LIMNOLOGY and OCEANOGRAPHY

Seasonal and functional variation in the trophic base of intermittent Alpine streams

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Abstract

In high-altitude Alpine streams, seasonal cycles of snowmelt, glacial melt, and rainfall drive variation in the availability of algal food resources. Yet, high-altitude streams also exhibit varying degrees of flow intermittency, ranging from solely winter-drying streams to others that dry periodically throughout summer and autumn. These environmental drivers may interact in different ways to determine the functional trophic base of macroinvertebrates inhabiting high-altitude streams. Here, we estimated the proportional contribution of autochthonous resources to the assimilated diets of benthic macroinvertebrates in 26 headwater streams of Val Roseg, a high Alpine glacial catchment, using stable isotope analysis (δ^{13}C and δ^{15}N) of different macroinvertebrate families and their potential food sources. We compared dietary estimates along a gradient of flow intermittency and across three seasons (Alpine spring, summer, and autumn). Assimilation from autochthonous sources was highest for collector-gatherers and filter feeders in spring, and for grazers in summer. Grazers had higher estimated assimilation from autochthonous sources in intermittent streams than in perennial streams, particularly in summer, while collector-gatherers showed little effect of flow intermittency on dietary estimates. However, responses were highly taxon-specific, with different responses to variation in flow intermittency and season across families within functional groups. Our results suggest that frequent summer-drying events represent tradeoffs between greater access to algal food resources and a higher risk of desiccation, but that differing life history and functional feeding traits across macroinvertebrate taxa drive marked variation in the risks or benefits associated with inhabitants of drying streams.

Many of the worlds' rivers and streams experience flow intermittency, particularly in regions where climatic aridity can drive a high frequency of drying events (Messager et al. 2021). Flow intermittency is also common in the headwaters of mesic catchments, such as high-altitude montane and subalpine areas (Robinson et al. 2016a; Paillex et al. 2020). In these regions, seasonal variability in the contribution of different water sources (rainfall, snowmelt, and glacial melt) and high gradient slopes with low transient storage volumes can create flashy flow regimes in streams (Malard et al. 2000). Drying events in high-altitude headwater streams can thus be common during low-rainfall periods in summer

and autumn, as well as winter freezing periods (Paillex et al. 2020). While the ecological effects of water source variation have been widely investigated for benthic communities in high-altitude streams (Brown et al. 2003; Milner et al. 2017), the effects of flow intermittency are only recently being described (Tolonen et al. 2019). In particular, there is little information on how seasonality in water source contributions interacts with seasonality in the frequency and duration of drying events; yet, flow intermittence is likely a key driver of ecological processes in high-altitude streams (Shama et al. 2011; Harjung et al. 2019).

Trophic dynamics in high-altitude streams may be particularly affected by seasonal variation in environmental gradients. Benthic macroinvertebrates in high-altitude streams generally rely on epilithic biofilms and algae as their primary food resource (Di Cugno and Robinson 2017; Sertić Perić et al. 2021; *see* review by Niedrist and Füreder 2017), which likely reflects the limitation of terrestrial organic matter inputs due to low cover and productivity of riparian vegetation (Zah and Uehlinger 2001) as well as the high nutritional quality of algae (Guo et al. 2016). The primary source of algae in

high-altitude streams is periphyton, particularly epiphyton and filamentous algae attached to cobbles and other rocky substrate (Rott et al. 2006). Yet, the quantity and form of algae available to macroinvertebrates can vary markedly across seasons. Periphyton and filamentous algae can proliferate in winter despite low temperatures (Gustina and Hoffmann 2000; Uehlinger et al. 2009), but the onset of spring snowmelt pulses can scour algal biomass and result in higher sestonic organic matter loads (Robinson et al. 2002).

Stream flows generally decrease through summer in Alpine environments, which together with higher temperatures, should favor the development of periphyton (although periphyton in predominantly glacier-fed streams remains limited by high water velocity and turbidity; Uehlinger et al. 2009). Flows generally increase in autumn again as rain and snowfall become more common, and autumn is also the time of greatest leaf-fall. Furthermore, these terrestrial organic matter inputs can be derived from relatively labile sources (e.g., the nitrogen-fixer *Alnus viridis*; Gessner et al. 1998), and may dilute the availability of algae in seston despite a general increase in overall loads (Robinson et al. 2002). Algae within high-altitude streams may therefore become concentrated seasonally as different food resources, from seston and deposited FPOM in spring, to periphyton in summer, and then a mix of periphyton and seston/FPOM in autumn (Fig. 1a,b). This resource variation may alternately favor organisms that filter-feed and/or gather amorphous detritus, or those that graze biofilms directly.

Overlaying these seasonal patterns in basal resource availability are the ecological effects of drying events. A higher frequency of drying events can reduce the quality of terrestrial organic matter within streams (Datry et al. 2018) and restrict the overall abundance of macroinvertebrates (Siebers et al. 2020), thereby increasing the relative value of algae to macroinvertebrates as well as reducing competition for this higher-quality food resource. Benthic macroinvertebrates in high-altitude streams often exhibit high dietary flexibility in response to environmental variability (Fell et al. 2017; Niedrist and Füreder 2017). Accordingly, a higher incidence of flow intermittency has been shown to increase dietary assimilation from autochthonous sources in high-altitude streams (Siebers et al. 2019a, 2020), even though drying events vary both seasonally and spatially.

Most high-altitude streams are likely to experience drying events in winter as water becomes "locked-up" in ice or snow. Snowmelt in spring may induce flow almost universally, but variation in the frequency and duration of drying events across streams becomes pronounced across summer and autumn (Robinson et al. 2016a; Paillex et al. 2020). Streams in high-altitude catchments therefore generally fall into four categories: (1) perennial streams that flow year-round, (2) winter-drying streams that freeze or dry during the coldest parts of the year (but flow otherwise), (3) moderately intermittent streams that may only dry during extended periods of low rainfall in summer and autumn (including glacier-melt driven

streams that continue to flow in summer but may dry in autumn), and (4) periodically intermittent streams that dry frequently through summer and autumn (Paillex et al. 2020). The effects of flow intermittency are thus most pronounced in summer and for periodically intermittent streams (Siebers et al. 2019a, 2020).

In addition to this variation in flow intermittency, the response of macroinvertebrates to drying events is likely to vary taxonomically and functionally. The abundance of rheophilic taxa such as Ephemeroptera and Plecoptera are likely to be strongly reduced by drying events. Most specialist grazing taxa in high-altitude streams are rheophilic (e.g., Baetidae, Heptageniidae; Robinson et al. 2010), and grazers as a group are thus likely to be strongly affected by drying events. Conversely, facultative omnivorous and generalist taxa such as Chironomidae or Limnephilidae may be more resistant to low flows (Siebers et al. 2020). However, other organisms that rely on amorphous detritus or seston may be highly rheophilic (e.g., filter feeders such as Simulidae). The effects of flow intermittency on macroinvertebrate diets may thus vary both seasonally and across functional groups, with spring lows and summer highs in the frequency of drying events affecting rheophilic and drying-tolerant taxa to different extents (Fig. 1c,d). Interactions between organic matter availability and the effects of flow intermittency might therefore induce several potential patterns in assimilation from autochthonous sources among different functional groups. Grazers are likely to be weakly reliant on autochthonous resources in spring but exhibit peaks of autochthonous assimilation in summer (Fig. 1e,f), with increases in assimilation from autochthonous sources with greater flow intermittency most apparent in summer and autumn and for rheophilic taxa (Fig. 1e). Generalist primary consumers such as collector-gatherers may show an opposite seasonal pattern to grazers, with peaks of assimilation from autochthonous sources in spring and autumn (Fig. 1g,h). Yet, the effect of flow intermittency may be similar in generalists as for grazers, with the greatest differences in autochthonous assimilation between sites in summer for rheophilic taxa (Fig. 1g).

In this study, we estimated the proportion of benthic macroinvertebrate dietary assimilation from autochthonous resources across three seasons (Alpine spring, summer, and autumn) in 30 high-altitude headwater streams with varying degrees of flow intermittency. We focused particularly on assimilated diet variation among macroinvertebrate functional groups. We predicted that (1) grazers would show strongly seasonal peaks of assimilation from autochthonous sources in summer, at which time they would also exhibit higher autochthonous assimilation in more highly intermittent streams; (2) filter feeders in perennial and winter-drying streams would exhibit higher assimilation from autochthonous sources in spring than summer, but that individuals in highly intermittent streams would maintain high levels of autochthonous assimilation across all seasons; and (3) collector-gatherers would be most reliant on autochthonous resources in spring, but
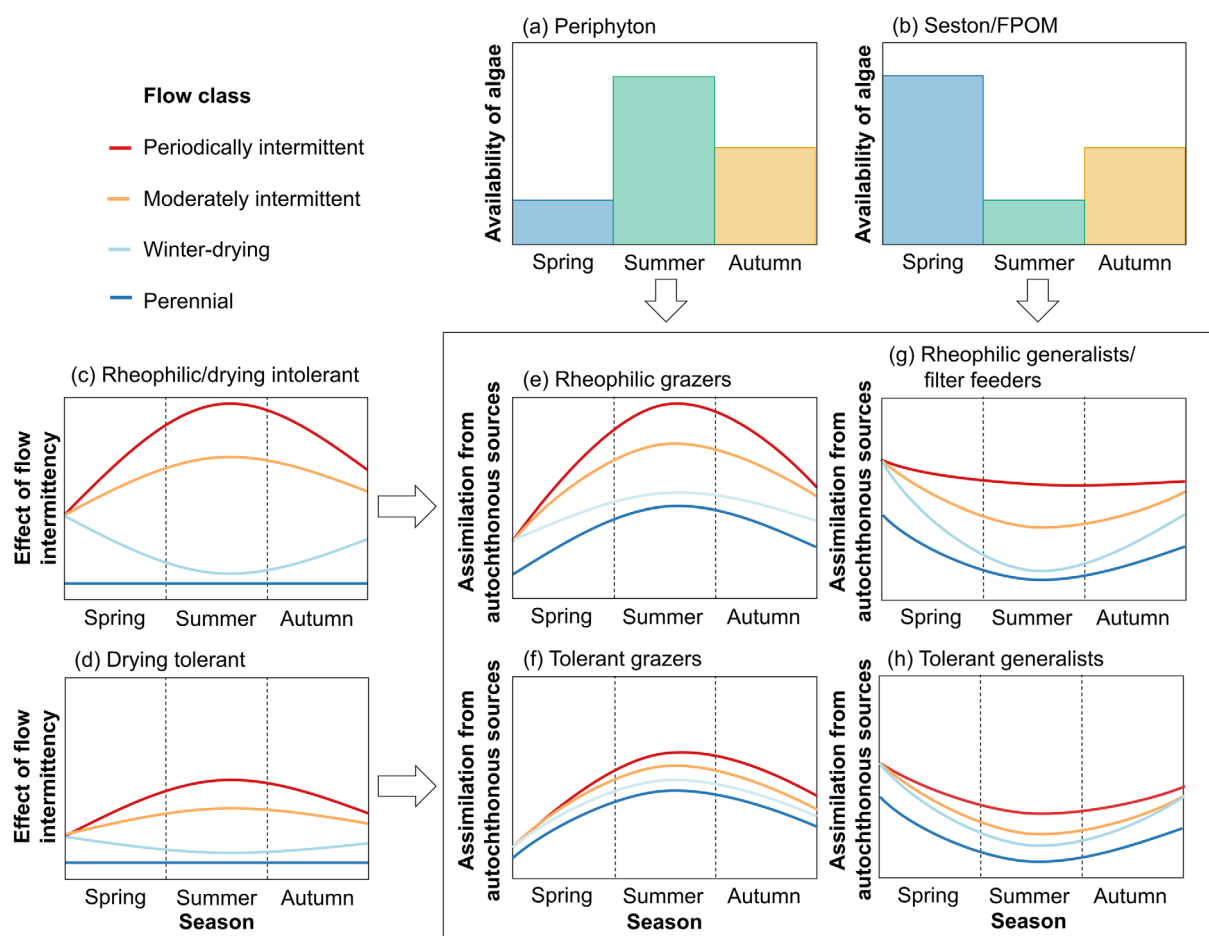
Fig. 1. Conceptual model of the interacting effects of algal organic matter availability and flow intermittency on the diets of benthic macroinvertebrates within high-altitude streams. Contrasting availability of algae as (**a**) periphyton and (**b**) seston and FPOM biomass across seasons, together with the contrasting effects of flow intermittency on assimilation from autochthonous sources for (**c**) rheophilic or drying-intolerant and (**d**) drying-tolerant taxa, create distinct patterns of assimilation from autochthonous sources across seasons based on a combination of functional feeding group and flow preference: distinctly summer-peaking assimilation in grazers, with either (**e**) strongly divergent diets in intermittent as opposed to perennial for rheophilic taxa, particularly in summer, or (**f**) little different in assimilation from autochthonous sources for drying-tolerant individuals across streams with varying flow intermittency; and distinctly spring and autumn-peaking assimilation in generalists and filter feeders, again with either (**e**) distinct differences in assimilation from autochthonous sources across intermittent as opposed to perennial streams for rheophilic taxa and (**h**) little difference across streams for drying-tolerant taxa. Lines in (**e–h**) represent means of patterns in (**a, b**) with those in (**c, d**) for each combination.

would exhibit little difference in diet across intermittent and perennial streams.

Methods

Site description and sampling design

We undertook this study in Val Roseg, a glacierized river valley located at high elevation (1800–2400 m a.s.l.) within the Bernina Massif in southeast Switzerland (Fig. 2a). Meltwater from two large glaciers feed a second-order braided river that flows along the valley floor, while numerous smaller headwater tributaries drain into the mainstem from valley side slopes. Headwaters are fed by spatially and seasonally variable contributions from glacial melt, rainfall, snowmelt, and hillslope groundwater. Varying water source contributions drive

marked expansion and contraction dynamics in the fluvial network (Malard et al. 2006), including a high incidence of flow intermittency across headwater streams (up to 90% of channels) (Robinson et al. 2016a; Paillex et al. 2020).

We sampled 30 headwater streams across Val Roseg as part of a long-term monitoring project that examined patterns of flow intermittency and its ecological effects across the valley (Siebers et al. 2019a; Paillex et al. 2020). Flow intermittency varies in a gradient across the 30 streams, from perennial channels with no drying events to others that lack surface flow for up to 60% of the year (Paillex et al. 2020; Siebers et al. 2021a). The 30 streams exist along a range of elevations (2002–2181 m a.s.l.) from the head of the catchment to the valley outlet, essentially incorporating the entire headwater network. The streams are typically small and high gradient
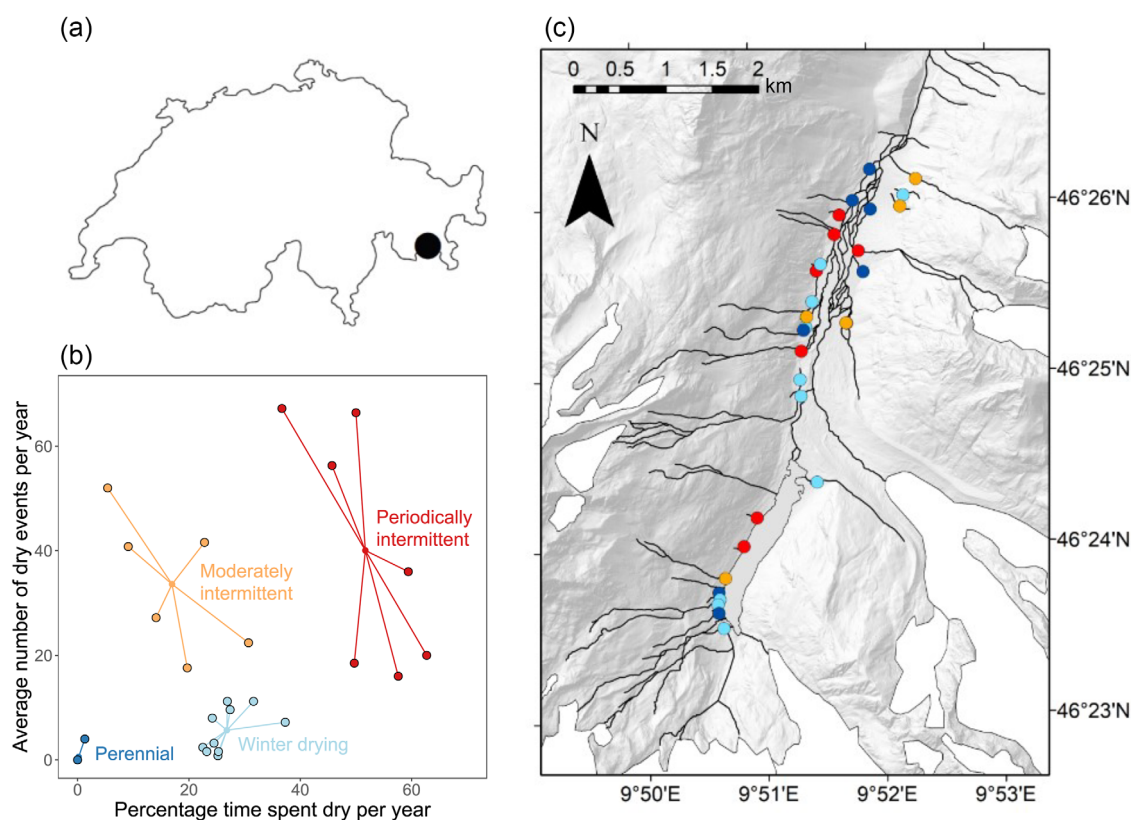
Fig. 2. (**a**) Location of Val Roseg within outline map of Switzerland; (**b**) categorization of headwater streams within Val Roseg into flow intermittency classes relative to the total duration of drying and average number of drying events per year; and (**c**) location of streams sampled within fluvial network of Val Roseg (black lines) with respect to flow intermittency class. Colors denoting flow classes are consistent between (**b**) and (**c**). Glaciers are colored white and glacial lake is colored gray in (**c**). Hillshade in (**c**) is derived from altitude data from 25 m DEM model of Switzerland (swisstopo 2018, swissTLM3D and swissALTI3D, Bundesamt für Landestopographie (Art.30 Geo IV): 5704 000). Note that six perennial sites overlap in (**b**) because of identical *x* and *y* values (0, 0).

(ca. 1–3 m wide, mean slope 13°; Paillex et al. 2020), with streambeds generally composed of cobbles and coarse gravels. The streams also occur across a range of riparian tree cover (0–53% at 100-m radius of channels), from higher elevation channels passing through alpine herb, grass and sedge fields (*Festuca* spp., *Carex* spp.) to channels that flow through European larch (*Larix decidua*) and stone pine (*Pinus cembra*) forests at the base of the valley (Siebers et al. 2019a).

Our sampling design follows that of Siebers et al. (2019a), who investigated the trophic structure of benthic macroinvertebrate assemblages across the 30 streams. We include here the same sites and data as that previous study (Siebers et al. 2019b), which was conducted in the Alpine autumn (September) of 2017. We sampled the same streams in the Alpine spring (June) and summer (August) of 2018 aiming to capture (1) the spring period in which most streams were either flowing continuously after winter-drying periods or were only experiencing infrequent, isolated drying events; and (2) the summer period of greatest differences in streamflow intermittency (Paillex et al. 2020).

Measurement of flow intermittency

To measure the presence/absence of surface water in each stream, we used HOBO Pendant Temperature/Light 64K data loggers (Onset Computer Corporation) modified to measure electrical resistance and temperature (detailed in Paillex et al. 2020; as per Chapin et al. 2014). We installed loggers at the thalweg of each stream in July 2017 and set them to record hourly. Loggers were removed briefly for maintenance in November 2017 and May 2018, and downloaded in October 2018. Two periods were modified in the dataset as per Siebers et al. (2021a): visual observations and data from a nearby logger were used to substitute for a logger that malfunctioned during winter 2017–2018; and data from a different logger were excised for 1.5 months following burial by a landslide in autumn 2017. Otherwise, we used hourly electrical resistance data for the entire July 2017 to October 2018 measurement period (Siebers et al. 2021a).

To characterize the degree of flow intermittency for each stream, we followed the approach of Paillex et al. (2020) and Siebers et al. (2021a) and classified sites into distinct flow classes. A cluster analysis (Ward agglomeration method) was used

to group sites based on the Euclidean distance between two standardized metrics: (1) the average percentage time each stream was dry over a year, and (2) the average number of drying events per year (Siebers et al. 2021a) (Fig. 2b). This approach follows observations that most variation in flow intermittency across Val Roseg is driven by the total duration and frequency of drying events (Robinson et al. 2016a; Siebers et al. 2019a, 2021a; Paillex et al. 2020). We grouped sites into four classes: perennial streams (including one stream that dried for only 1.3% yr^{-1}), winter-drying streams (20–40% dry yr^{-1}, < 15 events yr^{-1}), moderately intermittent streams (5–30% dry yr^{-1}, > 15 events yr^{-1}), and periodically intermittent streams (> 35% dry yr^{-1}, > 15 events yr^{-1}) (Supporting Information Figs. S1–S4), all of which were distributed throughout Val Roseg (Fig. 2c).

Sample collection and laboratory analysis

All samples were collected along a 20–30 m stream reach where data loggers were installed, with the same reaches sampled in September 2017, June 2018, and August 2018 (hereafter: "autumn," "spring," and "summer"). First, aquatic macroinvertebrates were collected by repetitive kick sampling (mesh size: 250 μm) within each study reach. We conducted a qualitative sweep including all substrate types present (e.g., cobbles, woody debris, and mosses) and using three kick-sample sweeps per stream. We conducted additional, targeted sweeps if it was deemed that rare or smaller species required more biomass to conduct isotope analysis (≥ 0.5 mg). Sweeps were not conducted if the channel was dry ($n = 6$ in summer, $n = 2$ in autumn). Aquatic macroinvertebrates were hand-picked from kick-net samples and immediately sorted into 50 mL plastic vials containing stream water. Predatory species were stored separately. Aquatic macroinvertebrates were stored at ambient temperature in stream water for ~ 8 h to void stomach contents, and then generally sorted to family (exceptions; subclass for Acari and Oligochaeta, order for adult Coleoptera) and stored at $-20°$C until analysis.

Where present, we collected coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), periphyton, and filamentous algae from each stream reach as samples of potential basal organic matter resources. Material for each resource was collected from at least three locations along the length of each sampling reach and then combined into a single sample (*see* Jardine et al. 2014). CPOM, FPOM, and filamentous algae were collected directly from the stream. Periphyton was scrubbed with a wire brush from the upward-facing side of at least three cobbles. All basal resource samples were stored at $-20°$C for transport to the laboratory. Periphyton and FPOM samples were briefly thawed, centrifuged for 12 min to separate out inorganic matter, and then stored at $-20°$C until analysis.

All macroinvertebrate, periphyton, algae, and FPOM samples were freeze-dried for 48 h in a Lyovac GT 2-E lyophilizer (STERIS GmbH, Hürth, Germany). Macroinvertebrates were finely chopped after drying. We weighed ~ 0.8 mg of each macroinvertebrate sample, wherever possible including parts from ≥ 3 individuals per

sample. We individually weighed ~ 1.2 mg of each periphyton, algae, and FPOM sample. CPOM samples were briefly thawed, triple-rinsed with distilled water, and then air-dried at $60°$C for 48–72 h. After drying, CPOM samples were finely ground in a coffee grinder. We individually weighed ~ 1.5 mg of each CPOM sample. Samples were combusted in a Vario PYRO Cube elemental analyzer (Elementar Analysensysteme GmbH) connected to an IsoPrime isotope ratio mass spectrometer (GV Instruments Ltd) for measurement of δ^{13}C and δ^{15}N. The δ^{13}C and δ^{15}N values are presented in permille (‰) after normalization to reference material (NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2, provided by Biogeochemical Laboratories, Indiana University). Analytical uncertainty was 0.1‰ for δ^{13}C and 0.2‰ for δ^{15}N.

Data analysis

We used Bayesian mixing models to estimate the proportional contribution of different basal food sources to macroinvertebrate dietary assimilation. First, we (1) grouped the isotope signatures of filamentous algae and periphyton (hereafter: periphyton) based on source δ^{13}C and δ^{15}N overlap and ecological similarity (Phillips et al. 2005), (2) excluded consumer isotope values ($n = 125$ out of 481 total) that were unsuitable for mixing model analysis (Smith et al. 2013) (Supplementary Information Methods 1), and (3) eliminated sites ($n = 4$) from the dataset where the source signatures of periphyton and CPOM (i.e., the two most distal isotope signatures; Siebers et al. 2019a) overlapped for both δ^{13}C and δ^{15}N (i.e., if the mean $\pm$ standard deviation values overlapped for both elements), as we expected that consumers from these sites would present unrealistically diffuse dietary estimates (Phillips et al. 2014). Basal resource isotope values were aggregated for each site across seasons (Supplementary Table S1), as: (1) we previously observed little variation in resource δ^{13}C and δ^{15}N from spring to autumn in Val Roseg (Siebers et al. 2020; although c.f. Sertić Perić et al. 2021); yet (2) we considered our sampling design (periphyton collected at a single time point per season) might have resulted in unrealistically low variance in estimated basal resource δ^{13}C and δ^{15}N, particularly periphyton, if season-specific values were used (*see* Jardine et al. 2014). Next, we used the mixing model framework MixSIAR (Stock et al. 2018) to estimate proportional source contributions (for CPOM, FPOM, and periphyton) to macroinvertebrates (Supplementary Information Methods 2). We created individual models for each site in each season (Supplementary Information Methods 2). All models were created using the MixSIAR package in R (v. 3.6.1). As our focus was on investigating patterns in the assimilation of autochthonous sources, we present here results for estimated proportions of periphyton in macroinvertebrate assimilated diets.

Mixing model results for each site were grouped post hoc into flow classes (perennial, winter drying, moderately intermittent, and periodically intermittent) for each season and summarized by median/quartile analysis in R (v. 3.6.1). While aggregating these values could potentially widen the resulting
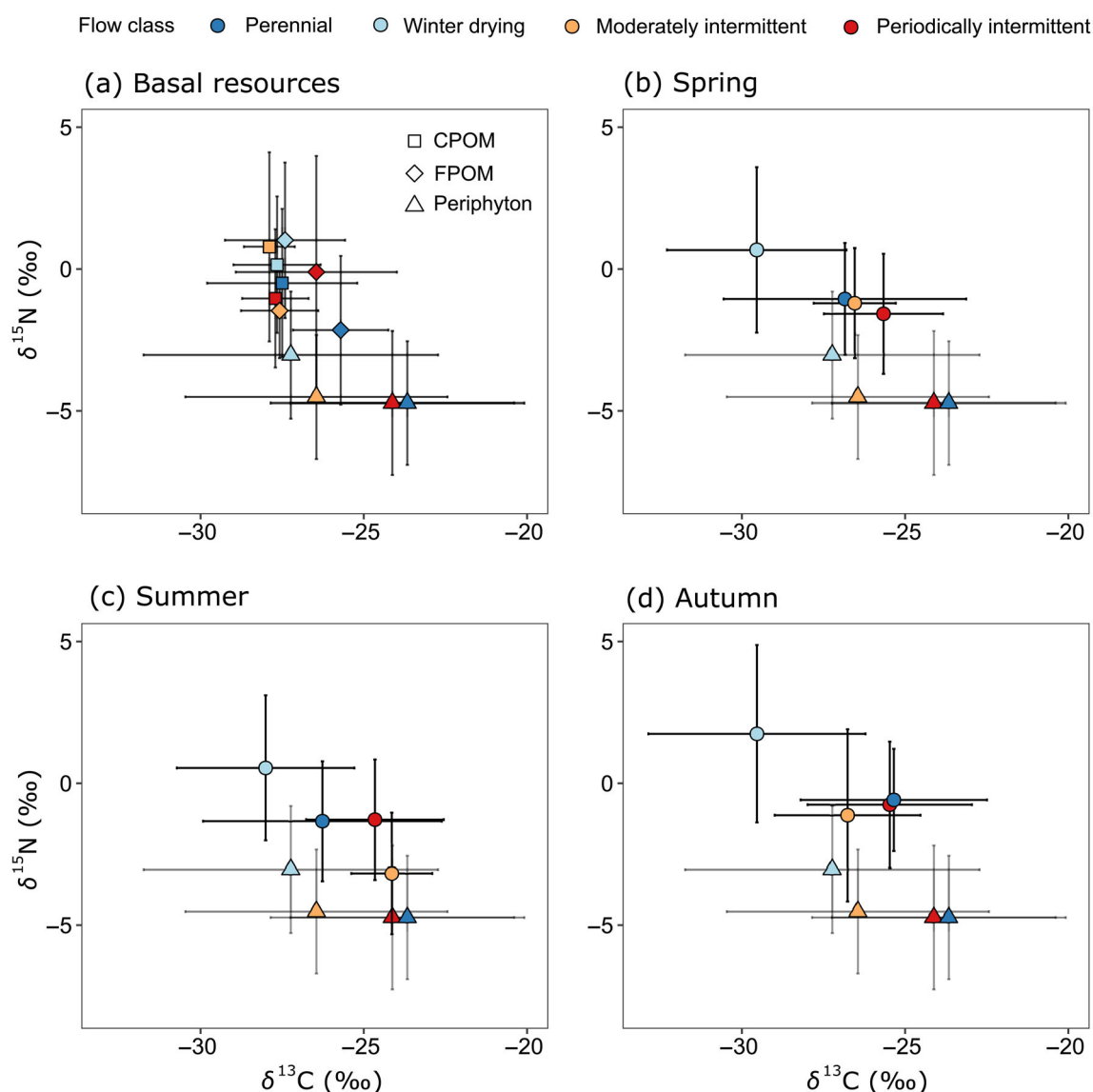
Fig. 3. Biplot of $\delta^{13}C$ and $\delta^{15}N$ values for (**a**) means ($\pm$ SD) of basal resources across all seasons, and individual macroinvertebrate samples (colored circles; all colors correspond to flow class of sampling site) shown in relation to periphyton means (triangles) for (**b**) spring (June 2018), (**c**) summer (August 2018), and (**d**) autumn (September 2017) samplings of streams in Val Roseg. Values are not corrected for trophic enrichment.

estimate distributions, the variance in the aggregated data (*see* the Results section) was similar to that at the individual site level (e.g., estimates of assimilation from autochthonous sources for Chironomidae, the most abundant taxon, had interquartile distances of consistently around 0.36 across sites and seasons). We summarized estimated proportions of periphyton contributing to macroinvertebrate assimilated diets at two levels. First, we grouped results by flow class and season, then (1) divided results for each flow class into broad functional feeding groups (grazers, filter feeders, gatherer-collectors, and predators). Functional feeding groups were defined by reference to Tachet et al. (2010) for each macroinvertebrate family. Next, we (2) divided results from the grazer functional feeding group (i.e., the group feeding obligately on local basal resources, and

thus likely to have the least error in differentiations between dietary sources) and the collector-gatherer functional feeding group (i.e., the most abundant individuals across sites) into specific macroinvertebrate families.

We describe results as differing where different flow classes within a season have nonoverlapping medians and upper or lower quartiles. We also report here the degree of dissimilarity between posterior distributions in the form of $1 - \eta\hat{}$, the "overlapping index" of Pastore and Calcagnì (2019), as an indication of the difference between result distributions when pairwise comparisons are discussed (values between 0 and 1 with higher values indicating more dissimilar results). Broadly analogous to effect sizes (Pastore and Calcagnì 2019), dissimilarities might thus be thought of in terms of $1 - \eta\hat{} > 0.5$ as "large," $0.5 > 1 - \eta\hat{} > 0.2$ as
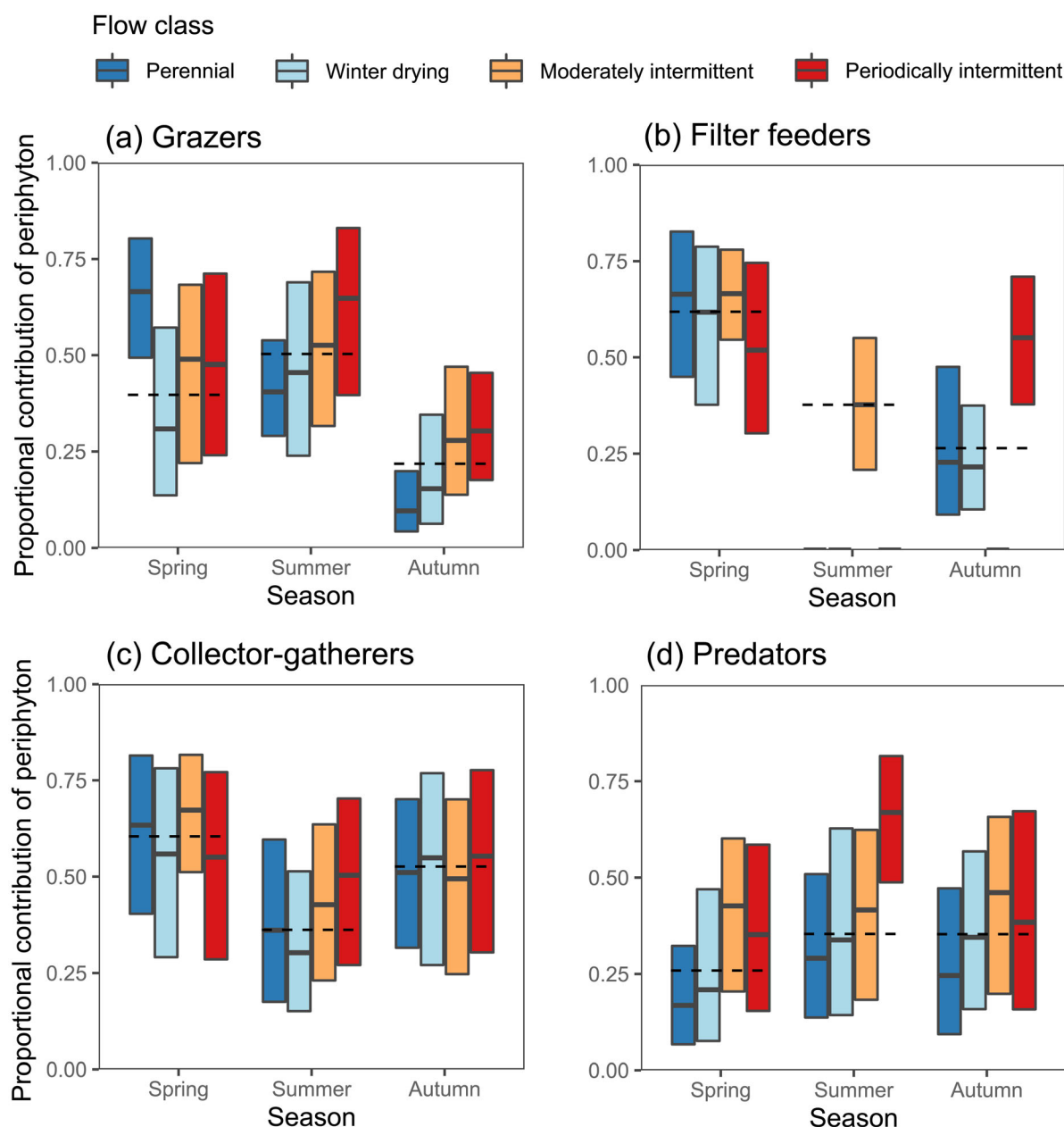
Fig. 4. Estimated proportional contribution of periphyton to assimilated diets of macroinvertebrates identified as belong to (**a**) grazer, (**b**) filter feeder, (**c**) gatherer-collector, and (**d**) predator functional feeding groups across spring (June 2018), summer (August 2018), and autumn (September 2017) sampling of headwater streams in Val Roseg. Boxes show medians and quartiles of mixing model posterior distributions, pooled by flow class (degree of flow intermittency) and season sampled. Dashed lines indicate median estimate for all sites within a season.

"moderate," and $1 - \eta^\wedge > 0.2$ as "weak." All $\eta^\wedge$ values were estimated using the overlapping package (Pastore 2018) in R (v 4.1.2).

Results

Seasonality in isotope signatures

The range of periphyton $\delta^{13}C$ (mean site values from $-33.6‰$ to $-17.4‰$) was higher than that of CPOM ($-29.8‰$ to $-24.7‰$) and FPOM ($-31.0‰$ to $-24.1‰$)

across all sites (Fig. 3a). Periphyton $\delta^{15}N$ values showed a similarly higher range ($-8.1‰$ to $0.2‰$) than those for CPOM ($-3.3‰$ to $3.7‰$) or FPOM ($-3.2‰$ to $3.0‰$) (Fig. 3a). Macroinvertebrate isotope signatures varied to a similar degree to that of periphyton across sites, with little difference in the range of $\delta^{13}C$ ($-33.3‰$ to $-19.6‰$) and $\delta^{15}N$ ($-6.2‰$ to $5.2‰$) across either spring (Fig. 3b), summer (Fig. 2c), or autumn (Fig. 3d) samples. There was also little difference in the range of macroinvertebrate $\delta^{13}C$ values across perennial ($-33.3‰$ to $-22.7‰$), winter-drying ($-30.3‰$ to $-20.1‰$),
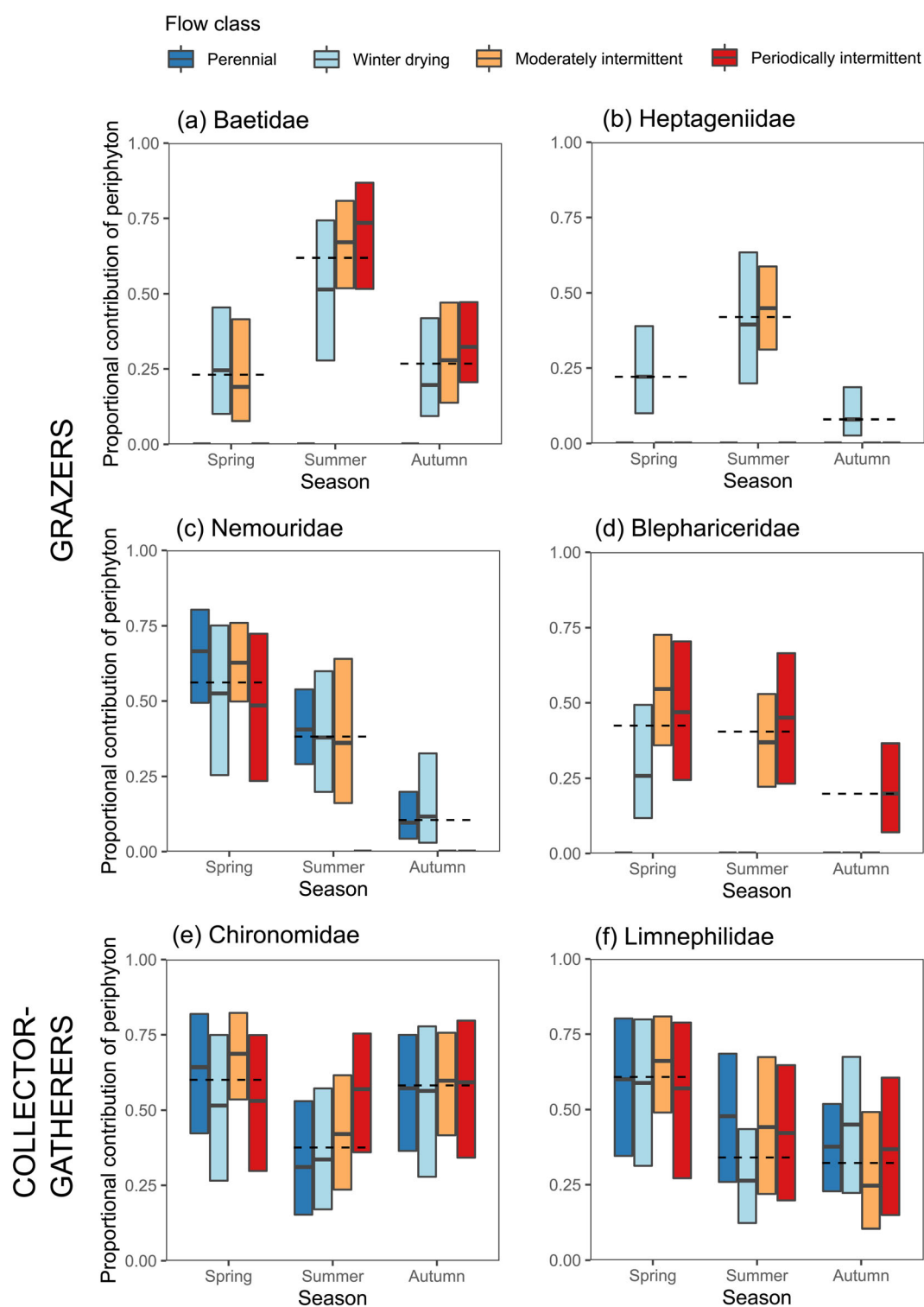
Fig. 5. Estimated proportional contribution of periphyton to: assimilated diets of macroinvertebrate families (**a**) Baetidae, (**b**) Heptageniidae, (**c**) Nemouridae, and (**d**) Blephariceridae belonging to the grazer functional feeding group; and assimilated diets of macroinvertebrate taxa (**e**) Chironomidae and (**f**) Limnephilidae belonging to the collector-gatherer feeding group. Estimates are shown compared across spring (June 2018), summer (August 2018), and autumn (September 2017) sampling of headwater streams in Val Roseg. Boxes show medians and quartiles of mixing model posterior distributions, pooled by flow class (degree of flow intermittency) and season sampled. Dashed lines indicate median estimate for all sites within a season.

moderately intermittent (−32.9‰ to −19.6‰), or periodically intermittent sites (−31.4‰ to −22.7‰); or in macroinvertebrate δ^{15}N values across perennial (−3.9‰ to 5.2‰), winter-drying (−5.8‰ to 5.1‰), moderately intermittent (−5.3‰ to 7.5‰), or periodically intermittent sites (−6.2‰ to 4.3‰) (Fig. 3b–d).

Variation in assimilation from autochthonous sources across functional groups

Different functional groups showed high variation in estimated periphyton assimilation across both sites and seasons (Fig. 4). Across sites, grazers had the highest median estimated periphyton assimilation in summer (0.50) and lowest in autumn (0.22; $1 - \eta^\wedge = 0.53$) (Fig. 4a). Predators had highest assimilation estimates in summer and autumn (0.35), and their lowest in spring (0.26), although the difference was weak ($1 - \eta^\wedge = 0.19$) (Fig. 4d). In contrast, both collector-gatherers (0.61) and filter feeders (0.62) had their highest periphyton assimilation in spring. Furthermore, collector-gatherers showed their lowest estimated assimilation in summer (0.36; $1 - \eta^\wedge = 0.44$), while filter feeders had their lowest estimated assimilation in autumn (0.26; $1 - \eta^\wedge = 0.59$) (Fig. 4b,c).

In summer and autumn, the estimated assimilation of periphyton by grazers was highest at periodically intermittent sites (summer 0.65, and autumn 0.30) and lowest at perennial sites (0.41 and 0.10; $1 - \eta^\wedge = 0.59$ and 0.63, respectively) (Fig. 4a). However, grazers at perennial sites had the highest periphyton assimilation in spring (0.67) (Fig. 4a). Assimilation of periphyton by filter feeders was also highest at periodically intermittent sites in autumn (0.55), although a lack of individuals in autumn and summer restricted comparisons across flow classes (Fig. 4b). Filter feeders were present across sites from all classes in spring, however individuals at periodically intermittent sites had the lowest estimated periphyton assimilation (0.52) (Fig. 4b). Across all seasons, the distribution of estimates for collector-gatherers was not distinct enough to separate different flow classes (Fig. 4c). Predators followed much the same pattern across flow classes as the results for grazers (see above): predators showed highest assimilation from periphyton at moderately intermittent sites in spring (0.43) and periodically intermittent sites in summer (0.67), while the distribution of estimates was too diffuse in autumn to separate different flow classes (Fig. 4d). Grazers therefore showed the most consistent pattern of increasing periphyton assimilation with higher flow intermittency, while collector-gatherers showed little change across this gradient (Fig. 4).

Variation in assimilation from autochthonous sources within functional groups

The different families making up the grazer functional group showed two largely similar patterns across seasons (Fig. 5). Baetidae (mayfly nymphs) showed higher estimates for periphyton assimilation in summer (median 0.62) than autumn (0.27; $1 - \eta^\wedge = 0.61$) and spring (0.23; $1 - \eta^\wedge = 0.62$)

(Fig. 5a). Heptageniidae (mayfly nymphs) also showed higher estimates for periphyton assimilation in summer (0.42) than in spring (0.22; $1 - \eta^\wedge = 0.46$) or autumn (0.08; $1 - \eta^\wedge = 0.72$) (Fig. 5b). In contrast, both Nemouridae (stonefly nymphs) and Blephariceridae (midge larvae) had higher estimated periphyton assimilation in spring (0.56 and 0.42, respectively) than in summer (0.38 and 0.40; $1 - \eta^\wedge = 0.37$ and 0.19) and autumn (0.11 and 0.20; $1 - \eta^\wedge = 0.72$ and 0.48) (Fig. 5c,d).

Across sites, Baetidae had higher estimates of periphyton assimilation at periodically intermittent sites in summer (median 0.74) and autumn (0.32) than at winter-drying sites in the same seasons (0.51 and 0.20; $1 - \eta^\wedge = 0.42$ and 0.45, respectively) (Fig. 5a). For Heptageniidae and Blephariceridae, results were too sparse to generally ascribe patterns across flow classes (Fig. 5b,d), although Blephariceridae had higher estimates of periphyton accrual at moderately intermittent (0.55) than at winter-drying sites (0.26) in spring ($1 - \eta^\wedge = 0.55$) (Fig. 5d). In this respect, only Nemouridae had enough individuals collected to compare estimates across all flow classes, and then only in spring, where individuals at periodically intermittent sites had lower estimated periphyton assimilation (0.49) than those at perennial sites (0.67) ($1 - \eta^\wedge = 0.42$) (Fig. 5c). As a result, only Baetidae showed a pattern of increasing periphyton assimilation estimates in more highly intermittent streams (Fig. 5).

Different families within the collector-gatherer functional group also showed varied responses to seasonality and flow intermittency (Fig. 5). Chironomidae (midge larvae) had higher estimates of periphyton assimilation in spring (median 0.60; $1 - \eta^\wedge = 0.42$) and autumn (0.58; $1 - \eta^\wedge = 0.39$) than in summer (0.38) (Fig. 5e). Limnephilidae (caddisfly larvae) also had their highest estimates of periphyton assimilation in spring (0.61), although estimates were lower in both summer (0.34; $1 - \eta^\wedge = 0.47$) and autumn (0.32; $1 - \eta^\wedge = 0.48$) (Fig. 5f). Chironomidae showed little difference in estimates of periphyton assimilation across perennial and intermittent sites in spring and autumn but had noticeably higher estimates in periodically intermittent sites (0.57) than at winter-drying sites (0.34; $1 - \eta^\wedge = 0.44$) or perennial sites (0.31; $1 - \eta^\wedge = 0.49$) in summer (Fig. 5e). In summer, Limnephilidae had higher estimates of periphyton assimilation at perennial (0.48) than at winter-drying sites (0.26; $1 - \eta^\wedge = 0.47$), but otherwise showed little distinction across flow classes in any season (Fig. 5f).

Discussion

We observed both seasonal and functional variation in the extent to which macroinvertebrates assimilated autochthonous resources within intermittent, high-altitude headwater streams. Macroinvertebrates within the Val Roseg derived much of their assimilated diets from autochthonous sources (periphyton and filamentous algae) across seasons. Consistent with our hypotheses, we observed (1) summer peaks in

assimilation from autochthonous sources and responses to flow intermittency for the grazer functional group, and (2) spring peaks in autochthonous assimilation for collector-gatherers, but no response to differences in flow intermittency across streams. These results suggest that the dominant form of autochthonous organic matter (seston and deposited FPOM vs. periphyton) and drying tolerance of taxa are interactive drivers of macroinvertebrate diets across seasons. However, both seasonality and the effect of flow intermittency varied among families within functional groups. The effect of flow intermittency on macroinvertebrate diets in these high-altitude streams may therefore vary according to taxon-specific life histories, rather than universal adaptations among functional groups. In this respect, our results emphasize that the effects of drying events are to accentuate local rather than general drivers and interactions (Larned et al. 2010). Knowledge of the specific dispersal and resistance abilities of different intermittent stream invertebrate taxa is thus likely essential in understanding their dietary variability, much as it is for other ecological attributes such as population structure (Robson et al. 2011).

In general, periphyton assimilation by grazers peaked in summer, while filter feeders and collector-gatherers peaked in spring and autumn. In this respect, our results support the hypothesis that seasonal differences in assimilation from autochthonous sources between grazers and collector-gatherers might be explained by differences in the predominant form of algal organic matter sources (periphyton vs. seston and FPOM). However, there were also seasonal differences between taxa within the same functional groups. For grazers, seasonal differences in assimilation from autochthonous sources align with those of assemblage composition: Ephemeroptera such as Baetidae and Heptageniidae tend to be most abundant in summer, while Blephariceridae and Nemouridae are more abundant earlier in spring (Siebers et al. 2020). Similarly for the collector-gatherers, Limnephilidae are more abundant in spring, while Chironomidae show low seasonal variation. Here, filter feeders are only represented by the Simulidae, which also peak in abundance in spring (Siebers et al. 2020). Development periods of larvae and nymphs in high-altitude streams generally fall into winter and summer-developing cohorts, which is commonly seen as an adaptation toward non-overlapping emergence periods (Harrison et al. 2008; Robinson et al. 2010). Emergence periods in the aquatic insects of high-altitude ecosystems are generally concentrated in summer to exploit short "windows of opportunity" for adult feeding and reproduction on land (Füreder et al. 2005), but different taxa still notably stagger emergence periods to avoid competition for resources in these relatively cold, low-productivity environments (Danks 2007). Yet, high-altitude streams are also generally low in productivity (Ward 1994) and access to high-quality but low-biomass algae might generally restrict growth and development in the aquatic environment (Niedrist et al. 2018). Competition for high-quality algal resources may therefore also be a driver of adaptation

toward staggered development periods in the larvae and nymphs of high-altitude benthic macroinvertebrates.

The effect of flow intermittency on assimilation from autochthonous sources was pronounced in summer and autumn for the grazer functional group, but there appeared to be little overall effect of flow intermittency on the diet of collector-gatherers. These results suggest that flow intermittency has the greatest effect on the diets of macroinvertebrates with low tolerance to reduced flows and drying, consistent with our second hypothesis. As with seasonality, however, there was high variation in the effects of flow intermittency on taxa within the same functional groups. The contrasting effects of flow intermittency might thus also be linked to differing development periods: simply put, summer-developing taxa are exposed to greater variation in flow intermittency than spring-developing taxa (Paillex et al. 2020). For grazers, the spring-dominant families (Nemouridae, Blephericeridae) showed little response to intermittency but the summer-dominant taxa (Ephemeroptera, i.e., Baetidae and Heptageniidae) showed distinct patterns of higher assimilation from autochthonous sources in more highly intermittent streams. Here, it is interesting to note that Nemouridae have no results in highly intermittent streams in summer and autumn, perhaps reflecting a complete exclusion from drying sites due to their high degree of rheophily (Tachet et al. 2010). Nemouridae are also often described as shredders (Piano et al. 2020), although the high degree of reliance on periphyton we estimated (> 50% in spring) suggests that the high-altitude species sampled here are facultative rather than obligate consumers of terrestrial organic matter. Nemouridae may therefore feed on algae in spring when competition with other rheophilic grazers (i.e., Ephemeroptera) is low, switching to leaf litter during peak abscission periods in autumn. As a contrast, Chironomidae in glacial-melt streams have been shown to maintain specialist diets consisting of high-quality food resources despite strongly limiting environmental factors (e.g., turbidity and low substrate stability; Niedrist and Füreder 2017). Resistance traits, particularly resistance to drying, are energy intensive (Strachan et al. 2015), and organisms may thus need to specialize on high-quality resources (i.e., algae) to remain within more frequently disturbed (e.g., more frequently drying) habitats. Conversely, low tolerance to environmental change may thus necessitate a higher degree of dietary flexibility (i.e., a need to draw from lower-quality resource pools at certain times to remain within a preferred habitat).

If environmental resistance is tied to dietary flexibility, then we might expect the largely nonrheophilic collector-gatherer taxa here to show stronger differences across seasons than flow classes. For the collector-gatherers, Limnephilidae showed roughly the same pattern in response to season and flow intermittency as Nemouridae, suggesting similar environmental constraints on diet (i.e., spring development). However, Limnephilidae do not appear to be excluded from highly intermittent sites in summer and autumn, supporting our assumption that they are not highly rheophilic.

Conversely, Chironomidae appeared to be strongly affected by flow intermittency in summer, with individuals in periodically intermittent streams exhibiting higher assimilation from autochthonous sources to a notably higher extent than those in perennial streams. This result contradicts our assumption that Chironomidae would be less affected by flow intermittency than more rheophilic taxa. We suggest that this result may reflect the coarse taxonomic resolution of our study, as Chironomidae are represented by several families that may have distinct dietary and environmental preferences (Robinson et al. 2010). Furthermore, while the other macroinvertebrate families are generally represented by one or two species within Val Roseg (Burgherr and Ward 2002), each Chironomid family can be represented by several taxa that may each have characteristic environmental niches (Robinson et al. 2016b). For example, Chironomidae often show marked changes in taxon composition along the first few reaches downstream of glacier inputs (Burgherr and Ward 2002). Given that Chironomidae are usually the most abundant inhabitants of high-altitude streams (Robinson et al. 2010), we suggest that distinct species might be associated with perennial and progressively more highly intermittent streams. Ultimately, however, our results reinforce the idea that summer-developing taxa may be more effective competitors for algae, particularly periphyton, and that taxa developing in spring may do so partly to escape this competition (*see* above). In this respect, the effects of flow intermittency on reduced competition (i.e., more highly intermittent streams have lower abundance of macroinvertebrates competing for roughly the same resources) are also stronger in summer-developing taxa.

Interestingly, the dietary estimates of predators here reflect those of grazers in both seasonality and the effect of flow intermittency, suggesting a potential preference for grazing prey. In other high-altitude streams, large predators such as Plecoptera often show a preference for grazing taxa such as Baetidae (Silveri et al. 2008; Khamis et al. 2015). Predators might not always need to select prey with a higher proportion of algae in their diet, contrary to an expectation that access to essential dietary elements from algae (e.g., fatty acids) might restrict growth and development in high-altitude streams (Niedrist et al. 2018). This likely reflects the closer stoichiometric match between predators and prey than between primary consumers and basal resources (Leroux and Schmitz 2015). These results also support our assumption that a release from predation pressure is one of the driving factors toward increased assimilation from autochthonous sources by primary consumers in intermittent streams (Siebers et al. 2020). Staying within a potentially drying reach during summer may represent a general tradeoff between the possibility of obtaining greater access to algal food resources against a higher risk of desiccation. However, these effects may be most pronounced in invertebrates that are highly dependent on biofilms on the surface of rocks, and their predators, rather than generalist collector-gatherers that may be able to facultatively switch between feeding on amorphous detritus, grazing, and omnivory (Zah et al. 2001; Clitherow et al. 2013). In a more general sense, our results also suggest that predator population dynamics might follow the abundance of specific prey and thus be disconnected from seasonal variation in basal resource availability (Rüegg et al. 2021), but instead respond more strongly to other environmental drivers (e.g., drying regimes).

In summary, seasonal variation in the diets of macroinvertebrates followed broadly the patterns we predicted at a functional level, with grazers and collector-gatherers showing different trends in assimilation from autochthonous sources across time. These patterns likely reflect general trends in resource availability (algae in periphyton vs. seston). Whether flow intermittency drives increased assimilation from autochthonous sources by specific taxa within these functional groups, however, is likely dependent on both their tolerance to drying and seasonal differences in development periods. In this respect, our results support earlier experimental findings that suggest flow intermittency has the greatest effect on rheophilic species with summer development periods (Siebers et al. 2020). As summer is also generally the time of highest primary productivity and macroinvertebrate abundance in high-altitude streams, we suggest that the degree to which autochthonous resources support food webs (i.e., energy flux) may also be most strongly affected by flow intermittency at this time. High-altitude benthic assemblages exist along a number of steep environmental gradients that limit their composition, abundance, and diet, such as water temperature and terrestrial vegetation (Milner et al. 2017). As with organic matter availability, our results suggest that the interactive effects of these gradients with flow intermittency will differ in accordance with species-specific life history strategies. Given that high-altitude streams are likely to be both warmer and have a higher frequency of drying events in the future (IPCC 2014), we suggest a possible, additional consequence of climate change is that the abundance of cold stenothermic taxa may become dominated by spring-developing species—those which do not face the dual, and likely increasing pressures of desiccation and competition for high-quality dietary sources.

Data availability statement

The datasets analyzed during the current study are available in the Dryad repository https://doi.org/10.5061/dryad.2bvq83brz (Siebers et al. 2021b).

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Acknowledgments

Conflict of Interest
None declared.