

Research

Flow intermittency influences the trophic base, but not the overall diversity of alpine stream food webs

Andre R. Siebers, Amael Paillex and Christopher T. Robinson

A. R. Siebers (<https://orcid.org/0000-0002-8326-1649>) ✉ (andre.siebers@eawag.ch), A. Paillex (<https://orcid.org/0000-0001-9255-3662>) and C. T. Robinson, Dept of Aquatic Ecology, Eawag, Swiss Federal Inst. of Aquatic Sciences, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland. CTR also at: Inst. of Integrative Biology, Zürich, Switzerland.

Ecography

42: 1523–1535, 2019

doi: 10.1111/ecog.04597

Subject Editor: Jani Heino

Editor-in-Chief: Miguel Araújo

Accepted 25 April 2019

Alpine streams can exhibit naturally high levels of flow intermittency. However, how flow intermittency in alpine streams affects ecosystem functions such as food web trophic structure is virtually unknown. Here, we characterized the trophic diversity of aquatic food webs in 28 headwater streams of the Val Roseg, a glacierized alpine catchment. We compared stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) trophic indices to high temporal resolution data on flow intermittency. Overall trophic diversity, food chain length and diversity of basal resource use did not differ to a large extent across streams. In contrast, gradient and mixing model analysis indicated that primary consumers assimilated proportionally more periphyton and less allochthonous organic matter in more intermittent streams. Higher coarse particulate organic matter (CPOM) C:N ratios were an additional driver of changes in macroinvertebrate diets. These results indicate that the trophic base of stream food webs shifts away from terrestrial organic matter to autochthonous organic matter as flow intermittency increases, most likely due to reduced CPOM conditioning in dry streams. This study highlights the significant, yet gradual shifts in ecosystem function that occur as streamflow becomes more intermittent in alpine streams. As alpine streams become more intermittent, identifying which functional changes occur via gradual as opposed to threshold responses is likely to be vitally important to their management and conservation.

Keywords: allochthonous, glacier, high altitude ecosystem, macroinvertebrates, organic matter, stable isotopes

Introduction

Intermittent rivers and ephemeral streams (IRES) experience recurrent periods without surface flow (Datry et al. 2017). These periodic drying events regulate the structure and diversity of aquatic communities, alter cycles of organic matter and nutrients, and govern the connections between freshwater and terrestrial ecosystems (Larned et al. 2010, Datry et al. 2014, Leigh et al. 2016). IRES likely make up at least 50% of the world's waterways (Datry et al. 2014), and flow intermittency is further increasing in extent and duration in response to changes in climate and land use (Leigh et al. 2016). Despite a

continually growing body of research on IRES (Dadry et al. 2017), substantial knowledge gaps of flow intermittency–ecosystem function relationships still exist (Leigh et al. 2016, Stubbington et al. 2018). In particular, little is known regarding the ecology of intermittent alpine streams, which can experience up to 90% intermittency in fluvial networks (Robinson et al. 2016). Alpine catchments are expected to experience a significant change in flow intermittency in the future, as increased temperatures and temporal shifts in precipitation (Horton et al. 2006, IPCC 2014) influence seasonal patterns of glacial melt, snow melt and groundwater contributions to streams (Brown et al. 2003, Malard et al. 2005, Robinson et al. 2016). These changes in flow intermittency will substantially influence ecosystem properties and processes (Milner et al. 2009, Slemmons et al. 2013, Cauvy-Fraunié et al. 2015). A comprehensive understanding of how flow intermittency structures and maintains alpine fluvial ecosystems is thus critical to the conservation of biodiversity and ecosystem function in alpine, as well as other, catchments.

Food webs characterize the energy flow through communities, thus integrating both biodiversity and ecosystem functioning (Thompson et al. 2012). Flow reduction results in habitat contraction in rivers and streams, which in turn results in smaller and less complex food webs due to restrictions on body size, dispersal, productivity and interaction strengths (Rolls et al. 2012). An essential component of food webs is trophic diversity, reflecting the range of dietary niches occupied within a web (Bearhop et al. 2004). In IRES, trophic diversity is strongly affected by drying through the exclusion of large, mobile and obligate aquatic predators (i.e. fish; Sabo et al. 2010, McHugh et al. 2015) that generally occupy the highest trophic levels in freshwater ecosystems (Post 2002a, Takimoto and Post 2013). IRES trophic diversity is thus hypothesized to be consistently limited in vertical dimensions (i.e. food chain length) by the lack of consumers able to fill higher-order trophic niches (Sabo et al. 2010, McHugh et al. 2015).

Experimental studies also have shown that the overall diversity of basal resource use within freshwater food webs is largely unaffected by flow intermittency, sometimes despite large changes in biomass flux and consumer mortality (Ledger et al. 2013, Boersma et al. 2014, Vander Vorste et al. 2016). Consequently, trophic diversity in IRES might not vary greatly across gradients of flow intermittency or hydrological isolation (McIntosh et al. 2017), somewhat contrary to the general theory that trophic diversity, particularly food chain length, should scale along gradients of ecosystem size and disturbance (Post 2002a). However, these results may reflect the large proportion of studies investigating trophic diversity or food-web size relationships that focused on reaches containing fish (Takimoto and Post 2013). Fish are strongly limited in body size and trophic position by the size of aquatic habitat (McIntosh et al. 2018), and, being largely intolerant to drying events, may actively avoid reaches that dry even briefly (McHugh et al. 2015).

In contrast, the macroinvertebrate fauna of IRES have many adaptations that confer resistance or resilience to drying events (Bogan et al. 2017). An increase in predatory semi-aquatic or terrestrial macroinvertebrate taxa also is common within drying channels, possibly maintaining overall trophic diversity despite the loss of obligate aquatic taxa (McIntosh et al. 2017).

Consequently, while aquatic habitat size may be the most important determinant of overall trophic diversity in ecosystems with fish (Takimoto and Post 2013), macroinvertebrate communities may respond to ecosystem ‘size’ or disturbance at a different scale, e.g. the frequency and duration of drying events. For example, McHugh et al. (2015) found that while food chain length was lower in fishless reaches overall, macroinvertebrate-dominated food chains contributed to an overall relationship between habitat size and trophic diversity in intermittent streams. Further, Hette-Tronquart et al. (2013) showed that much of the difference in food chain length between streams with differing variability in water temperature was due to the trophic position of filter feeders and shredders. Finally, in their meta-analysis of determinants of food chain length, Takimoto and Post (2013) found positive effects of ecosystem size on trophic diversity in the macroinvertebrate-dominated pitcher plant ecosystems studied by Baiser et al. (2011). These studies thus show a need for further work to identify the different constraints on trophic diversity that might occur in IRES as opposed to perennial systems, particularly in macroinvertebrate-dominated ecosystems.

In contrast with overall trophic diversity, the proportional contribution of different food sources to consumers in IRES is often highly spatially and temporally variable. This functional redundancy through high feeding variability may be a mechanism by which IRES food webs resist high environmental variability (Leigh et al. 2010, Schriever and Lytle 2016). Omnivory is thus common in IRES food webs, as are high proportions of generalist grazing and gatherer/collector taxa (Sánchez-Carmona et al. 2012, Blanchette et al. 2013). Consequently, while it is predicted that IRES should generally shift their trophic base from allochthonous to autochthonous sources as they dry (McIntosh et al. 2017), evidence for shifts in organic matter sources supporting IRES food webs as they become more intermittent have been largely equivocal. Both algae (Bunn et al. 2003, Dekar et al. 2009, Holgersson et al. 2016, Pettit et al. 2016) and terrestrial detritus (Reid et al. 2008, Leigh et al. 2010, Hunt et al. 2012) have been identified as key sources of the organic matter assimilated by metazoan consumers across intermittent and ephemeral freshwater habitats. Thus, the mechanisms underlying differences in the trophic base of IRES food webs might largely be accredited to differences in additional, regional ecological factors (e.g. riparian vegetation quality) rather than differences in flow intermittency alone (McIntosh et al. 2017). Alpine streams occur along a number of steep environmental gradients that may influence trophic structure in aquatic food webs, such as water temperature, channel stability and

organic matter quality (Brown et al. 2003, Uehlinger et al. 2009, Hotaling et al. 2017). Disentangling the effects of such strong environmental gradients from those of flow intermittency is thus crucial in understanding which aspects of trophic diversity and food-web structure are most affected by changes in the flow regime.

Collection of high-resolution data on flow intermittency is often time and labor intensive (Stubbington et al. 2018). Further, gauging stations are most often placed on large, perennial channels, rather than the extensive upper network of low-order streams that are more likely to dry (Meyer et al. 2007, Snelder et al. 2013). Thus, our understanding of the effects of flow intermittency on ecosystem function has frequently been limited to comparisons of perennial and intermittent reaches, rather than along a gradient of flow intermittency (Leigh et al. 2016). In this regard, ecosystem responses to flow intermittency might follow a ramp, threshold or stepped pattern (Boulton 2003, Lake 2003), which comparisons of perennial and intermittent reaches alone might not identify. Aquatic communities also are structured as a response to antecedent conditions (Sponseller et al. 2010), and may represent variability to antecedent flow conditions rather than conditions at the time of sampling. In this context, IRES exhibit wide variation in the frequency, timing and duration of flow intermittency (Costigan et al. 2017). Thus, characterizing the fine-scale spatial and temporal patterns of flow cessation could provide important insights into mechanisms of food-web variation in relation to flow intermittency gradients (Sánchez-Montoya et al. 2018), particularly when flow intermittency affects fluvial ecosystems in conjunction with other environmental stressors.

In this study, we quantified the trophic structure of naturally fishless alpine stream food webs along a fine-scale gradient in flow intermittency. We used high spatial and temporal-resolution data on flow cessation from electrical resistance sensors to explain variation in stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) composition of food webs among headwater streams of a glacierized alpine catchment. We expected that the increase in resolution of flow intermittency data would allow us to identify that 1) overall trophic diversity might decrease across more intermittent streams, largely driven by a reduction in food chain length; that 2) macroinvertebrate diets would show a change from allochthonous to autochthonous sources, without an overall reduction in basal resource diversity; and 3) that measures reflecting common limiting alpine environmental gradients, such as elevation and variation in water temperature, would interact strongly with flow intermittency as explanatory variables for trophic diversity.

Material and methods

Site description and sampling design

The Val Roseg is a glacierized river valley located in the Bernina massif in the eastern Swiss Alps. The catchment is hydrologically complex, with flow regimes affected by

seasonal and topographical combinations of glacial meltwater, rainfall and snowmelt (Malard et al. 2005). Meltwaters from two valley glaciers primarily feed a second-order braided river along the valley floor, while numerous headwater tributaries drain into the floodplain along valley side slopes. A high proportion ($\geq 75\%$) of the headwater channel network is likely to have intermittent surface flow (Zah et al. 2001b, 2003, Malard et al. 2005, Robinson et al. 2016). Vegetation in the valley consists of European larch *Larix decidua* and stone pine *Pinus cembra* forest along with shrubs (*Juniperus communis* subsp. *alpina*, *Rhododendron ferrugineum*) and small trees (*Alnus viridis*, *Salix* spp.), alpine herbs, grasses and sedges (*Festuca* spp., *Carex* spp.).

A field survey was carried out in June 2017 and used to identify intermittent streams within the fluvial network of the upper Roseg catchment (after Robinson et al. 2016). Based on the survey, 28 headwater streams within the upper catchment were selected for study. These streams were identified as being likely to express a range of flow intermittency from perennial to frequent (weekly to daily). Study streams were distributed both laterally (valley side slopes) and longitudinally across a gradient of altitude, and encompassed headwaters varying in flow (intermittency, water source) and environmental conditions (temperature, altitude, aspect, slope, vegetation). HOBO Pendant Temperature/Light 64K data loggers modified to record electric conductivity and temperature were installed in each stream. The loggers continually recorded (hourly) the presence and absence of surface flow and temperature, thus providing detailed information on flow intermittency (Chapin et al. 2014). Loggers were downloaded in early October 2017 to provide information on the antecedent flow regime for all streams.

Food web sampling

All streams were sampled in autumn (September 2017) for assessing aquatic food webs. All samples were collected from a 20 to 30 m reach of stream where loggers were installed. Benthic macroinvertebrates for stable isotope analysis were collected by repetitive kick-sampling (mesh size: 250 μm) at several sites within each study stream and included main substrate types present (e.g. cobbles, sediments, woody debris, mosses). Three kick-sample sweeps were conducted per stream, and additional sweeps were conducted targeting rare or smaller species if additional mass to conduct isotope analyses ($\sim \geq 0.5$ mg) appeared necessary. Macroinvertebrates were hand-picked from kick-net samples and immediately sorted into 50 ml plastic vials containing stream water, separating non-predator and predator taxa (with large predators further separated from each other), and left alive for ca 8 h to void stomach contents. Macroinvertebrates were then identified and sorted to family, and individual samples stored at -20°C until analysis. Fish are not present in the Val Roseg and thus not included in food web analyses.

We collected potential basal resources (i.e. organic matter) as material homogenized from several individuals, colonies, or accumulations from at least three locations

along the sampling reach of each stream (Jardine et al. 2014). Leaves of riparian plants and aquatic mosses were collected from living plants. Riparian plant samples were separated by species. Coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) were collected directly from the stream. Periphyton was collected as epilithon, scrubbed with a wire brush and rinsed from a minimum of three replicate stones. All samples were stored at -20°C until analysis.

Sample preparation and isotope analysis

All moss and CPOM samples were triple-rinsed with distilled water. Terrestrial plant and aquatic CPOM samples were air dried at 60°C for 72 h and then mechanically ground and homogenized. Periphyton and FPOM samples were centrifuged for 15 min to separate out any residual CPOM and invertebrates. Periphyton, FPOM, moss and invertebrate samples were freeze-dried for 48 h in a Lyovac GT 2-E lyophilizer. Moss and invertebrate samples were finely chopped and homogenized after drying. We weighed ~ 0.5 – 1.5 mg plant and animal samples and combusted them in an elemental analyzer connected to an isotope ratio mass spectrometer for measurement of total C content, total N content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Reference materials for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ derived from NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2 were provided by Biogeochemical Laboratories, Indiana University. Analytical precision was 0.01‰ for $\delta^{13}\text{C}$ and 0.02‰ for $\delta^{15}\text{N}$.

Data analysis

Flow intermittency of streams was determined from a principal components analysis (PCA) based on four metrics of flow intermittency derived from the logger data from 5 July to 11 October 2017. Flow metrics included the presence/absence of dry periods, total duration of dry periods (hours; range, 0–1429), length of individual drying periods (hours; range of means, 0–211), and the timing of dry periods (occurrence of first drying period, August–October 2017). The PCA values ordinated sites along a gradient of flow intermittency from permanently flowing streams to streams with multiple drying events (range; 1–15) throughout the specified period (Supplementary material Appendix 1 Fig. A1). Axis-1 explained 59% of the variation, and was associated with the occurrence, total duration, and average length of individual drying periods. Axis-2 explained 29% of the variation, and was associated with the timing of drying events. Total drying duration was linearly correlated with the average length of drying periods ($R^2 = 0.84$). We thus used PCA Axis-1 values as a proxy for the main components of flow intermittency (FI value) in further analyses. We first transformed Axis-1 data by reversing signs (Supplementary material Appendix 1 Fig. A1) so that progressively more intermittent streams had higher FI values, then applied a natural log transformation (\ln FI value for site minus minimum FI value across sites) to improve normality.

We further calculated a number of environmental variables which are well-described drivers of ecological change in alpine environments (Brown et al. 2003, Hotelling et al. 2017). Stream temperature data derived from the loggers were used to calculate average water temperature ($^{\circ}\text{C}$) and the coefficient of variation (c.v.) for each stream over the study period (Hette-Tronquart et al. 2013). Temperature readings from dry periods were thus excluded. Stream elevation was taken from the swissALTI3D digital elevation model (swisstopo 2018a) and tree cover (100-m radius of each site) from the swissTLM3D large-scale topographical landscape model (swisstopo 2018b) using the GIS software package QGIS 2.16.3 (<http://qgis.osgeo.org>). Distance from the head of the catchment to each site (as a proxy for stream age since loss of glacier cover; Malard et al. 2005, Robinson et al. 2016) was calculated as Euclidean distance (m) based on World Geodetic System (WGS84) coordinates. Finally, CPOM lability was measured by calculating C:N ratios from total C and N content. While these measures do not encompass all aspects of habitat heterogeneity, elevation in particular is closely correlated with several important habitat characteristics (e.g. riparian cover, slope and step-pool morphology, channel stability) across alpine catchments and thus may be considered a general proxy (Brown et al. 2003, Hotelling et al. 2017).

We used complimentary approaches to determine changes in food-web structure along environmental gradients. First, we characterized the trophic niche space occupied by assemblages (i.e. trophic diversity of macroinvertebrate food webs) using complementary metrics. We calculated overall trophic diversity as stable ellipse area (SEAc) (Jackson et al. 2011), maximum height of food webs as food chain length (FCL) (Post 2002b), and basal resource diversity as the $\delta^{13}\text{C}$ range of consumers (C_{range}) (Layman et al. 2007) at each site (Supplementary material Appendix 1 Methods A1).

Second, we used a gradient-based approach from $\delta^{13}\text{C}$ values of macroinvertebrates and measured basal resources. Given consistent $\delta^{13}\text{C}$ values of basal resources across streams, changing $\delta^{13}\text{C}$ values of macroinvertebrates indicate an increasing reliance of consumers on different basal resource pools. Conversely, gradients of change in $\delta^{13}\text{C}$ values of consumers equivalent to those of certain resources indicate a consistent reliance on that source (Rasmussen 2010). We separated primary from secondary consumers by comparison of trophic position (TP; Supplementary material Appendix 1 Methods A1). We selected a cut-off point of $\text{TP} \leq 2.5$ for primary consumers as the point at which well-described predators (Buffagni et al. 2018) began to occur in the dataset. Lastly, we used isotope mixing models to estimate the dietary contributions of basal food resource groups to primary consumers. After assessment of the suitability of the possible range of isotopic mixing models (Smith et al. 2013), we used the Bayesian mixing model SIAR (Parnell et al. 2010) to produce probability distributions of the contributions of basal resources to primary consumer isotope values (Supplementary material Appendix 1 Methods A2).

Table 1. Difference in deviance explained (%) between models predicting various isotope metrics as a response to flow intermittency, and models including both flow intermittency and an additional environmental variable as a predictor term. [†] $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Response	Additional predictor					
	Elevation (m a.s.l.)	Tree cover (%)	Temperature (°C)	Temp. variability (c.v.)	Dist. along catchment (m)	CPOM C:N ratio
Overall trophic diversity (SEAc)	-1.3	-2.2	48.8***	9.7 [†]	-2.0	-0.8
Food chain length (FCL)	0	2.0	24.6	9.8	0.5	12.9
Basal resource diversity (C _{range})	0.2	3.2	33.4*	1.6	0.2	0
Primary consumer $\delta^{13}\text{C}$	11.3	3.1	12.7 [†]	0.5	4.6	28.5***
CPOM consumption	44.1***	2.1	11.3	-0.6	27.3**	17.9*
Periphyton consumption	17.5*	0.3	10.6	2.4	4.5	11.5
FPOM consumption	36.8***	1.0	5.5 [†]	3.7	7.3	10.5*

We used generalised additive models (GAMs) to identify whether SEAc, FCL, C_{range}, $\delta^{13}\text{C}$ and median estimated dietary contribution values (Supplementary material Appendix 1 Methods A1, A2) varied across streams in response to gradients of flow intermittency and other measured environmental variables. First, we explored correlations between trophic diversity indices and flow intermittency as a single predictor variable using GAMs. Next, we identified the amount of additional variance explained by including additional environmental variables in the models. GAMs were built using a single variable in addition to flow intermittency (Table 1) and we calculated the difference in deviance explained (%) between these models and the model with flow intermittency alone. Significant differences in deviance explained were identified using Wald likelihood ratio tests. We did not include an autocorrelation term based on the geographical coordinates of pools, as exploratory data analysis revealed no correlation between residuals and geographic coordinates (Zuur et al. 2009). We restricted GAM predictors to 4 knots to avoid over-interpolation of models. All models were created using the package mgcv in R ver. 3.4.2 (<www.r-project.org>).

Data deposition

Data available from Zenodo: <<http://doi.org/10.25678/0000XX>> (Siebers et al. 2019).

Results

Food-web structure and trophic diversity

Periphyton was the most isotopically distinct basal resource, with higher $\delta^{13}\text{C}$ (mean \pm SD; $-24.1 \pm 4.6\text{‰}$) and lower $\delta^{15}\text{N}$ values ($-3.0 \pm 1.9\text{‰}$) than POM (Fig. 1). CPOM had similar $\delta^{13}\text{C}$ ($-28.1 \pm 1.8\text{‰}$) and $\delta^{15}\text{N}$ values ($-2.4 \pm 1.7\text{‰}$) to terrestrial plants and mosses, while FPOM had intermediate $\delta^{13}\text{C}$ values ($-26.5 \pm 2.2\text{‰}$) to CPOM and periphyton but was enriched in $\delta^{15}\text{N}$ ($-1.6 \pm 2.4\text{‰}$) relative to both (Fig. 1). Macroinvertebrate consumers generally had higher $\delta^{15}\text{N}$ values ($-0.6 \pm 2.2\text{‰}$) than basal resources, and large predatory Diptera larvae (Empididae, Brachycera, Athericidae), Planariidae, and adult diving beetles (Dytiscidae)

occupied the highest levels of food webs (Fig. 1). Periphyton (mean \pm SD; C:N = 7.4 ± 1.1) and FPOM (C:N = 9.0 ± 2.0) generally represented more nutritious resources than CPOM (C:N = 21.5 ± 8.3).

Overall trophic diversity (SEAc), food chain length (FCL), and basal resource diversity (C_{range}) did not significantly change along the gradient of flow intermittency (Fig. 2). Adding average water temperature as an additional predictor resulted in models explaining an additional 20% or more of the variation in all isotopic niche indices (Table 1). Overall trophic diversity (SEAc) decreased (GAM range; 34.0–3.5) when streams were both warmer and more highly intermittent (Fig. 3a). Food chain length (FCL) did not significantly change (GAM range; 0.6–1.6) across the gradients of flow intermittency and water temperature (Fig. 3). Basal

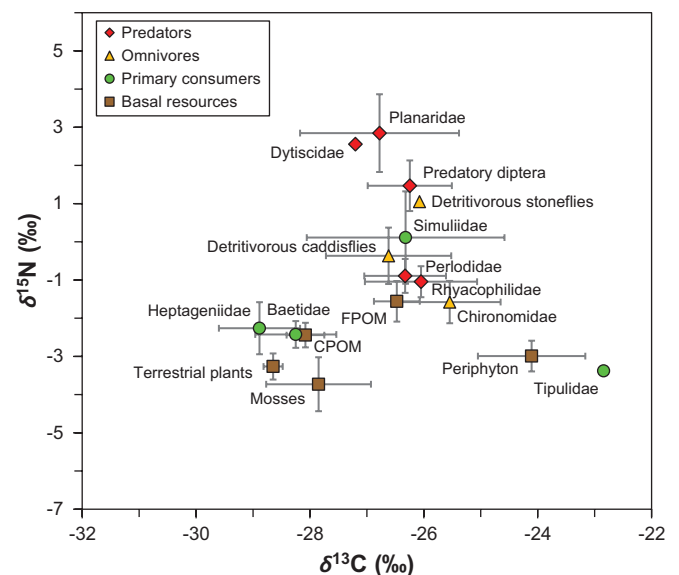


Figure 1. Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for basal resources and macroinvertebrates across the 30 study streams. Large predatory dipteran taxa (Brachycera, Athericidae, Empididae), detritivorous stoneflies (Nemouridae, Leuctridae) and detritivorous caddisflies (Limnephiliidae, Sericostomatidae) are pooled for visual clarity. Values are not corrected for trophic enrichment. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter.

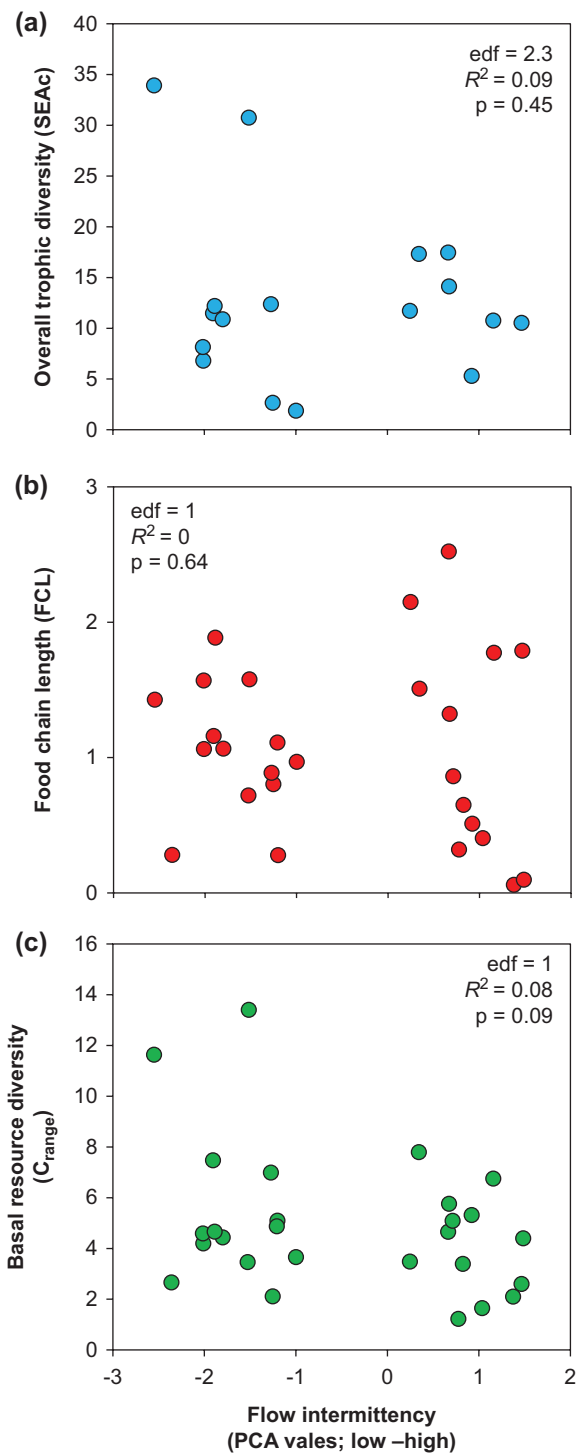


Figure 2. Patterns of isotopic niche space indices describing trophic diversity across flow intermittency gradients. (a) Median estimated overall trophic diversity (stable ellipse area corrected for sample size, SEAc) and associated generalized additive model (GAM). (b) Food chain length (FCL) and associated GAM. (c) Basal resource diversity (consumer $\delta^{13}C$ range, C_{range}) and associated GAM. GAM results are shown as fitted values (solid lines) and 95% confidence intervals for fitted values (dashed lines). R^2 -values are adjusted for sample size. edf=estimated degrees of freedom.

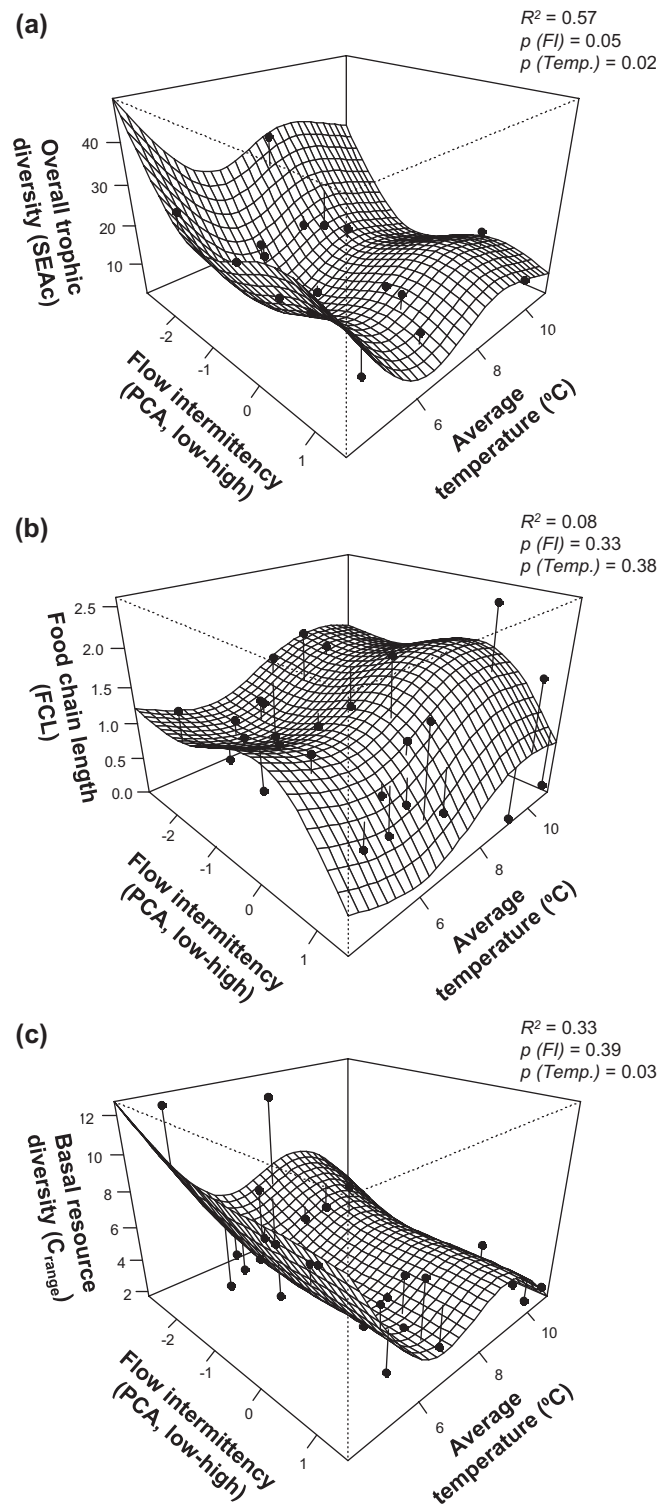


Figure 3. Three-dimensional plots of generalized additive model (GAM) predicting (a) overall trophic diversity (SEAc), (b) food chain length (FCL) and (c) basal resource diversity (C_{range}) relative to flow intermittency with average water temperature ($^{\circ}C$). Original data points and residuals relative to GAM fitted values are also shown. R^2 -values are adjusted for sample size. Temp.=water temperature.

resource diversity (C_{range}) decreased (GAM range; 10.7–1.8) in warmer streams (Fig. 3c).

Trophic base of food webs

Macroinvertebrate primary consumers had higher $\delta^{13}\text{C}$ values in streams with more intermittent flow regimes (GAM range; -29.9 to -24.2‰) (Fig. 4a). There was no corresponding change in $\delta^{13}\text{C}$ values for CPOM (-28.3 to -27.9‰), FPOM (-27.3 to -24.9‰), and periphyton (-27.2 to -20.6‰) along the gradient of flow intermittency (Fig. 4b, c, d).

Median predictions for the estimated contributions of CPOM to primary consumer diets declined (GAM range; 0.62 – 0.30) with increasing flow intermittency (Fig. 5a, b), while predicted contributions of periphyton to primary consumer diets rose (0.10 – 0.38) with increasing flow intermittency (Fig. 5c, d). Estimated contributions of FPOM were, in contrast, relatively consistent (0.24 – 0.33) across flow intermittency gradients (Fig. 5e, f).

In addition to flow intermittency, CPOM C:N ratios were the best additional predictor for primary consumer $\delta^{13}\text{C}$ values (Table 1). Primary consumer $\delta^{13}\text{C}$ values increased (GAM range; -31.5 to -24.0‰) as both flow intermittency and CPOM C:N ratios increased (Fig. 6a). Elevation explained more of the variation in estimates of periphyton

consumption (Table 1). Estimated periphyton consumption increased (GAM range; 0.02 – 0.46) with increasing flow intermittency but peaked at intermediate elevations (Fig. 6b). Elevation, CPOM C:N ratios, and distance along the catchment contributed most to explaining CPOM diet contributions (Table 1). Estimated CPOM consumption decreased (GAM range; 0.78 – 0.26) with flow intermittency and CPOM C:N ratios (Fig. 6c), but increased (GAM range; 0.11 – 0.78) with elevation (Fig. 6d). Estimated CPOM consumption also reduced as streams were located further along the catchment (Supplementary material Appendix 1 Fig. A2). Elevation and CPOM C:N ratios also contributed to further explaining estimated FPOM consumption (Table 1). FPOM consumption was lowest (GAM range; 0.61 – 0.18) at lower elevations (Supplementary material Appendix 1 Fig. A3).

Discussion

We observed little change in food-web trophic diversity across gradients of flow intermittency in 28 alpine headwater streams. In contrast, there was an increase in macroinvertebrate primary consumer $\delta^{13}\text{C}$ values with increasing flow intermittency. This pattern did not match any corresponding changes in organic matter $\delta^{13}\text{C}$ values, suggesting differences in diet were the cause of changing consumer isotopic

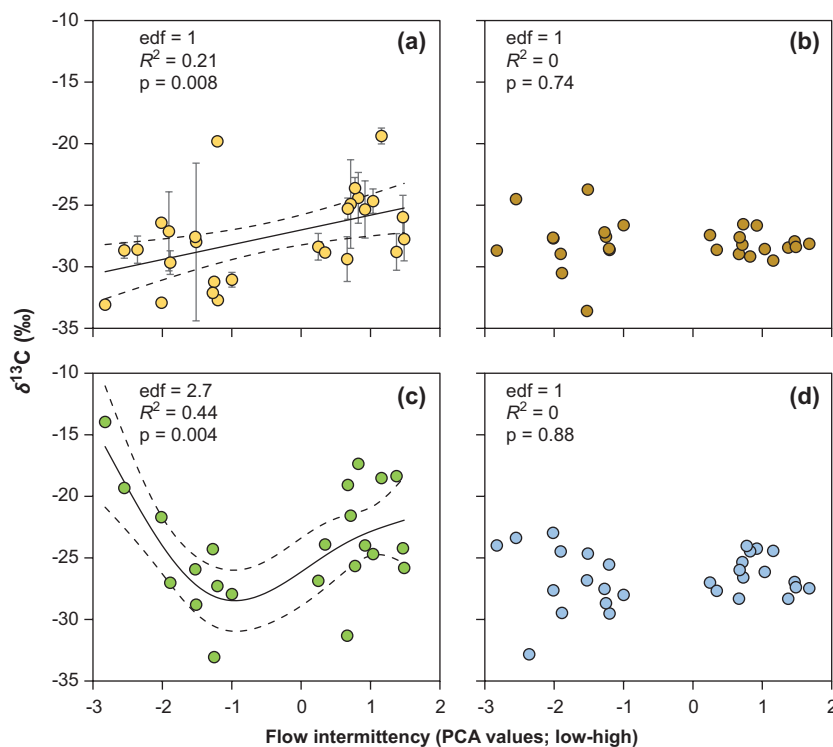


Figure 4. Patterns of organic matter and macroinvertebrate primary consumer $\delta^{13}\text{C}$ values across flow intermittency gradients. (a) Macroinvertebrate primary consumer $\delta^{13}\text{C}$ values (site mean \pm SD) and associated generalized additive model (GAM). (b) Coarse particulate organic matter (CPOM) $\delta^{13}\text{C}$ values and associated GAM. (c) Epilithic periphyton $\delta^{13}\text{C}$ values and associated GAM. (d) Fine particulate organic matter (FPOM) $\delta^{13}\text{C}$ values and associated GAM. GAM results are shown as fitted values (solid lines) and 95% confidence intervals for fitted values (dashed lines). R^2 values are adjusted for sample size. edf = estimated degrees of freedom.

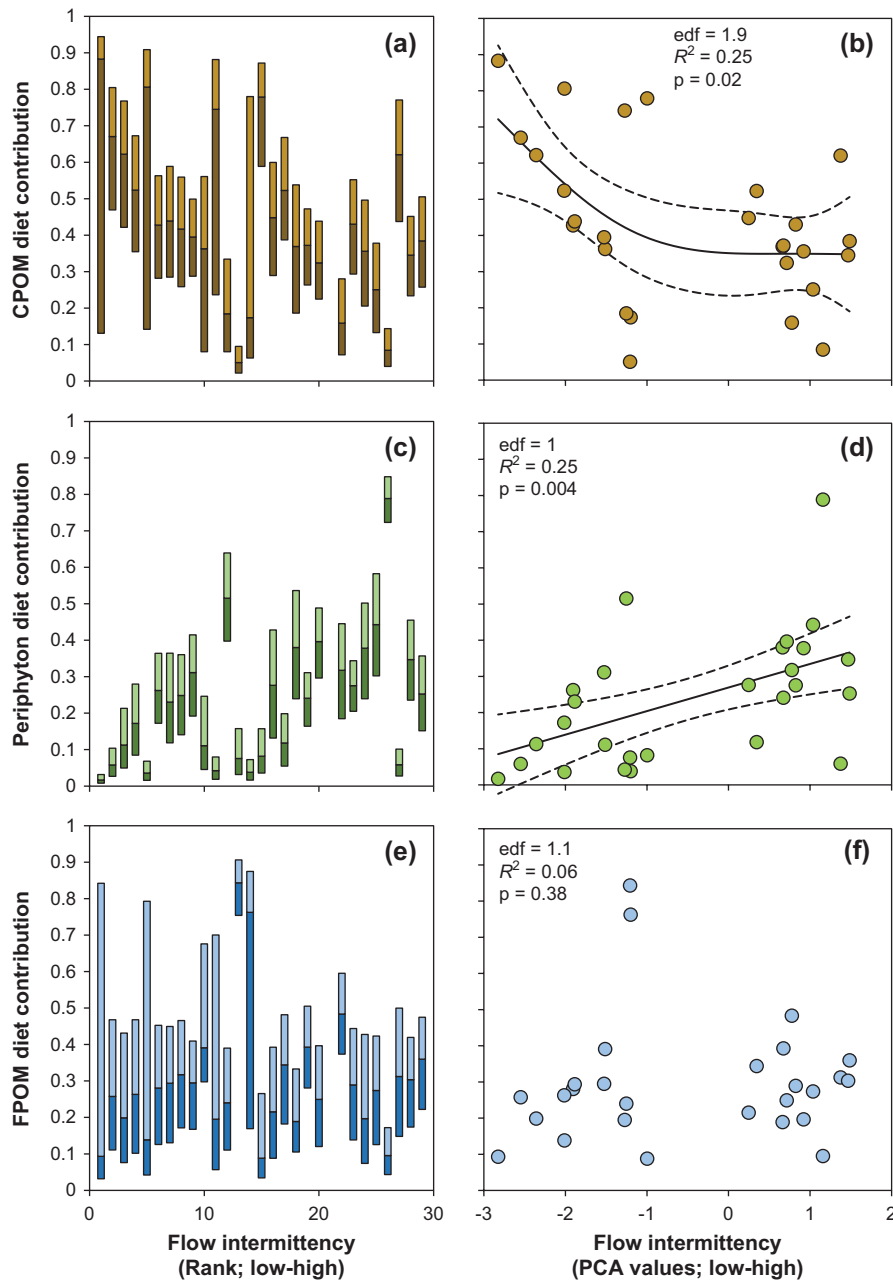


Figure 5. Estimated dietary contributions (as proportions of total) for three basal resource groups to macroinvertebrate primary consumers across flow intermittency gradients. Estimated contributions are shown as 25th percentile, median and 75th percentile of probability distributions for (a) dietary contribution of coarse particulate organic matter (CPOM), with (b) associated generalized additive model (GAM) predicting medians of probability distributions. (c) Dietary contributions of epilithic periphyton and (d) associated GAM. (e) Dietary contributions of fine particulate organic matter (FPOM) and (f) associated GAM. GAM results are shown as fitted values (solid lines) and 95% confidence intervals for fitted values (dashed lines). Note differences in x-axis scales; streams are ranked by flow intermittency (low-high) for visual clarity in (a), (c) and (e). R^2 values are adjusted for sample size. edf = estimated degrees of freedom.

signatures. While mixing model results for primary consumer diet proportions indicated multiple environmental factors were affecting invertebrate diets, models suggested that there was a greater proportion of periphyton and a lower proportion of CPOM being consumed as intermittency increased. Importantly, these results suggest that macroinvertebrates

changed the proportional contributions of basal resources in their diets as streams became more intermittent, without necessarily changing the overall diversity of resources being consumed. As CPOM C:N values were a significant predictor of both increasing primary consumer $\delta^{13}\text{C}$ values and estimated CPOM consumption, CPOM lability appears

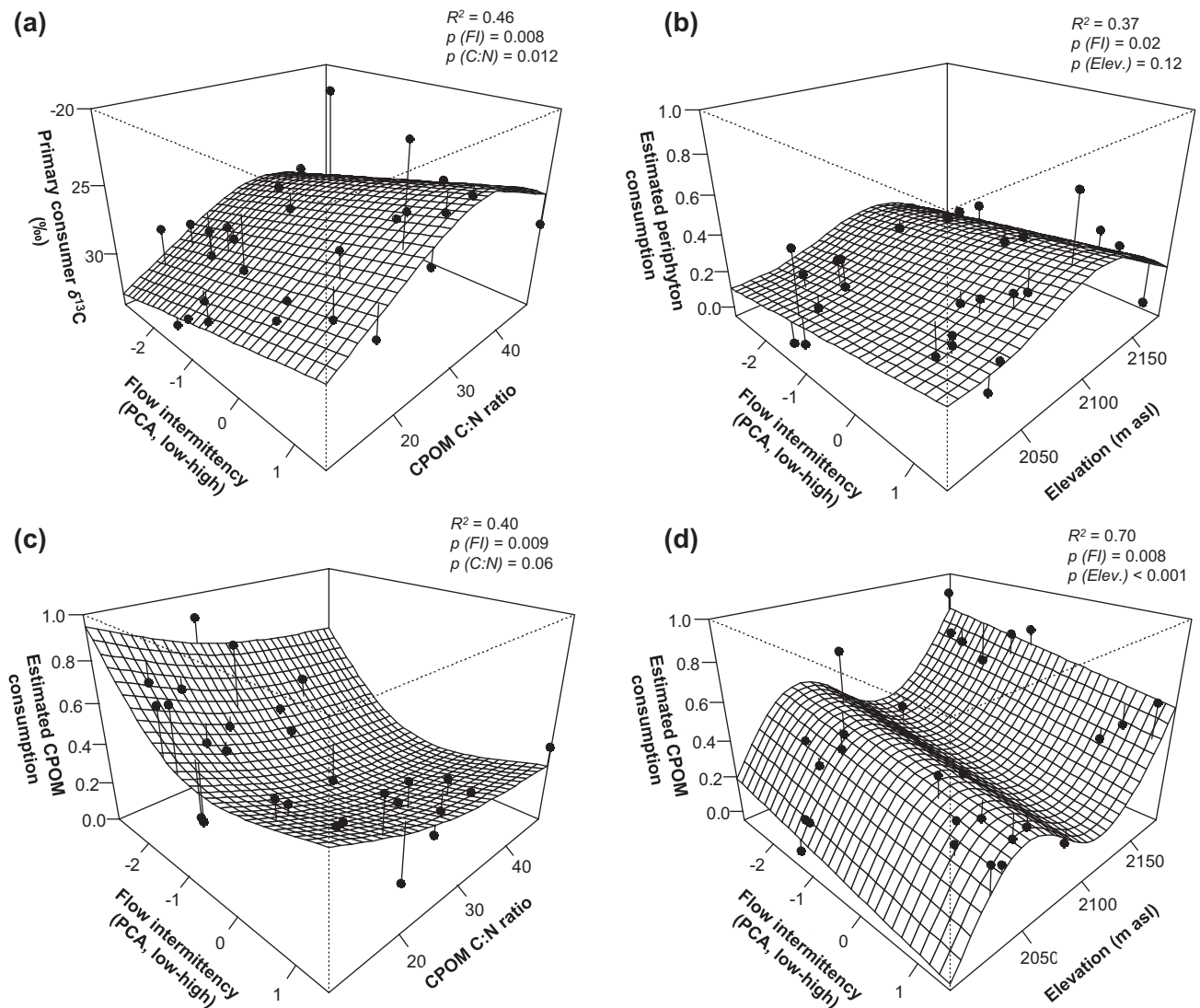


Figure 6. Three-dimensional plots of generalized additive models (GAMs) predicting (a) primary consumer $\delta^{13}C$ values and (c) median estimated coarse particulate organic matter (CPOM) consumption by primary consumers in relation to flow intermittency and site elevation, and (b) median estimated consumption of periphyton and (d) median estimated consumption of CPOM by macroinvertebrate primary consumers relative to flow intermittency and site elevation. Original data points and residuals relative to GAM fitted values are also shown. R^2 -values are adjusted for sample size. FI = flow intermittency. Elev. = elevation. C:N = CPOM C:N ratio.

to be the driving mechanism behind differences in trophic structure. Thus, this study shows that fundamental ecosystem properties can change gradually as streams become more intermittent, rather than only exhibiting substantial changes at hydrological thresholds.

Flow intermittency consistently limits overall trophic diversity

Flow intermittency was generally a poor predictor of trophic diversity. In this respect, our study adds to a growing body of evidence suggesting that trophic diversity, particularly food chain length (FCL), is consistently low across any level of

flow intermittency (Sabo et al. 2010, McHugh et al. 2015). However, average water temperature provided a significant increase in the amount of variability explained in trophic diversity. Higher average temperatures might act to affect trophic diversity through increased body mass and energy availability, allowing for larger predators at higher trophic levels (Woodward et al. 2010). However, our results do not provide conclusive evidence of such patterns, and instead suggest that trophic diversity decreases as these alpine streams warm through a reduction in basal resource diversity (Fig. 3). Trophic diversity also might change as higher temperatures increase productivity through enhanced decomposition and mineralization of organic matter together with

higher periphyton productivity (Friberg et al. 2009). Our results thus suggest that in these alpine streams temperature might have a greater effect on trophic diversity than flow intermittency, possibly through metabolically-costly adaptations to colder environments (Hotaling et al. 2017) and resource limitations (Uehlinger et al. 2009) that might possibly require macroinvertebrates to feed across a wider range of lesser quality basal resources to obtain enough energy. These effects also may lessen at lower altitudes, as species assemblages shift towards taxa with higher ranges of thermal tolerance (Hotaling et al. 2017).

The mechanisms behind limits on trophic diversity are often due to the habitat requirements of fish; which as mobile, obligate aquatic organisms are highly and consistently affected by drying events (McIntosh et al. 2018). Food webs in Val Roseg are instead dominated by macroinvertebrates, which have a multitude of mechanisms for resisting drying events (e.g. diapause, desiccation tolerance) (Bogan et al. 2017). In Val Roseg, these mechanisms might include hyporheic refuge use (Plecoptera, Ephemeroptera), desiccation resistance (Diptera), and semi-aquatic taxa (adult Dytiscidae) (Shama and Robinson 2009, Perić and Robinson 2015, Leys et al. 2016). The effects of high flows on trophic diversity in IRES, such as disturbance or resource subsidies, also are likely to be stronger for fish than macroinvertebrates (Sabo et al. 2010, Warfe et al. 2013, Ruhí et al. 2016). However, indicators of different water sources (e.g. temperature variability, distance along catchment) that should drive differences in flow across streams (Brown et al. 2003) were not predictors of trophic diversity in this study.

As in other intermittent catchments, food webs in Val Roseg consist largely of generalist grazers (Ephemeroptera) and gatherers (Chironomidae), with many omnivorous taxa (Zah et al. 2001a). Changes in food-web breadth, or basal resource use diversity, are more often related to the loss or gain of specialist taxa (Layman et al. 2007). Most macroinvertebrates in Val Roseg have aerial dispersal in the adult stage and headwaters are seldom farther than a few hundred meters from relatively perennial habitats. Consequently, there exists a regional/catchment level pool of taxa that are able to disperse across both perennial and intermittent sites (Shama et al. 2011, Leys et al. 2016), overriding local effects on species richness or trophic diversity (Warfe et al. 2013). Thus, the Val Roseg likely represents a highly-linked metacommunity rather than isolated stream ecosystems (Tonkin et al. 2018). Here, the absence of fish, the high resilience and resistance of macroinvertebrates to drying, a high proportion of generalist/opportunist taxa, and a closely-linked catchment species pool may all be interacting to drive the poor relationship between trophic diversity and flow intermittency. These mechanisms likely act as co-adaptations to both flow intermittency and the relatively harsh environmental conditions of alpine catchments (Füreder et al. 2003, Clitherow et al. 2013, Cauvy-Fraunié et al. 2015), which might largely restrict food webs to a consistent maximum size.

Flow intermittency affects the trophic base of alpine stream food webs

Trends in $\delta^{13}\text{C}$ values of macroinvertebrates and basal resources, together with estimates from the isotope mixing models, suggested that food webs were supported to a greater extent by periphyton in streams that dried more often. Autochthonous production and processing of OM usually peaks with time after flooding and aquatic habitat contracts (Humphries et al. 2014). Autotrophic microbial biomass can also recover rapidly following rewetting events in IRES, despite large changes in elemental stoichiometry during drying (Timoner et al. 2012). The incorporation of algal resources into IRES food webs is thus expected to increase as drying progresses, while CPOM is expected to represent a relatively constant resource across drying gradients (McIntosh et al. 2017). Importantly, we observed strong interacting effects between both flow intermittency and CPOM C:N ratios on the trophic base of food webs. In dry channels, C:N ratios of terrestrial plant litter increase as non-structural compounds are photodegraded or leached (Dieter et al. 2011, Detry et al. 2018). Litter breakdown by micro-organisms and shredding invertebrates also is greatly reduced under dry conditions; i.e. terrestrial CPOM lability in streams is reduced under dry periods (Austin and Vivanco 2006, Corti et al. 2011, von Schiller et al. 2017). As such, litter conditioning during aquatic stages, particularly when algae are included, is a major driver of terrestrial OM uptake into aquatic food webs (Brett et al. 2017). Here, increasing flow intermittency may have ultimately caused reduced lability of terrestrial plant litter in streams, leading to lower assimilation of CPOM by food webs upon rewetting.

CPOM use in IRES food webs is dependent on its lability, consequently the increased consumption of periphyton may partly be a response to allochthonous resource 'scarcity' rather than increases in autochthonous productivity. The relative importance of allochthonous and autochthonous resources to macroinvertebrate food webs is a long-standing issue, and the generality of conceptual models is often dependent on the characteristics of the study systems (e.g. seasonality of leaf litter inputs) (Thorp et al. 2006, Tank et al. 2010). For example, increased consumption of periphyton might be driven by algal productivity in IRES that have disconnected surface water pools (Bunn et al. 2003, Dekar et al. 2009). These pools likely act as refuges for aquatic biota and as biogeochemical 'reactors' allowing continued production and decomposition of OM through otherwise dry periods (Larned et al. 2010). This geomorphic context highlights the increasing importance of local scale factors as IRES dry and contract (Fisher et al. 1998, Larned et al. 2010, Humphries et al. 2014).

The interacting effects of elevation and CPOM C:N ratios on macroinvertebrate diet proportions may largely arise through the distribution of our streams along altitudinal gradients. In alpine environments, elevation should correlate with periphyton productivity through light attenuation, as

vegetation gradients shift to shrubs, herbs and grasses. But in alpine catchments, elevation also can restrict periphyton productivity through decreasing temperature, increasing turbidity and scour disturbance, and low nutrient concentrations (Uehlinger et al. 2009). These factors may thus correspond to the intermediate effect of elevation on periphyton consumption in Val Roseg. Elevation also corresponds with a lower mass of terrestrial OM inputs, although higher elevation vegetation (alpine shrubs, herbs) may have greater lability than lower elevation forests (pine, larch) due to lower proportions of structural compounds in plant tissue. Further, alpine trees also exhibit higher concentrations of non-structural compounds at higher elevations (Hoch and Körner 2012), thus high elevation food webs might rely on relatively labile terrestrial inputs as well as periphyton.

Ecosystem responses to increased flow intermittency

Globally, rivers and streams are expected to become more intermittent as temperatures rise and rainfall decreases or becomes more variable (Döll and Schmied 2012). These changes in flow intermittency are likely to have substantial ecological impacts in areas with complex environmental gradients, such as alpine and montane environments (Cauvy-Fraunié et al. 2015). Predicting the response of stream ecosystems to increased flow intermittency is difficult due to the threshold nature of many ecosystem responses and the high inherent variability of IRES food webs. Dramatic changes in food-web structure and function can occur once certain thresholds in flow cessation are reached (e.g. food chain length, biomass flux) (Ledger et al. 2013, McHugh et al. 2015). However, these thresholds can be precipitated by changes in other ecosystem properties, such as the energetic base of food webs (Bestelmeyer et al. 2011). Gradual changes in trophic dynamics may be obscured by the high overlap of feeding traits and functional resistance of IRES taxa to drying and contraction of aquatic habitats (Leigh et al. 2010, Boersma et al. 2014). In this context, our study shows that shifts in the trophic base of IRES can occur as gradual, ramped changes, and these shifts can be identified if flow intermittency is characterized at a fine scale.

A number of ecosystem functions might change gradually along gradients of flow intermittency, rather than exhibiting clear and dramatic threshold shifts upon increased drying. For example, aquatic macroinvertebrates can increase in density as habitats contract without species loss (Acuña et al. 2005, Dewson et al. 2007, Walters and Post 2011), but substantial losses of diversity follow thresholds of water loss (e.g. loss of lateral connectivity, loss of surface water) (Boulton 2003). Threshold changes in ecological function might occur when drying occurs as a supra-seasonal event (*sensu* Lake 2003) on the intrinsic scale of the organisms affected; i.e. the same level of flow intermittency might represent a seasonal disturbance for drying-adapted IRES taxa (Boersma et al. 2014) but a supra-seasonal disturbance for perennial stream taxa (Ledger et al. 2013), resulting in substantially different magnitudes of response in assemblage and

food-web structure. Whether changes in the trophic base of IRES food webs lead to fundamentally different food-web structure and function post-drying (Bogan and Lytle 2011, Cauvy-Fraunié et al. 2016) is an important avenue of further research. We therefore emphasize that aquatic ecosystem function may not be maintained or stable until thresholds in flow intermittency are reached, but might instead change fundamentally but gradually with even small increases in drying frequency or duration. As Alpine streams become more intermittent, identifying these gradual ecological changes is likely to be vitally important to management and conservation aimed at avoiding dramatic, threshold changes in ecological function.

Acknowledgements – We thank Jorrit Mesman (Univ. of Geneva) and Christian Ebi (Eawag) for assistance in the field. We further thank Christian Ebi for work on the electrical resistance loggers. We thank Zahrah Alghamdi (King Abdul-Aziz Univ.) for laboratory assistance. We thank Serge Robert (Eawag) for analysis of EA-IRMS samples, and the AuA Lab (Eawag) for analysis of water chemistry. We are grateful to Lucrezia and Wolfgang Pollak-Thom, and the staff of the Hotel Restaurant Roseg Gletscher, for their hospitality. *Funding* – Funding for this project was provided through Eawag Discretionary Funds for Research, the Ernst Göhner foundation, Gelbert foundation and Canton Graubünden.

References

- Acuña, V. et al. 2005. Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. – *J. N. Am. Benthol. Soc.* 24: 919–933.
- Austin, A. T. and Vivanco, L. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. – *Nature* 442: 555.
- Baiser, B. et al. 2011. Species richness and trophic diversity increase decomposition in a co-evolved food web. – *PLoS One* 6: e20672.
- Bearhop, S. et al. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. – *J. Anim. Ecol.* 73: 1007–1012.
- Bestelmeyer, B. T. et al. 2011. Analysis of abrupt transitions in ecological systems. – *Ecosphere* 2: 1–26.
- Blanchette, M. L. et al. 2013. Omnivory and opportunism characterize food webs in a large dry-tropics river system. – *Freshwater Sci.* 33: 142–158.
- Bogan, M. T. and Lytle, D. A. 2011. Severe drought drives novel community trajectories in desert stream pools. – *Freshwater Biol.* 56: 2070–2081.
- Bogan, M. T. et al. 2017. Resistance, resilience and community recovery in intermittent rivers and ephemeral streams. – In: Datry, T. et al. (eds), *Intermittent rivers and ephemeral streams: ecology and management*. Elsevier, pp. 349–376.
- Boersma, K. S. et al. 2014. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. – *Freshwater Biol.* 59: 491–501.
- Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. – *Freshwater Biol.* 48: 1173–1185.

- Brett, M. T. et al. 2017. How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? – *Freshwater Biol.* 62: 833–853.
- Brown, L. E. et al. 2003. Alpine stream habitat classification: an alternative approach incorporating the role of dynamic water source contributions. – *Arct. Antarct. Alp. Res.* 35: 313–322.
- Buffagni, A. et al. 2018. The taxa and autecology database for freshwater organisms. ver. 7.0, – <www.freshwaterecology.info>, accessed 24 May 2018.
- Bunn, S. E. et al. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. – *Freshwater Biol.* 48: 619–635.
- Cauvy-Fraunié, S. et al. 2015. Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. – *PLoS One* 10: e0136793.
- Cauvy-Fraunié, S. et al. 2016. Ecological responses to experimental glacier-runoff reduction in alpine rivers. – *Nat. Commun.* 7: 12025.
- Chapin, T. P. et al. 2014. Robust, low-cost data loggers for stream temperature, flow intermittency and relative conductivity monitoring. – *Water Resour. Res.* 50: 6542–6548.
- Clitherow, L. R. et al. 2013. Food web structure in a harsh glacier-fed river. – *PLoS One* 8: e60899.
- Corti, R. et al. 2011. Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river. – *Aquat. Sci.* 73: 537.
- Costigan, K. et al. 2017. Flow regimes in intermittent rivers and ephemeral streams. – In: Datry, T. et al. (eds), *Intermittent rivers and ephemeral streams: ecology and management*. Elsevier, pp. 51–78.
- Datry, T. et al. 2014. Intermittent rivers: a challenge for freshwater ecology. – *BioScience* 64: 299–235.
- Datry, T. et al. 2017. General introduction. – In: Datry, T. et al. (eds), *Intermittent rivers and ephemeral streams: ecology and management*. Elsevier, pp. 1–20.
- Datry, T. et al. 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. – *Nat. Geosci.* 11: 497–503.
- Dekar, M. et al. 2009. Shifts in the trophic base of intermittent stream food webs. – *Hydrobiologia* 635: 263–277.
- Dewson, Z. S. et al. 2007. Invertebrate responses to short-term water abstraction in small New Zealand streams. – *Freshwater Biol.* 52: 357–369.
- Dieter, D. et al. 2011. Preconditioning effects of intermittent stream flow on leaf litter decomposition. – *Aquat. Sci.* 73: 599–609.
- Döll, P. and Schmied, H. M. 2012. How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. – *Environ. Res. Lett.* 7: 014037.
- Fisher, S. G. et al. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. – *Ecosystems* 1: 19–34.
- Friberg, N. et al. 2009. Relationships between structure and function in streams contrasting in temperature. – *Freshwater Biol.* 54: 2051–2068.
- Füreder, L. et al. 2003. Dietary and stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses in alpine stream insects. – *Int. Rev. Hydrobiol.* 88: 314–331.
- Hette-Tronquart, N. et al. 2013. Variability of water temperature may influence food-chain length in temperate streams. – *Hydrobiologia* 718: 159–172.
- Hoch, G. and Körner, C. 2012. Global patterns of mobile carbon stores in trees at the high-elevation tree line. – *Global Ecol. Biogeogr.* 21: 861–871.
- Holgerson, M. A. et al. 2016. Reconciling the role of terrestrial leaves in pond food webs: a whole-ecosystem experiment. – *Ecology* 97: 1771–1782.
- Horton, P. et al. 2006. Assessment of climate-change impacts on alpine discharge regimes with climate model uncertainty. – *Hydrol. Process.* 20: 2091–2109.
- Hotaling, S. et al. 2017. Climate change and alpine stream biology: progress, challenges and opportunities for the future. – *Biol. Rev.* 92: 2024–2045.
- Humphries, P. et al. 2014. The river wave concept: integrating river ecosystem models. – *BioScience* 64: 870–882.
- Hunt, R. J. et al. 2012. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. – *Freshwater Biol.* 57: 435–450.
- IPCC. 2014. *Climate change 2014: synthesis report*. – Cambridge Univ. Press.
- Jackson, A. L. et al. 2011. Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. – *J. Anim. Ecol.* 80: 595–602.
- Jardine, T. D. et al. 2014. Understanding and overcoming baseline isotopic variability in running waters. – *River Res. Appl.* 30: 155–165.
- Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. – *Freshwater Biol.* 48: 1161–1172.
- Larned, S. T. et al. 2010. Emerging concepts in temporary-river ecology. – *Freshwater Biol.* 55: 717–738.
- Layman, C. A. et al. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? – *Ecology* 88: 42–48.
- Ledger, M. E. et al. 2013. Drought alters the structure and functioning of complex food webs. – *Nat. Clim. Change* 3: 223.
- Leigh, C. et al. 2010. Dynamic stability in dry season food webs within tropical floodplain rivers. – *Mar. Freshwater Res.* 61: 357–368.
- Leigh, C. et al. 2016. Ecological research and management of intermittent rivers: an historical review and future directions. – *Freshwater Biol.* 61: 1181–1199.
- Leys, M. et al. 2016. Distribution and population genetic variation of cryptic species of the Alpine mayfly *Baetis alpinus* (Ephemeroptera: Baetidae) in the central Alps. – *BMC Evol. Biol.* 16: 77.
- Malard, F. et al. 2005. Flood-pulse and riverscape dynamics in a braided glacial river. – *Ecology* 87: 704–716.
- Meyer, J. L. et al. 2007. The contribution of headwater streams to biodiversity in river networks. – *J. Am. Water Resour. Assoc.* 43: 86–103.
- McHugh, P. A. et al. 2015. Habitat size influences food web structure in drying streams. – *Ecography* 38: 700–712.
- McIntosh, A. R. et al. 2017. Food webs and trophic interactions in intermittent rivers and ephemeral streams. – In: Datry, T. et al. (eds), *Intermittent rivers and ephemeral streams: ecology and management*. Elsevier, pp. 323–347.
- McIntosh, A. R. et al. 2018. Capacity to support predators scales with habitat size. – *Sci. Adv.* 4: eaap7523.
- Milner, A. M. et al. 2009. Hydroecological response of river systems to shrinking glaciers. – *Hydrol. Process.* 23: 62–77.
- Parnell, A. C. et al. 2010. Source partitioning using stable isotopes: coping with too much variation. – *PLoS One* 5: e9672.

- Perić, M. S. and Robinson, C. T. 2015. Spatio-temporal shifts of macroinvertebrate drift and benthos in headwaters of a retreating glacier. – *Hydrobiologia* 75: 25–41.
- Petit, N. E. et al. 2016. Carbon sources for aquatic food webs of riverine and lacustrine tropical waterholes with variable groundwater influence. – *Mar. Freshwater Res.* 68: 442–451.
- Post, D. M. 2002a. The long and short of food-chain length. – *Trends Ecol. Evol.* 17: 269–277.
- Post, D. M. 2002b. Using stable isotopes to estimate trophic position: models, methods and assumptions. – *Ecology* 83: 703–718.
- Reid, D. J. et al. 2008. Terrestrial detritus supports the food webs in lowland intermittent streams of south-eastern Australia: a stable isotope study. – *Freshwater Biol.* 53: 2036–2050.
- Rasmussen, J. B. 2010. Estimating terrestrial contribution to stream invertebrates and periphyton using a gradient-based mixing model for $\delta^{13}\text{C}$. – *J. Anim. Ecol.* 79: 393–402.
- Robinson, C. T. et al. 2016. Flow intermittency, physico-chemistry and function of headwater streams in an Alpine glacial catchment. – *Aquat. Sci.* 78: 327–341.
- Rolls, R. J. et al. 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. – *Freshwater Sci.* 31: 1163–1186.
- Ruhí, A. et al. 2016. Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. – *Freshwater Biol.* 61: 1536–1549.
- Sabo, J. L. et al. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. – *Science* 330: 965–967.
- Sánchez-Carmona, R. et al. 2012. Food web structure in Mediterranean streams: exploring stabilizing forces in these ecosystems. – *Aquat. Ecol.* 46: 311–324.
- Sánchez-Montoya, M. M. et al. 2018. Understanding the effects of predictability, duration and spatial pattern of drying on benthic invertebrate assemblages in two contrasting intermittent streams. – *PLoS One* 13: e0193933.
- Schriever, T. A. and Lytle, D. A. 2016. Convergent diversity and trait composition in temporary streams and ponds. – *Ecosphere* 7: e01350.
- Shama, L. N. and Robinson, C. T. 2009. Microgeographic life history variation in an alpine caddisfly: plasticity in response to seasonal time constraints. – *Freshwater Biol.* 54: 150–164.
- Shama, L. N. et al. 2011. Bottlenecks drive temporal and spatial genetic changes in alpine caddisfly metapopulations. – *BMC Evol. Biol.* 11: 278.
- Siebers, A. R. et al. 2019. Data from: flow intermittency influences the trophic base, but not the overall diversity of alpine stream food webs. – *Zenodo*, <<http://doi.org/10.25678/0000XX>>.
- Slemmons, K. E. et al. 2013. The influence of glacial meltwater on alpine aquatic ecosystems: a review. – *Environ. Sci. Process. Impact* 15: 1794–1806.
- Smith, J. A. et al. 2013. To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. – *Methods Ecol. Evol.* 4: 612–618.
- Snelder, T. H. et al. 2013. Regionalization of patterns of flow intermittence from gauging station records. – *Hydrol. Earth Syst. Sci.* 17: 2685–2699.
- Sponseller, R. A. et al. 2010. Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. – *Global Change Biol.* 16: 2891–2900.
- Stubbington, R. et al. 2018. Biomonitoring of intermittent rivers and ephemeral streams in Europe: current practice and priorities to enhance ecological status assessments. – *Sci. Total Environ.* 618: 1096–1113.
- swisstopo. 2018a. swissALTI3D, Bundesamt für Landestopographie (Art.30 Geo IV) – 5 704 000 000, reproduced by permission of swisstopo/JA100119.
- swisstopo. 2018b. swissTLM3D, Bundesamt für Landestopographie (Art.30 Geo IV) – 5 704 000 000, reproduced by permission of swisstopo/JA100119.
- Takimoto, G. and Post, D. M. 2013. Environmental determinants of food-chain length: a meta-analysis. – *Ecol. Res.* 28: 675–681.
- Tank, J. L. et al. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. – *J. N. Am. Benthol. Soc.* 29: 118–146.
- Thompson, R. M. et al. 2012. Food webs: reconciling the structure and function of biodiversity. – *Trends Ecol. Evol.* 27: 689–697.
- Thorp, J. H. et al. 2006. The Riverine ecosystem synthesis: biocomplexity in river networks across space and time. – *River Res. Appl.* 22: 123–147.
- Timoner, X. et al. 2012. Functional responses of stream biofilms to flow cessation, desiccation and rewetting. – *Freshwater Biol.* 57: 1565–1578.
- Tonkin, J. D. 2018. The role of dispersal in river network metacommunities: patterns, processes and pathways. – *Freshwater Biol.* 63: 141–163.
- Uehlinger, U. et al. 2009. The physico-chemical habitat template for periphyton in alpine glacial streams under a changing climate. – In: Stevenson, R. J. and Sabater, S. (eds), *Global change and river ecosystems: implications for structure, function and ecosystem services*. Springer, pp. 107–121.
- Vander Vorste, R. et al. 2016. Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. – *Freshwater Sci.* 35: 164–177.
- von Schiller, D. et al. 2017. Nutrient and organic matter dynamics in intermittent rivers and ephemeral streams. – In: Detry, T. et al. (eds), *Intermittent rivers and ephemeral streams: ecology and management*. Elsevier, pp. 135–160.
- Walters, A. W. and Post, D. M. 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. – *Ecol. Appl.* 21: 163–174.
- Warfe, D. M. 2013. Productivity, disturbance and ecosystem size have no influence on food chain length in seasonally connected rivers. – *PLoS One* 8: e66240.
- Woodward, G. et al. 2010. Sentinel systems on the razor's edge: effects of warming on Arctic geothermal stream ecosystems. – *Global Change Biol.* 16: 1979–1991.
- Zah, R. et al. 2001a. Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. – *Freshwater Biol.* 46: 871–882.
- Zah, R. et al. 2001b. Long-term dynamics of the channel network in a glacial floodplain, Val Roseg, Switzerland. – *Arct. Antarct. Alp. Res.* 33: 440–446.
- Zah, R. et al. 2003. Glacial history and floodplain evolution. – In: Ward, J. V. and Uehlinger, U. (eds), *Ecology of a glacial floodplain*. Kluwer Academic Publishers, pp. 17–36.
- Zuur, A. F. et al. 2009. Violation of independence – part II. – In: Zuur, A. F. et al. (eds), *Mixed effects models and extensions in ecology with R*. Springer, pp. 161–191.

Supplementary material (available online as Appendix ecog-04597 at <www.ecography.org/appendix/ecog-04597>). Appendix 1.