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Microdistribution of chironomids (Diptera: Chironomidae) in Alpine streams: an autoecological perspective

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Abstract

Chironomid communities from three glacial and three non-glacial high mountain streams in three Alpine river basins were analyzed (Conca, Niscli, Cornisello, NE Italy, 46° N, 10° E). Eighteen sampling reaches belonging to five stream types (kryal, subkryal, glacio-rhithral, kreno-rhithral, outlet) were investigated. At each reach, geomorphological, physical, chemical and biological data were collected. Field surveys were carried out during three periods per year from 1996 to 1998: immediately after spring snowmelt, in mid-summer and in early autumn. In all, 439 zoobenthos samples were collected from 5 to 10 microhabitats of 0.1 m^2 in each reach and date using a standard pond net (mesh size of 250 μm). About 50% of individuals collected were chironomids (26 673 specimens, 53 taxa), with densities ranging from 4 to 2652 ind m^{-2}. With few exceptions, they dominated as number of taxa and individuals in all reaches. Chironomid subfamilies Diamesinae and Orthocladiinae were most abundant, especially in glacial reaches, where *Diamesa* spp. constituted up to 100% of the total fauna. Chironomid distribution was analyzed in relation to 37 abiotic variables, referring to stream origin, hydrology, geomorphology, physics and chemistry. *Diamesa steinboecki*, *D. latitarsis* gr. A and *Pseudokiefferiella parva* were the taxa best associated with 'glacial' conditions (i.e. high channel instability or presence of bedrock, high suspended solids and total phosphorous content, low conductivity and silica content, highly variable diel discharge and low mean temperature), while *Pseudodiamesa branickii*, *Corynoneura* spp., *Eukiefferiella* spp., *Parorthocladius nudipennis*, *Tvetenia calvescens/bavarica*, *Thienemaniella* spp. and *Micropsectra atrofasciata* were mostly associated with 'non-glacial' conditions. Substratum particle size, water depth, current velocity, the presence of riffles/pools and of mosses/algae (*Hydrurus foetidus*) were the major factors affecting microdistribution of chironomids in the investigated streams.

Introduction

The role of spatial heterogeneity in affecting the dynamics of populations, the structures of communities and the functioning of ecosystems has been widely highlighted by several authors (e.g. Townsend, 1989; Cooper et al., 1997; Beisel et al., 1998).

Habitat selection by benthic stream insects depends on the interaction of numerous abiotic (e.g. water temperature and substrate stability) and biotic (e.g. predation and competition) factors (Townsend, 1989; Rossaro, 1993; Palmer et al., 1996). Optimum conditions may be different even for different life stages of the same species (Rabeni & Minshall, 1977). Different species assemblages may be found at the same site and season in successive years as response to different climatic conditions (e.g. different thickness and duration of the winter snow/ice cover) (Rossaro, 1991; Schütz et al., 2001). Furthermore, the interaction of such factors makes it difficult to separate the effects of single variables on the fauna and to extract those most important for the biota (Rossaro & Lencioni, 2001; Rossaro et al., 2002).

At present, knowledge of invertebrate responses to abiotic factors in high mountain streams is rather scarce. Most studies have been limited to single streams or to a restricted sampling period, producing conclusions usually applicable to specific conditions (Rossaro et al., 2000; Lencioni et al., 2001a). Such habitats host a specialized invertebrate fauna, chironomids (Diptera: Chironomidae) often being the only group present (Lencioni et al., 2001b). This is the most widely distributed dipteran family in freshwaters and, with about 15 000 species (Cranston, 1995), represents 25% of aquatic insect species (Cure, 1985). Chironomids are well adapted to survive in a variety of environmental rigors such as desiccation, anoxia, low temperatures and freezing (Oliver, 1968; Danks, 1971; Danks & Oliver, 1972). In particular, their capacity to adapt in different ways to overwintering (i.e. migration activity, cocoon building, supercooling, freezing tolerance) (Irons et al., 1993) makes chironomids the dominant taxon in headwater ecosystems (Füreder, 1999).

Despite the attention this family has received from specialists (Cranston, 1995), chironomids have often been ignored or given little more than a brief mention in many ecological studies. This applies especially to lotic systems, which until recently were less studied than lake dwelling species (Hatwin, 1998). Detailed information about their life cycles in glacial meltwater streams is also fragmentary and autoecological studies are rare (Lods-Crozet et al., 2001). This is partly due to the harshness of these environments that hinders ecological surveys, and to the lack of complete and efficient keys to identify chironomid larvae at the species level. Species identification is a prerequisite for detailed ecological research, because most genera include species with different ecological demands that cannot be pooled into larger taxonomic units without loosing substantial information (Rossaro & Mietto, 1998).

The recent interest in headwaters is justified by the awareness that they represent our ultimate resource of unpolluted waters for the future, but they are threatened by local (e.g. tourism, water abstraction, artificial snow and pasture) and global (e.g. Greenhouse Effect and acid rain) environmental changes (McGregor et al., 1995). Because of their sensitivity and high resilience, remote aquatic ecosystems could become tools for detecting climatic changes and for developing predictive models of ecological changes (Brittain et al., 2001). Air temperature and precipitation patterns are likely to change under a scenario of global climate warming, with consequent effects on water temperature and hydrology that in turn could determine the local extinction of some species and the expansion into unsuitable habitats of others (Irons et al., 1993). Biota living in these habitats are extremely specialized and have developed unique survival strategies to face environmental constrains that could be modified due to climatic changes. In this prospect, chironomids are an excellent tool for the assessment of freshwater pollution and indicators of environmental changes. More knowledge regarding the response of species to different factors is needed, in order to be able to separate the effects of pollution from the effects of natural variables that affect community structures (Rossaro & Pietrangelo, 1993). As a response to these scientific demands, this paper focuses on the forces driving chironomid distribution in headwaters, at large (reach) and small (microhabitat) scales.

Study area

The study area is located in the Southern Alps, within the Adamello-Brenta Regional Park in the Trentino Region (NE Italy) (Fig. 1). Three glacial systems were investigated: Conca (46° 06′ N, 10° 36′ E), Niscli (46° 06′ N, 10° 36′ E) and Cornisello (46° 13′ N, 10° 41′ E), belonging to the crystalline Adamello-Presanella mountain group, with tonalite and granite as dominant bedrock (Bombarda, 1994). Glaciers in this area have been retreating from the end of the 19th century until the 1960s (from 1888 to 1962 the ice mass of Adamello-

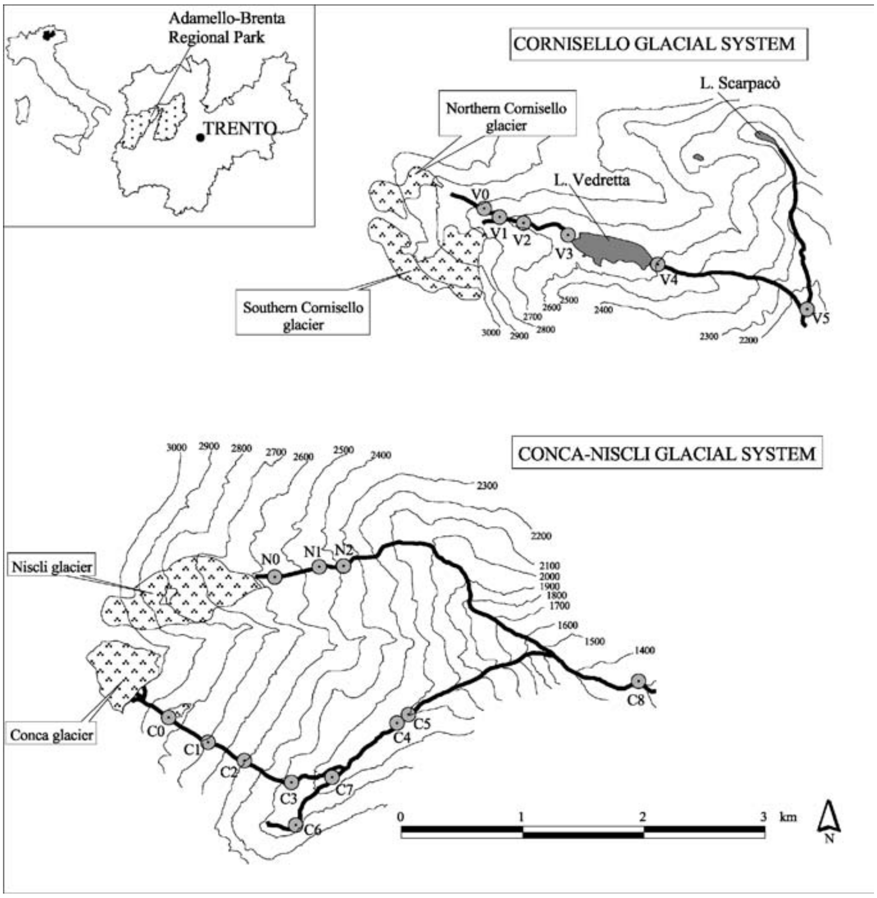

Figure 1. Study area (Southern Alps, 46° N). Eighteen sites were sampled on three glacial and their main non-glacial tributaries within the Adamello-Brenta Regional Park, in Trentino (NE Italy).

Presanella was reduced by about 50%, with a mean loss rate of 63 ha per year) (Bombarda, 1995). Since then, their ice mass has remained almost stable, with an area of 18 ha (Conca), 43 ha (Niscli) and 51 ha (Southern and Northern Cornisello together) (Bombarda, 1994). The glacial snouts are at an altitude of 2994 m a.s.l. (Conca), 2590 m a.s.l. (Niscli), 2775 m a.s.l. (Southern Cornisello) and 2876 m a.s.l. (Northern Cornisello) (CNR-CGI, 1998).

The study was carried out at 14 sampling sites on the three streams fed by the Conca (C0, C1, C2, C3, C4, C5, C8), Niscli (N0, N1, N2) and Cornisello (V0, V1, V2, V3) glaciers. Two additional stations (C6, C7) were selected on the main tributary of the Conca glacial stream (a short brook fed by snowmelt, rainfall and groundwater) and other two on the outlets of Lakes Vedretta (V4) and Scarpacò (V5), both in the Cornisello system. With the exception of C8, all the sampling sites selected were above the tree line.

The location and general features of the 18 sampling reaches are given in Table 1. Stream types were defined according to Ward (1994), Füreder (1999) and Hieber et al. (2002).

Methods

Field surveys were carried out during the melting season, from 1996 to 1997 in the Conca system, during 1997 in the Niscli system and from 1997 to 1998 in the Cornisello system. All sites were sampled during 5-day periods on three occasions per year (end of June, beginning of August and mid-September), except for C1 and C5, which were

Table 1. Location and general characteristics of sampling reaches

Reach	Altitude	Distance from source	Slope	Substrate stability	Type
C0	2833	0.31	0.40	33	Kryal
C1	2690	0.71	0.13	30	Kryal
C2	2507	1.07	0.28	32	Subkryal
C3	2252	1.52	0.22	38	Subkryal
C4	2115	2.60	0.02	25	Glacio-rhithral
C5	2100	2.74	0.07	27	Glacio-rhithral
C6	2285	0.18	0.01	18	Kreno-rhithral
C7	2170	0.71	0.03	21	Kreno-rhithral
C8	1300	4.60	0.13	36	Glacio-rhithral
N0	2565	0.16	0.03	35	Kryal
N1	2450	0.51	0.10	44	Subkryal
N2	2372	0.72	0.20	39	Subkryal
V0	2775	0.33	0.07	35	Kryal
V1	2720	0.17	0.05	42	Kryal
V2	2690	0.46	0.03	45	Kryal
V3	2605	0.94	0.02	60	Kryal
V4	2600	1.65	0.05	22	Outlet
V5	2120	2.98	0.05	30	Outlet

C = Conca, N = Niscli, V = Cornisello system. Altitude as m a.s.l., distance as km and slope as m m^{-1}. Substrate stability as Pfankuch's index (Pfankuch, 1975).

sampled only in 1996 due to redundancy, with C0 and C4 respectively, based on 1996 faunal results, and for C1, N2, V0 and V5, sampled on only one occasion. Within each catchment, it involved the collection of geomorphological and physico-chemical data and the sampling of epilithic algae and zoobenthos (Castella et al., 2001; Maiolini & Lencioni, 2001a).

Environmental variables

A geomorphological description (e.g. channel width, slope) was carried out on each 15 m long reach. The stream bottom component of the Pfankuck's index (Pfankuch, 1975) was used to assess channel stability by scoring five variables (rock angularity, bed-surface brightness, particle packing, percentage of stable materials, scouring and aquatic vegetation). Scores were summed to provide an overall index of channel stability, with a potential range of 15–60 (high scores representing unstable channels at the reach scale). Snow cover was registered at each reach and sampling occasion.

During each field survey, discharge was measured in each reach along a depth/velocity profile using a current meter (OTT Hydrometrie Z30) or by using a bucket in low flow conditions. Water temperature was monitored continuously in each reach by digital loggers (Gemini TinyTalk II, Gemini Data Loggers (UK) Ltd, Chichester, UK) during the sampling periods (5 days in each of the three occasions in 1996) and from June to September in 1997 and 1998. Point measurements of dissolved oxygen were also made during the faunal surveys using a field multiprobe (Hydrolab).

Water samples (1 l) were collected from each reach and analyzed for the following chemical parameters according to Standard Methods (APHA, 1992) and IRSA-CNR (1994): pH, conductivity, alkalinity, calcium, magnesium, sodium, potassium, silica, sulphate, chloride, nitrate nitrogen, ammonium nitrogen, orthophosphate and total phosphorous. Turbidity was measured as suspended solids, by filtering from 250 (at glacial sites) to 2500 (at non-glacial sites) ml of water through 0.45 μm membrane MFS filters and drying at 105 °C for 30 min. The standing crop of algae was estimated as chlorophyll *a* concentration

Table 2. List and codes of chironomids used in the ACCESS analysis

Taxon	Code
Zavrelimyia sp.	Zavrelim
Boreoheptagyia monticola	B.montic
Diamesa bertrami	D.bertr
D. steinboecki	D.stein
D. sp.2	D.sp2
D. sp.3	D.sp3
D. latitarsis gr.A	D.latgrA
D. latitarsis gr.B	D.latgrB
D. gr.A	D.grA
D. zernyi gr.	D.zerngr
D. cinerella gr.	D.cinegr
D. gr.B	D.zercin
D. dampfi gr.	D.damp
Pseudodiamesa branickii	P.bran
P. nivosa	P.nivosa
Pseudokiefferiella parva	P.parva
Syndiamesa sp.	Syndiam
Brillia bifida	B.bifida
Bryophaenocladius spp.	Bryoph
Chaetocladius spp.	Chaetocl
Corynoneura spp.	Corynon
Cricotopus fuscus	C.fuscus
Eukiefferiella brevicalcar/tirolensis	E.bretir
E. cyanea	E.cyanea
E. claripennis	E.clarip
E. coerulescens	E.coerul
E. devonica	E.devon
E. fuldensis	E.fulden
E. minor/fittkaui	E.minfit
Heleniella spp.	Helen
Heterotanytarsus apicalis	H.apical
Heterotrissocladius marcidus	H.marcid
Krenosmittia spp.	Krenosm
Limnophyes spp.	Limnoph
Metriocnemus sp.	Metriocn
Orthocladius (*E.*) *fuscimanus*	E.fuscim
Orthocladius (*E.*) *rivicola* gr.	E.rivigr
Orthocladius (*O.*) *frigidus*	O.frigid
Orthocladius s.str.	Orthsstr
Parakiefferiella sp.	Parakief
Parametriocnemus stylatus	P.stylat
Paratrichocladius rufiventris	P.rufiv
P. skirwithensis	P.skirw
Parorthocladius nudipennis	P.nudip
Pseudosmittia gracilis	P.grac
Rheocricotopus effusus	R.effus
Smittia sp.	Smittia
Thienemanniella spp.	Thienem
Tvetenia calvescens/bavarica	T.calvbav
Tokunagaia rectangularis	T.rect
Orthocladiinae juv.	Orthjuv
Polypedilum sp.	Polyped
Micropsectra atrofasciata	M.atrof

by scraping an area of 9 cm^2 at each reach and date from three stones selected randomly in the bed channel with a toothbrush. The toothbrush was washed in distilled water, then filtered through a Millipore filter funnel using a hand pump with a 4.7 cm GF/C filter paper. Chlorophyll *a* was extracted with 90% acetone and the concentration was read at 665 and 750 nm according to Standard Methods (APHA, 1992).

Chironomid sampling

Within each sampling reach, from 5 (in 1997 and 1998) to 10 (in 1996) replicate kick samples of zoobenthos were collected using a standard pond net (mesh size of 250 μm, mouth of 30 × 30 cm), disturbing the substrate for 1 min within an area of 0.1 m^2. Samples were washed through a 250 μm mesh funnel to remove excess water and then preserved in 75% ethanol. Prior to benthic sampling, water depth and current velocity were measured using a current meter at six points within each of 0.1 m^2 area, and bed composition was evaluated by visual assessment as percentage of boulders (>20 cm), cobbles (5–20 cm), gravel (0.2–5 cm), sand (0.01–0.2 cm) and silt–mud (<0.01 cm). For each microhabitat, the eventual presence of riffles, pools, mosses or of the chrysophyte *Hydrurus foetidus* (Villars) was noted.

Only larvae and pupae of chironomids are considered for this paper. For detailed information on non-chironomids see Lencioni (2000) and Maiolini & Lencioni (2001a, b). The stereomicroscope identification was confirmed at 1000/1600× by preparation of slides for each group identified. On account of difficulties in identifying the larval stages, morphospecies and discrete groups of species were established (Table 2), based on the morphology of the larvae according to Lods-Crozet et al. (2001). *D.* gr. A represents the first and second instars of *Diamesa steinboecki* Goetghebuer and *D. latitarsis* gr. A and B together, while *D.* gr. B represents the first and second instars of *D. zernyi* gr. and *D. cinerella* gr. together.

During sorting under the stereomicroscope, coarse benthic particulate organic matter (CPOM *sensu* Galas, 1993) was separated from the invertebrate samples, dried at 60 °C and ashed at 500 °C in a muffle furnace.

Data analysis

In all, 37 environmental factors (among these, eight dummy variables*) were considered to assess the spatial distribution of taxa. Of these factors, 13 vary at replicate level (presence of sheer rock*, % boulders, % cobbles, % gravel, % sand, % silt, current velocity, water depth, CPOM, presence of *H. foetidus**, of mosses*, of riffles* and of pools*) and 24 at reach level (altitude, distance from the source, level of glacial influence*, stream types*, slope, Pfankuch's index, presence of snow cover*, chlorophyll *a*, mean, minimum, maximum and range water temperature, discharge, pH, conductivity, alkalinity, sulphate, silica, nitrate nitrogen, ammonium nitrogen, orthophosphate and total phosphorous, suspended solids, dissolved oxygen).

Minimum, maximum, mean and range of water temperature referred to the three weeks before sampling or, when not available, to the 5-day sampling periods. For dummy variables, increasing presence of the specific condition was coded with a progressive number, from 0 (= absent) to 2 (= dominant/very abundant). Stream types (kryal, subkryal, glacio-rhithral, kreno-rhithral and outlet) were coded as 0 (= the reach does not belong to this type) or 1 (= the reach belongs to this type). Taxon codes used in the present analysis are listed in Table 2.

To test significant differences in time (June, August and September 1996, 1997 and 1998) and space (in all 18 stations in the Conca, Niscli and Cornisello catchments) of environmental factors and chironomid fauna, Student *t*-test and ANOVA were performed. Pearson's correlations between environmental factors and chironomid fauna were also calculated. The STATISTICA computer package was used for these analyses and values with $p < 0.05$ were considered significant.

Data were processed with Microsoft ACCESS in a relational database. Means and standard deviations weighted on species abundances were calculated for each environmental variable. Only taxa collected in more than five samples are discussed.

Results

Stream environmental features

The main environmental features of the sampling sites are given in Tables 1 and 3. All parameters listed in Table 3 were significantly different among the five stream types, apart from the percentage of boulders, sand and silt/mud.

The three systems were dominated by coarse substrate (sheer rock and/or boulders and cobbles), forming from 65% (Niscli and Cornisello) to 74% (Conca) of the bed sediment. Gravel was relatively abundant in some kryal sites (N0, V0, V2, V3), in the Conca stream after the confluence with its non-glacial tributary (C4) and in the outlets (V4, V5). Finer substrates were recorded in a relatively high percentage only in the delta region of the Cornisello stream (V3). Moderate to high channel stability was recorded in the Conca system (C6, C7) and in the Cornisello reaches located below the lake (V4, V5). Lower channel stability was recorded in the Niscli (mean Pfankuch's index of 41) and in the Cornisello reaches located above the lake, with a maximum of 60 for the Pfankuch's index at V3 (Table 1).

The highest mean values of discharge and current velocity were recorded in the Niscli sites and at C8, with an absolute maximum of 2050 l s^{-1} at C8 in June 1997 and of 1.46 m s^{-1} at N1 in September 1997. Mean discharge increased progressively downstream of the glacial snout in the three systems, and so from the kryal to the glacio-rhithral (Table 3). The same was not observed for current velocity, with means higher in highly steep kryal sites (C0) and/or water flowing over bedrock outcrop (C2).

The lowest mean, minimum and maximum water temperature were recorded in the kryal (with the only exception of C3 where a maximum of 15.4 °C was measured) and the lowest temperature range in the kreno-rhithral (Table 3). The

Table 3. Mean (±standard deviation) of the principal physico-chemical parameters of the sampling sites

	Unit	Kryal	Subkryal	Glacio-rhithral	Kreno-rhithral	Outlet
% Boulder[a]		43.0 ± 36.5	50.8 ± 37.7	41.9 ± 34.3	52.9 ± 38.6	47.4 ± 35.6
% Cobbles[a]		29.0 ± 22.2	23.3 ± 25.3	27.7 ± 23.4	17.2 ± 19.4	37.4 ± 20.0
% Gravel[a]		32.1 ± 26.1	15.4 ± 17.8	15.1 ± 20.0	21.2 ± 28.7	29.4 ± 25.0
% Sand[a]		11.7 ± 17.3	9.6 ± 20.7	16.4 ± 24.8	8.7 ± 19.3	12.6 ± 24.2
% Silt/mud[a]		0.2 ± 1.4	0.9 ± 6.1	0.5 ± 2.7	0.1 ± 0.5	1.2 ± 3.0
Sheer rock[a]		0.06 ± 0.24	0.15 ± 0.36	0.03 ± 0.16	0.06 ± 0.24	0.06 ± 0.25
Discharge	l s^{-1}	137.9 ± 199.8	287.8 ± 529.0	495.3 ± 534.1	20.5 ± 19.0	11.7 ± 6.0
Velocity[a]	m s^{-1}	0.74 ± 0.47	0.75 ± 0.56	0.51 ± 0.44	0.51 ± 0.50	0.79 ± 0.56
Depth[a]	cm	8.42 ± 4.59	7.15 ± 4.94	13.98 ± 7.86	9.72 ± 6.40	8.63 ± 4.34
T_{mean}	°C	1.5 ± 1.1	4.3 ± 2.0	6.3 ± 2.1	3.8 ± 1.2	5.4 ± 2.5
T_{min}	°C	0.4 ± 0.7	1.6 ± 1.0	3.9 ± 1.4	2.8 ± 1.2	3.7 ± 2.0
T_{max}	°C	3.5 ± 2.6	8.5 ± 4.0	9.1 ± 2.9	5.4 ± 1.7	7.3 ± 3.1
T_{range}	°C	3.1 ± 2.3	6.8 ± 3.4	5.2 ± 1.9	2.6 ± 1.6	3.6 ± 2.1
pH		5.8 ± 0.5	5.8 ± 0.5	6.2 ± 0.4	6.1 ± 0.4	6.0 ± 0.3
Conductivity	$\mu\text{S cm}^{-1}$	10.2 ± 5.4	7.6 ± 2.5	10.2 ± 1.5	10.9 ± 0.8	11.0 ± 0.7
Alkalinity	$\mu\text{eq l}^{-1}$	27.2 ± 47.0	1.6 ± 16.4	20.7 ± 9.4	17.6 ± 15.8	29.4 ± 9.4
SO_4	mg l^{-1}	0.87 ± 0.32	0.98 ± 0.29	1.15 ± 0.19	1.34 ± 0.13	0.89 ± 0.31
SiO_2	mg l^{-1}	1.26 ± 0.54	1.58 ± 0.89	2.46 ± 0.48	2.84 ± 0.41	1.72 ± 0.37
$N\text{-}NO_3$	$\mu\text{g l}^{-1}$	219 ± 119	189 ± 103	200 ± 48	248 ± 38	230 ± 47
$N\text{-}NH_4$	$\mu\text{g l}^{-1}$	45 ± 33	18 ± 14	10 ± 6	8 ± 6	23 ± 7
$P\text{-}PO_4$	$\mu\text{g l}^{-1}$	2 ± 1	1 ± 0	2 ± 1	2 ± 1	1 ± 0
TP	$\mu\text{g l}^{-1}$	23 ± 20	12 ± 16	6 ± 4	8 ± 9	20 ± 10
Turbidity[b]	mg l^{-1}	49.1 ± 71.7	11.3 ± 9.8	5.1 ± 4.4	2.7 ± 2.0	18.0 ± 12.3
% Oxygen	%	98.0 ± 8.6	92.8 ± 4.2	94.4 ± 3.8	94.1 ± 4.0	98.3 ± 13.5
Chlorophyll *a*	$\mu\text{g cm}^{-2}$	0.192 ± 0.204	0.343 ± 0.438	0.274 ± 0.108	0.388 ± 0.293	0.128 ± 0.126
BPOM[a]	g m^{-2}	2.21 ± 8.21	0.82 ± 1.70	5.44 ± 16.71	2.46 ± 4.83	0.35 ± 0.61
Snow cover		1.29 ± 0.54	1.28 ± 0.45	1.00 ± 0.00	1.12 ± 0.33	1.16 ± 0.37
Riffle[a]		0.03 ± 0.16	0.07 ± 0.26	0.19 ± 0.40	0.13 ± 0.34	0.09 ± 0.02
Pool[a]		0.03 ± 0.18	0.07 ± 0.26	0.11 ± 0.31	0.11 ± 0.31	0.03 ± 0.18
Hydrurus[a]		0.18 ± 0.38	0.02 ± 0.15	0	0.02 ± 0.15	0.03 ± 0.18
Moss[a]		0.04 ± 0.20	0.02 ± 0.15	0.03 ± 0.16	0.23 ± 0.42	0

Kryal (C0, C1, N0, V0, V1, V2, V3); subkryal (C2, C3, N2, N3); glacio-rhithral (C4, C5, C8); kreno-rhithral (C6, C7); outlet (V4, V5). C = Conca, N = Niscli, V = Cornisello system. Boulders (>20 cm), cobbles (5–20 cm), gravel (0.2–5 cm), sand (0.01–0.2 cm) and silt–mud (<0.01 cm). T = temperature.

[a] Parameters variable at replicate level.

[b] Turbidity as suspended solids.

absolute minimum temperature was recorded in the kryal (−0.1 °C at C0, V1, V2 and V3), affected for a longer period by snow cover than the other stream types. Minimum, maximum and mean temperatures increased significantly downstream in the three glacial streams, in all sampling years. In the Cornisello system, below the lake (V4), mean temperature varied from 2.8 °C (September 1998) to 5.3 °C (August 1997) higher than above (V3).

Low conductivity (2.5–23.9 $\mu\text{S cm}^{-1}$), low pH (4.5–6.6) and low alkalinity (−20 to 168.2 $\mu\text{eq l}^{-1}$) were recorded in the three glacial systems, with general lower values in the Conca system during the peak of ice/snow melting (end of June/beginning of August).

Mean sulphate and silica content showed similar spatial trends, both increasing with decreasing glacial influence (from kryal to kreno-rhithral). Temporal trends were also observed for the SO_4:Si ratio at the snouts of the three glaciers, being higher (>80%) in mid-summer (=higher subglacial input) and lower (<20%) in autumn (=higher groundwater input).

Ammonium was generally higher in late spring/early summer in the kryal sectors, with a peak of 77 $\mu g\ l^{-1}$ at C0 in June 1997, of 75 $\mu g\ l^{-1}$ at N0 in August 1997 and of 154 $\mu g\ l^{-1}$ at V1 in August 1998. In June nitrate was higher at the upper stations in all stream investigated, although also in September when snow cover was already present (e.g. C0 and C1 in 1996). The absolute maximum value of N-NO_3 was of 690 $\mu g\ l^{-1}$ at C1 in June 1996.

On average, turbidity was higher in the kryal and lower in the kreno-rhithral (Table 3). The highest turbidity was recorded in the Cornisello stream before the lake, with a maximum of 301.8 mg l^{-1} at V1 in August 1998. Lower values were measured in the Conca reaches, even in the kryal ones (14.2 ± 21.5 mg l^{-1} at C0). A similar trend was observed for total phosphorous (minimum of 2 $\mu g\ l^{-1}$ at C4 in June 1996 and maximum of 86 $\mu g\ l^{-1}$ at V1 in August 1998). Dissolved oxygen was always over 90% (Table 3).

Mean chlorophyll *a* was lower in the kryal and in the outlets (especially at V4) and higher in the kreno-rhithral with abundant mosses, while mean CPOM was lower in the subkryal and in the outlets and higher in the glacio-rhithral where allochthonous detritus from shrubs and herbs was more readily available. However, the absolute maximum of chlorophyll *a* (0.964 $\mu g\ cm^{-2}$) was recorded in a kryal reach (C1), when (August 1996) *H. foetidus* was found particularly abundant. This chrysophyte was found forming large thalli at all glacial sites, especially in mid-summer and early autumn.

Most of these parameters (Table 3) showed clear temporal trends, according to ice and snowmelt. Parameters such as discharge, turbidity, TP and nitrogen peaked at the end of June or early summer during the melting season in all reaches dominated by glacier runoff, while other parameters (e.g. conductivity and pH) were lowest in this period. Some parameters, such as discharge and conductivity, showed also daily variations, with maximum discharge and minimum conductivity during the peak of ice–snowmelt.

Highly significant positive correlations ($p < 0.001$) were found between glacial influence and altitude ($r = 0.561$), Pfankuch's index ($r = 0.479$), chlorophyll *a* ($r = 0.634$), N-NH_4 ($r = 0.842$), P-PO_4 ($r = 0.770$), TP ($r = 0.822$) and suspended solids ($r = 0.878$), while highly significant negative correlations ($p < 0.001$) were found between glacial influence and distance from the source ($r = -0.503$), minimum ($r = -0.764$), maximum ($r = -0.571$) and mean ($r = -0.592$) temperatures, conductivity ($r = -0.711$), SO_4 ($r = -0.877$), SiO_2 ($r = -0.896$) and N-NO_3 ($r = -0.578$).

Chironomid assemblage structure

54 625 aquatic invertebrates were sorted from 439 samples, with densities ranging from 14 (Cornisello system in 1997) to 4107 (Conca system in 1996) ind m^{-2}. Diptera, Ephemeroptera, Plecoptera, Trichoptera, Oligochaeta, Nematoda, Crustacea, Tricladida and Hydracarina were the major groups found in the study sites. Chironomids (Diptera Chironomidae) were the dominant faunal group represented, with 26 673 specimens and 53 taxa, accounting for about 50% of all individuals collected (see Table 2). The greatest number of taxa was collected in the Conca streams, followed by Cornisello and Niscli. Chironomid population density (4–2652 ind m^{-2}) showed clear inter-annual and seasonal differences with higher values in 1997 in all glacial-dominated reaches and peaks in autumn and minimum in mid-summer.

The numerical dominance of midges was recorded in all sites and dates except a few. Diamesinae were most abundant, especially in the kryal reaches, where *Diamesa* spp. reached almost 100% of the total fauna. This percentage decreased downstream, with decreasing glacial influence and increasing distance from the glacial snout, reaching a mean relative abundance < 50% in the subkryal and < 5% in the glacio-rhithral reaches. *Diamesa* spp. constituted around 10–20% in the kreno-rhithral (C6, C7) and outlet (V4, V5) reaches.

The kryal reaches were dominated by *Diamesa* gr. A, *D. steinboecki* and *D. latitarsis* gr. A, followed by *Pseudokiefferiella parva* (Edwards),

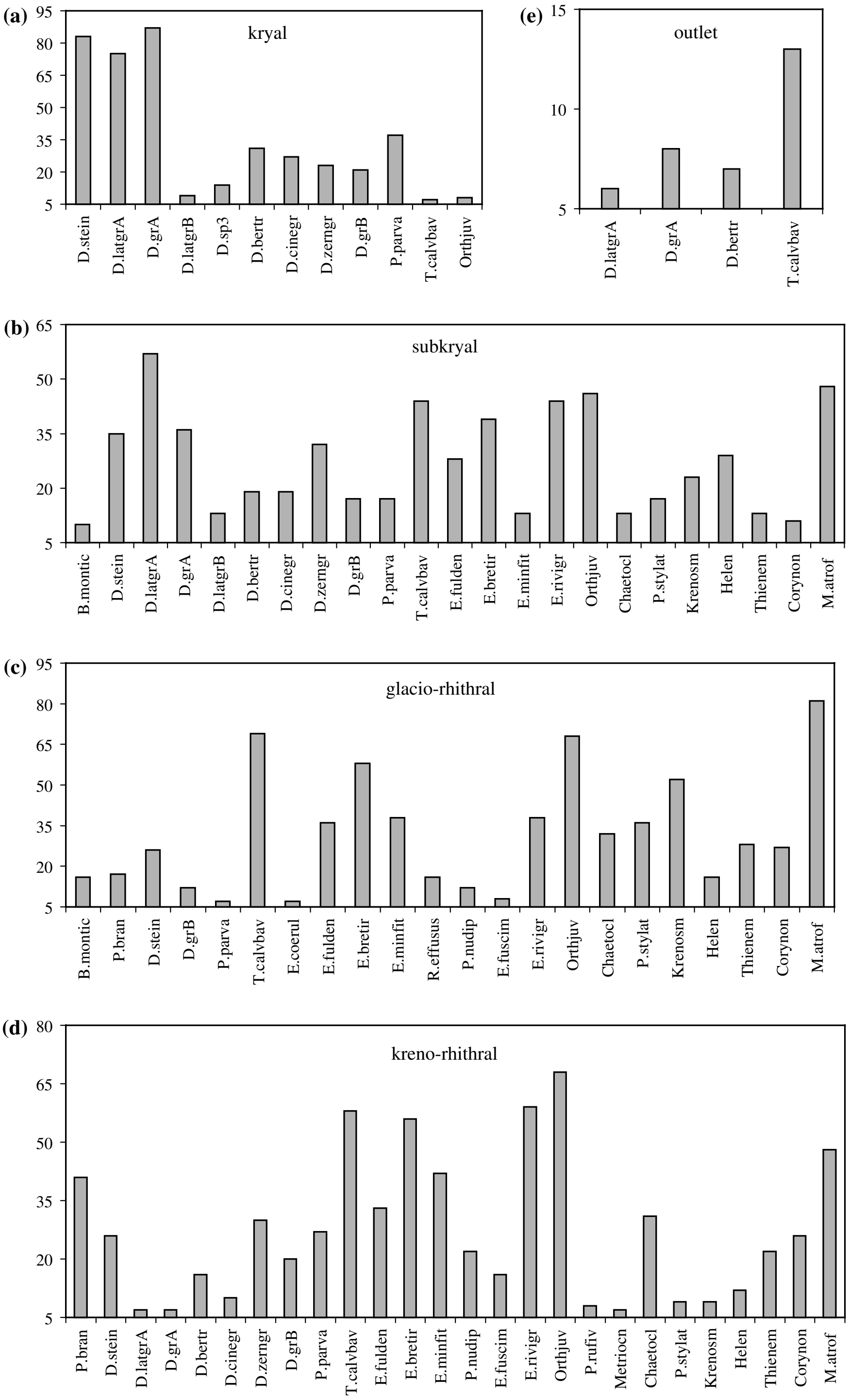

Figure 2. Chironomid taxa, in phylogenetic order, best represented in the (a) kryal, (b) subkryal, (c) glacio-rhithral, (d) kreno-rhithral and (e) outlet reaches. On the *y*-axis the sample size as number of records of each taxon per reach typology. Only taxa collected in more than five samples have been considered. Taxon codes as in Table 2.

D. bertrami Edwards, *D. zernyi* gr., *D. cinerella* gr., *D.* gr. B and *D.* sp. 3 (Fig. 2a). The first Orthocladiinae appearing in the kryal were first and second instar larvae and *Tvetenia calvescens* (Edwards)/*bavarica* (Goetghebuer).

The same *Diamesa* taxa dominated the subkryal reaches (Fig. 2b), with the exception of the station C3 where the mean relative presence of chironomids fell to below 50% of the total fauna and, among them, the abundance of *Diamesa* spp. strongly decreased to only 5% of the zoobenthos. Here, *Micropsectra atrofasciata* (Kieffer) (Chironominae) was, on average, the most abundant species, followed by early instar Orthocladiinae larvae, *T. calvescens*/*bavarica*, *Orthocladius* (*Euorthocladius*) *rivicola* gr. and *Eukiefferiella brevicalcar* (Kieffer)/*tirolensis* Goetghebuer. These taxa remained co-dominants besides other Orthocladiinae such as *Krenosmittia* spp., *Eukiefferiella minor* (Edwards)/*fittkaui* Lehmann, *Parametriocnemus stylatus* (Kieffer), *Eukiefferiella fuldensis* Lehmann and *Chaetocladius* spp., in the downstream reaches in the Conca stream (C4, C5, C8), then in the glacio-rhithral reaches (Fig. 2c). The most abundant Diamesinae in the glacio-rhithral was *D. steinboecki*. Orthocladiinae juveniles, *O.* (*E.*) *rivicola* gr., *T. calvescens*/*bavarica*, *E. brevicalcar*/*tirolensis*, *M. atrofasciata*, *E. minor*/*fittkaui* besides *Pseudodiamesa branickii* (Nowicki) were the most numerous groups in the kreno-rhithral reaches (Fig. 2d). Finally, the lake outlets (Fig. 2e) were dominated by Orthocladiinae (mostly *T. calvescens*/*bavarica* and, at V5, *E. minor*/*fittkaui*) followed by Diamesinae (only at V4) (mostly *D.* gr. A, *D. bertrami* and *D. latitarsis* gr. A). Chironominae (*M. atrofasciata*) were abundant only at V5.

During the study period (June–September), some taxa showed a clear temporal trend. For example, *O.* (*E.*) *rivicola* gr. and *D. latitarsis* gr. A were more abundant in late spring, while *D. zernyi*/*cinerella* gr., *D. bertrami*, *D. steinboecki* and *P. parva* peaked in mid-summer/early autumn in all sampling years in the three investigated systems. Some taxa had different relative abundances in the invertebrate community in different years. For example, *M. atrofasciata* increased in 1996 while it decreased in 1997 from June to September in both Conca streams while *D. bertrami* was found in the kreno-rhithral in 1996 and was also very abundant in the subkryal only in 1997 (especially in September) in the Conca system.

Generally, Diamesinae were more abundant in the glacial streams in mid-summer, Orthocladiinae in late spring and Chironominae in autumn or late spring. The same trend was observed for their relative importance in the zoobenthic community.

Environmental relationships

The 'upstream–downstream gradient' observed for the chironomid fauna was significantly correlated with the 'upstream–downstream gradient' observed for the environmental parameters, among which some exhibited a clear tendency to increase (i.e. pH, conductivity, CPOM, mean water temperature, discharge, sulphate and silica) and others to decrease (i.e. slope, N-NO_3 and abundance of *H. foetidus*) with decreasing altitude and glacial influence and with increasing distance from the source. The significant correlations calculated between abiotic (27) and biotic (26) factors are given in Appendix 1.

At the reach level, mean and minimum water temperatures, channel stability and water chemistry (conductivity, silica, nitrate and ammonium nitrogen and total phosphorous) were the main environmental factors driving the chironomid distribution in the investigated catchments. There was high variability among the replicates at each station and date.

According to the means weighted on taxon abundance calculated for each environmental variable, CPOM and granulometry were the two parameters that most influenced chironomid distribution, in addition to water depth, the presence of riffles/pools and of *H. foetidus*/mosses. These variables were significantly correlated with hydrological, geomorphological and chemical factors. In particular, CPOM correlated with distance from the source ($r = 0.556$), discharge ($r = 0.713$), % sand ($r = 0.645$), SiO_2 ($r = 0.494$), SO_4 ($r = 0.504$), N-NO_3 ($r = 0.545$), altitude ($r = -0.579$), % boulders ($r = -0.457$), chlorophyll *a* ($r = -0.507$) and N-NH_4 ($r = -0.469$). Water depth was correlated with current velocity ($r = -0.501$) and with the presence of pools ($r = 0.585$). The presence of riffles was correlated

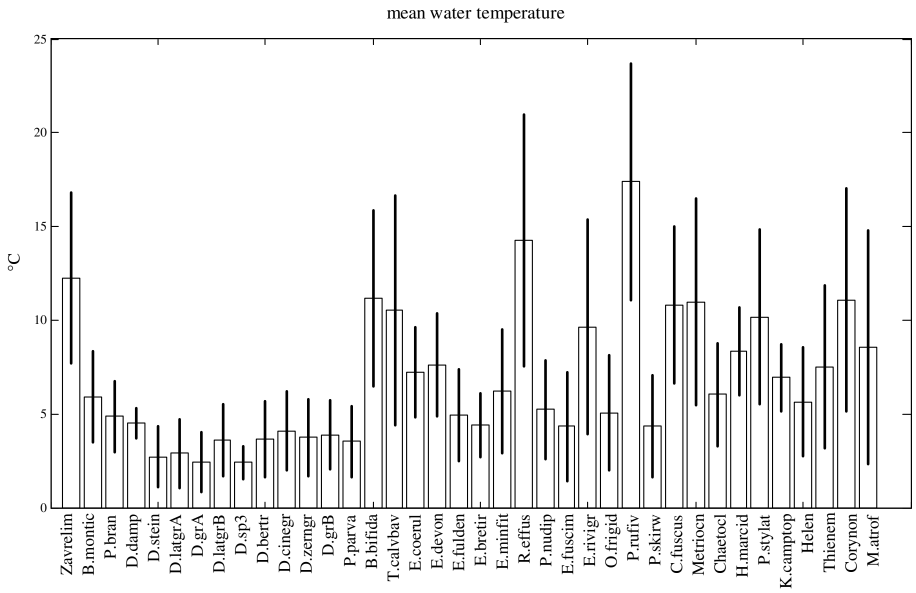

Figure 3. Distribution of chironomid taxa, in phylogenetic order, as a function of mean water temperature (°C). The means (±standard deviation) weighted on species abundance were calculated. Only taxa collected in more than 10 samples were included in the graph.

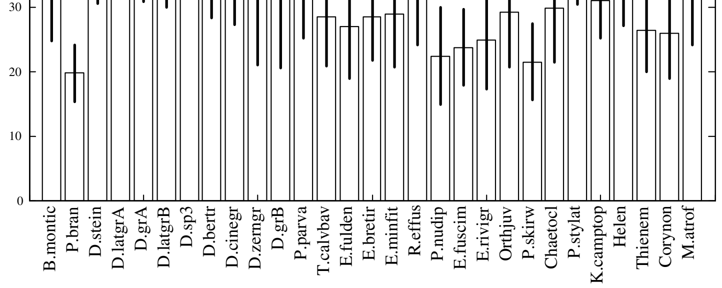

Figure 4. Distribution of chironomid taxa, in phylogenetic order, as a function of Pfankuch's index. The means (±standard deviation) weighted on species abundance were calculated. Only taxa collected in more than 10 samples were included in the graph.

with % gravel ($r = 0.538$), SiO_2 ($r = 0.625$), SO_4 ($r = 0.556$) and $N\text{-}NH_4$ ($r = -0.535$).

D. steinboecki, *D. latitarsis* gr. A and *P. parva* were the major colonizers of the cold and highly unstable kryal reaches (Figs 3 and 4). The lowest minimum, maximum, mean and range water temperatures correlated mainly with *D. steinboecki*, *D. latitarsis* gr. A, *P. parva* and *D.* sp. 3. Among *Diamesa* taxa, some (*D. bertrami*, *D. cinerella* gr. and *D. zernyi* gr.) were abundant in a wider range of conditions, in terms of both season and stream type. However, the records of these species and of

P. parva in the kryal were generally associated with the presence of *H. foetidus*. The occurrence of *D. steinboecki*, *D. latitarsis* gr. A and B and *D.* gr. A correlated also with the presence of the snow cover, indicating their capacity to continue, or to start early in spring, their life cycle even beneath the snow in glacial streams. The same ability was observed for the Orthocladiinae juveniles, *T. calvescens/bavarica* and *M. atrofasciata* in non-glacial reaches fed by snowmelt.

Fine sediments (gravel and sand) were mainly colonized by Orthocladiinae such as *E. brevicalcar/tirolensis*, *P. nudipennis*, *P. stylatus*, *Orthocladius* (*Eudactylocladius*) *fuscimanus* Kieffer, *Corynoneura* spp., *Thienemanniella* spp., as well as *P. branickii* (Diamesinae) and *M. atrofasciata* (Chironominae). These species, along with *Krenosmittia* spp. and the tanypod *Zavrelimyia* sp., were frequent in pools. Fine sediments were also successfully colonized by *Diamesa* spp. in glacial floodplains characterized by high channel instability (V3, in the delta region of the Cornisello glacial stream). *P. branickii*, *Paratrichocladius skirwithensis* (Edwards), *P. nudipennis*, *Metriocnemus* spp. and *Bryophaenocladius* spp. were the taxa most associated with stable substrates. The last two taxa, along with *Smittia* sp., were only found in low current conditions, while *P. stylatus*, *D. latitarsis* gr. A and B, *Rheocricotopus effusus* (Walker) and *O.* (*E.*) *rivicola* gr. were most frequent in high flow conditions.

Mosses were mainly colonized by Orthocladiinae such as *E. brevicalcar/tirolensis*, *E. minor/fittkaui*, *T. calvescens/bavarica*, *O.* (*E.*) *rivicola* gr., especially in riffles of non-turbid waters and those richer in dissolved ions.

Some taxa were associated with slightly acid conditions, as *Bryophaenocladius* spp., *P. skirwithensis*, *Heterotrissocladius marcidus* (Walker) and *Metriocnemus* sp., others with low conductivity and low silica content (Fig. 5), such as *D. steinboecki*. In contrast, several taxa such as *D. zernyi* gr., *Corynoneura* spp., *E. brevicalcar/tirolensis*, *E. minor/fittkaui*, *O. frigidus*, *Thienemanniella* spp. and *Tvetenia calvescens/bavarica* were associated with high silica content (Fig. 5).

Discussion

The results of this study support the hypothesis that chironomids are preadapted to rigorous habitats, dominating in terms of number of individuals and taxa in all stream types above

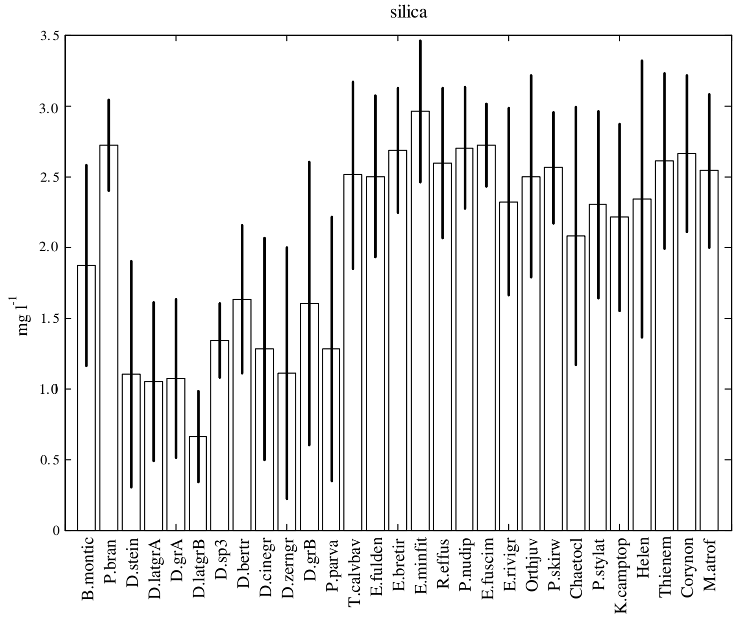

Figure 5. Distribution of chironomid taxa, in phylogenetic order, as a function of silica content (mg l^{-1}). The means (± standard deviation) weighted on species abundance were calculated. Only taxa collected in more than 10 samples were included in the graph.

the tree line. They evolved several hundred million years ago in cold running waters and secondly conquered almost all the other types of habitats (Oswood et al., 1991). Among chironomids, *Diamesa* species are the best appeared to be the best adapted to face the harshness of glacial freshwaters. Particularly, *D. steinboecki*, *D. latitarsis* gr. A and *P. parva* were the taxa best associated with 'glacial' conditions (i.e. high channel instability or presence of sheer rock and steep slopes, high suspended solids and high total phosphorous, low conductivity and low silica content, highly variable discharge during the day, low mean temperatures and presence of thalli of *H. foetidus*), while *P. branickii*, *Corynoneura* spp., *Eukiefferiella* spp., *Parorthocladius nudipennis* (Kieffer), *T. calvescens/bavarica*, *Thienemanniella* spp. and *M. atrofasciata* were the taxa most associated with 'non-glacial' conditions. However, among these taxa, some such as *Tvetenia* showed a tendency to colonize very cold and unstable kryal waters. These 'later colonizers' may be the 'first colonizers' of reaches once restricted to *Diamesa* species after the retreat of glaciers predicted by increasing air temperature due to global warming (Brittain et al., 2001; Milner et al., 2001).

Substrate particle size, organic matter deposit, water depth, current velocity and the presence of mosses or *H. foetidus*, appeared to be the major factors affecting microdistribution of chironomids in the study streams. These variables have been found by other authors (e.g. Malmqvist et al., 1999) to be major factors affecting microdistribution of stream insects. Current velocity influences all other environmental parameters: it sorts and separates the substrate particles, deposits or carries away silt, transports and shreds leaf detritus, and is necessary for respiration. However, other authors consider current velocity and a light deposition of silt play a secondary role, while substrate–detritus interactions have the overriding influence on insect microdistribution (Rabeni & Minshall, 1977). The number of organisms has been found to be directly related to the composition of stream substrate, with most benthic insects concentrated where the food is most abundant (small substrate) (Rabeni & Minshall, 1977). In fact, the substrate particles, especially those of small size, act as collectors of detritus which does not accumulate in the larger-size substrata, where the interstices are larger and current velocity is higher. However, physically complex substrate types (wood, leaves, gravel or cobbles, macrophytes, mosses) generally support a more diverse zoobenthic community than structurally simple substrates (sand or bedrock) (Miserendino, 2001). In this scenario, kryal and subkryal reaches dominated by sheer rock or boulders represent an exception when covered by large masses of *Hydrurus*. Algal mats such as thalli of *H. foetidus* trap organic particles that act as food supply for invertebrates. Furthermore, these thalli contribute to the development of stable microhabitats where current velocity is reduced, and constitute a valid substrate for epiphytic diatoms, thus playing an important indirect role for the diet of invertebrates (Nolte, 1989; Gíslason et al., 2001). Algal and moss mats have also been emphasized as oviposition habitats (Nolte, 1989).

Conclusions

This research highlighted the necessity of replication (Halse et al., 2002) to study all different microhabitats in a stream reach, to collect the greatest proportion of the species present, due to high habitat heterogeneity. Long-term monitoring of the same reaches and, within them, of the same microhabitats, is also necessary in glacial streams, characterized by high seasonality but also diurnal variability. In different hours of a summer day, hydrological and physico-chemical features vary and different zoobenthic assemblages can be found in the same microhabitats, as result of mortality, flux among patches or between the streambed or catastrophic drift (Palmer et al., 1996; Lencioni et al., 2002). It is known that benthic organisms often use the hyporheic zone as a refuge from a variety of environmental disturbances such as warm summer temperatures, floods and predation (Füreder, 1999; Malard et al., 2002). This is true especially for taxa living in glacial streams during the melting season. For this reason sampling in glacial streams should be done in the early morning, before the peak of discharge.

In conclusion, the clumped distribution of specimens observed in the investigated streams highlighted the importance of habitat heterogeneity as a better predictor of chironomid assemblages than large-scale patterns in landscape diversity.

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Appendix 1. Significant Pearson's correlations ($p < 0.05$) between chironomid taxa and environmental factors. Records > 5 were considered. Taxon codes as in Table 2.

	r	*p*
D.grA		
Snow cover	0.529	0.017
pH	0.490	0.028
D.latgrA		
Pfankuch's index	0.452	0.045
Snow cover	0.499	0.025
$N\text{-}NH_4$	0.466	0.038
% Silt/mud	0.499	0.025
D.stein		
Glacial influence	0.502	0.024
Chlorophyll *a*	0.479	0.033
T_{min}	−0.459	0.042
Conductivity	−0.561	0.010
SiO_2	−0.522	0.018
$N\text{-}NO_3$	−0.533	0.015
$N\text{-}NH_4$	0.454	0.045
TP	0.589	0.006
Turbidity*	0.587	0.007
D.zerngr		
Glacial influence	−0.580	0.007
SiO_2	0.463	0.040
Riffle	0.617	0.004
Hydrurus	0.541	0.014
D.cinegr		
Hydrurus	0.571	0.009

Continued on p. 76

Appendix 1. (Continued)

	r	*p*
P.bran		
% Sand	0.623	0.003
Pool	0.978	0.000
P.parva		
Chlorophyll *a*	−0.473	0.035
% Boulder	−0.468	0.037
Riffle	0.466	0.038
Hydrurus	0.466	0.038
Chaetocl		
Slope	0.538	0.014
Riffle	0.667	0.001
Corynon		
Glacial influence	−0.592	0.006
SiO_2	0.507	0.023
% Boulder	−0.512	0.021
% Gravel	0.639	0.002
Riffle	0.653	0.002
E.bretir		
Glacial influence	−0.633	0.003
Chlorophyll *a*	−0.507	0.022
SiO_2	0.628	0.003
$N\text{-}NH_4$	−0.528	0.017
TP	−0.447	0.048
% Boulder	−0.582	0.007
% Gravel	0.689	0.001
Riffle	0.757	0.000
E.cyanea		
% Gravel	0.447	0.048
E.clarip		
% Sand	0.585	0.007
Pool	1.000	< 0.001
E.coerul		
Depth	0.636	0.003
E.fulden		
Chlorophyll *a*	−0.467	0.038
SiO_2	0.546	0.013
$N\text{-}NH_4$	−0.461	0.041
% Gravel	0.602	0.005
E.minfit		
Altitude	−0.576	0.008
Glacial influence	−0.615	0.004
SiO_2	0.512	0.021
Riffle	0.708	0.000
Krenosm		
Discharge	0.620	0.004
pH	−0.552	0.012
BPOM	0.671	0.001
E.fuscim		
% Gravel	0.447	0.048
Riffle	0.459	0.042
E.rivigr		
BPOM	0.705	0.001
O.frigid		
Glacial influence	−0.553	0.011
SiO_2	0.459	0.042
% Boulder	−0.456	0.043
% Gravel	0.612	0.004
Riffle	0.629	0.003
Hydrurus	0.594	0.006
P.stylat		
Discharge	0.639	0.002
pH	−0.569	0.009
% Sand	0.691	0.001
BPOM	0.741	0.000
Pool	0.774	0.000
P.nudip		
% Boulder	−0.451	0.046
% Gravel	0.450	0.047
% Sand	0.453	0.045
Depth	0.456	0.043
BPOM	0.481	0.032
Thienem		
Glacial influence	−0.614	0.004
SiO_2	0.509	0.022
% Gravel	0.583	0.007
Riffle	0.698	0.001
T.calvbav		
Glacial influence	−0.592	0.006
SiO_2	0.479	0.033
Riffle	0.478	0.033
T.rect		
Slope	0.852	0.000
T_{range}	0.724	0.000
Riffle	0.459	0.042
Orthjuv		
T_{mean}	0.465	0.039
T_{min}	0.457	0.043
M.atrof		
Altitude	−0.757	0.000
Distance from source	0.566	0.009
Glacial influence	−0.597	0.005
Chlorophyll *a*	−0.621	0.003
SiO_2	0.715	0.000
$N\text{-}NO_3$	0.450	0.047
$N\text{-}NH_4$	−0.617	0.004
TP	−0.567	0.009
Turbidity	−0.510	0.022
% Boulder	−0.495	0.026
% Sand	0.471	0.036
BPOM	0.687	0.001
Riffle	0.544	0.013

* Turbidity as suspended solids.