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THE INFLUENCE OF ENVIRONMENTAL VARIABLES ON THE DISTRIBUTION OF DIATOM COMMUNITIES IN AN ALPINE PROGLACIAL STREAM, TAILLON-GABIÉTOUS CATCHMENT, FRENCH PYRÉNÉES

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ABSTRACT.– Algae are important components of stream ecosystems but their distribution in alpine streams has received little attention. We studied diatom communities within a small alpine glacierized catchment (Taillon-Gabiétous, French Pyrénées) to explore longitudinal patterns in diatom genera and identify principal physicochemical habitat variables determining distributions. Diatoms, hydrochemical and physical habitat data were collected from four sites along the Taillon Glacier stream and one site on a groundwater fed tributary (Tourettes) between July-August, 2002 (peak glacial melt). Diatom genera increased from three at the glacier snout to 13 approximately 1.2 km downstream, influenced predominantly by increased water temperature, channel stability and conductivity. Cymbella, Fragilaria *and* Navicula *dominated at all sites.* Cocconeis *was relatively abundant in the Tourettes groundwater stream where higher water temperature may have enhanced colonisation.*

RÉSUMÉ.– Bien que les algues soient d'importants composants des écosystèmes des eaux courantes, leur distribution dans les torrents de montagne a été peu étudiée. Nous avons étudié ici les communautés de Diatomées dans un petit bassin alpin soumis à l'influence glaciaire (Taillon-Gabiétous, Pyrénées françaises) dans le but d'explorer les modèles de distribution longitudinale des genres de Diatomées et d'identifier les principaux paramètres physico-chimiques de l'habitat qui les conditionne. Aussi bien les Diatomées que les données hydrochimiques et physiques ont été échantillonnés en quatre points au long du ruisseau du glacier du Taillon et sur un autre point dans l'eau d'un ruisseau tributaire (Tourettes) entre Juillet et Août 2002, précisément pendant la période de fusion maximale. Les genres de Diatomées augmentent depuis 3 au bord du glacier jusqu'à 13 à 1,2 km plus bas, grâce à l'augmentation de la température de l'eau, à sa meilleure stabilité et à sa conductivité. Cymbella, Fragilaria *et* Navicula *prédominent* *en tous les points, alors que* Cocconeis *était relativement abondant dans l'eau du fond de Tourettes, où la température plus élevée de l'eau en facilitait la colonisation.*

RESUMEN.– *Aunque las algas son importantes componentes de los ecosistemas de aguas corrientes, su distribución en los arroyos de montaña ha merecido poca atención. Hemos estudiado aquí las comunidades de diatomeas en una pequeña cuenca alpina sometida al glaciarismo (Taillón-Gabieto, Pirineos franceses) con el fin de explorar los patrones de distribución longitudinal de los géneros de diatomeas e identificar las principales varialbes fisicoquímicas del hábitat que los condicionan. Tanto las diatomeas como los datos hidroquímicos y físicos se tomaron en cuatro puntos a lo largo del arroyo del Glaciar del Taillón y otro punto en el agua de un arroyo tributario (Tourettes) entre Julio y Agosto de 2002, precisamente durante el máximo de fusión. Los géneros de diatomeas aumentan de 3 en el borde del glaciar hasta 13 a 1,2 km aguas abajo, gracias al incremento de la temperatura del agua, a su estabilidad mayor y a su conductividad.* Cymbella, Fragilaria *y* Navicula *dominaban en todos los puntos, mientras que* Cocconeis *era relativamente abundante en el agua del fondo de Tourettes, donde la temperatura algo mayor del agua facilitaba la colonización.*

Key-words: Diatom genera, water temperature and conductivity, glaciar stream, Central Pyrenees, France.

1. Introduction

Recent work has greatly enhanced our understanding of alpine stream ecology, particularly with respect to benthic macroinvertebrate communities in glacial streams (reviewed by MILNER *et al.*, 2001). However, despite the important role of algae within stream food webs, the distribution and diversity of algal communities in alpine streams has received little consideration (KAWECKA, 1971, 1980; UEHLINGER *et al.*, 1998; HIEBER *et al.*, 2001). In alpine (above the treeline) environments, riparian vegetation is typically limited to grasses and small shrubs so benthic algae may act as the main source of energy input to these systems (ZAH *et al.*, 2001).

Diatoms are an important algal sub-group as short cell cycles enables rapid reaction to environmental perturbation (JÜTTNER *et al.*, 1996), potentially allowing them to inhabit physically 'harsh' glacial streams. Water temperature and channel stability change with distance from glaciers drives predictable changes in benthic macroinvertebrate community composition (e.g. MILNER *et al.*, 2001). However, studies of diatom communities in relation to environmental conditions in glacial streams are mainly from Arctic and Antarctic regions (e.g. ELSTER & SVOBODA, 1996) and little data exists regarding alpine glacial streams.

This study reports upon a short-term preliminary study of diatom communities in a small alpine glacierized catchment (Taillon-Gabiétous, French Pyrénées) and aims to:

(1) establish if distinct longitudinal patterns in diatoms, similar to benthic macroinvertebrate communities (MILNER *et al.*, 2001), are evident downstream of a small glacier, (2) identify the principal environmental variables determining any longitudinal distributions of diatom genera, and (3) assess the effect of water input from a groundwater tributary, upon the longitudinal diatom community gradient. Previous work in the catchment has identified substantial differences in physical and chemical properties of different stream sections (e.g. SMITH *et al.*, 2001; SNOOK & MILNER, 2001). In this study we investigated whether this large variation would be reflected in the relative abundance of diatom genera.

2. Methodology

2.1 Study Area

Fieldwork was undertaken between 16 July and 10 August 2002 within the Taillon-Gabiétous catchment (43°6'N, 0°10'W), Cirque du Gavarnie, French Pyrénées (Figure 1), during a period of relatively high glacial ice-melt. The catchment covers an area of 6.4 km^2, and spans an altitudinal range from 3144 m to 1850 m at the most downstream point sampled (see SMITH *et al.*, 2001 for further details). The study area was located in alpine meadow above the treeline where stream channels were unshaded.

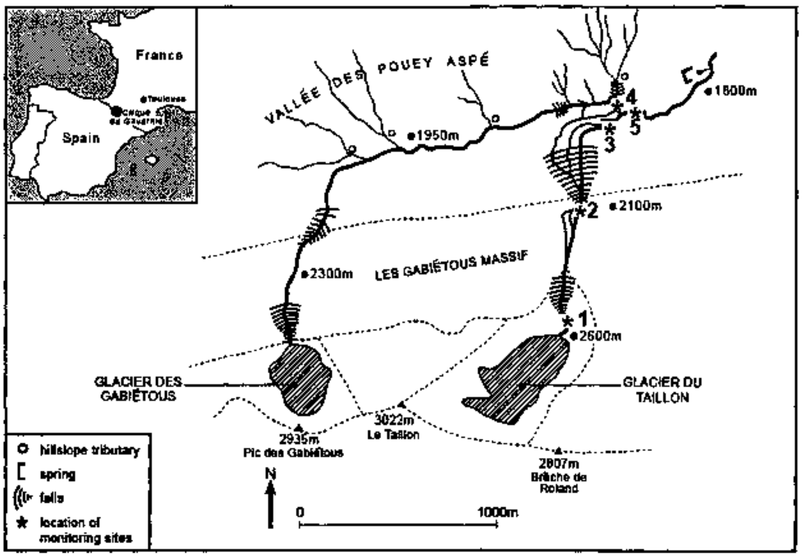

Figure 1. Map of Taillon-Gabiétous catchment showing study sites.

2.2 *Field Monitoring*

Diatom sampling was undertaken on two occasions at five sites (Figure 1). Four sites were studied on the Taillon stream (Figure 1; Table 1) from the glacier snout to approximately 1.2 km downstream, spanning an altitudinal range of 660 m. A fifth site (Site 4) was located on the Tourettes tributary, predominantly fed from hillslope and upwelling groundwaters (BROWN *et al.*, 2004). Stream length from Site 1 to Site 5 was approximately 2 km due to a series of steep falls between Sites 1 and 3 (Figure 1).

Table 1. Characteristics of the five study sites. For locations within the catchment see Figure 1.

Site	Stream	Distance from glacier margin (m)	Altitude (m a.s.l.)	Gradient ($m\ m^{-1}$)	Mean Depth (m)	Mean Width (m)	Mean Discharge ($m^3\ s^{-1}$)
1	Taillon	50	2500	0.079	0.07	3.32	-
2	Taillon	900	2200	0.085	0.08	1.66	-
3	Taillon	1100	1850	0.041	0.09	2.97	0.06
4	Tourettes	N/A	1843	0.030	0.08	2.72	0.05
5	Taillon	1180	1840	0.017	0.14	3.27	0.17

2.3 *Physical habitat variables*

Water temperature was monitored using synchronised Campbell Scientific combined conductivity-temperature probes and CR10X/CR21X dataloggers, or Gemini TinyTag dataloggers (for further details see BROWN *et al.*, 2004). Temperature data were recorded every 15 mins. Temperatures for Site 2 were spot measurements. Channel stability was evaluated using the bottom component of the Pfankuch (PFAN) index (PFANKUCH, 1975), and as Macroscale channel stability (MSS):

$$MSS = [(w1/v1) + (w2/v2) + (w3/v3)]/3$$

where $w1$ to $w3$ are the combined widths (m) of channels containing flow at mid reach and 10 m upstream and downstream of this point; and $v1$ to $v3$ are the full channel width (m) to the point of continuous bank vegetation. Froude Number, was calculated for each sample according to STATZNER *et al.* (1988):

$$Fr = U / \sqrt{gD}$$

Where U is current velocity, g is acceleration due to gravity and D is water depth. Current velocity was measured using a Sensa RC2 meter at 0.6x stream depth. Suspended sediment concentrations (SSC; mg L^{-1}) were determined from 500 ml water samples. Water samples were filtered through preweighed Whatman cellulose nitrate filter papers (0.45µm), dried at 30°C for 24 hrs, and reweighed to determine SSC.

2.4 *Hydrochemical variables*

Electrical conductivity was measured every 15 min at Sites 3, 4 and 5. Spot measurements were taken weekly (low/high flow) at Sites 1 and 2 using a WPA CM25 probe. Weekly measurements of pH were taken at all sites (low/high flow) using a Jenway 3150 meter. Water samples were taken weekly at all sites except Site 2. Samples were filtered through 0.45 µm Whatman cellulose nitrate filter papers, stored in 75 ml HDPE bottles and frozen prior to analysis. Samples were analysed for major anions (Cl^-, NO_3^-, SO_4^{2-}) and cations (Ca^{2+}, K^+, Mg^{2+}, Na^{2+}) using a Dionex 4000i ion chromatograph. Soluble reactive phosphate and NH_4^+ concentrations were measured by standard colorimetric analyses. Silica concentrations were measured with the molybdosilic acid method (see WADHAM *et al.*, 1998).

2.5 *Diatom Communities*

For each site, five cobbles (median b-axis = 10 cm) were selected randomly from riffles on two sampling dates. Diatoms from the stone surfaces were removed with a stiff nylon brush into a tray. To prevent cross-contamination, a different brush was used for each site. Samples were stored in polyethylene bottles and preserved in 4% formaldehyde. In the laboratory, samples were prepared using hydrogen peroxide. Cleaned material was mounted in Naphrax. As this was a preliminary study, a sub-sample of 50 diatom frustules was identified from each sample stone. In total, 500 diatom frustules were identified for each site (50 frustules x 5 stones x 2 sampling dates).

2.6 *Data Analysis*

Diatom assemblages were related to environmental variables by direct gradient analysis (Canonical Correspondence Analysis; CCA) in CANOCO 4.0 (TER BRAAK & SMILAUER, 1998). Forward selection determined which subset of the 21 habitat variables explained a significant ($p < 0.05$) proportion of the variance within the data set. The significance of the constrained model was tested against 199 Monte-Carlo permutations. Because no hydrochemical data were available for Site 2, these samples were made supplementary. Therefore, they do not influence the definition of the ordination axes but are added by projection (i.e. regression onto the existing ordination axes).

3. Results

3.1 Physical habitat and hydrochemical variables

Sites on the Taillon stream were characterised by increasing water temperatures with distance from the glacier snout (Table 2). Temperatures increased from 0.3°C at Site 1 to 9.4°C at Site 5. Water temperature was warmest and least variable at Site 4 (see also BROWN *et al.*, 2004). Daily mean and maximum temperatures were found to co-vary (Pearson's correlation; r = 0.894) therefore only mean temperatures were used in subsequent analyses.

Table 2. Water temperature regime and measures of channel/hydraulic stability (Susp. Sed. Conc. = Suspended Sediment Concentration) (PFAN = Pfankuch Index, MSS = Macroscale Stability Index) for the five study sites.

	Temperature (°C)			Channel Stability Indices			
Site	Mean	Min	Max	PFAN	MSS	Froude No. (mean)	Susp. Sed. Conc. (mg/L)
1	0.28	-0.25	1.55	42	0.68	1.01	119.2
2	6.20	–	–	41	0.70	0.81	–
3	8.42	4.12	13.72	37	0.49	0.68	51.9
4	10.16	7.08	13.06	25	0.81	0.55	9.14
5	9.38	5.25	14.81	33	0.48	0.71	60.3

Channel stability was lowest at the glacial snout and consistently increased downstream on the Taillon stream to Site 5. The most stable channel was the Tourettes tributary (Table 2). Macroscale stability showed a less consistent trend ,increasing from Site 1 to 2, but then decreasing sharply at Site 3 and remaining low at Site 5 (Table 2). Froude Number varied between individual samples, but a general trend of lower average values was evident with distance from the glacier (Table 2). Therefore, all measures of channel and hydraulic stability show a longitudinal pattern of increasing stability with distance from the glacier snout. Suspended sediment concentration was highest at the Taillon Glacier snout, and decreased downstream. Concentrations were higher at Site 5 than at Site 3, due to a glacial tributary input below Site 3, which carries elevated sediment loads. Lowest suspended sediment concentrations were found at Site 4 (Table 2).

Conductivity increased downstream and was highest in the Tourettes tributary (Table 3). Concentrations of all major ions except Mg^{2+}, NO_3^- and SO_4^{2-} were highest at Site 4 (Table 3). Greatest NO_3^- concentrations were recorded at Site 1 close to the glacial snout. Mg^{2+} and SO_4^{2-} concentrations were highest at Site 2. Phosphate concentrations ranged by 1.7 µeq L^{-1} but showed no clear downstream pattern. Silica concentration was lowest at Site 1 but almost doubled downstream at Site 3. Concentrations of silica were greatest in the Tourettes tributary (Site 4). Water pH was highest at Site 1 with average values decreasing with distance downstream (Table 3). Ammonium concentrations were greatest at Site 1 and decreased downstream, and were lowest at Site 4.

Table 3. Mean values of major ion and silica concentrations, and conductivity and pH for the five study sites.

Site	Ca^{2+} (µeq/l)	Mg^{2+} (µeq/l)	Na^+ (µeq/l)	K^+ (µeq/l)	Cl^- (µeq/l)	NO_3^- (µeq/l)	SO_4^{2-} (µeq/l)	Si (mg/l)	NH_4^+ (µeq/l)	PO_4^- (µeq/l)	Conductivity (µs cm^{-1})	pH
1	544.79	364.49	12.75	1.20	18.60	23.42	160.79	0.20	1.92	3.85	46	8.17
2	–	–	–	–	–	–	–	–	–	–	69	8.12
3	845.04	397.68	13.67	1.74	13.96	13.47	183.61	0.36	0.68	5.50	97	8.04
4	853.74	340.19	24.07	2.33	19.12	19.25	164.12	0.81	0.55	4.62	116	7.77
5	836.57	381.14	15.69	1.71	16.00	19.96	166.54	0.43	0.68	3.94	106	7.98

3.2 Diatom Community Structure

A total of 14 taxa (four families) were identified from the Taillon-Gabiétous catchment. Most taxa belonged to either Biraphidineae (6) or Araphidineae (5), with Monoraphidineae (2) and Raphidineae (1) also present. The most abundant taxa were *Fragilaria, Navicula, Cymbella* and *Diatomella* (Table 4). The number of genera progressively increased along the Taillon stream from three (Site 1) to 13 (Site 5; Table 4), with clear variations in relative abundance at the five sites (Table 4).

At Sites 1 and 2, *Fragilaria* dominated the community with *Cymbella* and *Navicula* (Table 4). Of the seven other genera at Site 2, *Diatomella* and *Hannaea* were most common. *Fragilaria* and *Navicula* were co- dominant at Site 3, with *Diatomella Hannaea, Meridion* and *Tabellaria* more abundant than Site 2. Three additional genera colonized Site 3 (*Achnanthes, Nitzschia* and *Synedra),* but *Diatoma,* and *Eunotia* found at Site 2 were absent (Table 4). *Navicula* and *Diatomella* were most abundant at the groundwater-fed Site 4. *Nitzschia* found at Site 3 was absent in the Tourettes stream, but *Cocconeis* was added and abundant compared with other taxa. At Site 5 below the confluence of the two streams, *Fragilaria* and *Navicula* were the most abundant genera. *Cocconeis* was found in the Taillon stream at Site 5, although in less abundance than in the Tourettes tributary (Table 4).

Table 4. Number of diatom frustules counted (relative abundance in parentheses) and number of diatom genera (richness) at the five study sites.

Taxa	Site 1	Site 2	Site 3	Site 4	Site 5
Cymbella	189 (0.38)	53 (0.11)	62 (0.12)	25 (0.05)	24 (0.05)
Fragilaria	196 (0.39)	282 (0.56)	153 (0.31)	143 (0.29)	195 (0.39)
Navicula	115 (0.23)	87 (0.17)	113 (0.23)	123 (0.25)	121 (0.24)
Diatoma	–	2 (<0.01)	–	4 (0.01)	7 (0.01)
Eunotia	–	1 (<0.01)	–	3 (0.01)	–
Hannaea	–	13 (0.03)	22 (0.04)	29 (0.06)	12 (0.02)
Meridion	–	4 (0.01)	30 (0.06)	9 (0.02)	30 (0.06)
Pinnularia	–	3 (0.01)	6 (0.01)	1 (<0.01)	2 (<0.01)
Tabellaria	–	4 (0.01)	14 (0.03)	5 (0.18)	17 (0.03)
Diatomella	–	51 (0.1)	75 (0.15)	91 (0.03)	77 (0.15)
Achnanthes	–	–	9 (0.02)	17 (0.03)	3 (0.01)
Nitzschia	–	–	3 (0.01)	–	1 (<0.01)
Synedra	–	–	13 (0.03)	17 (0.03)	8 (0.02)
Cocconeis	–	–	–	33 (0.07)	3 (0.01)
Richness	3	10	11	13	13

3.3 The influence of environmental variables upon diatom communities

Forward selection identified mean water temperature and PFAN as the most significant physical habitat variables, and conductivity, Si and Ca^{2+} as the most significant hydrochemical variables in determining the diatom distributions. Of these five retained variables, mean temperature, channel stability (PFAN) and conductivity explained most of the diatom assemblage variance on both axes (93.5%). The constrained CCA explained 35% of the variance in the diatom data ($\lambda_1 = 0.19$, $\lambda_2 = 0.07$). Interset correlations of environmental variables with CCA axes revealed that variation along the first axis (22% of total variation; $r = 0.897$, Monte-Carlo $p = 0.05$; 63.0% of taxa-env. relation) was related to mean temperature, conductivity and PFAN (Table 4). Axis 2 ($r = 0.750$) accounted for 7% of the total variation and 21.5% of the total taxa-environment variation, and was weakly correlated with silica concentration (Table 4). Diatom taxa distribution along the environmental gradients is shown in Figure 2.

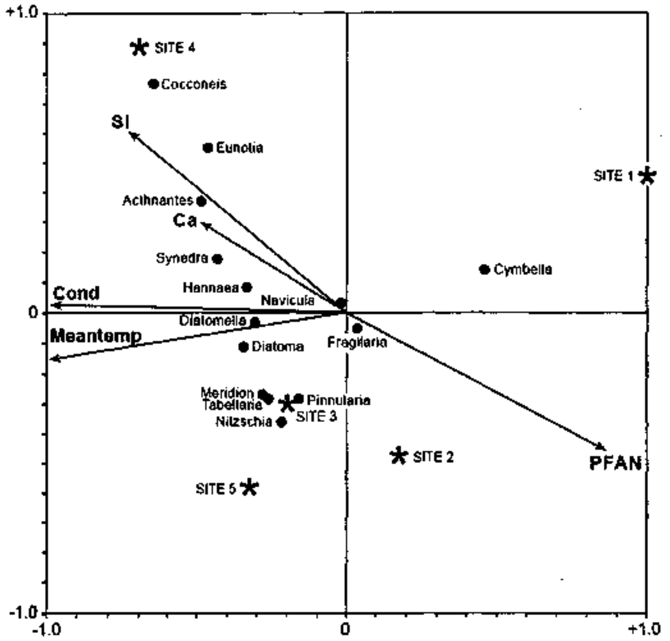

Figure 2. Ordination of diatom taxa in relation to environmental variables at the five study sites. Cond = Electrical conductivity, Meantemp = mean water temperature, PFAN = Pfankuch stability index.

Cymbella was common at Site 1, which was associated with the coldest water temperatures, and low channel stability (Figure 2). At glacial stream Sites 2, 3 and 5 *Meridion, Tabellaria, Pinnularia* and *Nitzschia* were associated with intermediate water temperatures, channel stability and conductivity. *Cocconeis,* as well as *Achnanthes* and *Synedra* characterised the groundwater-fed Tourettes tributary (Site 4). *Fragilaria* and *Navicula* were positioned centrally relative to channel stability and mean water temperature reflecting their widespread distribution at all five sites.

4. Discussion

The longitudinal position of a site downstream from the glacier margin influenced diatom community composition and richness. *Cymbella, Fragilaria* and *Navicula,* the only genera found at Site 1, were also relatively abundant at all other sites. These genera are common inhabitants of glacial streams in the

Himalayas and the Alps (CANTONATI *et al.*, 2001), indicating their ability to tolerate a range of relatively inhospitable conditions typical of alpine streams. *Fragilaria* and *Cymbella* were also found in glacial streams in the Val Roseg catchment, Switzerland (UEHLINGER *et al.*, 1998; HIEBER *et al.*, 2001). *Navicula* spp. dominance at Site 1 may be attributed to a resistance to disturbance and severe scour events by certain species of this genus, as observed in other studies (e.g. ROUNICK & GREGORY, 1981).

The less harsh conditions at Site 2 and Site 3 permitted richer diatom communities to become established. Although *Achnanthes*, as a group, exhibit high resilience to disturbance and are typical of glacier-fed streams with frequent shifting of the channel bed and high abrasion from suspended sediments (UEHLINGER *et al.*, 1998), few cells were found in glacial stream sites in this study. Moreover, in the predominantly groundwater-fed Tourettes tributary, *Achnanthes* abundance was relatively high, suggesting an ability to adapt to a wide range of habitats. Furthermore, *Achnanthes* are known to be resistant to grazing pressure, and may therefore compete better with other diatom genera where macroinvertebrate taxa are abundant (i.e. Site 4; SNOOK & MILNER, 2001). However, it is likely that the genus may have been represented by different species in the glacial and groundwater streams.

The presence of *Cocconeis* at Site 4 was probably due to a preference for warm water conditions, as their abundance is known to be greatest above 10°C (VINSON & RUSHFORTH, 1989). Downstream of the confluence of the Tourettes and Taillon streams, cells of *Cocconeis* were rare. As *Cocconeis* are tightly adherent adnate taxa, this genus can resist high flow velocities and scour (e.g. ROUNICK & GREGORY, 1981) but may be unable to colonise the glacial stream in large numbers due to the cool water temperatures (BROWN *et al.*, 2004). Thus, the Tourettes tributary may contribute to the diversity of stream communities by providing more favourable habitat conditions. Furthermore, *Cocconeis* and *Achnanthes* are often found together at disturbed (grazed) sites, as their smaller size and adnate/prostrate growth form means they are less susceptible to ingestion by grazers. Relatively large numbers of these genera were found at Site 4, where densities of grazers including *Baetis alpinus*, *Thremma gallicum*, *Eukiefferiella* spp. and *Rithrogena* spp. were found in large numbers during the study period (L.E. Brown, unpublished data).

Diatom community structure was strongly influenced by variations in water temperature and channel stability, but further longitudinal patterns with distance from the Taillon Glacier may be revealed if diatom taxa were identified to species level. Although genus level taxonomy decreases the power of data to reveal longitudinal patterns, identification to genus provided a clear picture of community and relative abundance changes, and may therefore be useful when comparing results with longitudinal distributions of macroinvertebrate taxa, which are often modelled at family/genus level (e.g. MILNER *et al.*, 2001). However, future studies should aim to identify diatoms to species where possible, particularly to identify whether ubiquitous genera (e.g. *Cymbella, Fragilaria* and *Navicula*) contain the same complement of species in streams fed from different water sources.

The most important environmental variables influencing diatom community composition with increasing distance from the Taillon Glacier snout were water temperature and channel stability, similar to macroinvertebrates (MILNER *et al.*, 2001). Electrical conductivity was also strongly related to diatom community composition. Although average temperature increases between Sites 1 and 2 were marked (see also BROWN *et al.*, 2004), changes in channel stability were minimal, suggesting water temperature may be most important in determining the observed patterns. Further temperature and channel stability increases downstream do not appear to restrict the distribution of *Cymbella, Fragilaria* and *Navicula,* yet enable colonisation by other diatom taxa. HIEBER *et al.* (2001) emphasized the role of water temperature upon alpine stream algal communities, in addition to suspended sediment concentration/turbidity influencing light availability for photosynthesis. Suspended sediment concentrations in the Taillon stream may not strongly influence diatom distribution due to shallow water depths.

In summary, the longitudinal distribution of diatom genera was closely associated with increasing water temperature, channel stability and conductivity. These diatom community changes may be due to the rapid changes in physical and hydrochemical habitat that occur over a very short distance (<2 km) in the Taillon-Gabiétous catchment. This is because the dominance of glacial runoff contribution to streamflow is limited to a short distance from the Taillon glacier due to its relatively small size. More detailed spatial and temporal surveys are needed to determine whether similar longitudinal gradients in diatom communities occur in glacial streams in other catchments, and to assess the role of seasonal variations in contributions from snowmelt, ice-melt and groundwater (e.g. BROWN *et al.*, 2003). Such studies may improve our understanding of the potential response of glacial and alpine streams to future climate and hydrological change.

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References

BROWN, L. E.; HANNAH, D. M. & MILNER, A. M. (2003). Alpine stream habitat classification: An alternative approach incorporating the role of dynamic water source contributions. *Arctic, Antarctic and Alpine Research*, 35: 313-322.

BROWN, L. E.; HANNAH, D. M. & MILNER, A. M. (2004). Spatial and temporal water column and streambed temperature dynamics within an alpine catchment: Implications for benthic communities. *Hydrological Processes* (in press).

CANTONATI, M.; CORRADINI, G.; JUTTNER, I. & COX, E. J. (2001). Diatom assemblages in high mountain streams of the Alps and the Himalaya. *Nova Hedwigia*, Beiheft 123: 37-61.

ELSTER, J. & SVOBODA, J. (1996). Algal diversity, seasonality and abundance in, and along glacial streams in Sverdrup Pass, 79°N, Central Ellesmere Island, Canada. *Mem. National Institute of Polar Research*, Special Issue 51: 99-118.

HIEBER, M.; ROBINSON, C. T.; RUSHFORTH, S. R. & UEHLINGER, U. (2001). Algal Communities Associated with Different Alpine Stream Types. *Arctic, Antarctic and Alpine Research*, 33: 447-456.

JÜTTNER, I.; ROTHFRITZ, H. & OSMEROD, S. J. (1996). Diatoms as indicators of river quality in the Nepalese Middle Hills with consideration of the effects of habitat-specific sampling. *Freshwater Biology*, 36: 475-486.

KAWECKA, B. (1971). Zonal distribution of alga communities in streams of the Polish High Tatra Mts. *Hydrobiologia*, 13: 393-414.

KAWECKA, B. (1980). Sessile algae in European mountain streams, I. The ecological characteristics of communities. *Hydrobiologia*, 22: 361-420.

MILNER, A. M.; BRITTAIN, J. E.; CASTELLA, E. & PETTS, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental condition: a synthesis. *Freshwater Biology*, 46: 1833-1847.

PFANKUCH, D. J. (1975). *Stream Reach Inventory and Channel Stability Evaluation*. US Department of Agriculture Forest Service, Region 1, Missoula, MO, USA.

ROUNICK, J. S. & GREGORY, S. V. (1981). Temporal changes in periphyton standing crop during an unusually dry winter in streams of the Western Cascades, Oregon. *Hydrobiologia*, 83: 197-205.

SMITH, B. P. G.; HANNAH, D. M.; GURNELL, A. M. & PETTS, G. E. (2001). A hydrogeomorphological context for ecological research on alpine glacial rivers. *Freshwater Biology*, 46: 1579-1596.

SNOOK, D. L. & MILNER, A. M. (2001). The influence of glacial runoff on stream macroinvertebrate communities in the Taillon catchment, French Pyrénées. *Freshwater Biology*, 46: 1609-1624.

STATZNER, B.; GORE, J. A. & RESH, V. H. (1988). Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, 7: 433-455.

TER BRAAK, C. J. F. & SMILAUER, P. (1998). *CANOCO Reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4)*. Wageningen: Microcomputer Power, Ithaca, NY.: 352.

UEHLINGER, U.; ZAH, R. & BURGI, H. (1998). The Val Roseg project: temporal and spatial patterns of benthic algae in an Alpine stream ecosystem influenced by glacial runoff. In *Hydrology, Water Resources and Ecology in Headwaters*. IAHS Publication 248: 419-424.

VINSON, D. K. & RUSHFORTH, S. R. (1989). Diatom species composition along a thermal gradient in the Portneuf River, Idaho, USA. Hydrobiologia 185: 41-54.

WADHAM, J. L.; HODSON, A. J.; TRANTER, M. & DOWDESWELL, J. A. (1998). The hydrochemistry of meltwaters draining a polythermal based, high Arctic glacier, south Svalbard. I. The ablation season. *Hydrological Processes*, 12: 1825-1849.

ZAH, R.; BURGHERR, P.; BERNASCONI, S. M. & UEHLINGER, U. (2001). Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology*, 46: 871–882.