Long-term patterns of chironomid assemblages in a high elevation stream/lake network (Switzerland) — Implications to global change

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A long-term monitoring program was initiated in 2002 on running and standing waters in a high elevation cirque landscape (Macun) in the Swiss National Park. The region comprises contrasting basins with different water sources, a glacier-fed basin and two precipitation-fed basins. Sampling of 26 permanent and temporary ponds (or small lakes) and of interconnecting streams (10 sites) was conducted from 2002 to 2010. Pond macroinvertebrate assemblages were dominated by chironomids with 42 taxa. The Orthocladiinae were the dominant subfamily in richness and abundance with 22 taxa. The greatest diversity was found in ponds located in the south and outlet basins. The inter-year variability for the same pond is high, but no clear temporal trend was noticed in ponds frequently monitored ponds. The Orthocladiinae subfamily was also the richest in the stream sites where 33 taxa were collected. The north and south basins were separated on the basis of chironomid assemblages. The chironomid assemblages in the stream network shows a temporal trend from 2002 but it cannot be linked to any clear change at the community structure level. The higher richness and abundance in stream sites and ponds of the south basin could be related to a greater heterogeneity in water physico-chemistry and substrata, and by the presence of Bryophyta. The understanding of the environmental factors that influence faunal assemblages is crucial for the protection of this sensitive alpine pond network where a relatively high overall regional diversity (49 taxa) is detected. From the literature, temperature is recognized as the driving force on changes in chironomid assemblages in alpine systems. Our results support the use of chironomids as flagship indicators in the assessment of climatic change in alpine landscapes.

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INTRODUCTION

High-elevation catchments in the Swiss Alps often include numerous small waterbodies interconnected by streams. Most alpine waterbodies originate during glacial recession, so-called cirque lakes, and many have inlet and outlet streams forming lake or pond chains along a large hydrographic system (Maiolini et al. 2006; Robinson & Oertli 2009). Moreover, catchment characteristics can strongly influence their physico-chemistry (Robinson & Matthai 2007). Water sources can vary among surface waters, originating from glacier melt, groundwater, precipitation, and combinations of these (Tockner et al. 1997; Brown et al. 2003). Ephemeral and intermittent streams also are quite common in alpine environments (Robinson et al. 2003; Ruegg & Robinson 2004). Alpine lakes range in size and degree
of connectedness; some being isolated waterbodies, while others are inter-connected by streams forming lake/pond chains. The juxtaposition of lakes and streams in alpine catchments enhances overall habitat heterogeneity and potentially enhances biodiversity. Relatively harsh environmental conditions such as very long winters under snow cover and low pond productivity and temperature further limit the composition and abundance of macroinvertebrates found in alpine freshwaters (Lods-Crozet et al. 2001a; Ilg & Castella 2006). Most studies of alpine streams and lakes document relatively low taxon richness and invertebrate abundances (Lods-Crozet et al. 2001a; Burgherr et al. 2002; Knispel & Castella 2005; Hieber et al. 2005; Lencioni & Rossaro 2005; Oertli et al. 2008; Hinden et al. 2005; Boggero & Lenci0ni 2006; Maiolini et al. 2006; Robinson et al. 2007).

This study is part of a long-term monitoring programme started in 2001 by the Swiss National Park, at the high altitude “Macun cirque”. One of the preliminary steps towards monitoring was to establish the distribution patterns of macroinvertebrates with a specific focus on the taxonomic composition of assemblages. Previous investigations (Robinson et al. 2007; Oertli et al. 2008) revealed that chironomids were predominant with communities characterized by stenothermic species in such high alpine ponds and streams. These considerations made them sensitive indicators of environmental change. It appears that the chironomid assemblages are a key group for monitoring.

The present study examined chironomid assemblages along two lake/pond chains interconnected by stream stretches in the same alpine catchment, each having a different water source (glacial and snowmelt/groundwater).

The objective of this paper was to summarize the distribution patterns of the chironomid fauna of permanent and temporary lakes/ponds and streams. A second objective was to analyse temporal changes over a 9 year period of study.

Study area
The Macun catchment (46°44′EN 10°08′E) is a high alpine cirque (> 2600 m a.s.l.) in the Canton Graubünden, Switzerland (Figure 1). The 3.6 km² region was annexed to the Swiss National park in 2000 and currently is an area designed for long-term monitoring of alpine waterbodies (springs, streams, ponds, lakes).

The region comprises more than 35 small lakes or permanent ponds and around 10 small temporary ponds scattered within two sub-basins. A north basin is fed mostly by snowmelt and groundwater, whereas the south basin is fed by glacial melt from a number of rock glaciers. The surrounding peaks reach 3400 m and the outlet stream of the Macun (Zezmina) drains north to the river Inn in lower Engadine (Robinson & Oertli 2008). Precipitation is low, typically being around 850 mm per year. Air temperature ranges from over 20°C in summer to below -25°C in winter with a extended ice cover (9 months) (Robinson & Kawecka 2005). Bedrock geology is crystalline (ortho-gneiss) rock. The area is above the tree line and the drainage area of each pond is characterised by a mixture of two types of land cover, rock and alpine grassland.

Of the 35 standing waterbodies, a subset of 26 ponds was selected for sampling (Figure 1), including 21 permanent and 5 temporary ponds. The choice included all types of ponds: different sizes (area and depth) and magnitude of water level fluctuations, permanence or temporarity, location in the north or south basin, and connected or not to streams. A description of pond morphometry and selected physico-chemical parameters is presented in Table 1. Low pH (mean: 6.3 – 6.8) and low conductivity (mean: 10.4 – 16.3 µS/cm), except in pond M6 (84 µS/cm) characterized these waterbodies. Aquatic vegetation is present in 9 ponds. Bryophyta (7 taxa) are the main aquatic plants. Helophytes colonised the lower elevation pond (M6) with four taxa (Eleocharis sp., Eriophorum scheuchzeri, Glyceria sp., Saxifraga stellaris). Five of the sampled ponds (M4, M5, M14, M16, M17) had fish (Salmo trutta fario, Salvenius namaycush, Phoxinus phoxinus), and were last stocked in 1993 (Oertli et al. 2008).

Ten sites were sampled for streams: four in the north basin (sites 1 - 4), three in the south basin (5 – 8) and two in the outlet stream (9 – 10) (Figure 1). The sites were situated at the inlets and outlets of the prominent lakes in each basin along a longitudinal gradient.

The different origin in each basin affects the physico-chemical characteristics of the running waters (Robinson & Matthaei, 2007). The south basin had temperatures on average 4°C cooler and temperature generally increased for all sites for years grouped as 2001-2004 and those grouped as 2006-2010 (Robinson & Oertli 2009). Total dissolved nitrogen levels in the south basin were twice the amounts found in the north basin (Table 2). Conductivity was low but increasing along the longitudinal gradient (mean: 6.6 -15.1 µS/cm). The pH of the stream was acid or near neutral (6.0 – 7.5). The turbidity was low in the stream network and higher in the outlet stream (site 10) due to a strong influence of a rock glacier.
Table 1. Description of environmental parameters characterising permanent and temporary ponds sampled between 2002 and 2009.

|                      | 21 permanent ponds (ponds x dates = 29) | 5 temporary ponds (ponds x dates = 10) |
|----------------------|----------------------------------------|----------------------------------------|
|                      | mean  | SD   | min  | max  | mean  | SD   | min  | max  |
| Altitude (m a.s.l.)  | 2651.8| 38.2 | 2551.0| 2714.0| 2633.8| 32.7 | 2600.0| 2669.0|
| Pond area (m²)       | 2099.9| 2855.0| 98   | 12750| 40.6  | 31.3 | 18   | 122  |
| Mean depth (m)       | 1.2   | 1.0  | 0.3  | 4.5  | 0.1   | 0.0  | 0.05 | 0.15 |
| Max depth (m)        | 2.5   | 2.2  | 0.7  | 10   | 0.2   | 0.1  | 0.1  | 0.35 |
| pH                   | 6.3   | 0.5  | 5.3  | 7.5  | 6.8   | 1.2  | 5.5  | 8.52 |
| Conductivity (µS/cm)| 10.4  | 18.6 | 1.7  | 84   | 16.3  | 10.2 | 5.3  | 35.3 |
| Total nitrogen (mg/L)| 0.25  | 0.10 | 0.05 | 0.50 | 0.3   | 0.1  | 0.13 | 0.36 |
| Alpine grassland in drainage area (%) | 48 | 27 | 10 | 100 | 40.0 | 30.8 | 10 | 80 |

*a Measured on a subset of 18 ponds x date

Table 2. Description of environmental parameters characterising stream sites sampled between 2002 and 2010.

|                      | North basin | South basin | Outlet stream |
|----------------------|-------------|-------------|---------------|
|                      | mean  | SD   | min  | max  | mean  | SD   | min  | max  | mean  | SD   | min  | max  |
| Temperature (°C)     | 12.4  | 3.5  | 3.9  | 19.5 | 8.9   | 3.2  | 2.1  | 14.2 | 9.0   | 3.1  | 2.8  | 15.4 |
| pH                   | 6.8   | 0.4  | 6.1  | 7.8  | 6.7   | 0.5  | 6.0  | 7.6  | 6.9   | 0.3  | 6.4  | 7.3  |
| Conductivity (µS/cm 20°C) | 6.6 | 0.8  | 5.3  | 9.0  | 10.2  | 3.9  | 5.3  | 24.0 | 15.1  | 13.5 | 2.6  | 79.0 |
| Turbidity (NTU)      | 1.9   | 2.4  | 0.2  | 18.2 | 1.8   | 2.0  | 0.1  | 9.1  | 6.0   | 7.5  | 0.3  | 27.9 |
| Total dissolved nitrogen (mg/L) | 0.14 | 0.09 | 0.05 | 0.61 | 0.25  | 0.13 | 0.05 | 0.52 | 0.21  | 0.12 | 0.05 | 0.47 |

**METHODS**

**Chironomid sampling**

The biomonitoring of the small stagnant waterbodies were initiated in summer 2002 (16-22 July), followed by collections in 2004 (27 July- 2 August), 2005 (17-26 July), 2007 (27-28 July) and 2009 (2-5 August). The standardised procedure “PLOCH” (Oertli et al. 2005) was used for sampling macroinvertebrates. They were collected by a small-framed hand-net (rectangular frame 14 x 10 cm, mesh size 0.5 mm). For each sample, the net was swept through the water intensively for 30 to 60 seconds. The number of samples taken ranged from 2 to 20, depending on pond size. Sampling was stratified for the dominant habitats (from the land-water interface to a depth of 2 m): stones, gravel, sand and bryophytes.

For streams, the biomonitoring was done in summer 2002 (16-22 July), 2004 (16-22 July- 2 August), 2006 (17-27 July), 2007 (27-28 July) and 2010 (29-30 July). Chironomid larvae and pupae were sampled semi-quantitatively using a timed (5 min) kick-net approach (250 mm mesh). Along a 30-m reach, benthic substrata were disturbed and the loosened material collected in the net (250 mm mesh). Primary habitat types (e.g., pools, runs, riffles) were sampled proportionally during the 5 min sample. In all cases, the collected material was preserved in 70% ethanol and then sorted in the laboratory. Chironomid specimens (larvae and pupae) were identified to species / genus (Wiederholm 1983, 1986; Langton 1991; Schmid 1993; Saether 1995; Brooks et al. 2007; Lencioni et al. 2007; Ilyashuk et al. 2010). Collection material was deposited in the Museum of Zoology in Lausanne (Switzerland).

**Data analysis**

Physico-chemical data were summarized as means and standard deviations for the different study sites. Chironomids were summarized first using species group as one taxon for estimates of taxon richness, abundances per sample and occurrence (as %). Mean richness and abundance were compared between north and south basin stream sites using a non-parametric Mann-Whitney U-test.

Given the heterogeneity of abundances between samples, the taxonomic richness was calculated using the rarefaction procedure (Heck et al. 1975; Krebs 1999). Rarefaction simulates random draws of a fixed number of individuals within the samples (or combined samples) to be compared. The number of individuals drawn is based upon the least abundant sample. Rarefied richness is not an estimate of the total community richness, but it allows an unbiased comparison between samples of unequal abundances. It can also be regarded as a diversity measure, because, for a given number of observed taxa in a sample, rarefied richness will increase with the evenness of
the distribution of abundance between taxa. Calculations were performed with the function "rarefy" from the "vegan" library in the R software (R Development Core Team 2009). The function calculates the rarefied richness for a given number of individuals from the Hurlbert (1971) formula, together with a standard error following Heck et al. (1975). Stream data from regrouped taxa (Diamesa gr. latitarsis, D. gr. zernyi/cinerella, Corynoneura spp., Eukiefferiella spp.) and representing at least 5% of occurrence were then examined using Correspondence analysis (CA) on log-transformed values and associated with between-class Correspondence Analyses (Doledec & Chessel 1987, 1989). A Monte-Carlo permutation test (999 replicates) was then performed. All multivariate analyses were carried out using the ade4 library (Chessel et al. 2004) for the R software (R development core team 2009).

RESULTS

Chironomid assemblages in Macun permanent and temporary ponds

In the 26 ponds sampled between 2002 and 2009, 42 taxa were collected, 24 of which were identified to the species level. The Orthocladiinae were the dominant subfamily with 22 taxa followed by Diamesinae, tribe Tanytarsini (9 and 8 taxa each) and Tanypodinae (3 taxa) (Table 3).

In 21 permanent ponds sampled one to four times through the sampling period, 37 taxa were found. Zavrelionyma melanura (Meigen) (63%) was the most frequent species followed by Paratanytarsus austriacus (Kieffer) (50%), Heterotrissocladius marcidus (Walker) (47%), Corynoneura scutellata gr. (43%), Pseudodiamesa nivosa (Goetghhebuer) and Limnophyes sp.
vegetation, had chironomid assemblages characterized by a
mainly associated with the largest and deepest lakes in the
with a higher conductivity (76.1 ± 0.7) in the outlets (6.5 ± 0.6) and similar abundances were found between inlets (197 ± 79.8 ind/sample) and outlets (161 ± 29.1 ind/sample).

The CoA results on 20 taxa at 50 sites x dates distinguished
3 major groups of sites: north basin sites, south basin sites, and Zeznina basin sites 9 and 10 (permutation test, p = 0.002). The first two axes of the CoA explained 23.3 % of the variation among sites. The two basins were separated from the outlet stream (site 10) along axis-1 according to the chironomid assemblages (Corynoneura spp. and Microspera spp.) (Figure 3). Site 9 was placed intermediate along axis-2. Axis-2 separated the two basins: north basin with Diamesa zernyi/cinerella, Pseudodiamesa branickii, Rheocricotopus effusus (Walker) and south basin with Diamesa gr. latitarsis, Pseudoki fferiella parva, Tokunagaia rectangularis, Tve nia calvescens.

The between class CoA showed a clear separation in the chironomid assemblages (permutation test, p = 0.001) between periods 2002-04 and 2006-07-10 (identified by the water
Table 3. List of Chironomidae species identified, occurrence (%) and abundance (no per site-year) in 21 permanent and 5 temporary ponds between 2002 and 2009; S: south basin; N: north basin; O: outlet basin, n: number of samples.

| Pond      | M7 2004 | M8 2004 | M9 2004 | M10 2004 | M11 2004 | M12 2004 | M13 2004 | M14 2004 | M15 2005 | M15 2009 |
|-----------|---------|---------|---------|----------|----------|----------|----------|----------|----------|----------|
| Year      | 2004    | 2004    | 2004    | 2002     | 2004     | 2004     | 2004     | 2002     | 2004     | 2004     |
| Basin     | S       | S       | S       | S        | S        | S        | S        | S        | S        | S        |
| n         | 2       | 2       | 2       | 3        | 4        | 2        | 2        | 2        | 8        | 1        |
| Species   |         |         |         |          |          |          |          |          |          |          |
| Macropelopia sp |         |         |         |          |          |          |          |          |          |          |
| Procladius choraus (Meigen) |         |         |         |          |          |          |          |          |          |          |
| Zavrelimyia melamora (Meigen) |         |         |         |          |          |          |          |          |          |          |
| Diamesa steinboecki (Goetgebuer) | 2       |         |         |          |          |          |          |          |          |          |
| Diamesa bartramii Edwards |         |         |         |          |          |          |          |          |          |          |
| Diamesa latitarsis gr | 6       | 4       |         |          |          |          |          |          |          |          |
| Diamesa xenyi gr | 8       | 3       | 9       |          |          |          |          |          |          |          |
| Diamesa spp (fuv) |         |         |         |          |          |          |          |          |          |          |
| Pseudodiamesa sp |         |         |         |          |          |          |          |          |          |          |
| Pseudodiamesa branickii (Nowicki) | 4       | 2       | 3       |          |          |          |          |          |          |          |
| Pseudodiamesa niveoa (Goetgebuer) | 6       | 78      | 1       | 4        | 25       | 1        | 6        |          |          |          |
| Pseudokiefferiella parva (Edwards) | 8       | 6       | 3       |          |          |          |          |          |          |          |
| Bryophaeonocladius sp | 1       | 2       | 2       | 3        | 6        |          |          |          |          |          |
| Chaetocladius sp | 17      | 8       | 3       |          |          |          |          |          |          |          |
| Corynoneura scutellata gr |         |         |         |          |          |          |          |          |          |          |
| Cricotopus (Cricotopus) sp |         |         |         |          |          |          |          |          |          |          |
| Cricotopus / Orthocladius sp | 7       | 4       |          |          |          |          |          |          |          |          |
| Eukiefferiella / Tokunagasia sp | 3       | 93      | 212     |          |          |          |          |          |          |          |
| Heterotrissocladius grimshawi (Edwards) |         |         |         |          |          |          |          |          |          |          |
| Heterotrisocladius marcicus (Walker) |         |         |         |          |          |          |          |          |          |          |
| Limnoglyns sp | 11      | 3       | 2       | 8        | 3        | 31       | 2        | 6        | 3        |          |
| Metriocnemus eurymon (Holmgren) | 1       |         |          |          |          |          |          |          |          |          |
| Metriocnemus urusmus (Holmgren) | 39      | 2       |          |          |          |          |          |          |          |          |
| Metriocnemus sp |          |         |          |          |          |          |          |          |          |          |
| Orthocladius (Euorthocladius) sp |          |         |          |          |          |          |          |          |          |          |
| Orthocladius (Orthocladius) sp |          |         |          |          |          |          |          |          |          |          |
| Parametriocnemus stylatus Kieffer | 1       | 23      |          |          |          |          |          |          |          |          |
| Paraphaeonocladius sp |          |         |          |          |          |          |          |          |          |          |
| Parorthocladius radipennis (Kieffer in Kieff & Then) |          |         |          |          |          |          |          |          |          |          |
| Psectrocladius sordidellus (Zettistedt) |          |         |          |          |          |          |          |          |          |          |
| Pseudomittia arenaria Strenzke | 1       | 1       |          |          |          |          |          |          |          |          |
| Pseudomittia oxamiana (Edwards) | 2       |          |          |          |          |          |          |          |          |          |
| Rheoacricotopus affinis (Walker) | 18      |          |          |          |          |          |          |          |          |          |
| Tokunagasia rectangularia (Goetgebuer) | 6       | 2       |          |          |          |          |          |          |          |          |
| Microspectra juncti (Meigen) |          |         |          |          |          |          |          |          |          |          |
| Microspectra notescens (Walker) | 4       |          |          |          |          |          |          |          |          |          |
| Microspectra radiola (Goetgebuer) |          |         |          |          |          |          |          |          |          |          |
| Microspectra sp | 2       | 5       |          |          |          |          |          |          |          |          |
| Paratanytarsus austriacus (Kieffer) | 2       | 1       |          |          | 1        | 5        | 3        |          |          |          |
| Tanytarsus sp |          |         |          |          |          |          |          |          |          |          |
| Tanytarsus bathophilus Kieffer |          |         |          |          |          |          |          |          |          |          |
| Tanytarsus simunus Goetgebuer |          |         |          |          |          |          |          |          |          |          |

Nbt taxa: 9 5 1 10 15 2 2 6 5 7 3 4 5

a: among which C. melaleucus (Meigen)
b: among which P of pseudobritas Strenzke
| M23 | M4 | M5 | M16 | M17 | M18 | M19 | M20 | M20 | M20 | M20 | M21 | M22 | M90 | M6 | M6 | Occurrence | Abundance % |
|-----|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|----------|-------------|
| 2   | 2  | 7  | 2   | 2   | 1   | 2   | 2   | 7   | 6   | 3   | 2   | 1   | 2   | 5   | 13| 3        | 3           |
| 3   | 2  | 6  | 1   | 2   | 0   | 0   | 2   | 0   | 1   | 0   | 1   | 0   | 0   | 2   | 0  | 0        | 6           |
| 4   | 4  | 7  | 2   | 2   | 1   | 2   | 1   | 2   | 1   | 2   | 1   | 2   | 1   | 1   | 1  | 1        | 1           |
| 4   | 1  | 1  | 2   | 7   | 2   | 2   | 1   | 2   | 2   | 2   | 1   | 2   | 1   | 1   | 1  | 1        | 1           |
| 4   | 1  | 1  | 2   | 7   | 2   | 2   | 1   | 2   | 8   | 42  | 46  | 338 | 85  | 338 | 85 | 34       | 7           |
| 8   | 2  | 2  | 3   | 1   | 2   | 3   | 1   | 4   | 177 | 790 | 500 | 42  | 1   | 1   | 1   | 1        | 1           |
| 2   | 11 | 4  | 10  | 5   | 5   | 5   | 5   | 5   | 5   | 5   | 3   | 2   | 1   | 5   | 7  | 12       |              |

Continued on next page
| Pond | M8t 2002 | M8t 2004 | M8t 2005 | M8t 2007 | M2tt 2007 | M9t 2004 | M9t 2007 | Occurrence | Abundance |
|------|---------|---------|---------|---------|---------|---------|---------|------------|-----------|
| Basin | S 1 2 3 2 5 1 1 2 1 1 | | | | | | | | |

| Taxa | Occurrence | Abundance |
|------|------------|-----------|
| Macropelopia sp | 0 0 | 0 |
| Procladius chorua (Meigen) | 0 0 | 0 |
| Zavrelmiylea melanura (Meigen) | 4 | 91 4 |
| Diamesa stehbuchi (Goetghheber) | 1 | 91 1 |
| Diamesa bertramis Edwards | 1 | 91 1 |
| Diamesa latitarsis gr | 22 71 163 | 79 15 | 45 5 350 |
| Diamesa spp (juv.) | 0 0 | 0 |
| Pseudeoxanius spp | 135 | 91 135 |
| Pseudeoxanius brevioculis (Nowicki) | 16 80 | 18 2 96 |
| Pseudeoxanius nivea (Goetghheber) | 25 8 | 1 | 27 3 34 |
| Pseudeoxanius parva (Edwards) | 4 9 4 13 | 36 4 30 |
| Broyphaisicladia sp | 1 1 2 2 | 27 3 4 |
| Chaetocladius sp | 12 | 91 12 |
| Corynoneura scutellata gr | 0 0 | 0 |
| Cricotopus (Lasiocladia) sp | 0 0 | 0 |
| Cricotopus / Orthocladius sp | 0 0 | 0 |
| Eukiefferiella / Takanoساطa sp | 0 0 | 0 |
| Heterotrissocladius grimschis (Edwards) | 0 0 | 0 |
| Heterotrissocladius mearichis (Walker) | 2 | 91 2 |
| Limnophyes sp | 3 8 19 | 2 | 36 4 32 |
| Metriocnemus eurynotus (Holmgren) | 4 | 91 4 |
| Metriocnemus urinatus (Holmgren) | 4 3 1 | 1 | 36 4 9 |
| Metriocnemus sp | 5 50 | 18 2 55 |
| Orthocladius (Euvamocladia) sp | 1 | 91 1 |
| Orthocladius (Orthocladius) sp | 9 | 91 9 |
| Parameiocnemus stylatus Kieffer | 8 14 5 3 6 | 45 5 36 |
| Paraphaenocladius sp | 20 1 | 18 2 21 |
| Paraphaenocladius nigripennis (Kieffer in Kieff & Thien) | 0 0 | 0 |
| Pseurocladius sordidellus (Zetterstedt) | 0 0 | 0 |
| Pseurocladius australis Strenzke | 0 0 | 0 |
| Pseurocladius oaxianus (Edwards) | 0 0 | 0 |
| Rheocricotopus affinis (Walker) | 1 | 91 1 |
| Tokanoساطa rectangulosa (Goetghheber) | 0 0 | 0 |
| Microspectra junct (Meigen) | 0 0 | 0 |
| Microspectra notescens (Walker) | 0 0 | 0 |
| Microspectra radialis Goetghheber | 0 0 | 0 |
| Microspectra sp | 0 0 | 0 |
| Paratanytarsus australis (Kieffer) | 0 0 | 0 |
| Tanytarsus sp | 9 | 91 9 |
| Tanytarsus bithoraxus Kieffer | 0 0 | 0 |
| Tanytarsus sinuatius Goetghheber | 0 0 | 0 |

a: among which C. melaleucus (Meigen)
b: among which P. cf. pseudoirritus Strenzke
| n° site  | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 |
|---------|----|----|----|----|----|----|----|----|----|----|
| 2002    |    |    |    |    |    |    |    |    |    |    |
| Zavrelinyia melamora (Meigen) | Zav mel | 1 |    |    |    |    |    | 1  |    | 1  |
| Diamesa bertrami Edwards | Diam ber | 3 | 3  | 2  | 24 | 31 | 8  | 3  | 3  | 16 |
| Diamesa latitarsis gr | Diam lat | 8 |    | 1  |    |    |    |    |    |    |
| Diamesa steinboeki (Goetghebuer) | Diam ste | 1 |    |    |    |    |    | 5  |    |    |
| Diamesa zernyi/cinerella gr | Diamzercin | 29 | 56 | 17 | 191 | 4 | 12 | 54 | 12 | 55 |
| Diamesa zernyi Meigen | Diam zern | 24 |    | 3  | 4  |    |    |    |    |    |
| Diamesa zernyi Edwards | Diam zern | 2  |    |    |    |    |    |    |    |    |
| Pseudodiamesa branckii (Nowicki) | Pseu bra | 6 | 6  | 101 | 56 | 143 | 8 | 58 | 18 | 42 |
| Pseudodiamesa nivosa (Goetghebuer) | Pseu niv | 3 | 9  | 6  |    | 10 | 16 | 38 |    |    |
| Pseudokiefferiella parva (Edwards) | Pseu par | 14 | 1  | 6  | 4  | 1  |    |    |    |    |
| Chaetocladius spp | Chaend |    |    |    |    |    |    |    |    |    |
| Corynoneura scutellata gr | Coryscu | 1 | 72 | 2  | 3  | 6  | 4  | 3  | 1  | 2  |
| Corynoneura lobata Edwards | Corylob |    |    |    |    |    |    |    |    |    |
| Cricotopus (C) tremulus (Linnaeus) | Cric tre |    |    |    |    |    |    |    |    |    |
| Enkiefferiella brevicor (Kieffer) | Euki bre |    |    |    |    |    |    |    |    |    |
| Enkiefferiella dittmar Lehmann | Euki dit |    |    |    |    |    |    |    |    |    |
| Enkiefferiella lobifera Goetghebuer | Euki lob |    |    |    |    |    |    |    |    |    |
| Enkiefferiella minor? | Euki min/fit | 13 | 67 | 13 | 43 | 13 | 4  | 15 | 3  | 3  |
| Enkiefferiella sp A (sensu Schmid 1992) | Euki spA | 1  | 2  | 2  | 1  | 2  | 1  | 11 | 2  | 2  |
| Heleniella spp | Heleind | 1  |    |    |    |    |    |    |    |    |
| Heterotrissocladius marcidus (Walker) | Hete mar | 1  | 3  | 6  |    |    |    |    |    |    |
| Limnophyes spp | Limnind | 1  |    |    |    |    |    |    |    |    |
| Orthocladius (E) lutetii Goetghebuer | Orth lut | 1  |    |    |    |    |    | 6  |    | 1  |
| Orthocladius (O) frigidus Zetterstedt | Orth fri | 1  | 2  | 6  | 2  | 4  | 10 | 3  | 100 | 1   |
| Orthocladius spp | Orthind | 2  |    |    |    |    |    |    |    |    |
| Parametriocnemus sylatus Kieffer | Parastiy | 7 | 1  | 1  | 2  | 2  | 1  | 11 | 2  | 2  |
| Parorticocladius nudipes (Kieffer) | Para ind |    |    |    |    |    |    |    |    |    |
| Paraphaenocladius sp | Paromud | 2  | 2  | 1  | 25 | 2  | 2  | 13 |    | 20 |
| Rheocricotopus effusus (Walker) | Rheoeff |    |    |    |    |    |    |    |    | 62 |
| Tokunagaia rectangularis (Goetghebuer) | Tokugree | 1  |    |    |    | 34 | 201 | 5  | 24 | 200 |
| Tvetena calvescens (Edwards) | Tvet cal | 1  | 7  | 18 | 27 | 1515 | 123 | 5  | 8  | 19 |
| Micropspectra spp | Micrind |    |    |    |    |    |    |    |    |    |
| Micropspectra ignotobus-type | Miergins | 2  | 11 | 2  | 24 |    |    |    |    |    |

Richness: 8 9 8 12 12 7 11 14 11 7 5 2 5 8 14 7 7 6 5 10
Abundance: 21 54 248 138 461 1548 308 201 330 98 32 78 70 109 318 78 449 740 353 135

Continued on next page
| Species                                      | Site | 2006 | 2007 |
|----------------------------------------------|------|------|------|
| Zavrelimyia melanura (Meigen)                | Zavr mel | 1 | 1 |
| Diamesa bermanni Edwards                     | Diam ber | 10 | 1 |
| Diamesa latticae gr                           | Diam lat | 2 | 1 |
| Diamesa steinboecki (Goetghebuer)            | Diam ste | 18 | 1 |
| Diamesa zenny/tenella gr                     | Diam zen | 18 | 1 |
| Diamesa anera Meigen                        | Diam ana | 18 | 1 |
| Diamesa zenny Edwards                       | Diam zeny | 18 | 1 |
| Pseudodiamesa branchi (Nowicki)              | Pseu bra | 5 | 1 |
| Pseudodiamesa nivoso (Goetghebuer)           | Pseu niv | 8 | 1 |
| Pseudokiefferella parva (Edwards)            | Pseu par | 8 | 1 |
| Chactocladus spp                             | Chaeind | 3 | 1 |
| Corynoneura scuillata gr                     | Cory scu | 3 | 1 |
| Corynoneura lobata Edwards                   | Cory lob | 3 | 1 |
| Cricotopus (C) tremulius (Linnaeus)          | Cric tre | 3 | 1 |
| Enkciefferiella breviset (Kieffer)           | Euki bre | 3 | 1 |
| Enkciefferiella ditmar Lehmann               | Euki dit | 3 | 1 |
| Enkciefferiella lobifera Goetghebuer         | Euki lob | 3 | 1 |
| Enkciefferiella minor/fitkani                | Euki min/fit | 3 | 1 |
| Enkciefferiella sp A (sensu Schmid 1992)     | Euki spA | 3 | 1 |
| Helenies spp                                 | Heleind | 3 | 1 |
| Heterotrissocladius marcius (Walker)         | Hete mar | 3 | 1 |
| Limnophyes spp                               | Limnind | 3 | 1 |
| Orthocladius (E) lutes (Goetghebuer)         | Orth lut | 3 | 1 |
| Orthocladius (O) fridias Zetterstedt         | Orth fri | 3 | 1 |
| Orthocladius spp                             | Orthind | 3 | 1 |
| Parametriocnemus stylatus Kieffer           | Para sty | 3 | 1 |
| Parorthocladius mulipennis (Kieffer)         | Para ind | 3 | 1 |
| Paraphoanocladus sp                          | Para nud | 3 | 1 |
| Rheocricotopus effusus (Walker)              | Rheo eff | 3 | 1 |
| Tokunaga rectangularis (Goetghebuer)         | Teku grec | 3 | 1 |
| Tvetena calvescens (Edwards)                 | Tvet cal | 3 | 1 |
| Micropsectra spp                             | Micrind | 3 | 1 |
| Micropsectra insignilobus-type               | Micrins | 3 | 1 |

Richness | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
Abundance | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| No. site | 2010 Occurrence | Abundance | Richness |
|----------|-----------------|-----------|----------|
| Zavrelimia melanura (Meigen) | Zavr mel | 6 0 | 3 |
| Diamesa bertrami Edwards | Diam ber | 1 1 3 | 18 0 | 93 |
| Diamesa latariasis gr | Diam lat | 38 89 20 | 4 0 | 9 |
| Diamesa steinboecki (Goetghebuer) | Diam ste | 4 0 | 6 |
| Diamesa zermeyi/cinerella gr | Diam zerm | 1 2 17 2 21 7 111 157 122 2 | 38 0 | 1581 19 |
| Diamesa cinerea Meigen | Diam cin | 6 0 | 31 3 |
| Diamesa zermeyi Edwards | Diam zer | 2 0 | 2 |
| Pseudodiamesa branickii (Nowicki) | Pseu bra | 3 1 10 | 20 3 70 | 30 0 | 575 15 |
| Pseudodiamesa nivosa (Goetghebuer) | Pseu niv | 12 0 | 82 6 |
| Pseudokiefferiella parva (Edwards) | Pseu pur | 2 27 2 3 9 1 1 | 10 0 | 26 5 |
| Chaetocladius spp | Chaeind | 2 0 | 5 1 |
| Corynoneura scutellata gr | Cory scu | 18 0 | 94 9 |
| Corynoneura lobata Edwards | Cory lob | 9 4 1 1 | 10 0 | 118 5 |
| Cricotopus (C) tremulus (Linnaeus) | Cric tre | 2 0 | 1 1 |
| Eukiefferiella breviscalcar (Kieffer) | Euki bre | 6 0 | 11 3 |
| Eukiefferiella dimmari Lehmann | Euki dit | 4 0 | 2 2 |
| Eukiefferiella lobifera Goetghebuer | Euki lob | 2 0 | 2 1 |
| Eukiefferiella minor/fitilkanu | Euki min/fiti | 1 2 7 1 | 18 0 | 174 9 |
| Eukiefferiella sp A (sensu Schmid 1992) | Euki spA | 4 0 | 121 2 |
| Heterotricocladius marcidus (Walker) | Hete mar | 4 0 | 8 0 | 11 4 |
| Limnophyes spp | Limnind | 2 0 | 1 1 |
| Orthocladius (E) luteipes Goetghebuer | Orth lut | 6 0 | 8 3 |
| Orthocladius (O) frigidus Zetterstedt | Orth fri | 2 1 1 1 | 18 0 | 129 9 |
| Orthocladius spp | Orthind | 2 0 | 2 1 |
| Parametrocennus sylvars Kieffer | Para sty | 1 1 1 2 1 2 | 20 0 | 49 10 |
| Parorthocladius nudipennis (Kieffer) | Para nip | 2 0 | 1 1 |
| Paraphaenocladius sp | Paro nud | 4 7 2 2 | 18 0 | 167 9 |
| Rhoeicricotopus effiusus (Walker) | Rheo eff | 2 3 | 4 0 | 70 2 |
| Tokunagia rectangularis (Goetghebuer) | Tokugrec | 1 2 14 24 7 | 16 0 | 526 8 |
| Tvetenia cabrescens (Edwards) | Tvet cal | 3 2 3 1 2 | 2 30 0 | 1818 15 |
| Micropsectra spp | Micrind | 2 0 | 1 1 |
| Micropsectra insignitus-type | Micrins | 1 4 | 10 0 | 49 5 |

Richness 8 10 37 9 89 34 225 212 231 20
Table 5. Mean (SD) number of taxa and abundance of chironomids collected by kick net in the study stream sites during summer 2002-2010 (n = 5); p = significance of a Mann-Whitney test.

| Site             | Number | Type      | Basin       | Taxon richness | Abundance | p      |
|------------------|--------|-----------|-------------|----------------|-----------|--------|
| Grond-OL         | 1      | outlet    | North       | 3.6 (1.1)      | 14.8 (5.3)|        |
| Mezza-gliina-inlet| 2      | inlet     | North       | 4.0 (1.3)      | 46.0 (11.0)|        |
| Mezza-gliina-outlet| 3      | outlet    | North       | 6.2 (0.7)      | 89.4 (40.1)|        |
| Immez-north      | 4      | inlet     | North       | 5.2 (2.0)      | 54.2 (28.7)|        |
| Sura OB          | 5      | outlet    | South       | 8.4 (1.4)      | 225.0 (71.4)|        |
| Sura-inlet       | 6      | inlet     | South       | 6.8 (0.4)      | 371.2 (294.4)|        |
| Sura-outlet      | 7      | outlet    | South       | 7.6 (0.7)      | 247.8 (70.1)|        |
| Immez-south      | 8      | inlet     | South       | 8.2 (1.3)      | 317.4 (106.0)|        |
| Immez-outlet     | 9      | outlet    | outlet      | 7.0 (1.5)      | 227.6 (55.1)|        |
| Zeznina          | 10     | stream    | outlet      | 6.8 (0.7)      | 65.2 (23.0)|        |
| North basin      | 1, 2, 3, 4 | all     | all         | 4.7 (0.7)      | 51.1 (13.1)| 0.002  |
| South basin      | 5, 6, 7, 8 | all     | all         | 7.7 (0.5)      | 290.3 (76.5)| 0.001  |
| North basin      | period 2002-04 | all | period 2002-04 | 6.5 (1.1)      | 93.4 (26.0)| 0.038  |
|                  | period 2005-10 | all | period 2005-10 | 3.6 (0.6)      | 22.9 (5.5)| 0.04   |
| South basin      | period 2002-04 | all | period 2002-04 | 9.0 (1.0)      | 512.6 (163.5)| > 0.05  |
|                  | period 2005-10 | all | period 2005-10 | 6.9 (0.3)      | 142.2 (23.0)| 0.009  |

temperature variable) on the CoA (Figure 4).

**Chironomid diversity in the Macun system**

A total of 49 taxa were collected during this long-term monitoring (2002-10), among which half (25 taxa) were common to ponds and interconnected streams. These results reflected the influence of a lake/pond system on the outlet chironomid fauna. The presence of genera such as *Metriocnemus*, *Paraphaenocladius* and *Pseudosmittia* suggested that the damp soil, the splash-zone of littoral and mosses are also habitats for chironomid larvae.

**DISCUSSION**

Chironomids were the most diverse and abundant macroinvertebrate group found in high mountain streams (Lods-Crozat et al. 2001a; Burgherr et al. 2002; Hieber et al. 2005) and lakes/ponds (Boggero & Lencioni 2006; Fürder et al. 2006; von Gunten et al. 2008; Oertli et al. 2008; Catalan et al. 2009). As expected, most of the chironomid taxa in the Macun system are stenothermic, typical of oligotrophic waters and high mountain streams. The assemblage of Macun cirque consisted of mostly oligostenothermic species often occurring in high densities (e.g. *Zavrelimya, Pseudodiamesa, Heterotrissocladius*) (Langton 1991, Brooks et al. 2007, Ilyashuk et al. 2009). This phenomenon could be explained by the ability of a few well-adapted species to use time-restricted input of food resources under extreme climatic conditions (Ciamporova-Zat’ovicova et al. 2010). This biomonitoring is among the first to study chironomid communities in a high alpine lake/pond chain over a long-term period using semi-quantitative sampling. Indeed, 26 ponds/lakes sampled between 1 to 5 occasions and 10 stream sites were monitored during 9 years may explain the overall high regional diversity (49 taxa) for a high mountain pond/lake network. The chironomid diversity could be therefore underestimated since drift pupae and adult collection were not investigated.

The local diversity was relatively low in stream sites (range 3.6 – 8.4) and in pond/lake littorals (3.5 – 10.0) compared to lowland sites (e.g. Lods-Crozet & Castella 2009; Koperski 2010; Bouchard & Ferrington 2011), reflecting the general perception that the harsh conditions determine the species able to persist and complete their life cycle in high elevation waterbodies. The Diamesinae and few Orthocladinae from the *Eukiefferiella* complex (*Eukiefferiella, Tokunagia, Tvetenia*) are known to be the first taxa colonizing glacial-fed streams, being able to tolerate the cold water temperature (Lods-Crozat et al. 2001a, 2001b; Müller et al. 2001). *Pseudodiamesa* spp. are cold-adapted to harsh physical environments, including freezing and drying (Ilyashuk et al. 2009). The larvae are able to complete their life cycle at water temperatures never exceeding 2 °C (Lods-
Crozet et al. 2001b; Milner et al. 2001; Ilyashuk et al. 2009). Furthermore, the presence in ponds M7 and M23 of Diamesa steinboecki, species characteristic of the uppermost glacial waters stretches, confirmed the glacial origin of waters feeding these two ponds in the south basin. Paratanytarsus australicus is often associated with Bryophyta (more than half of the ponds) and is the dominant taxa in pond M6 which was colonized by a rich and diverse aquatic vegetation. Moreover, Cricotopus and Psectrocladius sordidellus indicated that enough littoral food or organic habitat is available (Langton 1991). Zavrelimyia and Corynoneura larvae, dominant genera in permanent ponds, are typical littoral dweller in high alpine lakes living on periphyton (Brooks et al. 2007). Limnophyes spp. frequently occurred in permanent and temporary ponds (40%) and their larvae lived in moss in moist soil or stream/littoral zones of lakes (Langton 1991).

The Macun chironomid assemblages are mostly herbivorous and detritivorous, feeding mainly on diatoms that are diverse in the catchment and reflecting the heterogeneity of physicochemical conditions (Robinson & Kawecka 2005). Despite streams in both basins having stable substrata because of low gradients and flows (Robinson & Matthaei, 2007) compared to glacial-fed streams, the chironomid fauna were dominated in abundance by the Diamesinae subfamily. The total richness is relatively high (33 taxa) if compared to the one of a glacial-fed stream in the Rhône glacier region at the same range of altitude, where Lods-Crozet et al. (2001a) documented only 10 taxa.

In addition, it can be noted that Tanypodinae, Orthocladiinae and Tanytarsini (88%) contributed most to the abundance in permanent ponds while Diamesinae and Orthocladiinae (88%) contributed most in temporary ponds. This was partially noted by Boggero & Lencioni (2006) that Tanypodinae and Tanytarsini were abundant in the littoral of high elevation lakes in the Alps. A comparison with four lakes located above 2400 m a.s.l., studied by Boggero & Lencioni (2006), showed the same range in the number of taxa by lake, the presence of the same dominant taxa (Zavrelimyia, Heterotrissocladius, Corynoneura, Paratanytarsus) and a total richness of 22 taxa. In inlets/outlets, 34 taxa were also identified with the predominance of orthoclads (25 taxa). This species composition seems to be a general feature of alpine lakes under extreme conditions and situated above 2000 m a.s.l. (Ciamporova-Zat’ovicova et al. 2010, Lotter et al. 2000, Boggero & Lencioni 2006; Füréder et al. 2006).

No obvious temporal trend was detected among the chironomid fauna in ponds frequently monitored (M15, M20, M8) and the spatial variability between ponds seemed higher than the temporal between years. In contrast, chironomid assemblages in the stream network showed a temporal trend from 2002 to 2009 but it cannot be linked to any clear change at the species level. The higher richness and abundance in stream sites of the south basin could be related to a greater heterogeneity in water physico-chemistry and substrata, and by the presence of moss beds.

As noticed above, the Chironomidae is the most diverse group in this high alpine ponds/lakes and stream network with almost 50 taxa and represent twice of all the other macroinvertebrate groups such as Oligochaeta, Plecoptera, Coleoptera and other Diptera (Robinson & Oertli 2009, Oertli et al. 2008). Similar results were found in alpine lakes in the Tatra mountains (Slovakia) where chironomids and oligochaetes were the dominant groups (Kownacki et al. 2000, Ciamporova-Zat’ovicova et al. 2010).

The understanding of environmental factors that influence faunal assemblages is crucial for the protection of these sensitive ecosystems at the catchment level. For example, recent studies highlight the importance of vegetation cover in the catchment for the distribution of macroinvertebrates (Füréder et al. 2006). These aspects are going to become essential in the future, especially in the recognition of a continuous changing world. The reconstruction of past July air temperature from a remote high mountain lake based on chironomid remains by Ilyashuk et al. (2009) shows that the changes in chironomid assemblages were mainly driven by the temperature gradient.

Due to the insular nature of alpine environments, many of the cold stenothermal species will be subject to extinction if water temperatures increase above a certain threshold, perhaps by only a few degrees (e.g. Rosset & Oertli 2011). Others, such as eurythermic taxa, may act as fugitive species and may expanding their distribution due to temperature changes (Robinson et al. 2006). At the same time, an indirect impact on chironomids through food source changes can also be expected. The epilithic algal biomass could be enhanced by the change in light availability resulting from earlier ice melt and consequently improved environmental conditions for life.

Despite the fact that larval identification is time consuming and requires special taxonomic expertise, our results support the use of chironomids as flagship indicators in the assessment of climatic change in alpine landscapes. The present study contributes to the overall understanding of environmental effects on high mountain waterbodies and ecosystems, and assists in refining research and conservation strategies for the forecasting of expected changes.

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