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Zoobenthic communities of inlets and outlets of high altitude Alpine lakes

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Abstract

Due to their sensitivity, remote mountain lakes and streams are not only vulnerable to environmental change but also excellent sensors of such changes. Notwithstanding their importance as an ultimate resource of unpolluted waters, the alpine biome remains one of the less studied ecosystems in the world. This study involved the analysis of a database of zoobenthic communities collected in 36 inlets and 44 outlets of Swiss (Canton Bern) and Italian (Piedmont, Trentino-Alto Adige) Alpine lakes. All the streams are above the tree line and were sampled qualitatively in September/October (mostly in 2000) by disturbing the substrate and concentrating the dislodged animals with a standard pond net (250 μm mesh size). Generally higher population densities and taxon richness were found in the outlets than in the inlets. Fifty-seven per cent of taxa were common to the two stream types, with 17% found exclusively in the inlets and 26% in the outlets. Piedmont had the highest number of taxa found only in the region, Trentino-Alto Adige the lowest number. Insects represented 89% and 81% of the zoobenthic community of inlets and outlets, respectively. Among the insects, Diptera prevailed, with Chironomidae accounting for 68% of the mean inlet communities and 45% of those found in the outlets. The subfamily of Diamesinae was far more abundant in the inlets (16%) than in the outlets (1%). In contrast, the outlets hosted more Ephemeroptera, Trichoptera, Plecoptera, Oligochaeta and Tricladida. Some significant differences regarding the distribution of some species were found along the West–East and South–North gradients. The lakes appeared to affect the structure of the stream zoobenthic community by ameliorating the harsh physico-chemical conditions of the tributaries but no evidence was found indicating an increase in organic matter. In fact, filter-feeding invertebrates did not show any significant increase in the outlets, though the number of these taxa was higher downstream of the lakes.

Introduction

In the last decade growing attention has been paid by the scientific community and public administrations to headwater lotic ecosystems and the definition of their functionality and integrity is becoming a priority demand (Brittain & Milner, 2001). Headwaters are the most sensitive aquatic ecosystems, the focal point of mountain landscapes, supporting unique plant and animal communities and determining the quality and quantity of lowland rivers. Human activities affect the most remote areas on a local (water abstraction, tourism, artificial snow, etc.) and global scale (global warming, acid rains, etc.) (McGregor et al., 1995). Because of their sensitivity, remote mountain streams and lakes are not only vulnerable to environmental changes but also excellent sensors of such changes (Rieredevall et al., 1998). Notwithstanding their importance, the alpine biome remains to date one of the least studied ecosystems in the world (Bowman & Seastedt, 2001).

In the 1990s several studies were carried out in the central-western Alps (Piedmont – Italy and Canton Bern, Switzerland) (e.g., Boggero et al., 1996; Boggero & Nobili, 1998; Fjellheim et al., 2000; Lods-Crozet et al., 2001; Rossaro & Lencioni, 2001; Burgher, 2002; Ward, 2002) and in the central-eastern Alps (Trentino-Alto Adige, Italy and Austria) (e.g., Kownacki & Kownacka, 1994; Füreder et al., 2001; Maiolini & Lencioni, 2001). Earlier research on Alpine headwater stream ecology was performed by Kownacka & Kownacki (1975). Yet information on the taxonomy and ecology of aquatic invertebrates from high altitude lotic systems is still scarce, as is their role in revealing habitat changes. This is particularly true for the Italian Alps: to date, about 90 papers have been published on benthic fauna from Italian high altitude streams since the 1930s, mainly referring to Plecoptera, Trichoptera, Ephemeroptera, Diptera Chironomidae and Simuliidae from the central-western Alps and the Apennines (Lencioni et al., 2001). Most of these data result from hand collections carried out by entomologists interested in a specific taxon, rather than from long-term ecological researches on entire communities (Lencioni et al., 2001). More knowledge of the species response to different abiotic factors is needed, in order to distinguish the effects of pollution from the natural variability affecting community structures (Rossaro & Pietrangelo, 1993). In fact it is known that different species belonging to the same genus (e.g., the chironomids, *Diamesa*, *Eukiefferiella*, *Orthocladius* and *Paratrichocladius*) respond differently to the same environmental variables (Rossaro & Mietto, 1998).

Different stream types can be identified in Alpine headwaters with distinctive abiotic and biotic features: glacier-fed streams (kryal), spring brooks (krenal) and streams fed by rainfall and/or snowmelt (rhithral) (Ward, 2002). Harsh environmental conditions characterise the glacier-fed streams, especially in summer during the melting season. In this period, the temperature does not exceed 4–6 °C, turbidity is high (>200 mg l^{-1} of suspended solids), discharge is highly variable during the day (up to 5–10 times higher in the afternoon than in the morning), current velocity reaches 2–3 m s^{-1}, the substrate is highly unstable, aquatic macrophytes are absent and the biofilm is codominated by cyanobacteria (Maiolini & Lencioni, 2001). In summer, Diamesinae (Diptera Chironomidae) are almost the only inhabitants of these streams. In autumn/winter, when the chrysophyte *Hydrurus foetidus* (Villars) grows, glacial streams can host, besides Diamesinae, other Diptera (mainly Limoniidae), Plecoptera and Trichoptera (Milner et al., 2001; Robinson et al., 2001; Lencioni & Maiolini, 2002). Less harsh environmental conditions and a more diverse and abundant invertebrate community are generally present in non-glacial streams, characterised by transparent and cool waters (summer temperature from 2 to 15 °C), with low discharge and low current velocity fluctuations during the day. Dissolved oxygen is generally fully saturated and carbon dioxide concentration can be very high, favouring the development of algae, mosses and liverworts. The zoobenthic community is codominated by chironomids (Diamesinae and Orthocladiinae), Plecoptera, Ephemeroptera and Trichoptera (Castella et al., 2001). Adverse conditions in these streams may be due to summer or winter droughts. Lake outlets represent a unique stream type, with physical, hydrological and chemical features directly influenced by the source lake (Milner & Petts, 1994; Hieber et al., 2002). Generally, outlets benefit from more stable physico-chemical and hydrological conditions, buffered by the lake. In contrast to outlets of lowland lakes, oligotrophic Alpine lakes may act as sinks rather than sources for organic matter so an increase in filter feeders is not expected and non-insect taxa may prevail (Hieber et al., 2002).

The present paper analyses the zoobenthic communities of 80 high altitude streams with the aim of highlighting the "lake effect" on the upstream–downstream invertebrate distribution and the consistence of lake outlets as a distinctive alpine stream type on a local and inter-regional scale.

Study area

The inlets and outlets of 48 high altitude lakes were investigated in two different Countries (Switzerland and Italy) and two different Italian Regions (Piedmont and Trentino-Alto Adige) for a total of three Alpine areas (Fig. 1): Canton Bern/Switzerland (10 lakes, 17 streams) in the Bernese Alps, Piedmont/Italy (14 lakes, 23 streams) in the Pennine-Lepontine Alps, Trentino-Alto Adige/Italy (24 lakes, 40 streams) in the Rhaetian Alps (Table 1).

The study area is located between latitude 46° N (Pennine-Lepontine and eastern Rhaetian Alps) and 47° N (Bernese and western Rhaetian Alps) and, in a west to east range, between longitude 7–8° E (Pennine-Lepontine and Bernese Alps), and 10–12° E (eastern and western Rhaetian Alps). All but three study sites are located above the tree line, from 1592 (Hinterstockensee, Bernese Alps) to 2705 m a.s.l. (Lake Marmotte, Rhaetian Alps). The Swiss Bernese lakes are located at the lowest altitude (mean 1989 ± 227 m a.s.l.), followed by those of the Pennine-Lepontine (2230 ± 126 m a.s.l.) and Rhaetian Alps (2341 ± 231 m a.s.l.). Most of the Italian study sites are in protected areas, in National and Regional Parks: Val Grande (Piedmont/Pennine-Lepontine) and Stelvio National Park (Trentino-Alto Adige/Rhaetian) and Adamello-Brenta Regional Park (Trentino-Alto Adige/Rhaetian). The 80 investigated streams are located in the catchments of two major Italian lakes (Maggiore and Garda) and rivers (Po and Adige), whereas the Swiss lakes are in the catchment of the river Aare (a tributary of the river Rhine). The lake catchments are dominated by crystalline rocks (granite, diorite, gneiss) except for the Bernese and one of the northern Rhaetian sites, which are located in calcareous areas. All lakes have glacial origins and 31 of the 48 have a permanent inlet and outlet, in the others one of the two is ephemeral.

The Pennine-Lepontine and Rhaetian streams are characterised by lower conductivity, pH and alkalinity than those in the Bernese Alps, as was to be expected from the watershed lithology (Boggero et al., this volume). The Pennine-Lepontine and Rhaetian surface waters, with a median pH of 6.6 and 6.3 and an alkalinity of 38 and 51 μeq l^{-1} respectively, are therefore sensitive to indirect anthropogenic impacts related to airborne pollutants, including potential acidification according

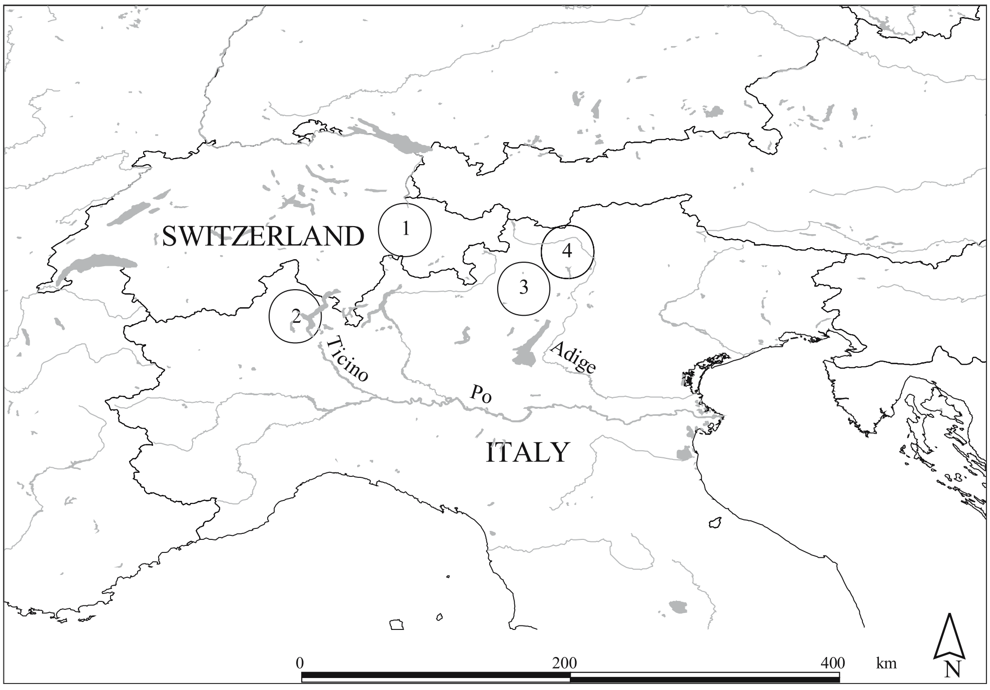

Figure 1. Study areas in the Alps: Switzerland (1, Canton Bern) and Italy (2, Piedmont; 3, Trentino; 4, Alto Adige).

Table 1. Study sites. 80 streams were investigated in the Bernese (Canton Bern, Switzerland), in the Pennine-Lepontine (Piedmont, Italy) and in the Rhaetian Alps (Trentino-Alto Adige, Italy)

Lake	°N	°E	Altitude	Main river basin	Region/Province	Country	Inlet	Outlet	Date
Hinterstockensee	47	8	1592	Aare/Rhine	Canton Bern	Switzerland	1		2000
Seebergsee	47	7	1831	Aare/Rhine				1	2000
Engstlensee	47	8	1850	Aare/Rhine			1	1	2000
Sulsseewli	47	8	1920	Aare/Rhine			1		2000
Sägistalsee	47	8	1935	Aare/Rhine			1	1	2000
Seebodensee	47	8	2042	Aare/Rhine			1	1	2000
Flueseeli	46	7	2045	Aare/Rhine			1	1	2000
Bachsee	47	8	2265	Aare/Rhine			1	1	2000
Hagelseewli	47	8	2339	Aare/Rhine			1	1	2000
Triebtenseewli	47	8	2365	Aare/Rhine			1	1	2000
Paione Inferiore	46	8	2002	Toce/Po	Piedmont	Italy	1	1	2000
Panelatte	46	8	2063	Ticino/Po				1	1991
Matogno	46	8	2087	Toce/Po			1	1	2000
Capezzone	46	8	2100	Toce/Po				1	2000
Variola medio	46	8	2123	Toce/Po			1	1	2000
Paione di mezzo	46	8	2147	Toce/Po				1	2000
Variola superiore	46	8	2190	Toce/Po			1	1	2000
Grande	46	8	2269	Toce/Po			1	1	2000
Paione superiore	46	8	2269	Toce/Po				1	2000
Campo	46	8	2293	Toce/Po			1	1	2000
Pojala	46	8	2305	Toce/Po			1	1	2000
Boden Inferiore	46	8	2334	Toce/Po			1	1	1994
Boden Superiore	46	8	2343	Toce/Po				1	1994
Sfondato	46	8	2422	Toce/Po			1	1	2000
Malghette	46	10	1891	Noce/Adige	Trentino-Alto Adige	Italy	1	1	1995
San Giuliano	46	10	1935	Sarca/Po			1	1	1996
Ritorto	46	10	2058	Sarca/Po			1	1	1996
Scuro delle Malghette	46	10	2160	Sarca/Po			1	1	1996
Artuich	46	10	2166	Sarca/Po			1	1	1996
Nero di Cornisello	46	10	2233	Sarca/Po				1	1996
Tre Laghi I	46	10	2256	Sarca/Po			1	1	1996
Lambin	46	10	2327	Sarca/Po				1	1996
Serodoli	46	10	2371	Sarca/Po			1	1	1996
Mandrone	46	10	2399	Sarca/Po			1	1	1996
Scarpacò	46	10	2469	Sarca/Po				1	1997
Lungo	46	10	2550	Noce/Adige			1	1	2000
Ghiacciato	46	10	2571	Sarca/Po			1		1996
Vedretta	46	10	2605	Sarca/Po			1[a]	1	1997
Marmotte	46	10	2705	Noce/Adige			2	1	2000
Gruensee	47	12	2043	Adige			1	1	2000
Kratzbergersee	47	11	2119	Adige				1	2000
Klammsee	47	12	2258	Adige			1	1	2000
Alplanersee	46	11	2387	Adige			1	1	2000
Kofelrrastersee	47	11	2405	Adige				1	2000
Timmelsschwarzsee	47	11	2514	Adige			1		2000

Continued on p. 221

Table 1. (Continued)

Lake	°N	°E	Altitude	Main river basin	Region/Province	Country	Inlet	Outlet	Date
Milchsee	47	11	2540	Adige				1	2000
Schwarzsee	47	12	2551	Adige			1	1	2000
Rasasser See	47	10	2682	Adige				1	2000

Latitude as °N, longitude as °E, altitude as m a.s.l., and the number of inlets and/or outlets are given for each lake. Date = year of sampling.
[a]Glacier-fed stream.

to Camarero et al. (1995). On the basis of nutrient concentrations, chlorophyll *a* (0.5–4.2 μg l^{-1} as mean on the water column) and transparency (total or equal to half the maximum depth), the investigated lakes can be considered ultra-oligotrophic to oligo-mesotrophic (Cantonati et al., 2002; Boggero et al., this volume).

Most of the lakes are subject to various forms of anthropogenic impact such as tourism, cattle grazing, fish stocking and water abstraction for potable use, or for hydroelectric power generation. American char and brown trout have been introduced into most lakes, while natural minnow populations are common. Detailed information on the lakes discussed in this paper can be found in Boggero et al. (this volume).

Methods

The database considered in this paper refers to the zoobenthic community of 80 streams, 36 inlets (of which one is glacial) and 44 outlets (Table 1). At all sites, surveys were carried out once in September/October (mostly in 2000), a period in which all the lakes were ice-free (Table 1). Qualitative kick samples (Frost et al., 1971) were collected using a standard pond net (250-μm mesh size); different microhabitats in 10–15 m long stations were investigated for 2–5 min. The outlets were sampled at lake-source and/or approximately 100–200 m downstream of the lake. In the Bernese, Pennine-Lepontine and western Rhaetian sites, most surveys were carried out within the EC-project EMERGE and in eastern Rhaetian within the EC-project AASER and the regional project HIGHEST. For this reason the eastern Rhaetian sites (Trentino) were separated from those in the western Rhaetian area (Alto-Adige), on account of the different sampling periods and number of stations per stream, though the two provinces belong to the same region.

Animals were preserved in the field in 75% ethanol and sorted and identified in the laboratory to genus and species level (Tricladida, Ephemeroptera, Plecoptera, Trichoptera, Diptera Chironomidae and Simuliidae) or higher taxonomical level (all the other aquatic invertebrates, with the exception of Nematoda from western Rhaetian streams and Oligochaeta and Hydracarina from Pennine-Lepontine and western Rhaetian ones, which were identified to species).

The relative composition of the zoobenthic community was standardised to the same identification level, and, when more than one station was sampled, the mean number of individuals per stream was considered. α-diversity was measured as number of species and the Shannon–Wiener index (Shannon & Weaver, 1948) and Simpson dominance Index were calculated. Significant differences between inlet and outlet communities were tested with the *t*-Student test and ANOVA using the STATISTICA computer package. Values with $p < 0.05$ were considered significant. Correlations between total number of taxa, total density, EPT taxa, Oligochaeta + Chironomidae/total fauna (taxa) in the outlets and lake altitude and area were calculated. Values with $p < 0.05$ were considered significant.

Non-parametric multivariate analysis (clustering) was applied to faunal data, using the weighted arithmetic average linkage method (WPGMA) on Bray–Curtis similarity matrix (Clarke, 1993).

Samples for chemical analyses were taken at lake-source outlet or, in its absence, in an area of the lake not influenced by inlet flow, at the same time as biological samples (Rogora et al., 2001).

Chemical analyses were performed for the major variables following the procedures found in Tartari & Mosello (1997). No specific chemical samples were taken from the inlets, thus an inlet/outlet comparison was not possible.

Results

A total of 20,536 individuals were collected, distributed over 224 taxa. The highest abundance and richness were found in Piedmont and Trentino, which also had the highest Shannon diversity (Table 2).

A higher number of individuals (13,544) and of taxa (186) were found in the outlets than in the inlets (6992 individuals and 165 taxa). However, no significant difference was found in the Shannon diversity (2.98 and 3.05 mean values for outlets and inlets, respectively). The highest diversity was recorded in the eastern Rhaetian inlets (Trentino), the lowest in those in the western Rhaetian (Alto Adige) (Table 2).

Thirty-eight taxa (17%) were exclusive to the inlets, and most of these taxa were rare (30) and found in only one stream, seven in two and only one in three streams. The outlets had more exclusive taxa (59 = 26%), of which 40 were recorded in only one location, 14 in two and 5 in three or four stations. One hundred and twenty-seven taxa (57%) were common to both stream types. Of these, 33 (26%) were more abundant in the inlets, 58 (46%) in the outlets and 36 (28%) were present in the same number of inlets and outlets.

No genus or species was common to all 80 streams. The most frequent species was the triclad *Crenobia alpina* (Dana) present in 50 streams (63%), followed by the chironomid *Tvetenia calvescens* (Edwards) and the mayfly *Baetis alpinus* (Pictet) present respectively in 30 (38%) and 28 (35%) streams. All the others were recorded in fewer than 30 sites, and 70 in only one site.

Piedmont had the highest number of taxa exclusive to the region, while western Rhaetian had the highest number of taxa common to the four study areas (Fig. 2).

Both inlet and outlet communities were dominated by insects, representing respectively 89 and 81% of the zoobenthic community (Appendix). Diptera prevailed among the insects, with Chironomidae (53 genera and 63 species/groups of species) accounting for 68% of the inlet and 45% of the outlet communities. Though Chironomidae were always the most abundant taxon, they displayed the highest relative abundance (more than 70%) in the Piedmont and Trentino inlets. Most Chironomids belonged to the subfamily Orthocladiinae, which represented 44% of the individuals found in the inlets and 32% of those in the outlets. Chironominae (mainly Tanytarsini) and Tanypodinae had similarly low abundances in inlets and outlets while Diamesinae were far more abundant in the inlets (16%) than in the outlets (1%) (Appendix). In terms of genera, *Tvetenia*, *Eukiefferiella*, *Orthocladius* (subgenera *Orthocladius*, *Euorthocladius* and *Eudactylocladius*), *Corynoneura* and *Micropsectra* were the most frequent, occurring in more than 30% of the sites. Some of

Table 2. Number of streams, mean number of individuals/stream, number of taxa, Shannon diversity (H') and Simpson dominance (D) indices for Swiss (S), Piedmont (P), Trentino (Tn) and Alto Adige (AA) inlets (in) and outlets (out)

	S_in	S_out	P_in	P_out	Tn_in	Tn_out	AA_in	AA_out
Streams	9	8	9	14	13	14	6	7
Individuals	85	114	273	340	248	437	91	250
Taxa	60	51	82	110	89	73	38	53
H'	3.15	2.81	3.15	3.24	3.34	2.85	2.54	3
D	0.002	0.004	0.082	0.085	0.028	0.190	0.002	0.010
Individuals	99		307		342		171	
Taxa	82		133		113		61	
H'	3.28		3.41		3.34		3.13	
D	0.064		0.068		0.070		0.062	

In the lower part of the table values are also presented at the regional scale.

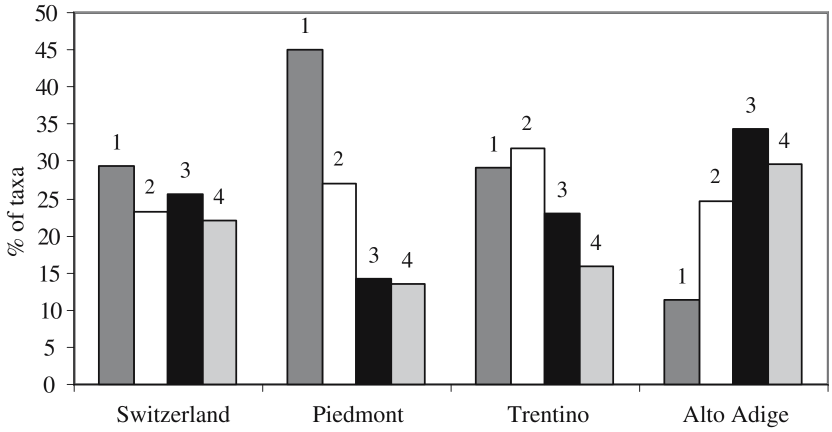

Figure 2. Percentage of taxa exclusive (1), common to two (2), three (3) and four (4) regions.

these (*Tvetenia*, *Eukiefferiella*, *Corynoneura*, *Micropsectra*), along with *Diamesa* and *Heterotrissocladius* were also the most abundant. In terms of species/groups of species, *Eukiefferiella brevicalcar* (Kieffer), *Tvetenia calvescens* (Edwards) and *Diamesa cinerella* gr. were those most frequently found in the inlets (≥10 sites), while *T. calvescens* ($p = 0.016$), *Rheocricotopus effusus* (Walker), *Heterotrissocladius marcidus* (Walker), *Corynoneura lobata* Edwards, *Paratanytarsus austriacus* (Kieffer) and *T. bavarica* (Goetghebuer), were the most common in the outlets.

The second dipteran family in order of abundance was Simuliidae. The typical high altitude species *Prosimulium latimucro* (Enderlein) was more widespread and abundant in the inlets while *Simulium aureum* gr., *S. cryophilum* (Rubtsov), *S. monticola* Friederichs, *S. noelleri* Friederichs and *S. vernum* Macquart prevailed, though in small numbers, in the outlets.

Ephemeroptera were generally present in low numbers with the exception of two outlets in eastern Rhaetian, where they were collected in stations at lower altitudes. In these two cases Baetidae and Heptageniidae were both much more abundant than in the respective inlets. To a lesser extent, Ephemeroptera also prevailed in outlets in Piedmont, but not in the Swiss and western Rhaetian sites. *B. alpinus* was the most widespread (28 sites) and abundant species, followed by *B. rhodani* (Pictet) (7 sites) and *B. muticus* (Linné) found in only one Swiss outlet. *B. alpinus* was one of the best represented species in the outlets, accounting for 13% of all individuals. The family Heptageniidae was recorded in only a few sites, the most widespread taxa being *Ecdyonurus venosus* gr. found in 7 sites, mostly outlets, *E. helveticus* gr. in two inlets and two outlets and *E. auranticus* (Burmeister) in a single outlet in Piedmont. The genus *Heptagenia* was found only in three outlets while *Epeorus alpicola* (Eaton), *Rhithrogena hybrida* gr. and *R. loyolaea* gr. prevailed in the inlets.

Plecoptera were more abundant and widespread in the outlets, with the exception of the Swiss sites. Nemouridae was the best represented family, with the genus *Nemoura* prevailing in density and distribution in the outlets, particularly the species *N. mortoni* (Ris) followed by *N. cinerea* (Retzius) and *N. obtusa* (Ris), found in only one location. *Nemurella pictetii* Klapálek was equally distributed in 3 inlets and 3 outlets. Perlodidae (mostly *Isoperla* spp.) were found in larger numbers in the outlets (10 sites) than in the inlets (6 sites), with the sole exception of *Dictyogenus fontium* (Ris), restricted to two inlets. The genus *Leuctra* was recorded in 15 inlets and in an equal number of outlets, with similar low abundances. In contrast, the genus *Capnia*, belonging to the same family, was found only in three inlets.

Most of the Trichoptera were found in the Piedmont and eastern Rhaetian sites and were generally more diverse, abundant and widespread in the outlets than in the inlets. Limnephilidae were everywhere the dominant family, *Drusus discolor* (Rambur) being locally abundant in the outlets. Rhyachophilidae were in all regions more abundant in the outlets and filterers such as the philopotamid *Philopotamus ludificatus* McLachlan and the polycentropodid *Plectrocnemia conspersa* (Curtis) were locally present in the outlets. Eleven species were exclusive to outlets, generally in low numbers and few locations: *Silo nigricornis* (Pictet), *Melampophylax mucoreus* (Hagen), *Odontocerum albicorne* (Scopoli), *Philopotamus montanus* (Donovan), *Plectrocnemia conspersa* (Curtis), *Rhyacophila aurata* Brauer, *R. dorsalis* (Curtis), *R. glareosa* McLachlan, *R. italica* Moretti, *R. occidentalis* McLachlan and *R. stigmatica* (Kolenati).

Five taxa were restricted to inlet habitats: *Drusus biguttatus* (Pictet), *Halesus* cf. *radiatus* (Curtis), *Micropterna* sp. and *Wormaldia* sp.

Other insect orders such as Odonata, Hemiptera, Coleoptera and Megaloptera were sporadically found comprising few individuals.

The most abundant and widespread of non-insect taxa was the triclad *C. alpina*, recorded with a relative abundance of 2% in 22 inlet and 6% in 28 outlet communities. In all the regions *C. alpina* was more than twice as abundant in the outlets than the inlets. Among the Oligochaeta, the most abundant families were Naididae and Enchytraeidae, respectively 5 and 3 times more abundant in the outlets than in the inlets. Haplotaxidae, Lumbriculidae and Lumbricidae were everywhere rare. The only species present in both Piedmont and western Rhaetian sites was *Nais communis* Piguet. In Piedmont, the abundance and diversity of Hydracarina were twice as high in the outlets (12 taxa) than in the inlets (6 taxa) and only three species shared both stream types (*Feltria minuta* Koenike, *Lebertia tuberosa* Thor and *Sperchon glandulosus* Koenike). Gastropoda (*Limnea* sp.) were found in high numbers only in one Swiss outlet.

Along the west–east gradient, significant differences were found only in the relative abundance of some taxa: *C. lobata* ($p < 0.001$), *Eukiefferiella claripennis* Lundbeck ($p < 0.013$) and *B. rhodani* ($p = 0.039$) decreased in abundance, while *Pseudokiefferiella parva* (Edwards) ($p = 0.004$), *Pseudodiamesa branickii* (Nowicki) ($p = 0.043$), *Eukiefferiella tirolensis* Goetghebuer ($p = 0.006$) and *Stilocladius montanus* (Rossaro) ($p = 0.018$) showed an increase.

Some taxa (e.g., *Heleniella ornaticollis* (Edwards), *Micropsectra bidentata* (Goetghebuer), *Baetis muticus* (Linnaeus)), appeared to be significantly better represented on the northern than in the southern side of the Alps. *Eukiefferiella claripennis* Lundbeck, and *Baetis rhodani* (Pictet) were found to be significantly more abundant in the western Alps while *Pseudokiefferiella parva* (Edwards) and *Prosimulium latimucro* (Enderlein) in the eastern Alps.

The observed distribution of macroinvertebrate species justify the site separation observed in Figure 3.

Based on macroinvertebrate distribution, the Trentino streams were clearly separated from the others, with about 10% similarity with all others sites. A low similarity was calculated between inlets and outlets in all regions (the highest was of about 40% between inlets and outlets in the Piedmont region).

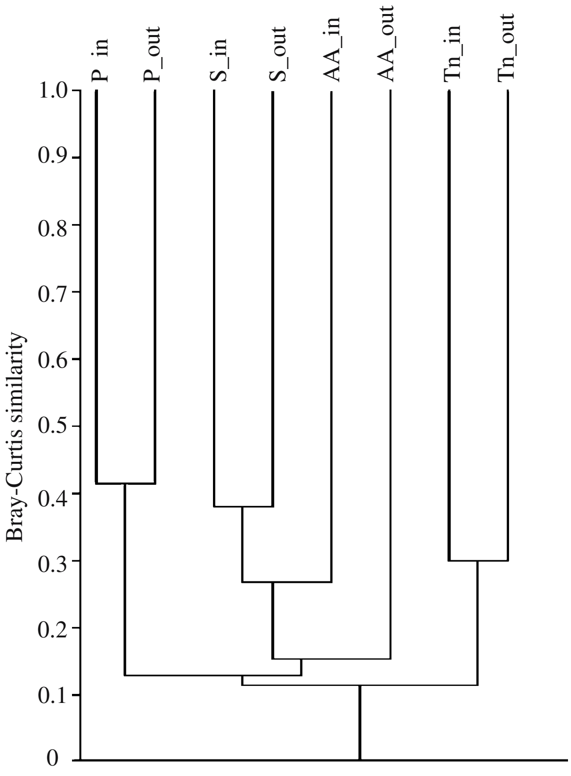

Figure 3. Hierarchical classification of the sampling sites based on macroinvertebrate taxa using the weighted arithmetic average linkage method (WPGMA) on Bray–Curtis similarity matrix.

Significant correlation was found between total number of taxa and lake area (Fig. 4).

This correlation was particularly evident when lake area is higher than 20 ha. In case of areas lower than 4–5 ha, the number of taxa ranged in a wide interval (10–49 taxa, median 21 ± 8), while in outlets of larger lakes the richness ranged from 7 to 20 taxa with a median of 13 ± 5.

Discussion

Ameliorated habitat conditions in terms of discharge regime, turbidity, temperature range and substrate stability are generally present in the outlets in comparison to the generally more harsh environment of the inlets, determined by the presence of lakes. Furthermore, a higher abundance of filter feeders is expected in the outlets, exploiting a higher organic matter amount (Müller, 1954; Richardson & Mackay, 1991). This condition is not always present in oligotrophic high mountain lake ecosystems, where no evidence can be found of increasing densities of filter feeding taxa downstream of the lakes, acting such lakes more as sinks rather than sources of organic matter (Lencioni, 2000; Milner et al., 2001; Hieber et al., 2002). However, the relationship between transported organic matter and the presence of filter-feeders (e.g. Simuliidae) is not always evident, as found in the intermittent outlet of a small lake in the Tatra Mountains (1600 m a.s.l.) with the former decreasing downstream and the latter increasing (Kownacki et al., 1997). In this case the zoobenthic community of the outlet was mostly represented by scraper-feeding organisms (mainly the Oligochaeta *N. communis*).

The studied outlets, save few exceptions, were poor in filter feeders, had higher population densities but not always a higher richness than inlets.

Lake area seemed to affect the total richness in the outlets, richness decreasing with increasing lake area. This could be associated also to the trophic status of the studied lakes, being the largest also the deepest and ultraoligo-oligomesothrophic ones.

It is difficult to make comparisons with existing literature as most published studies focus on glacier-fed Alpine streams, while all but one of the inlets (Vedretta, Trentino) investigated in this work were rhithral or krenal reaches. Evidence was produced demonstrating that the Roseg proglacial lake (Switzerland, 2159 m a.s.l) raised average summer temperatures in the lake outlet by 3.3 °C compared to the adjacent kryal stream segment and interrupted downstream transport of coarse sediments (Uhelinger et al., 2003). Due to the ameliorated habitat conditions (channel stability, increased temperature and stable discharge patterns), the zoobenthic community of the outlet exhibited less variability in total and relative abundance than that in the kryal biotope. While Chironomidae clearly dominated the latter, Ephemeroptera, Plecoptera and Trichoptera were abundant in the outlet, but no predominance of filter-feeding organisms was observed (Burgher & Ward, 2001). In a comparable

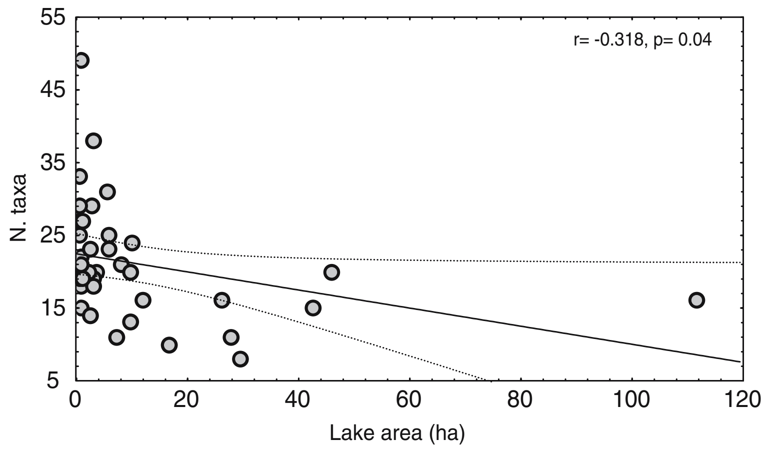

Figure 4. Response functions for the total number of macroinvertebrate taxa in the outlets on lake area. The dashed lines are approximate 95% confidence intervals around the smooth function. The significance of correlations is given as *r* and *p* value.

area in the Italian Alps, the kryal inlet and the outlet of Lake Vedretta (2605 m a.s.l., Trentino) showed a similar trend, with Chironomidae (mainly Diamesinae) dominating the kryal benthos (> 80%) while Simuliidae, Plecoptera, Trichoptera and Oligochaeta were seasonally abundant in the outlet. During the ice-melt season, a ''trap-effect'' was evident for suspended solids (on average, 57.6 ± 80.4 above and 20.9 ± 12.6 mg l^{-1} below the lake), while water temperature was higher below the lake than above (mean value 5 and 2 °C, respectively) (Lencioni. 2000).

The main results are generally consistent with comparable studies in the Alps, in particular:

– both inlet and outlet communities were dominated by insects, specifically by Diptera Chironomidae, but other insects (mainly Baetidae) and non-insects (mainly Tricladida and Oligochaeta) had higher relative abundance in outlets than the inlets;
– Diamesinae (Chironomidae) were confined almost entirely to the inlets, while the relative abundance of Orthocladiinae and Chironominae was higher in the outlets.

As highlighted by Rossaro et al., (this volume), there are a number of differences in the distribution of some chironomid species along the west–east and north–south gradients in the Alps. Among these, *H. ornaticollis* was better represented on the northern side of the chain, while *H. serratosioi* Ringe was more common in Italy.

Further biogeographical conclusions are hindered by the scarcity of material identifiable to species (i.e. pupal exuviae and pharate adult males) in the collected material.

Conclusions

On the basis of the distribution of the 224 taxa identified, the four regions appeared to be rather well separated and the same was observed between inlets and outlets within the same region (Fig. 3). This hindered, on the basis of this database, the definition of a type-community for Alpine inlets and outlets. In our opinion, different levels of invertebrate identification by the working groups affected this result.

Among abiotic variables, lake morphometry should be considered in explaining stream biodiversity, especially in the outlets where a negative correlation between lake area and number of taxa found. This could depend on a higher sink effect of organic matter in larger oligotrophic lakes.

The aim of this study was to verify differences induced in the zoobenthic communities of headwater Alpine streams by the presence of a lake along their course – and this was achieved to a certain extent. A more detailed analysis was hampered by the fact that the sampling effort that generated the database did not have this objective as its ultimate aim. In this sense constraints were represented by: (i) the lack of information regarding seasonality; (ii) an insufficient variety of inlet types (only one glacier-fed stream was included); and (iii) the lack of environmental data for inlets and outlets.

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Appendix

Relative abundance of families or higher taxonomic levels in the Swiss (S), Piedmont (P), Trentino (Tn) and Alto Adige (AA) inlets (in) and outlets (out). Chironomid subfamilies and tribes of Chironominae (Chironomini and Tanytarsini) are included. In italics the total number of individuals counted

	S_in	S_out	P_in	P_out	Tn_in	Tn_out	AA_in	AA_out
N. individuals	*761*	*915*	*2456*	*4766*	*3228*	*6111*	*547*	*1752*
TRICLADIDA	5.3	12.3	2.9	9.6	1.0	2.6	0.4	1.3
NEMATODA	2.2	2.0			0.1		3.7	11.3
GASTROPODA	0.4	2.4		0.1				
BIVALVIA	0.1	0.2	0.5	0.3				
OLIGOCHAETA	21.9	10.2	11.3	22.8	0.7	0.5	1.5	7.7
HYDRACARINA	0.7		0.9	0.8	0.1	0.2	8.0	7.8
EPHEMEROPTERA	8.4	2.8	1.8	2.7	3.2	34.0	36.9	2.6
Baetidae	4.6	2.6	1.3	1.8	1.9	27.7	36.6	2.5
Heptageniidae	3.8	0.2	0.5	0.8	1.2	6.3	0.4	0.1
ODONATA			0.1	0.02				
PLECOPTERA	11.0	5.0	5.3	12.2	7.3	17.3	4.0	2.2
Plecoptera juv.					0.1	2.7	0.2	
Chloroperlidae	0.1							
Perlidae					0.04	0.3		
Perlodidae	0.4	0.1		1.0	0.6	1.5	0.2	0.3
Leuctridae	7.4	2.7	1.8	2.3	1.6	0.4	2.4	0.9
Nemouridae	3.2	2.2	3.5	8.9	4.6	12.3	1.3	0.8
Taeniopterygidae					0.3			0.1
HEMIPTERA				0.04				
COLEOPTERA			0.04	0.1	0.1	0.05		
Dytiscidae			0.04	0.1		0.02		
Elminthidae				0.02				
Helophoridae					0.1	0.03		
Hydraenidae					0.03			
Hydroporinae				0.02				
MEGALOPTERA			0.6	0.02				

Continued on p. 229

Appendix (Continued)

	S_in	S_out	P_in	P_out	Tn_in	Tn_out	AA_in	AA_out
DIPTERA	49.5	64.3	76.2	46.4	85.6	43.5	42.6	66.7
Diptera juv.	1.4	1.3						
Limnoniidae			1.4	0.7	0.9	0.7	1.5	0.5
Tipulidae	0.1		0.3	0.02				
Psychodidae		0.3	0.6	0.04		0.5		
Dixidae				0.1		0.02		
Thaumaleidae				0.04	0.4	0.05		
Simuliidae	0.1			2.2	10.8	4.7		0.2
Ceratopogonidae			0.2	0.04		0.02		
Chironomidae	47.7	62.6	73.4	42.8	72.4	37.6	41.1	65.2
Chironomidae juv.					2.6	1.9		
Tanypodinae	2.0	0.1	4.0	5.4	0.9	0.1	0.4	1.1
Diamesinae	5.7	0.8	1.9	1.0	29.9	1.0	9.0	3.5
Prodiamesinae		0.1	0.0					
Orthocladiinae	37.7	41.7	55.8	28.4	38.0	26.6	30.5	58.4
Chironomini	0.1	6.9	0.3	0.1				
Tanytarsini	2.2	13.0	11.4	8.0	1.0	8.0	1.3	2.2
Stratiomydae						0.05		
Athericidae				0.02				
Empididae	0.1		0.3	0.4	1.1			0.9
TRICHOPTERA	0.4	0.8	0.4	4.9	2.0	1.8	2.9	0.5
Goeridae				0.1	0.2			
Hydropsychidae				0.02	0.03			
Limnephilidae			0.3	2.5	1.1	0.9	2.7	0.2
Odontoceridae				0.2		0.1		
Philopotamidae	0.4	0.3		0.7	0.2		0.2	0.1
Polycentropodidae			0.04	0.2	0.1	0.3		
Psychomyiidae					0.03			
Rhyachophilidae		0.4	0.04	1.2	0.4	0.4		0.2
Sericostomatidae						0.03		