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Author(s): Dean Jacobsen, Patricio Andino, Roger Calvez, Sophie Cauvy-Fraunié, Rodrigo Espinosa and Olivier Dangles

Source: Freshwater Science, 33(1):32-45.

Published By: The Society for Freshwater Science

URL: <http://www.bioone.org/doi/full/10.1086/674745>

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Temporal variability in discharge and benthic macroinvertebrate assemblages in a tropical glacier-fed stream

Dean Jacobsen^{1,5}, Patricio Andino^{2,6}, Roger Calvez^{3,7}, Sophie Cauvy-Fraunié^{2,4,8}, Rodrigo Espinosa^{2,9}, and Olivier Dangles^{2,4,10}

¹Freshwater Biological Laboratory, Department of Biology, University of Copenhagen, Universitetsparken 4, 2100 Copenhagen, Denmark

²Laboratorio de Entomología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador

³Institut de Recherche pour le Développement (IRD), UMR G-EAU, CEMAGREF, 361 Rue Jean-François Breton, BP 5095 34196 Montpellier Cedex 5, France

⁴Institut de Recherche pour le Développement (IRD), UR 072, LEGS, UPR 9034, CNRS 91198 Gif-sur Yvette Cedex, France and Université Paris-Sud 11, 91405 Orsay Cedex, France

Abstract: High flows are major disturbances in streams and cause benthic communities to vary temporally. Meltwater runoff in glacier-fed streams at temperate–arctic latitudes primarily follows a strong seasonal pattern. In contrast, such streams at the equator show less seasonal, but more-pronounced diel variability in discharge that tracks a year-round diurnal melting–nocturnal freezing cycle of glaciers. Consequently, qualitative and quantitative differences in temporal variability of macrobenthos communities should be expected between high-latitude and tropical glacier-fed streams. We explored temporal variability in density, taxon richness, and community composition of benthic macroinvertebrates and analyzed community responses to flow events at 3 sites along a glacier-fed stream in equatorial Ecuador (0.05, 1.6, and 4.3 km from the glacier front). We obtained continuous flow recordings and sampled fauna at approximately quarterly intervals over 30 mo. Temporal variability in the fauna was aseasonal. However, the overall magnitude of the coefficient of variability (CV) at the 3 sites was not lower than the CV at temperate latitudes. The explanatory power of flow did not differ among discharge parameters 3, 6, 9, 21, and 45 d before sampling. The effect of flow (slopes of regressions of faunal metrics vs flow) did not differ among sites, but the amount of variation explained by flow was significant only at the 2 downstream sites. Little synchrony was found in variability among sites, possibly because of differences among sites in physical characteristics (e.g., refugia space), which moderated the effect of disturbances, and taxonomic composition of communities. Our study is the first to show a close link between hydrological and biological fluctuations in an equatorial glacier-fed stream, a prerequisite for subsequent predictions of consequences of tropical glacier melting on diversity, composition, and stability of stream communities.

Key words: Ecuador, Andes, dynamics, flow, macrobenthos, fauna, communities, diversity-stability hypothesis

High-flow events are one of the most prevalent forms of natural disturbance in riverine systems (Lake 2000, Bunn and Arthington 2002). They have the potential to remove macroinvertebrates (Death 2008) and reduce food resources by carrying away benthic detritus and scouring benthic algae (Peterson and Stevenson 1992, Biggs et al. 1999), and thereby maintain nonequilibrium communities (e.g., Resh et al. 1988, Townsend 1989). Flow regime in glacier-fed streams is controlled primarily by glacial melt-

ing, which varies on a diel and seasonal basis. At temperate latitudes, discharge peaks during summer glacial melting and is almost nil during winter (Milner and Petts 1994, Smith et al. 2001, Brown et al. 2003). Therefore, the composition of biological communities in temperate glacier-fed streams varies greatly over the year, with density and diversity reaching maxima during seasons of low flow (e.g., Füreder et al. 2001, Lods-Crozet et al. 2001, Robinson et al. 2001). Glaciers at the equator have different dy-

E-mail addresses: ⁵djacobsen@bio.ku.dk; ⁶puchitricio@gmail.com; ⁷roger.calvez@ird.fr; ⁸sophie.cauvy@gmail.com; ⁹reespinosab@yahoo.com; ¹⁰olivier.dangles@legs.cnrs-gif.fr

namics because melting occurs throughout the year (Favier et al. 2008). Thus, the main variability in discharge takes place on a diel basis because of diurnal melting and nocturnal freezing. Therefore, temporal variability in equatorial glacier-fed stream communities is expected to differ quantitatively and qualitatively from that in temperate glacial streams.

Glacier-fed streams typically originate as physically unstable, cold, and nutrient-poor habitats (Milner et al. 2001). With increasing distance from the glacier, the stream environment becomes less influenced by the glacial source, and stream temperature, channel stability, and ionic strength of the water usually increase (Milner et al. 2001, Jacobsen et al. 2010). Therefore, benthic macroinvertebrate communities in glacier-fed streams show a characteristic increase in species diversity and turnover along the stream (Jacobsen et al. 2012).

This longitudinal increase in species richness is a result of decreasing environmental harshness (Jacobsen and Dangles 2012) in terms of the abiotic environment and resource availability. In general, extreme or severe environmental conditions (e.g., very cold, hot, dry, saline, acidic, or O₂-depleted) are assumed to limit species richness compared to more benign conditions (Connell 1975, Currie et al. 2004). According to the diversity–stability hypothesis (MacArthur 1955, Elton 1958), high species richness is expected to stabilize fluctuations in community density, biomass, and diversity (for reviews see, e.g., Cottingham et al. 2001, Cardinale et al. 2006, Jiang and Pu 2009). Thus, this hypothesis suggests an indirect link between environmental harshness and community stability, through species richness. Depending on how harshness and community stability are defined, the expectation is that as harshness increases, species richness and community stability decrease.

One aspect of environmental harshness could be temporal environmental variability or disturbance, which may have a direct effect on temporal variability of communities, regardless of whether these are poor or rich in taxa. Glacier-fed streams seem to be particularly harsh environments because of a high degree of environmental variability (Hieber et al. 2002, Ilg and Castella 2006). Factors that may affect a community's response to a given disturbance are habitat properties, such as refuge space where organisms may escape the impact of disturbances (Townsend and Hildrew 1994, Townsend et al. 1997).

Interconnected sites along glacier-fed streams potentially share the same taxon pool. They are ideal systems in which to explore relationships between temporal variability in discharge and benthic macroinvertebrate assemblages because they are subject to the same frequency of disturbances in the form of discharge variability, but differences in taxon richness are produced by a natural and steep gradient in environmental harshness. Equatorial glacier-fed streams are

particularly interesting because they are not constrained by seasonal short windows of favorable conditions that occur in temperate glacier-fed streams (Uehlinger et al. 2002). We obtained continuous records of discharge and did approximately quarterly sampling of benthos over 30 mo at 3 sites at varying altitudes and distances along a glacier-fed stream in equatorial Ecuador.

Differences in environmental characteristics and macroinvertebrate communities between sites along the stream have been explored previously (Jacobsen et al. 2010, Kuhn et al. 2011). Here, our purpose was to obtain insight into the temporal variability in benthic macroinvertebrate communities in a tropical glacier-fed stream. Our results should contribute to our understanding of the possible consequences of melting of tropical glaciers on aquatic communities. Our objectives were to: 1) document the spatio-temporal variability (CV) in the benthic macrofauna of a tropical glacier-fed stream and to discuss this variability in a broader context in a review of literature from glacier-fed streams in temperate regions, and 2) analyze the linkage between flow events (discharge) and the response of the fauna (density, taxon richness, and community composition) at different sites along the stream that differ with respect to habitat characteristics, taxon richness, and community composition. The hypotheses that we wanted to test were that: 1) temporal variability in the macroinvertebrate communities would be aseasonal, 2) broad-scale patterns in variability (coefficient of variability [CV]) would reveal lower values for our equatorial stream compared to temperate streams and that CVs would increase with glacial influence and duration of study, 3) the fauna at different sites along the stream would vary in a synchronous way, and 4) faunal variability and the amount of that variability explained by variations in runoff would decrease with increasing taxon richness and distance from the glacier.

METHODS

Study area

Our study stream, the Río Antisana, is a headwater of the River Napo, a main tributary of the upper Amazon River. It originates from the Crespo glacier on Mount Antisana in the eastern cordillera of the Andes of Ecuador (lat 0°28'S, long 78°09'W). The Crespo glacier covers an area of ~1.8 km² and originates at the summit of the mountain (5760 m asl). The ablation zone extends from ~5150 m to the glacier snout at 4730 m asl and is retreating 10 to 20 m of stream distance/y. Air temperature, humidity, and radiation do not vary systematically during the year, but precipitation, cloud cover, and wind speed are more seasonally variable (Cadier et al. 2007). The annual precipitation (mostly snow and hail) is ~800 mm (Maisincho et al. 2007), but hydrology is dominated by glacial meltwater (see

below). Mean annual air temperature varies from $\sim 3.7^{\circ}\text{C}$ at the lowest site to 1.3°C at the upper site (Cáceres et al. 2005). The vegetation of the lower part of the study area is páramo, a moorland type of vegetation with scattered bushes characteristic of the northern Andes. Above ~ 4600 m asl vegetation is present only in the form of sporadic tufts of grasses and cushion plants. For more information on the study area, refer to Jacobsen et al. (2010) and Kuhn et al. (2011).

We selected 3 sites along a stretch of the stream that had no visible tributaries and, therefore, was ideal for studying the effect of the same hydrological regime on different communities. Site A (0.5–5 m wide) at 4730 m asl was ~ 50 m from the glacier on a wide plain with wandering, braided threads of water. It was fed directly from the glacier snout, but the stream seemed to freeze and cease flowing at night. The site conformed well to the model proposed by Smith et al. (2001) for a high-altitude stream controlled by sediment regime and fed by a rapidly retreating glacier. Site B (1–2 m wide) was 4490 m asl and 1.62 km from the glacier, and site C (1–2 m wide) was 4225 m asl and 4.30 km from the glacier. Sites B and C were in a confined, but eroding flood valley. Glacial cover was ~ 100 , 67, and 42% of the catchment area of sites A, B, and C, respectively (Maisincho et al. 2007).

Environmental setting

We obtained data on the hydrological regime by continuously recording discharge during 2008–2010 at a gauging station at site B, which provided us with daily minimum, maximum, and mean discharge (Institut de Recherche pour le Développement [IRD], Instituto Nacional de Hidrología y Meteorología [INAMHI], Empresa Municipal de Alcantarillado y Agua Potable de Quito [EMAAP-Q]). We did not have discharge data from all 3 sites, so we used the discharge at site B indexed to maximum recorded discharge prior to each sampling as a standardized and comparable measure of intensity and predictability of disturbance at all sites (*sensu* Poff 1992). To ensure that discharge varied similarly at all 3 sites, we recorded water level continuously and simultaneously at all sites during April 2009 (Hobo loggers; Onset Computer Corporation, Bourne, Massachusetts).

We tested the presumed gradient in harshness along the stream by measuring a number of environmental variables that we suspected might influence macroinvertebrates. We measured temperature regime and O_2 saturation (precision: 0.1°C and 1% O_2) from data loggers (Oxylog, OxyGuard®, Birkerød, Denmark) placed in the stream and set to record every 30 min for 5 to 8 wk during January–March 2008 and for 2 to 5 wk during December 2011–February 2012. The O_2 probes hung freely from metal tubes inserted between boulders along the banks, and we

placed them as close to the stream bed as possible where the current was swift. The equipment was initially calibrated in situ based on altitude (e.g., 100% O_2 saturation at sea level, 59.2% at 4200 m asl and 55.4% at 4700 m asl), and the O_2 saturation and water temperature verified with an YSI® 58 O_2 meter (Yellow Springs Instruments, Yellow Springs, Ohio) while introducing and retrieving the loggers.

Conductivity (at 25°C) and pH were measured with portable meters, model Cond 315i and pH 315i, respectively (WTW, Weilheim, Germany), on every visit to the study sites (10–12 measurements). Water turbidity was measured 5 to 6 times at each site with a Eutech TN-100 Turbidimeter (Eutech, Nijkerk, The Netherlands) and current velocity 2 to 3 times at each site by dilution gauging (White 1978). We added a known amount of dissolved salt (volume and conductivity) at the upstream end of the 15- to 25-m stream reach, and we measured the conductivity every 5 or 10 s at the downstream end of the reach. Mean current velocity was calculated as the time needed for $\frac{1}{2}$ of the salt to pass the stream reach divided by the length of the reach. We measured stream slope at each site with a transparent plastic tube that carried flowing water from the upstream to the downstream end of the reach. Slope was calculated as the difference between the water level inside the tube when raised until flow stopped and that of the surface of the stream water at the downstream end, divided by the distance between the upstream and downstream ends of the tube (~ 25 m).

We estimated the food resources available to macroinvertebrates by sampling pebbles for quantification of epilithic algae and collecting the benthic detritus obtained in Surber samples (see below). At each site, we collected 9 small pebbles (~ 2 – 4 cm) at random (but we avoided pebbles with filamentous algae), placed 3 pebbles in each of 3 containers, and extracted chlorophyll *a* in 96% ethanol for 1 to 3 d in the dark until further processing in the laboratory where we gave the containers a 10-min ultrasonic bath to increase extraction efficiency. After settlement for a few hours, we transferred a sample to a spectrophotometer and measured absorption at 665 and 750 nm. We calculated the concentration of total chlorophyll *a* (including phaeopigments) according to the method published by Københavns Universitet (1989). Stone surface area was estimated with the formula

$$A = 1.15(LW + LH + WH) \quad (\text{Eq. 1})$$

proposed by Graham et al. (1988), where *L* is length, *W* is width, and *H* is height of the stones.

We quantified benthic detritus by collecting all material (inorganic and organic) present in the Surber samples after sorting out the animals. This material was dried at

80°C for ~24 h and weighed. We used mass loss upon combustion at 550°C as the ash-free dry mass (AFDM) of organic material >200 µm in the sample.

To obtain comparable estimates of environmental variability and disturbance level of the stream sites, we applied 4 measures: 1) the CV in water depth obtained from the loggers, 2) the average of the CVs for all nonflow variables (temperature, O₂, conductivity, pH, turbidity, benthic chlorophyll *a*, and detritus), 3) the skewness of the dilution-gauging curve used to measure current velocity (y = conductivity, x = time), where a large skewness is a measure of hydraulically dead space, which we considered as a measure of low-stress refugia for macroinvertebrates (low-flow areas are important refugia during high-flow events; Lancaster and Hildrew 1993, Rempel et al. 1999), and 4) a scoring system (15–60, with 60 as the most unstable) based on the channel-bottom component of the Pfankuch Index (Pfankuch 1975) evaluating properties, such as rock angularity, brightness, particle packing, stability of substratum, scouring and deposition, and clinging vegetation. The Pfankuch Index has been widely used to quantify channel bed stability in glacial streams (e.g., Castella et al. 2001).

Macroinvertebrate sampling

We sampled macroinvertebrates between April 2008 and September 2010 at intervals of 2 to 5 mo. At each site, we collected 5 quantitative Surber samples (500 cm²; mesh size = 200 µm) randomly from pebble–cobble substratum in riffle/run habitats. All samples were collected during the day and preserved in the field in 70% ethanol. In the laboratory, the samples were rinsed through a 200-µm sieve and sorted without use of magnification. We applied subsampling to samples with large numbers of chironomids.

Complete species analysis of the Ecuadorian stream fauna was not possible because only a few groups can be identified to a taxonomic level lower than family. Invertebrates other than Chironomidae were identified mostly to family with keys published by Roldán (1996), Merritt and Cummins (1996), and Fernández and Domínguez (2001) and were separated into morphospecies. We sorted larval chironomids with the aid of a stereomicroscope at 10× magnification, dehydrated them in 96 and 99% ethanol, and mounted them in Euparal. Larvae were identified to subfamily with the aid of a compound microscope at maximum 400× magnification with keys in the current taxonomic literature (Wiederholm 1983, Ruiz-Moreno et al. 2000, Epler 2001). Larvae of Orthoclaadiinae were not identified further.

Data analysis

We analyzed 2 univariate faunal metrics based on the Surber samples: density (number of individuals in samples) and local taxon richness (number of taxa in samples). We

generated autocorrelation function (ACF) plots in Minitab® (version 15.1.20.0; Minitab, State College, Pennsylvania) to test for temporal independence, periodicity, and seasonality in these faunal metrics and in monthly discharge measures.

We used CV as a measure of variability of faunal metrics. We compared our results with data from temperate systems to place our equatorial stream data in a broader context. However, we had to take into account 2 confounding factors that might influence temporal variability, variability of glacial influence among sites and the duration of study. In temperate systems, we expected studies including both summer and winter sampling to show higher variability than studies in which sampling occurred only in summer or only in winter. Therefore, we represented CVs of density and taxon richness in contour plots as a function of study duration (mo) and of the Glacial Index proposed by Jacobsen and Dangles (2012). This index is a simple and comparable measure of glacial influence at stream sites and is highly correlated with taxonomic richness in glacier-fed streams. It is related to the extent (area) of the feeding glacier and inversely related to the distance from the glacier. A value of 0 means no influence and 1 means maximum glacial influence. We made contour plots with a quadratic distance interpolation method in Minitab.

We used nonmetric multidimensional scaling (NMDS) ordination based on Bray–Curtis similarity (on $\log[x + 1]$ -transformed data to down-weight the influence of very abundant taxa) to examine spatial patterns and temporal variability in community composition among sites. The NMDS goodness-of-fit was estimated with a stress function, which ranges from 0 to 1 with values close to 0 indicating a good fit. The composition of macroinvertebrate communities among sites was compared with analysis of similarities (ANOSIM). ANOSIM tests the null hypothesis that within-site similarity is equal to between-site similarity. ANOSIM generates a statistical parameter *R*, which indicates the degree of separation between groups. A score of 1 indicates complete separation, and a score of 0 indicates no separation. We used Monte Carlo randomizations (10,000) of the group labels to generate null distributions to test the hypothesis that within-group similarities are higher than would be expected by chance. These analyses were done on the data for specific dates (pooling the 5 Surber samples) in Primer (version 5.2.4, PRIMER-E, Plymouth, UK).

To test for periodicity in community composition, we compared Bray–Curtis similarities between temporal neighbor samples with those of all other possible combinations. To test for seasonality, we compared samples collected at about the same date in different years (maximum 1-mo difference) with those of all other possible combinations. These tests were done as *t*-tests in Excel (version 2003; Microsoft Corporation, Redmond, Washington).

We used 1-way analyses of variance (ANOVAs) followed by Tukey post hoc comparisons of means to test for differences in faunal metrics ($\log[x + 1]$ -transformed data with replication) among the 3 sites, among sampling dates, and to test for differences between environmental factors ($\log[x + 1]$ -transformed data without replicates). We used F -tests to test for differences in variances in faunal metrics between sites. All of these tests were done in Excel.

To obtain a measure of community-wide synchrony in the variability of taxon densities within each site, we applied the statistic provided by Loreau and de Mazancourt (2008), which permits comparison of communities with different number of taxa. The statistic is standardized between 0 (perfect asynchrony) and 1 (perfect synchrony).

From the measurements of environmental variables, we extracted minimum, maximum, and mean values, and CV (in %). Because the study included only 3 sites, these values were easily distinguished without use of multivariate analyses on environmental variables. We made an initial exploration of the effect of flow events on the benthos by relating faunal density, taxon richness, and NMDS axis-1 coordinates to mean, maximum, and mean maximum discharge extracted from the last 3, 6, 9, 21, and 45 d before sampling. We used individual and simple regression analyses because our interest here was not to optimize (often ecologically meaningless) modeling of relationships between faunal metrics and discharge, relationships were clearly either linear or exponential, and correlation coefficients between the above mentioned discharge measures were generally high ($r_p > 0.85$). We tested for differences between regression slopes of faunal metrics at 3 sites vs discharge measures with analysis of covariance (ANCOVA) using the freeware PAST (version 2.03; Hammer et al. 2001).

RESULTS

Environmental setting

The 3-y discharge records at site B showed significant periodic correlation with a lag of 1 mo ($p < 0.05$) and a tendency toward seasonality at lags of 6 and 12 mo (minimum values generally occurred in June–August and maximum values during January–March; Fig. 1A). Short-term (day-to-day) variability was considerable (Fig. 1A), and within-day variability in discharge (max – min) ranged from 1 to 359 L/s. Daily minimum discharge (usually reached during early morning hours) was 5 to 93 L/s (median = 16 L/s); mean flow was 7 to 193 L/s (median = 47 L/s), and the afternoon maximum flow was 8 to 411 L/s (median = 114 L/s) (Fig. 1B). Precipitation had negligible effect on short-term variability in stream discharge because neither minimum, maximum, nor mean discharge was significantly correlated with daily precipitation records from the same day or the previous day. Measurements of daily maximum water depth obtained during April 2009 at site B were

highly correlated with independent records of daily maximum discharge at that site (Fig. 1C). Water-level loggers at the 3 sites showed very similar patterns during April 2009 (Fig. 1D), so we assume a parallel hydrological regime at all 3 sites during the entire study period. However, in mid-April the depth curve at site 1 was displaced relative to the depth curve at the other 2 sites (Fig. 1D).

Mean temperature and O_2 saturation differed significantly among all 3 sites, whereas conductivity and benthic chlorophyll *a* differed significantly between 2 of the 3 sites (Table 1), and these 4 variables increased downstream. The Pfrankuch Index was much higher (less physical stability) at site A (58) than at sites B (24) and C (21). In contrast, pH, turbidity, and detritus did not differ among sites (Table 1).

Overall faunal distribution

The total numbers of taxa found at each site during the entire study were 19, 29, and 48 at sites A, B, and C, respectively. Both measures of mean taxon richness (mean per sampling date and mean per Surber sample) increased significantly with increasing distance from the glacier (Table 2). Mean density did not differ among sites ($F_{2,24} = 0.40$, $p = 0.67$).

Overall community composition differed significantly among the 3 sites (Global $R = 0.909$, $p < 0.001$; Fig. 2, Table 3), and community composition differed for each pairwise comparison (all $p < 0.001$). Mean Bray–Curtis similarity was $46 \pm 3\%$ (SD) between sites A and B, $38 \pm 10\%$ between sites B and C, and $19 \pm 7\%$ between sites A and C.

The community at site A was completely dominated by chironomids (96.7% of all individuals), in particular Podonominae type 3 (77.4%) (Table 3). The abundance of this species decreased along the stream, and at site B, the fauna was dominated by Orthocladiinae and Podonominae type 1, two Diamesinae species, the caddisfly *Cailloma*, and *Simulium* blackflies. At site C, Orthocladiinae was still dominant, together with the midge *Alluaudomyia*, *Simulium*, the mayfly *Andesiops*, and the elm mid beetle *Neoelmis*.

Seasonality and periodicity

Temporal variability in density and richness seemed to follow to some degree the periodic fluctuations in discharge (Fig. 3A, B). Nevertheless, these 2 faunal metrics were temporally independent at all sampling lags and showed neither a periodic nor a seasonal cycle at any of the 3 study sites ($p > 0.05$). Temporal variability in the community composition (Fig. 2), defined as mean Bray–Curtis dissimilarity among dates, did not follow a seasonal pattern at any site ($p > 0.05$) but did show a significant periodic pattern at sites B and C ($t_{43} = 2.787$, $p = 0.008$;

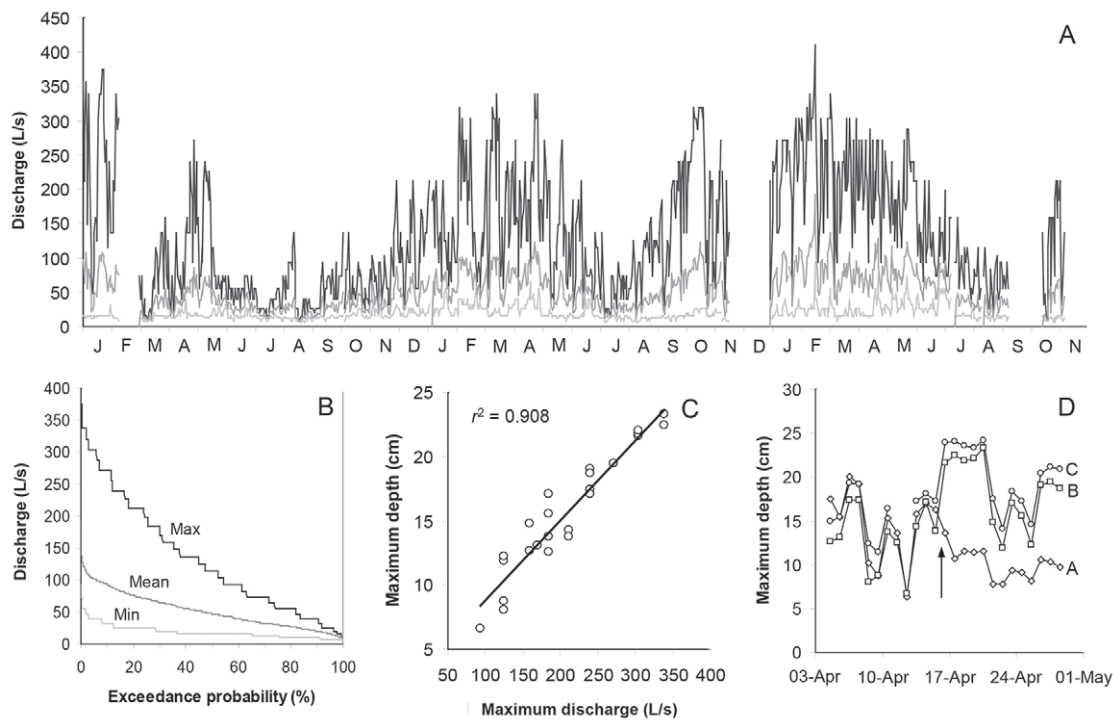


Figure 1. A.—Daily maximum, mean, and minimum discharge at site B (4490 m asl and 1.60 km from the Crespo glacier) during 2008–2010. B.—Exceedance probability in % of daily maximum, mean, and minimum discharge at site B. C.—Linear regression between independent records of maximum discharge (from gauge) and maximum depth (from Hobo® pressure logger) at site B during April 2009. D.—Daily maximum depth recordings from Hobo pressure loggers placed at each of the 3 study sites during April 2009. The vertical arrow indicates when recordings at site A were displaced with respect to the other 2 sites.

$t_{43} = 2.890$, $p = 0.006$, respectively). So, these data largely support our hypothesis that temporal variability in the macroinvertebrate communities would be aseasonal.

Broad-scale patterns in variability (CVs)

Analysis of the literature data showed that CV in density was almost always higher than CV in richness, and these 2 measures were not significantly related ($r_p = 0.326$, $p = 0.091$; Fig. 4A). The CV in density was related to neither the Glacial Index ($r_p = 0.21$, $p > 0.05$) nor the duration of the study ($r_p = 0.12$, $p > 0.05$; Fig. 4B). In contrast, CV in taxon richness increased significantly with the Glacial Index ($r_p = 0.61$, $p < 0.001$) but was unrelated to the duration of the sampling period ($r_p = 0.24$, $p > 0.05$) (Fig. 4C). In terms of CVs, our equatorial sites did not differ from the rest of the data. This result refutes our hypotheses that the overall magnitude of variability would be low compared to temperate latitudes and that it would increase with glacial influence and duration of study.

Synchrony in variability

The effect of sampling date on the variability in density (site A: $F_{8,36} = 4.36$, $p = 0.001$; site B: $F_{9,40} = 13.67$, $p < 0.001$; site C: $F_{9,40} = 6.23$, $p < 0.001$) and mean taxon rich-

ness per Surber sample (site A: $F_{8,36} = 3.48$, $p = 0.004$; site B: $F_{9,40} = 4.10$, $p = 0.001$; site C: $F_{9,40} = 4.32$, $p < 0.001$) was significant at all 3 sites, and the variability did not differ significantly among sites (F -tests, $p > 0.05$). However, synchrony between sites was far from perfect, and the variability in density and richness of pairwise correlations between sites were all nonsignificant ($p > 0.05$). Our hypothesis that sites at different distances along the stream should vary synchronously was not supported.

Mean CV in population (taxon) densities within communities tended to increase in a downstream direction (198, 211, and 225%), whereas synchrony in variability in population densities decreased downstream (0.791, 0.614, and 0.230 at sites A, B, and C, respectively).

Responses to flow

Only slight differences were found in the ability of the 3 discharge parameters and the length of period to explain variation in faunal metrics (Fig. 5A–C). Therefore, we chose maximum discharge the 3 d before sampling for further analyses (Fig. 6A–C). Density was negatively related to discharge, which explained 9.9 ($p = 0.430$), 81.0 ($p < 0.001$), and 73.0% ($p = 0.001$) of the variability at sites A, B and C, respectively. The pattern was similar for

Table 1. Mean, maximum, minimum, and coefficient of variation (CV) of environmental variables for the 3 stream sites. n = the number of single measurements that were performed at each site, respectively. For each variable, bold indicates significant differences among sites. Means with the same letter are not significantly different. Max = maximum, min = minimum, AFDM = ash-free dry mass.

Variable	Summary statistic	Site A	Site B	Site C	p
Slope (%)		1.4	8.7	9.0	
Mean current velocity (m/s)		0.22	0.38	0.21	
Pfankuch Index		58	24	21	
Skewness (hydrological dead space)		1.97	1.78	2.26	
Mean CV of all variables below except water depth		82	65	50	
Water depth (cm) (n = logging)	Mean	5	6	8	na
	Max	20	23	24	
	Min	0	0	0	
	CV	78	78	64	
Temperature (°C) (n = logging)	Mean	1.0 ^a	3.2 ^b	5.3 ^c	<0.001
	Max	15.0	9.8	19.4	
	Min	0.0	0.0	0.0	
	CV	209	57	66	
O ₂ (%) (n = logging)	Mean	52 ^a	55 ^b	58 ^c	<0.001
	Max	64	59	69	
	Min	45	43	48	
	CV	6	2	4	
Conductivity (µS/cm) (n = 13, 17, 18)	Mean	8 ^a	11 ^{ab}	13 ^b	0.008
	Max	22	22	25	
	Min	2	3	5	
	CV	83	58	46	
pH (n = 11, 12, 13)	Mean	7.5	6.8	7.0	0.109
	Max	8.6	7.9	8.2	
	Min	6.0	6.1	6.3	
	CV	12	9	10	
Turbidity (NTU) (n = 4, 4, 5)	Mean	661	453	444	0.464
	Max	956	774	841	
	Min	285	298	264	
	CV	46	49	52	
Benthic chlorophyll <i>a</i> (µg/cm ²) (n = 9, 10, 10)	Mean	1.0 ^a	2.9 ^b	3.6 ^b	<0.001
	Max	3.2	7.0	11.5	
	Min	0.2	1.1	0.2	
	CV	84	153	105	
Benthic detritus (g AFDM/m ²) (n = 9, 10, 10)	Mean	13.6	14	17.6	0.337
	Max	48.2	62.6	42.2	
	Min	0.1	3.4	3.4	
	CV	131	130	64	

richness. Flow accounted for 23.3 ($p = 0.180$), 51.9 ($p = 0.022$), and 51.3% ($p = 0.022$) of the variability in taxon richness and 9.5 ($p = 0.440$), 80.8 ($p < 0.001$), and 21.4% ($p = 0.184$) of the variability in community composition at sites A, B, and C, respectively. However, regression slopes for density ($F_{2,22} = 3.241$, $p = 0.060$), taxon richness

($F_{2,22} = 1.595$, $p = 0.228$), and NMDS axis-1 coordinates ($F_{2,22} = 0.716$, $p = 0.501$) did not differ among the 3 sites. Thus, the rate at which the fauna changed with flow was the same but the amount of the variation explained was different among sites. Therefore, our hypotheses that fauna variability and the amount explained by variation in runoff

Table 2. Mean, maximum, minimum, and coefficient of variation (CV) of density (individuals/Surber sample) and taxon richness (number of taxa/Surber sample). Means with the same letter are not significantly different ($p > 0.05$).

Variable	Site A	Site B	Site C
Density			
Mean	80.0 ^a	81.1 ^a	98.5 ^a
Max	277.8	279.6	200.6
Min	17.4	12.6	15.9
CV (%)	101.5	103.9	68.6
Taxon richness			
Mean	4.4 ^a	6.9 ^b	9.8 ^c
Max	5.6	9.2	12.2
Min	2.4	4.2	5.2
CV (%)	26.8	22.0	24.2

would decrease with increasing distance from the glacier were refuted.

DISCUSSION

Environmental setting and overall faunal distribution

The clear longitudinal patterns of mean faunal metrics reported here correspond well with results of our earlier studies on the same stream (Jacobsen et al. 2010, Kuhn et al. 2011) and with results from glacier-fed streams in general (Jacobsen and Dangles 2012). We assume that these patterns are caused by a steep gradient in environmental harshness along the stream (Jacobsen and Dangles 2012). Site A probably was more physically disturbed than the other sites by abrupt changes in stream channel morphology caused by substratum movement, the highly unstable moraine surroundings, and the diel freeze–thaw cycle of the stream (Jacobsen et al. 2010). Freezing is an important form of disturbance that can affect macroinvertebrate communities in Arctic streams (Irons et al. 1993, Parker and Huryn 2011). This effect was seen in a considerably higher Pfanckuch Index (particularly a loose and easily moved substratum with no packing and consisting of only 0–20% stable materials) at site A than at sites B and C. In addition, average conditions of low mean temperature, conductivity, and benthic algal food availability, and higher mean CV in environmental variables should contribute to the harshness of site A and, thus, to the difference in taxon richness and community composition between sites A and B.

Sites B and C appeared to be quite comparable with respect to Pfanckuch Index (24 and 21, respectively) and all measured environmental factors, and these 2 sites differed significantly only with respect to water temperature and % O₂ (Table 1). The increase in richness and change in community from site B to C seems to be a matter of temperature or O₂ levels (Jacobsen 2008a).

Seasonality and periodicity

As expected for a supposedly aseasonal environment at the equator, we did not find significant seasonal or periodic patterns in the variability of faunal metrics, even though the discharge of the stream did, in fact, show signs of seasonality and periodicity. This result indicates that faunal variability in the study stream is driven more by stochastic short-term flow variability than by seasonality per se. However, shorter sampling intervals could have revealed temporal dependency and, thus, a higher degree of periodicity. In 2 nearby rhithral streams that were sampled monthly/bimonthly during 1 y, temporal variability in density (CV = 39 and 95%) was about the same as in the glacier-fed stream and showed no seasonal cycle in density and richness (Jacobsen 2008b). Thus, the temporal variability in fauna in our glacier-fed stream seems to be comparable to that in other alpine streams at the equator with rain runoff as the main hydrological source.

In Bolivia, Molina et al. (2008) found CVs in density and richness of macroinvertebrates that were 20 to 25 and 70 to 90%, respectively, from quarterly samplings during 1 y at 3 sites (0.46–3.63 km) along a stream originating from a glacier on Mount Mururata. However, only their highest site was primarily glacier-fed. The lower sites had major contributions of rainwater runoff from tributaries. This runoff contribution probably explains why the highest site on the Mururata stream was largely aseasonal, whereas the 2 lower sites showed clear seasonality with high density and richness during the pronounced dry season of the outer tropics of Bolivia.

Broad-scale patterns of variability

In spite of the different seasonal flow dynamics in temperate and tropical glacier-fed streams (seasonal vs diel),

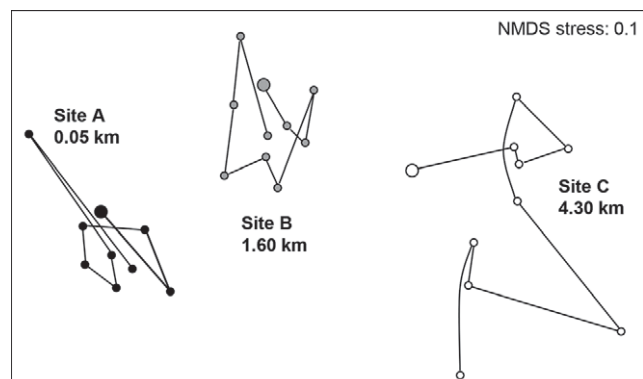


Figure 2. Nonmetric multidimensional scaling (NMDS) ordination plot based on Bray–Curtis similarities ($\log[x + 1]$ -transformed) of community data from the 10 sampling dates at the 3 sites. Stress is low (0.1), indicating a relatively good 2-dimensional representation of the placements of sites. The large data points denote the 1st sample from each site. Distances are from the glacier snout.

Table 3. Taxa making up >1% of total richness at each of the 3 study sites. The mean proportion of the total (%), the coefficient of variation (CV) in density (%), and the Pearson correlation coefficient between density and mean maximum flow are shown. Bold indicates significant correlation ($p < 0.05$).

Taxon	Site A			Site B			Site C		
	% total	CV (%)	r	% total	CV (%)	r	% total	CV (%)	r
<i>Andesiops</i> sp.							7.3	122.4	-0.26
<i>Neoelmis</i> sp. 1 (L)							6.9	71.2	-0.13
<i>Neoelmis</i> sp. 1 (A)							1.1	106.8	0.02
<i>Atopsyche</i> sp. 1							2.0	149.1	-0.46
<i>Cailloma</i> sp. 1				6.5	96.8	-0.56	1.3	81.0	-0.59
<i>Chelifera</i> sp.							1.4	121.6	-0.58
<i>Limnophora</i> sp. 1				1.6	123.3	-0.27			
<i>Simulium</i> sp. 1				5.6	83.9	-0.65	10.9	104.2	-0.72
<i>Alluaudomyia</i> sp.1							20.3	218.8	-0.25
Podonominae sp. 1	13.9	68.5	-0.02	22.4	89.5	-0.72	1.2	145.4	-0.42
Podonominae sp. 3	77.4	124.6	-0.44	3.9	91.5	-0.73			
Podonominae sp. 4	5.4	92.5	-0.34						
Diaesinae sp. 1				8.8	251.4	-0.32			
Diaesinae sp. 2				4.5	232.5	-0.32			
Orthoclaadiinae	1.3	74.8	-0.30	45.5	134.1	-0.62	39.1	123.7	-0.65

the overall magnitude of variability (CV) in faunal metrics in the equatorial Antisana stream sites did not differ from the magnitude of variability in European temperate sites (Fig. 4A). Most studies of temperate sites cover only summer, but a few include winter. Brown et al. (2006) sampled 3 sites with low glacial inflow in the French Pyrenees in July and August in 2 consecutive years, and their data showed, in order of decreasing glacial influence, CVs in density of 184 (61 if 1 sample with extraordinarily high density is omitted), 58, and 47% and in richness of 12, 15, and 13%. Burgherr and Ward (2001) sampled from June to November at 10 sites along the Roseg River in Switzerland. They reported mean CVs in density of 139% at proglacial sites, 60% on the braided floodplain, and 90% along the lower constrained reach. CVs in taxon richness were 31, 31, and 20% along the same reaches, respectively. Lods-Crozet et al. (2001) sampled the Swiss Mutt stream in June, August, and September and found that CVs in density and richness at the glacier snout of 89 and 101%, respectively, decreased to 42 and 13% 3.6 km further downstream. On the other hand, Robinson et al. (2001) sampled monthly during a full year at 7 sites close to glaciers in Switzerland where they found CVs in density of 53 to 132% and richness of 33 to 59%. Monthly sampling during 2 y at 2 stream sites at 1200 and 3350 m from a glacier in Austria gave CVs in density of 100 and 215% and in richness of 38 and 28%, respectively (Schütz et al. 2001).

Our hypotheses were that temporal variability would be highest in studies covering seasons with very different runoff regimes and at sites close to (large) glaciers. We expected CVs to peak in the upper right-hand corner of

the plots in Fig. 4B, C. However, the data from the studies mentioned above revealed that overall, neither the CV in density nor richness was significantly related to the duration of the study (Fig. 4B, C). Apparently, like in tropical glacier-fed streams, short-term variations in temperate glacier-fed stream faunas may be as pronounced as seasonal differences. In contrast, the CV in taxon richness, but not density, did indeed increase significantly with the Glacial Index (Fig. 4C). Thus, our expectation regarding the importance of glacial influence was only partially supported, perhaps because of zoogeographic differences among sites and local environmental conditions not captured through the Glacial Index.

Synchrony in variability

Our expectation of synchrony among sites in variability in density and taxon richness also was not met, probably because of differences in physical-habitat characteristics and composition of the fauna among sites (Fig. 2). For example, Orthoclaadiinae spp. composed 45 and 39% of the fauna, and the linear regression with flow explained 45 and 50% of the temporal variability in density of Orthoclaadiinae at sites B and C, respectively, whereas this group made up only 1% of the fauna at site A (Table 3). We found a similar pattern for *Simulium*. In contrast, Podonominae spp. contributed 97, 26, and 1% of the fauna at sites A, B, and C, respectively, but was significantly related to discharge only at site B ($r^2 = 0.60$) and not at sites A ($r^2 = 0.13$) and C ($r^2 = 0.15$). The response of benthic organisms to hydraulic stress is taxon-

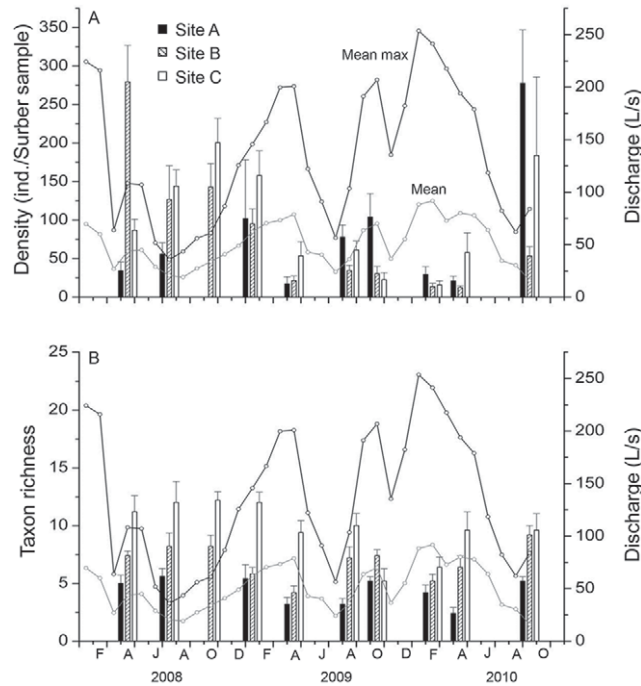


Figure 3. Mean (± 1 SE) density of individuals (A) and taxon richness per Surber sample (B) at the 3 sampling sites during 2008–2010. Monthly mean and mean maximum discharge are superimposed. Ind. = individuals.

specific (Lancaster and Hildrew 1993, Snook and Milner 2002). Macroinvertebrate taxa differ with respect to a wide array of biological/functional traits that determine their realized abiotic niches and competitive interactions (Lamouroux et al. 2004, Statzner et al. 2004). In glacier-fed streams, resilience and resistance traits (e.g., small size, high adult mobility, habitat and feeding generalist, clinging behavior) are particularly dominant in species assemblages living close to glaciers. Such traits provide an obvious advantage for coping with harsh and disturbed environmental conditions (Füreder 2007). Gradual replacement of these traits by others along the stream (Ilg and Castella 2006) may explain the observed asynchrony among sites.

Even though differences were nonsignificant, mean CV in population (taxon) densities increased slightly and variability in community density decreased downstream. In other words, mean CV in population density was inversely related to CV in community density. Increased taxon richness downstream probably leads to a more moderated overall response because each species responds individually to flow. This result is in agreement with most model predictions for the diversity–stability hypothesis (Lehman and Tilman 2000). If we assume that community density may be used as a proxy for community biomass, then our finding of increasingly asynchronous variation of populations within downstream communities supports the notion that asynchronous species fluctuations driven by

different responses among species to a temporally variable environment can stabilize community biomass (Cottingham et al. 2001, Loreau and de Mazancourt 2008, Allan et al. 2011).

Responses to flow

The effect of flow events was larger on density than on richness, a commonly observed response in streams (Giller and Malmqvist 1998). Short-term high-flow events in temperate streams are often stochastic and unpredictable

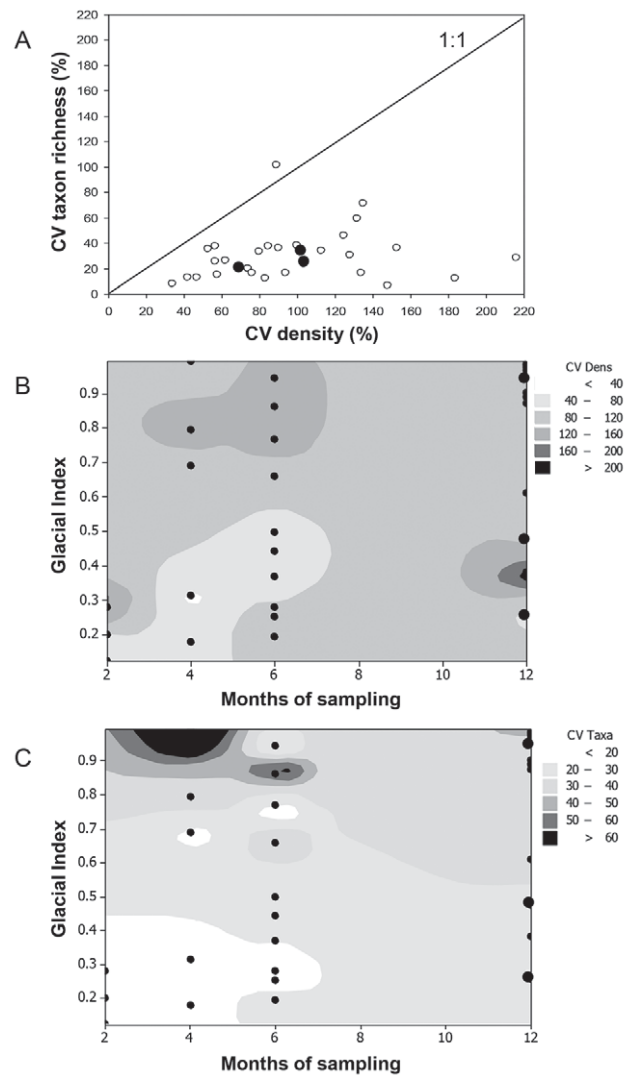


Figure 4. Coefficient of variation (CV) in taxon richness as a function of CV in density at various sites in different streams (A), and CV in density (B) and taxon richness (C) as a function of the Glacial Index (GI) and the number of months that the sampling covered. The GI was proposed by Jacobsen and Dangles (2012) as a proxy for environmental harshness. Values close to 1 are obtained close to large glaciers (see Methods for details). Large black dots = this study. Data from Brown et al. (2006), Robinson et al. (2001), Burgherr and Ward (2001), Lods-Crozet et al. (2001), Schütz et al. (2001), and this study.

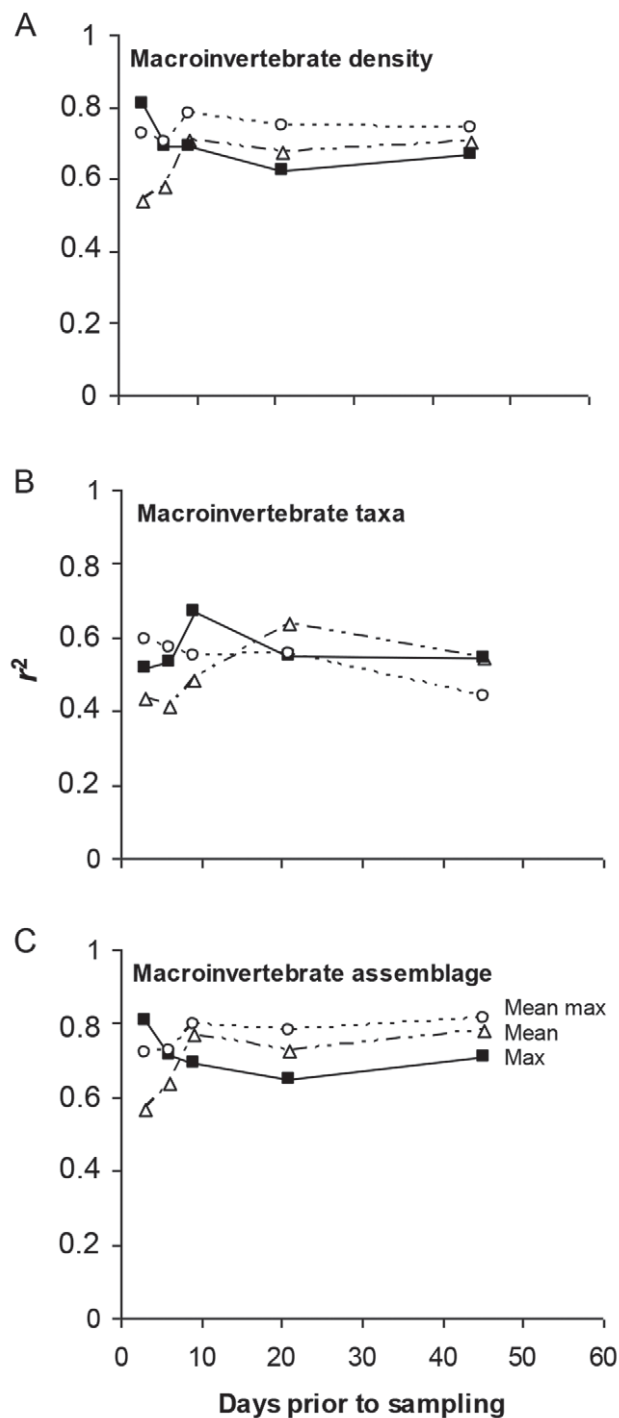


Figure 5. r^2 values from exponential regressions of density (A), taxa richness (B), and nonmetric multidimensional scaling (NMDS) axis-1 coordinates (C) against mean, maximum, and mean maximum discharge during the last 3, 6, 9, 21, and 45 d before sampling of benthic macroinvertebrates.

(Resh et al. 1988). In contrast, benthic macroinvertebrates in tropical glacier-fed streams are subjected to quite predictable increases in hydraulic stress mostly on a daily basis that follows the diel freeze–melt cycle of the glacier (even though the magnitude of these diel fluctuations may

be quite variable and largely unpredictable). If macroinvertebrates had adapted to this predictable regime, we might not expect to find a large effect of daily fluctuations in discharge on the macrofauna. However, we did indeed find significant relationships between faunal metrics and all 3 discharge parameters (mean, maximum, mean maximum), calculated for periods from 3 to 45 d prior to sampling (Fig. 5A–C). These discharge parameters were all highly correlated across all period lengths (all $r_p > 0.85$). Consequently, we could not distinguish between short-term and longer-term effects of flow on the fauna. However, these results enhance the robustness of our finding that flow events do indeed drive temporal variability in the fauna of equatorial glacier-fed streams.

If disturbance level varies among sites, simple CVs in faunal metrics may not allow us to disentangle the effect of disturbance level from that of taxon richness on community stability, even if we increased explanatory power by including more sites. Regressions between quantified disturbances (flow events) and faunal metrics should better reflect relative community response. However, the slopes of these regression lines, i.e., the effect of flow events on the faunal metrics, also did not differ significantly among the 3 stream sites (Fig. 6A–C). The explanatory power of flow was not significant for any faunal metric at site A, probably because of overriding effects of other stochastic disturbances in the highly unstable morainic environment at site A.

We did not calculate mean boundary shear stress at the reach scale because the DuBoys equation is applicable only under uniform flow conditions in wide channels ($W/H > 20$) (Schwendel et al. 2010), but the lower mean current velocity, depth, and slope at site A compared to site B should lead to lower shear stress at site A. That combined with a higher skewness index (\sim refugia space) at site A suggests that a given flow event had less effect on the fauna at site A than at site B. Likewise, if we assume that the lower mean current velocity, higher skewness index, and lower CV in water depth at site C probably diminished the effect of a given flow event on the fauna at site C (thereby reducing the regression slope) compared to site B, then regression slopes for density (Fig. 6A) and community composition (Fig. 6C) should be similar for the 3 sites. In contrast, site C, the most taxon rich, should be the most variable with respect to taxon richness. Thus, these results do not support our expectations of reduced influence of glacial runoff along the stream or the predictions of the diversity–stability hypothesis that high taxon richness should reduce community variability as a response to disturbance. Again, relationships between flow and community metrics seem to be the outcome of a complex interaction between habitat-specific characteristics and differing communities composed of species with different resilience/resistance traits (Füreder 2007).

Future investigators of temporal variability in communities along glacial-fed streams could take advantage of

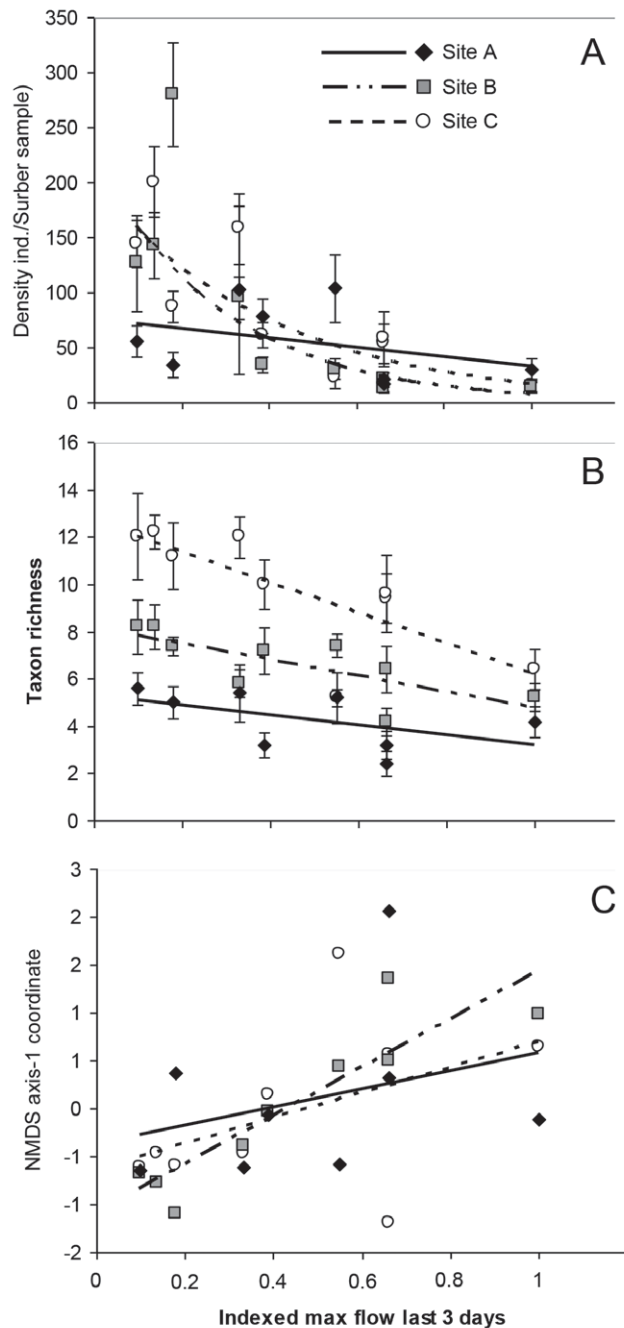


Figure 6. Linear regressions of faunal density (A), taxon richness (B), and nonmetric multidimensional scaling (NMDS) axis-1 coordinates (C) as functions of indexed maximum (max) flow during the last 3 d before sampling benthic macroinvertebrates. Error bars denote SE. Ind. = individuals, max = maximum.

this perfect model system and design studies specifically to test the diversity–stability hypothesis (which was not our goal). We also need to know how species specialized and endemic to glacier-fed streams depend upon and respond to hydrologic regime (Cauvy-Fraunié et al. 2013). Many glaciers are shrinking, and all monitored tropical Andean glaciers are shrinking quickly (Vuille et al. 2008). Glacial

shrinkage certainly will cause changes in the hydrological regime of meltwater streams (Milner et al. 2009), but the nature of such changes may be highly stream- and region-specific. Therefore, predicting effects of glacial shrinkage on aquatic communities will be challenging. Nevertheless, understanding how benthic communities respond to hydrological regime and disturbances is a prerequisite for subsequent predictions of consequences of tropical glacier melting on diversity, composition, and stability of communities in glacier-fed streams.

ACKNOWLEDGEMENTS

We thank 2 anonymous referees and editor Pamela Silver for their effort to improve this paper. We also thank Ladislav Hamerlik for help with the Chironomidae identifications. José Delgado kindly permitted access to the study area (Reserva Ecológica Antisana). The funding by a WWF-Novozymes grant 2008 to DJ and an Ecofondo grant no. 034-ECO8-inv1 to OD is greatly appreciated.

LITERATURE CITED

- Allan, E., W. Weisser, A. Weigelt, C. Roscher, M. Fischer, and H. Hillebrand. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences of the United States of America* 108:17034–17039.
- Biggs, B. J. F., R. A. Smith, and M. J. Duncan. 1999. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. *Journal of the North American Benthological Society* 18:222–241.
- Brown, L. E., D. M. Hannah, and A. M. Milner. 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., A. M. Milner, and D. M. Hannah. 2006. Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. *Hydrobiologia* 560:159–173.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Burgherr, P., and J. V. Ward. 2001. Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps). *Freshwater Biology* 46: 1705–1721.
- Cáceres, B., L. Maisincho, J. D. Taupin, B. Francou, E. Cadier, F. Delachaux, R. Bucher, M. Villacís, D. Paredes, J. P. Chazarin, A. Garcés, and R. Laval. 2005. Glaciares del Ecuador: Antisana y Carihuayrazo. Informe del Año 2004. Institut de Recherche pour le Développement, Instituto Nacional de Hidrología y Meteorología, Empresa Municipal de Alcantarillado y Agua Potable de Quito, Quito, Ecuador.
- Cadier, E., M. Villacís, A. Garcés, P. Lhuissier, L. Maisincho, R. Laval, D. Paredes, B. Cáceres, and B. Francou. 2007. Variations of a low latitude Andean glacier according to global and local climate variations: first results. Glacier mass balance changes and meltwater discharge. *International Association of Hydrological Sciences Press Publications* 318:66–74.

- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the function of trophic groups and ecosystems. *Nature* 443:989–992.
- Castella, E., H. Adalsteinsson, J. E. Brittain, G. M. Gislason, A. Lehmann, V. Lencioni, B. Lods-Crozet, B. Maiolini, A. M. Milner, J. O. Olafsson, S. J. Saltveit, and D. L. Snook. 2001. Macroinvertebrate richness and composition along a latitudinal gradient of European glacier-fed streams. *Freshwater Biology* 46:1811–1831.
- Cauvy-Fraunié, S., P. Andino, R. Espinosa, R. Calvez, F. Anthelme, D. Jacobsen, and O. Dangles. 2013. Glacial flood pulse effects on benthic fauna in equatorial high-Andean streams. *Hydrological Processes*. doi: 10.1002/hyp.9866
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M. L. Cody and J. Diamond (editors). *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts.
- Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters* 4:72–85.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guégan, B. A. Hawkins, D. M. Kaufman, D. M. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121–1134.
- Death, R. G. 2008. Effects of floods on aquatic invertebrate communities. Pages 103–121 in J. Lancaster and R. A. Briers (editors). *Aquatic insects: challenges to populations*. CAB International, Wallingford, UK.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Epler, J. H. 2001. Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. A guide to the taxonomy of the midges of the southeastern United States, including Florida. Special Publication SJ2001-SP13. North Carolina Department of Environment and Natural Resources, Raleigh, North Carolina, and St Johns River Water Management District, Palatka, Florida.
- Favier, V., A. Coudrain, E. Cadier, B. Francou, E. Ayabaca, L. Maisincho, E. Praderio, M. Villacís, and P. Wagnon. 2008. Evidence of ground water flow on Antizana ice-covered volcano, Ecuador. *Hydrological Sciences Journal* 53:278–291.
- Fernández, H. R., and E. Domínguez (editors). 2001. *Guía para la determinación de los artrópodos bentónicos sudamericanos*. Editorial Universitaria de Tucumán, Tucumán, Argentina.
- Füreder, L. 2007. Life at the edge: habitat condition and bottom fauna of alpine running waters. *International Review of Hydrobiology* 92:491–513.
- Füreder, L., C. Schütz, M. Wallinger, and R. Burger. 2001. Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. *Freshwater Biology* 46:1673–1689.
- Giller, P. S., and B. Malmqvist. 1998. *The biology of streams and rivers*. Oxford University Press, Oxford, UK.
- Graham, A. A., D. J. McCaughan, and F. E. McKee. 1988. Measurement of surface area of stones. *Hydrobiologia* 157:85–87.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological statistics software package for educational and data analysis. *Palaeontologia Electronica* 4(1).
- Hieber, M., C. T. Robinson, U. Uehlinger, and J. D. Ward. 2002. Are alpine lake outlets less harsh than other alpine streams? *Archiv für Hydrobiologie* 154:199–223.
- Ilg, C., and E. Castella. 2006. Patterns of macroinvertebrate traits along three glacial stream continuums. *Freshwater Biology* 51:840–853.
- Irons, J. G., L. K. Miller, and M. W. Oswood. 1993. Ecological adaptations of aquatic macroinvertebrates to overwintering in interior Alaska (U.S.A.) subarctic streams. *Canadian Journal of Zoology* 71:98–108.
- Jacobsen, D. 2008a. Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia (Berlin)* 154:795–807.
- Jacobsen, D. 2008b. Tropical high-altitude streams. Pages 219–256 in D. Dudgeon (editor). *Tropical stream ecology*. Elsevier Science, London, UK.
- Jacobsen, D., and O. Dangles. 2012. Environmental harshness and global richness patterns in glacier-fed streams. *Global Ecology and Biogeography* 21:647–656.
- Jacobsen, D., O. Dangles, P. Andino, R. Espinosa, L. Hamerlík, and E. Cadier. 2010. Longitudinal zonation of macroinvertebrates in an Ecuadorian glacier-fed stream: do tropical glacial systems fit the model? *Freshwater Biology* 55:1234–1248.
- Jacobsen, D., A. M. Milner, L. E. Brown, and O. Dangles. 2012. Biodiversity under threat in glacier-fed river systems. *Nature Climate Change* 2:361–364.
- Jiang, L., and Z. Pu. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *American Naturalist* 174:651–659.
- Københavns Universitet. 1989. *Limnologisk Metodik*. Akademisk Forlag, University of Copenhagen, Denmark.
- Kuhn, J., P. Andino, R. Calvez, R. Espinosa, L. Hamerlík, S. Vie, O. Dangles, and D. Jacobsen. 2011. Spatial variability in macroinvertebrate assemblages along and among neighbouring equatorial glacier-fed streams. *Freshwater Biology* 56:2226–2244.
- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19: 573–592.
- Lamouroux, N., S. Dolédec, and S. Gayraud. 2004. Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society* 23:449–466.
- Lancaster, J., and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* 12:385–393.
- Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. *American Naturalist* 156:534–552.
- Lods-Crozet, B., E. Castella, D. Cambin, C. Ilg, S. Knispel, and H. Mayor-Simeant. 2001. Macroinvertebrate community structure in relation to environmental variables in a Swiss glacial stream. *Freshwater Biology* 46:1641–1661.
- Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist* 172:E48–E66.
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536.

- Maisincho, L., B. Cáceres, C. Manciat, C. Loyo, E. Cuenca, M. Villacís, D. Paredes, A. Garcés, R. Laval, S. Mailler, R. Bucher, F. Delachaux, D. Freire, J. P. Chazarin, B. Francou, and E. Cadier. 2007. Glaciares del Ecuador: Antisana y Carihuayrazo. Informe del Año 2005. Institut de Recherche pour le Développement, Instituto Nacional de Hidrología y Meteorología, Empresa Municipal de Alcantarillado y Agua Potable de Quito, Quito, Ecuador.
- Merritt, R. W., and K. W. Cummins (editors). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.
- Milner, A. M., J. E. Brittain, E. Castella, and G. E. Petts. 2001. Trends in macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. *Freshwater Biology* 46:1833–1847.
- Milner, A. M., L. E. Brown, and D. M. Hannah. 2009. Hydroecological response of river systems to shrinking glaciers. *Hydrological Processes* 23:62–77.
- Milner, A. M., and G. E. Petts. 1994. Glacial rivers: physical habitat and ecology. *Freshwater Biology* 32:295–307.
- Molina, C. I., F. M. Gibon, J. Pinto, and C. Rosales. 2008. Aquatic macroinvertebrate structure in a high-Andean stream of the Cordillera Real, Bolivia: annual and longitudinal variations in relation to environmental factors. *Ecología Aplicada* 7:105–116.
- Parker, S. M., and A. D. Huryn. 2011. Effects of natural disturbance on stream communities: a habitat template analysis of arctic headwater streams. *Freshwater Biology* 56:1342–1357.
- Peterson, C. G., and R. J. Stevenson. 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73:1445–1461.
- Pfankuch, D. J. 1975. Stream reach inventory and channel stability evaluation. Region 1, US Department of Agriculture Forest Service, Missoula, Missouri. (Available from: <https://wiki.umn.edu/pub/Nieber/WebHome/Pfankuch.pdf>)
- Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* 11:86–92.
- Rempel, L. L., J. S. Richardson, and M. C. Healey. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. *Journal of the North American Benthological Society* 18:34–48.
- Resh, R. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.
- Robinson, C. T., U. Uehlinger, and M. Hieber. 2001. Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. *Freshwater Biology* 46:1663–1672.
- Roldán, G. 1996. Guía para el Estudio de los Macroinvertebrados Acuáticos del Departamento de Antioquia. Fondo Fen Colombia, Colciencias, Universidad de Antioquia, Bogotá, Colombia.
- Ruiz-Moreno, J. L., R. Ospina-Torres, H. Gómez-Sierra, and W. Riss. 2000. Guía para la identificación genérica de larvas de quironómidos (Diptera: Chironomidae) de la sabana de Bogotá. III. Subfamilias Tanypodinae, Podonomidae y Diametinae. *Caldasia* 22:34–60.
- Schütz, C., M. Wallinger, R. Burger, and L. Füreder. 2001. Effects of snow cover on the benthic fauna in a glacier-fed stream. *Freshwater Biology* 46:1691–1704.
- Schwendel, A. C., R. G. Death, and I. C. Fuller. 2010. The assessment of shear stress and bed stability in stream ecology. *Freshwater Biology* 55:261–281.
- Smith, B. P. G., D. M. Hannah, A. M. Gurnell, and G. E. Petts. 2001. A hydrogeomorphological context for ecological research on alpine glacial rivers. *Freshwater Biology* 46:1579–1595.
- Snook, D. L., and A. M. Milner. 2002. Biological traits of macroinvertebrates and hydraulic conditions in a glacier-fed catchment (French Pyrenees). *Archiv für Hydrobiologie* 153: 245–271.
- Statzner, B., S. Dolédec, and B. Hugueny. 2004. Biological traits composition of European stream invertebrate communities: assessing the effects of various filter types. *Ecography* 27:470–488.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36–50.
- Townsend, C. R., and A. G. Hildrew. 1994. Species traits in relation to a habitat template for river systems. *Freshwater Biology* 31:265–275.
- Townsend, C. R., M. R. Scarsbrook, and S. Dolédec. 1997. The intermediate disturbance hypothesis: refugia and biodiversity in streams. *Limnology and Oceanography* 42:938–949.
- Uehlinger, U., K. Tockner, and F. Malard. 2002. Ecological windows in glacial stream ecosystems. Pages 20–21 *in* Alpine streams. EAWAG News No. 54. EAWAG, Duebendorf, Switzerland.
- Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. *Earth-Science Review* 89: 79–96.
- Wiederholm, T. 1983. Chironomidae of the Holarctic Region. Part 1: Larvae. *Entomologica Scandinavica Supplement* 19.
- White, K. E. 1978. Dilution methods. Pages 47–55 *in* R. W. Herschy (editor) *Hydrometry*. John Wiley and Sons, Chichester, UK.