia pallidula              | 615 | 13.54  | 5.83    | 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  |
| Brilla bifida                        | 202 | 11.38  | 4.76    | 0.19  | −0.69 |
| Tetenia calciscens                   | 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 |
| Rheoricotopus eftasus                | 124 | 13.15  | 5.83    | −0.16 | −0.49 |
| Rheoricotopus fascipes               | 245 | 16.97  | 7.97    | 0.06  | −1.49 |
| Synthecladius semivirens             | 128 | 13.38  | 4.42    | −0.16 | −0.78 |
| Orthocladius (Eurothocladius) risica | 366 | 9.85   | 4.7     | 0.52  | −0.01 |
| Orthocladius frigida                 | 261 | 6.17   | 3.72    | 1.25  | 1.4   |
| Orthocladius obidens                 | 138 | 9.18   | 5.5     | 1.16  | 0.21  |
| Orthocladius rhychobius              | 212 | 12.14  | 4.02    | −0.15 | −0.24 |
| Orthocladius rubicandus              | 111 | 12.45  | 3.19    | 0.55  | 0.91  |
| Paratrichocladius rafusentris        | 253 | 17.33  | 6.32    | 0.17  | −0.82 |
| Cricotopus annulatus                 | 161 | 14.24  | 4.79    | 0.09  | 0.16  |
| Cricotopus bicinctus                 | 276 | 14.63  | 5.08    | −0.23 | −1.04 |
| Cricotopus (fusocladius) sylvestris  | 183 | 11.19  | 5.08    | 0.82  | −0.09 |
| Parametromnema 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 abidorsum            | 269 | 14.59  | 5.11    | 0.63  | −1.05 |
| Paratanytarsus lauterborni           | 101 | 10.53  | 3.01    | 3.1   | 9.11  |
| Microsectra atrifacilata             | 490 | 13.79  | 5.33    | 0.52  | 0.88  |
| Microsectra pallidula                | 125 | 6.3    | 3.58    | 1.1   | 0.44  |
| Pagastiella orophila                 | 115 | 8.12   | 4.63    | 1.43  | 0.75  |
| Pseudochironomus prasinatus          | 269 | 13.95  | 6.56    | 0.02  | −1.37 |
| Paratendipes albinus                 | 351 | 12.22  | 4.43    | 1.35  | 0.65  |
| Microtendipes pedellus               | 394 | 12.29  | 2.73    | 0.6   | 1.06  |
| Polypedilum conviculum               | 138 | 15.44  | 4.07    | −0.61 | 0.44  |
| Polypedilum laetum                   | 112 | 16.65  | 5.52    | −0.14 | −0.38 |
| Polypedilum tuberculatum             | 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 anfractus                 | 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 |
| Demicrochironomus sulnatus           | 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 bertramii* 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 3.67°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) had 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 330 m depth) characterized by low temperatures.

Similarly, it was possible to compare the response of *Polyplepidum tuberculatum* 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 *Microsceptrum 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 ($r^2=0.66$, 76 df, $P<0.01$, Figure 10). At high altitudes, *Zavrelia barbatipes*, *Corynoneura scutellata*, *Paratanytarsus australiacus* showed an optimum water temperature higher than predicted by altitude, whereas *D. bertramii*, *Polyplepidum tuberculatum*, *Orthocladius (Eudactylocladius) fuscinus* had temperature optima lower than expected by altitude; at

![Figure 4](image)

**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](image)

**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).

| Life stage | Habitat     | n  | m (°C) | SD (°C) | g1  | g2  |
|------------|-------------|----|--------|---------|-----|-----|
| Larvae     | Rhithral    | 363| 14.20  | 6.17    | 0.42| −0.33|
| Larvae     | Potamal     | 37 | 13.50  | 5.48    | −0.03| −1.02|
| Larvae     | Alpine lakes| 48 | 14.05  | 4.62    | 0.67| 2.47 |
| Pupal exuviae | Rhithral | 89 | 13.24  | 4.11    | 0.45| 0.58 |
| Pupal exuviae | Potamal | 37 | 13.50  | 5.48    | −0.03| −1.02|
| 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.
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| 457         | 303          | 2.42| 7.53 |
| Macropleopida nebulosa         | 274 | 1278        | 524          | -0.95| -0.67|
| Ablabesmyia monilis            | 143 | 662         | 513          | 1.97| 3.43 |
| Zavrelimyia barbatipes         | 243 | 1961        | 540          | -3.09| 3.16|
| Conchapelopia pallidula        | 1005| 363         | 285          | 3.14| 14.63|
| Rheopelopia ornata             | 137 | 177         | 160          | 2.22| 8.04 |
| Pseudodiamesa brunickii        | 262 | 1913        | 611          | -1.09| 0.11|
| Diamesa steinboecki            | 171 | 2213        | 572          | -1.60| 2.59|
| Diamesa bertrami               | 277 | 1933        | 653          | -0.86| 0.64 |
| Diamesa tonsa                  | 409 | 897         | 654          | 1.27| 0.75 |
| Diamesa zernyi                 | 353 | 363         | 298          | 1.76| 6.13 |
| Pseudokiefferiella parsa       | 119 | 2348        | 475          | -1.52| 2.49|
| Prodiamesa olivacea            | 393 | 300         | 421          | 3.56| 12.80|
| Bratia longifurca              | 413 | 434         | 298          | 0.87| 0.95 |
| Cardiocladia fascas            | 148 | 677         | 750          | 1.60| 0.77 |
| Tettexia calcsrens             | 840 | 1281        | 945          | 0.14| -1.81|
| Eukiefferiella brevicalcar     | 162 | 2013        | 461          | -1.55| 2.01|
| Eukiefferiella claraeppensis   | 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 efusus          | 205 | 866         | 743          | 1.17| -0.33|
| Rheocricotopus fascipes        | 515 | 361         | 242          | 3.10| 17.76|
| Synorthocladius semisimilis    | 212 | 451         | 280          | 4.10| 22.43|
| Orthocladius (Eudactylocladius) fuscimanus | 124 | 1825 | 709 | -1.25| -0.09|
| Orthocladius (Eoorthocladius) niscola | 618 | 1052 | 902 | 0.66| -1.40|
| Orthocladius exigaxs           | 141 | 335         | 152          | 1.96| 15.17|
| Orthocladius frigidas          | 463 | 1767        | 743          | -0.90| -0.49|
| Orthocladius obildens          | 179 | 305         | 188          | 1.73| 2.60 |
| Orthocladius rhyacobus         | 312 | 422         | 228          | 0.79| 1.82 |
| Orthocladius rubicandus        | 204 | 409         | 214          | 1.19| 6.43 |
| Paratrichocladius raffinskis   | 456 | 737         | 610          | 0.81| -1.18|
| Paratrichocladius skirntiss    | 210 | 1849        | 538          | -1.57| 1.75|
| Cricotopus annulatus           | 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 (foleocladius) sylvestris | 276 | 322         | 593          | 2.89| 6.69 |
| Metriocnemus bygroepetnica     | 180 | 937         | 685          | 0.88| -0.59|
| Chaetocladia laminatus         | 142 | 1628        | 913          | -0.44| -1.62|
| Paratrichocladius excerptus    | 114 | 434         | 242          | -0.07| -0.01|
| Heterotrichocladius marcidus   | 174 | 1936        | 595          | -1.45| 1.02|
| Parametriocnemus stylatus      | 349 | 1137        | 876          | 0.51| -1.19|
| Paratrichocladius bathophila   | 165 | 226         | 138          | 4.06| 28.87|
| Thienemanniella partita       | 173 | 1141        | 904          | 0.19| -1.69|
| Coroninaea scattellata         | 355 | 2130        | 447          | -3.37| 11.70|
| Stermellina borei              | 115 | 426         | 209          | 0.00| -1.67|
| Tanytarsus grigarius           | 652 | 561         | 577          | 1.21| -0.31|
| Cladostyanus atridorsum        | 342 | 406         | 136          | 1.92| 17.06|
| Paratanytarsus australis       | 135 | 2087        | 311          | -2.58| 8.72|
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 airofasciata   | 890 | 425          | 361           | 3.06  | 10.30 |
| Micropsectra contracta      | 386 | 402          | 114           | 8.52  | 93.32 |
| Micropsectra nolescens      | 108 | 327          | 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 abtinumus      | 464 | 308          | 172           | 2.83  | 17.00 |
| Microtendipes pedellus      | 510 | 264          | 213           | 3.86  | 18.41 |
| Polyplectanum convictum     | 145 | 347          | 167           | −0.32 | −1.23 |
| Polyplectanum laetum        | 199 | 340          | 294           | 3.06  | 15.31 |
| Polyplectanum cattalam      | 100 | 142          | 153           | 1.68  | 2.34  |
| Polyplectanum tuberculatum  | 812 | 228          | 143           | 5.21  | 61.77 |
| Phaenopsectra flavipes      | 149 | 399          | 429           | 2.03  | 3.05  |
| Endochironomus tendans      | 140 | 148          | 198           | 6.14  | 57.78 |
| Stictochironomus pictulas   | 101 | 460          | 443           | 2.21  | 2.90  |
| Dicrotendipes nervosus      | 373 | 270          | 104           | 1.28  | 1.94  |
| Glyptotendipes pallens      | 237 | 241          | 67            | 1.54  | 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 sibiralam       | 390 | 238          | 133           | 6.26  | 70.75 |
| Parachironomus arcazuas     | 113 | 195          | 98            | 2.73  | 16.60 |
| Parachironomus camptolabis  | 107 | 631          | 546           | 1.21  | 0.57  |
| Parachironomus nigratum     | 188 | 388          | 55            | 10.07 | 221.97|
| Cryptochironomus defectus   | 606 | 305          | 136           | 0.93  | 0.25  |
| Demicryptochironomus subnervatus | 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. airofasciata 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 puncticollis* and the lower for *Orthocladius oblidens*, *Pagastiella orophila*, *Parakiefferiella bathophila*, *Prodiamesa olivacea*, *Dianassa tona*.

**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 (*Microspectra contracta*, *Paracladopelma nigritulum*), others had maxima at lower depth (*e.g.* at 20-25 m, *Procladius choraeus*, *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 optimal 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 73 species present in ≥81 samples. The relation is shown in Figure 12, with r²=0.33 (73 df, P<0.01) fitting a linear model. As expected, cold stenothermal species had optimum near the stream source (*e.g.* *Dianassa* species) while euthermal ones (*Endochironomus tendens*, *C. riparius*, *Glyptotendipes pallens*, *C. sylvestris*, *Cricotopus triannulatus*, *Cricotopus bicinctus* and *C. s. sylvestris*, *C. riparius*, *Glyptotendipes pallens*, *C. sylvestris*, *C. riparius*, *Glyptotendipes pallens*) showed optimum at high distance from source.

### Table 6. Response of lacustrine species (larvae) to water depth (m depth) in Alpine ecoregion lowland lakes: number of samples, weight mean, standard deviation, skewness and kurtosis of species abundance vs sampling depth values

| Species                          | n | m (m depth) | g1 | g2 |
|----------------------------------|---|-------------|----|----|
| **Procladius choraeus**          | 1046| 21.02        | 3.17 | 23.24 |
| **Conchapelopia pallidula**      | 328| 4.87         | 3.34 | 4.05 |
| **Prodiamesa olivacea**         | 179| 21.70        | 1.08 | 6.27 |
| **Psectrocladius (Psectrocladius) oxyura** | 255| 4.97         | 1.67 | 4.75 |
| **Orthocladius oblidens**       | 110| 4.99         | 1.97 | 4.37 |
| **Parakiefferiella bathophila** | 113| 5.86         | 2.22 | 5.64 |
| **Tanytarsus gregarius**        | 459| 10.15        | 4.62 | 23.67 |
| **Cladotanytarsus atridorsum**  | 253| 3.62         | 2.65 | 17.66 |
| **Microspectra contracta**      | 116| 7.10         | 2.69 | 13.03 |
| **Pagastiella orophila**        | 212| 4.26         | 6.85 | 140.29 |
| **Pseudochironomus prasinatus** | 285| 6.20         | 3.64 | 8.51 |
| **Paratendipes albitormus**     | 228| 6.06         | 1.54 | 3.00 |
| **Microtendipes pedellus**      | 377| 3.27         | 1.12 | 126.29 |
| **Polypedilum nubeculosum**     | 113| 13.69        | 8.41 | 113.15 |
| **Cladotanytarsus atridorsum**  | 253| 3.62         | 2.65 | 17.66 |
| **Microspectra contracta**      | 116| 7.10         | 2.69 | 13.03 |
| **Pagastiella orophila**        | 212| 4.26         | 6.85 | 140.29 |
| **Pseudochironomus prasinatus** | 285| 6.20         | 3.64 | 8.51 |
| **Paratendipes albitormus**     | 228| 6.06         | 1.54 | 3.00 |
| **Microtendipes pedellus**      | 377| 3.27         | 1.12 | 126.29 |
| **Polypedilum nubeculosum**     | 113| 13.69        | 8.41 | 113.15 |
| **Cladotanytarsus atridorsum**  | 253| 3.62         | 2.65 | 17.66 |
| **Microspectra contracta**      | 116| 7.10         | 2.69 | 13.03 |
| **Pagastiella orophila**        | 212| 4.26         | 6.85 | 140.29 |
| **Pseudochironomus prasinatus** | 285| 6.20         | 3.64 | 8.51 |
| **Paratendipes albitormus**     | 228| 6.06         | 1.54 | 3.00 |
| **Microtendipes pedellus**      | 377| 3.27         | 1.12 | 126.29 |
| **Polypedilum nubeculosum**     | 113| 13.69        | 8.41 | 113.15 |
| **Cladotanytarsus atridorsum**  | 253| 3.62         | 2.65 | 17.66 |

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

**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 pluri-modal 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*, *Microspectra pallidula*), showed low optima for water temperature (cold stenothermal) and low tolerance (stenoeccious). These species often showed: i) optima close 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
available for the same species in different habitats, as for Orthocladius (Eurhocladius) ricicola, optimum values are lower in krenal (2.83°C) and kryal (5.23°C) than in rithral (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 (rithral, 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-Zaťovičová 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 Doorslaer 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 Diamena 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 CHID8 data showed that some species colonizing high altitude lakes such as Zavrelimyia spp., Heterotrissocladius marcius, C. scutellata and P. austriacus are more warm stenothermal than predicted by altitude, while species living in kryal, rithral or potamal 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, Microspectra radialis and C. plumosus as well as species living in lowland springs such as Brilli a bitida, 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. latrinirosteinhoeki (juvenilia), Appendix) and Tanytarsus spp.
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 laitartis             | 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|
| Brilia bifida                 | 302 | 19.64  | 31.95   | 3.35 | 19.85|
| Cardiocladius fascus          | 115 | 18.68  | 79.56   | 13.42| 331.58|
| Tretenia calciscens           | 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|
| Pecrotroclus (Pecrotroclus) ayana | 162 | 60.00  | 16.03   | 0.20 | 52.13|
| Rheocricotopus effusus        | 138 | 28.92  | 30.16   | 0.67 | −0.12|
| Rheocricotopus fascipes       | 391 | 48.28  | 98.83   | 5.40 | 30.02|
| Synorthocladus semivirens     | 163 | 22.23  | 40.18   | 3.74 | 29.23|
| Orthocladius (Eoorthocladius) nivicola | 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 obtidens         | 121 | 55.14  | 26.38   | 0.47 | 7.27|
| Orthocladius rhyacobius       | 215 | 35.31  | 89.49   | 5.16 | 85.39|
| Orthocladius rubicandus        | 106 | 57.75  | 43.71   | 0.40 | −0.22|
| Paratrichocladius rafivenstris| 317 | 3.76   | 35.13   | 29.05| 1517.03|
| Paratrichocladius skirathensis| 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 hygrotrichus     | 332 | 31.94  | 50.11   | 4.62 | 42.91|
| Chaeotroclus 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 scutellarata      | 233 | 12.58  | 61.42   | 6.02 | 39.72|
| Tanytarsus gregarius          | 238 | 67.50  | 30.09   | 10.27| 181.68|
| Cladopelma viridulum          | 131 | 50.98  | 23.96   | −1.54| 0.53|
| Cryptochironomus nivicola     | 236 | 35.41  | 66.56   | 8.86 | 269.38|
| Micropsectra atrifasciata     | 529 | 3.76   | 22.29   | 2.80 | 15.69|
| Microtendipes pedellus        | 235 | 14.01  | 23.29   | 2.15 | 3.32|
| 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 | 113.56  | 0.91 | 2.90|
| Chironomus anthracinus        | 273 | 57.22  | 19.98   | −1.93| 2.80|
| Chironomus plamosus           | 262 | 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 nivicola| 134 | 53.81  | 16.62   | −2.59| 5.90|

n, number of samples; m, weighted mean; SD, standard deviation; g1, skewness; g2, kurtosis.
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 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
adaptations by acclimation and genetics is also needed (Hogg et al., 2010; Sauer et al., 2011). To this purpose, more understanding into species adaptations by acclimation and genetics is also needed (Hogg et al., 1998; Van Doorslaer et al., 2009).

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 Doorslaer 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., GIACHINi L., 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., FERRARiESE U., et al., 2004 - 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 Kråkånes 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 Vetenskapsakademiens Handlingar, series 4. 11: 1-472.

CASPERs N., 1983 - Chironomiden-Emergenz zweier Lunzer Bäche. - J. Paleolimnol. 23: 77-89.

CATAAN 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-ZATOVIČOVÁ 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., MORGE 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 bioclimatic indicators of thermal alteration. - Hydrobiologia. 679: 61-76.

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

FERRARiESE U., 1983 - Chironomidi, 3 (Diptera: Chironomidae). - Syst. Entomol. 37: 172-188.

FERRARiESE U., OLIVER D.R., 1987 - Problems in Holarctic chironomid biogeography. - Entomol. Scand. 29: 51-56.

FERRARESE U., ROSSARO B., 1981 - Chironomidi, 1 (Diptera, Chironomidae: Generalità, Diamesinæ, Prodiamesinae). Guide per il riconoscimento delle specie animali delle acque interne italiane. - Consiglio Nazionale delle Ricerche: no. 26. AQ/1/204.

FERRARESE U., 2013 - Chironomidi, 3 (Diptera: Chironomidae: Tanypodinæ). Guide per il riconoscimento delle specie animali delle acque interne italiane. - Consiglio Nazionale delle Ricerche: no. 12. AQ/1/204.

FERRARESE U., ROSSARO B., MARZIAlI L., GIACHINi R., PARACCHINI B., et al., 2009 - Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake
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 Palaeartic 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 thoraxic horn development and dissolved oxygen in Chironomini (Diptera: Chironomidae). - Fund. Appl. Limnol. 169: 331-339.
SAUER O.A., 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: 2-121.
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. - Available from: http://www.freshwaterecology.info/
SERRA-TOSIO B., 1973 - Ecologie et biogéographie des Diamesini d’Europe (Diptera: Chironomidae). - 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 lake-types. - Verb. Int. Ver. Theor. Angew. Limnol. 29: 1811-1816.
TER BIAAK 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 local 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., JANSSEN M., JANSSEN 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: 3048-3055.
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.
WIEDEMÖRHELM T., 1980 - Use of benthos in lake monitoring. - J. Water Pollut. Control Fed. 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.