

1 **Title:** Trophic flexibility and hydrology structure alpine stream food webs: Implications for a  
2 fading cryosphere

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4 **Running title:** Alpine stream food webs

5

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17

18 **Keywords:** Alpine stream, food webs, stable isotopes, macroinvertebrates, climate change,

19 *Hydrurus*

20

21 **Abstract:**

22           Understanding biotic interactions and how they vary across habitats is important for  
23 assessing the vulnerability of communities to climate change. Receding glaciers in high  
24 mountain areas can lead to the hydrologic homogenization of streams and reduce habitat  
25 heterogeneity, which are predicted to drive declines in regional diversity and imperil endemic  
26 species. However, little is known about food web structure in alpine stream habitats, particularly  
27 among streams fed by different hydrologic sources (e.g., glaciers or snowfields). We used gut  
28 content and stable isotope analyses to characterize food web structure of alpine  
29 macroinvertebrate communities in streams fed by glaciers, subterranean ice, and seasonal  
30 snowpack in the Teton Range, Wyoming, USA. Specifically, we sought to: (1) assess community  
31 resource use among streams fed by different hydrologic sources; (2) explore how variability in  
32 resource use relates to feeding strategies; and (3) identify which environmental variables  
33 influenced resource use within communities. Average taxa diet differed among all hydrologic  
34 sources, and food webs in subterranean ice-fed streams were largely supported by the gold alga  
35 *Hydrurus*. This finding bolsters a hypothesis that streams fed by subterranean ice may provide  
36 key habitat for cold-water species under climate change by maintaining a longer growing season  
37 for this high-quality food resource. While a range of environmental variables associated with  
38 hydrologic source (e.g., stream temperature) were related to diet composition, hydrologic source  
39 categories explained the most variation in diet composition models. Less variable diets within  
40 versus among streams suggests high trophic flexibility, which was further supported by high  
41 levels of omnivory. This inherent trophic flexibility may bolster alpine stream communities  
42 against future changes in resource availability as the mountain cryosphere fades. Ultimately, our

- 43 results expand understanding of the habitat requirements for imperiled alpine taxa while
- 44 empowering predictions of their vulnerability under climate change.

45 **Introduction:**

46           Understanding biotic interactions within communities and how they vary across  
47 environmental gradients is important for assessing vulnerability to climate change (Blois et al.  
48 2013, HilleRisLambers et al. 2013, Perkins et al. 2010). For example, the trophic level of a  
49 species can influence its resilience to flooding or drought, with higher trophic levels having  
50 lower stability (Post 2002). Additionally, identifying the basal resources supporting food webs  
51 can help identify stoichiometric imbalances that may result from climate change, such as lower  
52 growth rate in *Daphnia* fed algae grown under elevated CO<sub>2</sub> levels (Urabe et al. 2003).  
53 Ecosystems above tree line in the alpine (hereafter referred to as alpine ecosystems) are models  
54 for studying the effects of climate change due to their rapid warming, habitat loss, low  
55 organismal density, and the presence of species living close to their thermal limits (Perkins et al.  
56 2010).

57           As climate change proceeds, aquatic habitats in the alpine are becoming increasingly  
58 homogenized as meltwater sources recede (Hotaling et al. 2017, Birrell et al. 2020). This  
59 ongoing habitat homogenization is predicted to decrease regional stream diversity and eliminate  
60 range-restricted species (Jacobsen et al. 2012, Giersch et al. 2017). However, recent work  
61 suggests that alpine macroinvertebrate diversity may persist longer than previously expected,  
62 despite glacier loss (Muhlfeld et al. 2020), perhaps due to cold refugia from subterranean  
63 meltwater sources such as rock glaciers (Brighenti et al. 2021, Tronstad et al. 2020). While  
64 macroinvertebrate community composition in alpine streams is well-known to vary with  
65 hydrologic source (Hieber et al. 2005, Brown et al. 2007, Tronstad et al. 2020), the structure of  
66 food webs and resource availability in these ecosystems is less clear (Niedrist & Füreder 2017,  
67 Fell et al. 2017), particularly as it relates climate-induced loss of meltwater sources.

68 Theory suggests that organisms in harsh and unstable environments, such as alpine  
69 streams, require trophic flexibility to maintain stability (Saint-Béat et al. 2015, Bartley et al.  
70 2019). Trophic flexibility can increase the resilience of aquatic taxa and communities to  
71 environmental perturbation, including rising temperatures, pollution, invasive species, and fire  
72 (Lisi et al. 2018, Lewis et al. 2014, Colossi Brustolin et al. 2019, Kortsch et al. 2015). Many  
73 aquatic taxa can change their feeding habits in response to seasonal resource pulses, habitat  
74 disturbances, or during development (Mihuc 1997, Larson et al. 2018, Lancaster et al. 2005).  
75 Flexible feeding strategies may facilitate survival in harsh cold-water environments due to  
76 limited and seasonally variable resource availability (Laske et al. 2018, Beaudoin et al. 2001,  
77 Zah et al. 2001, Clitherow et al. 2013, Al-Shaer et al. 2015). Macroinvertebrate communities in  
78 glaciated catchments can have overlapping trophic niches (Sertić Perić et al. 2021) and can  
79 uniformly rely on autochthonous resources despite taxonomic differences (Zah et al. 2001). The  
80 inherent dietary flexibility that may be required for life in alpine streams may bolster these  
81 communities against climate change and the shifting resources it brings to headwaters.

82 Dominant hydrologic source is a key driver of habitat makeup and resource availability in  
83 high mountain streams (Ren et al. 2019, Slemmons et al. 2013). Thus, a comprehensive  
84 understanding of alpine food webs requires insight into how hydrologic sources influence trophic  
85 ecology. Important hydrologic sources in alpine streams include glaciers, subterranean ice (e.g.,  
86 rock glaciers and other “cold rocky landforms”, Brighenti et al. 2021), and snowfields. Glacier-  
87 fed streams are phosphorous limited due to high nitrogen and low phosphorous, and have low  
88 water temperatures (Slemmons et al. 2013, Ren et al. 2019, Robinson et al. 2002). Additionally,  
89 they have low light penetration and high scouring due to large amounts of suspended solids.  
90 Rock glacier-fed streams have similar macronutrient and average temperature levels to glacier-

91 fed streams but lower suspended solids (Williams et al. 2007). In contrast, snowmelt streams  
92 have high light penetration, more variable temperatures, lower suspended solids, and are more  
93 often nitrogen limited (Slemmons et al. 2013, Beck et al. 2021, Warner et al. 2017). These  
94 environmental differences can result in snowmelt-fed streams having a larger quantity of  
95 autochthonous resources than glacier streams (Uehlinger et al. 2009, Cauvy-Fraunié et al. 2016).

96 Combining gut content and stable isotope analyses (SIA) is a well-established approach  
97 for understanding resource use (e.g., Whitley & Rabeni 1997, Davis et al. 2012). Previous  
98 stable isotope investigations of alpine stream food webs have focused on glacier-fed streams (but  
99 see Di Cugno & Robinson 2017). Comparing food webs across streams fed by different  
100 hydrologic sources provides a larger range of conditions to explore the influence of  
101 environmental variables on macroinvertebrate diets and the extent of trophic flexibility, and is  
102 therefore necessary to adequately characterize the baseline conditions of alpine stream food  
103 webs. It is particularly useful that SIA can distinguish between algal biofilms and the  
104 multicellular gold algae *Hydrurus foetidus* (hereafter *Hydrurus*), due to its low carbon isotope  
105 signature (Zah et al. 2001, Niedrist and Füreder 2018). *Hydrurus* is widely distributed and  
106 abundant during the spring in cold meltwater streams and is likely important for the growth of  
107 macroinvertebrates (Niedrist & Füreder 2017, Ward 1994). However, the true scale of this  
108 connection, and its geographic scope, is unclear. Additional information from gut content and  
109 stable isotope analyses is necessary to assess what resources support the base of alpine food  
110 webs and what other trophic connections exist among alpine macroinvertebrate taxa.

111 Here, we explored how the food web structure of macroinvertebrate communities varied  
112 among alpine streams fed by glaciers, subterranean ice, or perennial snowfields. Our primary  
113 objectives were: 1) to estimate how the importance of major basal resources (biofilm, plant

114 detritus, and *Hydrurus*) vary with hydrologic sources; (2) to explore how variability in resource  
115 use relates to the feeding strategies employed by macroinvertebrates; and (3) to assess  
116 relationships between environmental variables (e.g., stream temperature) and resource use within  
117 stream communities. We hypothesized that autochthonous resource use would be highest in  
118 snowmelt streams, intermediate in subterranean ice streams, and lowest in glacier-fed streams.  
119 We also expected that most taxa would display trophic flexibility in response to limited resource  
120 availability. Finally, we hypothesized that biofilm importance would be positively correlated  
121 with temperature and negatively correlated with total suspended solids, due to their effect on  
122 algal growth within biofilms.



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Figure 1. Map of study sites within Grand Teton National Park and the adjacent Jedediah Smith Wilderness in Wyoming, USA.

127

128 **Methods:**

129 *Study area*

130 We conducted our study on nine alpine streams in Grand Teton National Park and the  
131 adjacent Jedediah Smith Wilderness in Wyoming, USA (Figure 1). The Teton Range is a useful  
132 model for our study in several respects. First, glaciers in the Rocky Mountains are melting  
133 rapidly (Rice et al. 2018, Edmunds et al. 2012, Hall & Fagre 2003) and glaciers in the Teton  
134 Range are already quite small, with the largest—the Teton Glacier—less than 0.22 km<sup>2</sup>  
135 (Edmunds et al. 2012). These glaciers are likely past peak runoff (Chesnokova et al. 2020),  
136 which provides insight into the future for other glaciated watersheds. Additionally, the Teton  
137 Range hosts glaciers, snowfields, and many rock glaciers (Goff 2019). The range also harbors  
138 several species of management concern, including two stoneflies: *Zapada glacier* and *Lednia*  
139 *tetonica* (Hotaling et al. 2019; Green et al. 2022). *Zapada glacier* and a close relative of *L.*  
140 *tetonica* that inhabits similar habitat in Glacier National Park, *Lednia tumana*, were both recently  
141 listed as Threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 2019).  
142 Finally, the community composition of macroinvertebrates in these streams suggests that  
143 subterranean ice-fed streams could act as climate refugia for cold-water taxa (Tronstad et al.  
144 2020).

145

146 *Field sampling*

147 Our nine focal streams included two fed by subterranean ice, three fed by surface  
148 glaciers, and four fed by perennial snowfields. One of our two subterranean ice-fed streams  
149 (Wind Cave) is fed by ice within a cave system and the other (Alaska Basin) is fed by a rock



150 glacier. All sites lacked canopy cover except for one glacier-fed site (Delta), which is at treeline  
151 and partially shaded by riparian conifers. All streams were fishless and were sampled near their  
152 source and above any lakes to capture as much of the dominant hydrologic source as possible.

153 From 6–17 August 2020, we collected samples for isotope analysis from each stream.  
154 Macroinvertebrates, algae, plant detritus, and any other identifiable food resources were hand-  
155 picked from all available stream habitat types (e.g., riffles, pools, etc.). Invertebrates were  
156 identified using a hand lens to the lowest taxonomic level (usually genus), which was facilitated  
157 by our detailed understanding of what taxa are typically present at these sites (e.g. Tronstad et al.  
158 2020). We degutted invertebrate samples for isotope analysis in the field using forceps and  
159 placed the body tissue in snap-cap microcentrifuge tubes by taxa. Invertebrates that were too  
160 small to dissect (e.g., midge larvae) were kept in vials for several hours to void their gut  
161 contents. At least three replicates of each food item were collected. Macroalgae and stream plant  
162 detritus were placed in vials or plastic bags. We also sampled terrestrial plants to ensure the  
163 collection of all contributors to stream plant detritus. At least three rocks were scrubbed for  
164 biofilm using a plastic brush and stream water. The resulting homogenized slurries were filtered  
165 onto pre-weighed Whatman GF/F glass-fiber filters (0.45- $\mu$ m pore size) using a 60-ml syringe  
166 before being stored in tinfoil. We kept isotope samples cool on overnight backpacking trips by  
167 burying them in snow or submerging them within a stream., and they were frozen within 36  
168 hours. Additional samples were collected during 20-28 July 2021 to supplement samples of  
169 *Hydrurus* or biofilm.

170 We also collected macroinvertebrate samples for visual gut content analysis in August  
171 2020 and July 2021. Individuals of abundant taxa were preserved in 95% ethanol (2020) or  
172 Kahle’s solution (2021) at the field site. We switched to Kahle’s solution (Rosi-Marshall et al.

173 2016) for easier dissection and observed that both methods seemed to preserve the gut contents  
174 well. Samples of each food resource were also preserved for reference materials.

175 We collected quantitative benthic invertebrate samples and measured a suite of  
176 environmental variables at each site in August 2020. Invertebrate abundance and diversity were  
177 calculated from three Surber samples taken along the length of the reach. Dissolved oxygen  
178 (DO), specific conductivity (SPC), and pH were measured using a Yellow Springs Instrument  
179 (YSI) Professional Plus multiparameter sonde that was calibrated at the trailhead (SPC and pH)  
180 or at the site (DO). Recorded volumes of water were filtered onto ashed and pre-weighed 25 mm  
181 glass-fiber filters to measure total suspended solids (TSS). We collected filtered water samples to  
182 be analyzed for anions (nitrate, sulfate, chloride, and fluoride). Temperature loggers (HOBO Pro  
183 v2, Onset Computer Corporation) were secured to rocks on the streambed to record stream  
184 temperature every hour year-round. Elevation, slope, and aspect were compiled from  
185 measurements from previous sampling years.

186

### 187 *Laboratory analyses*

188 We analyzed macroinvertebrates and food resources for carbon (C) and nitrogen (N)  
189 isotopes. We dried isotope samples at 60 °C for at least 72 hours. Invertebrate samples were  
190 homogenized in microcentrifuge tubes using pestles and were tinned whole or homogenized  
191 individually or in groups to achieve adequate sample mass. We weighed biofilm samples on  
192 filters, calculated biofilm mass by subtracting the initial filter weight, and then tinned the filters.  
193 Plant samples and detritus were homogenized with a mortar and pestle, and *Hydrurus* samples  
194 were homogenized with a pestle in a microcentrifuge tube before tinning. Samples were analyzed

195 at the University of Wyoming Stable Isotope Facility for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  using a Carlo Erba 1110  
196 Elemental Analyzer coupled to a Thermo Delta V isotope-ratio mass spectrometer (IRMS).

197 Gut contents were visually quantified following Rosi-Marshall et al. (2016) with the  
198 following modifications. The foregut or front third of the invertebrate guts were mounted onto  
199 slides. We photographed two random transects across each slide at 200x magnification using a  
200 compound microscope. We assigned particles to the following categories: diatoms, *Hydrurus*,  
201 plant detritus, animal material, or “other.” Particles assigned to “other” made very small  
202 contributions to the total area measured and included other filamentous algae, fungal hyphae, and  
203 moss rhizoids. The area of each category was measured across multiple photos and then divided  
204 by the total area of those photos to calculate proportional cover. For abundant particles, 3-5  
205 photos were used, while rare particles were measured across both transects (~50 photos). We  
206 calculated percent composition of each diet item by dividing proportional cover by the sum of  
207 proportional covers for all categories and multiplying by 100. The percent assimilated from each  
208 diet item was calculated from the percent composition with assimilation factors of 0.3 for  
209 diatoms, 0.1 for plant detritus, 0.3 for filamentous algae (which we used for *Hydrurus*), and 0.7  
210 for animal material (Benke & Wallace 1980, Cross et al. 2013).

211 We analyzed environmental variables to assess differences in the physical and chemical  
212 habitat among streams. We dried TSS samples for at least 72 hours at 60 °C and calculated TSS  
213 as the difference between the sample and filter dry weight and the initial filter weight. Filtered  
214 water samples were measured for anion concentrations using an Ion Chromatograph (Thermo  
215 Scientific Dionex Dual Integrion RFIC). For a few data points that were below the detection  
216 limit, we used values halfway between zero and the detection limit (12.27  $\mu\text{g/L}$  for nitrate and  
217 21.48  $\mu\text{g/L}$  for fluoride). We calculated the mean ( $T_{\text{mean}}$ ) and max ( $T_{\text{max}}$ ) water temperatures for

218 the two-week period prior to our 2020 sampling. For Wind Cave, temperature data from 2019  
219 were used due to a lost temperature logger in 2020, which was likely similar to 2020 because the  
220 stream temperature at this site is very stable across years (Tronstad et al. 2020, Hotaling et al.  
221 2019). The aspect data were transformed using the formula  $A' = \cos(45 - A) + 1$ , where A is the  
222 aspect in degrees (Beers et al. 1966).

223 Macroinvertebrates from the Surber samples were used to calculate diversity and  
224 biomass. We measured the lengths of up to 40 individuals of each taxon from each sample. We  
225 calculated the biomass of each taxon using taxon-specific length-mass regressions from Benke et  
226 al. (1999). Invertebrate diversity was estimated for Shannon and Simpson diversity indices  
227 (Shannon 1948, Simpson 1949).

228

### 229 *Statistical analyses*

230 All statistical analyses and generation of figures were conducted in R (v4.0.2, R Core  
231 Team 2020). We used the Bayesian mixing-model package ‘MixSIAR’ (Stock et al. 2018) to  
232 estimate the proportional contribution of resources to invertebrate tissues and establish food web  
233 linkages. Separate models were run for each site. Taxon was included as a fixed effect in all  
234 models and the default generalist priors were used. We included both process and residual error  
235 in the models to incorporate variation in taxa consuming material from different locations on the  
236 source distributions and consumer variation not explained by source isotopic value (e.g.,  
237 individual assimilation, metabolism), respectively (Stock & Semmens 2016). We used Trophic  
238 Enrichment Factors (TEFs) of  $0.4 \pm 1.4$  ‰ for  $\delta^{13}\text{C}$  (Post 2002) and  $1.4 \pm 1.4$  ‰ for  $\delta^{15}\text{N}$  (Bunn  
239 et al. 2013). TEF selection is discussed further in Appendix 1. Model convergence was assessed  
240 by the Gelman diagnostic, the Geweke test, and visual assessment of trace plots.

241 The food resources included in our model were biofilm, coarse particulate organic matter  
242 (CPOM), and *Hydrurus*. Plant and within-stream plant detritus samples were combined into  
243 CPOM due to overlapping isotope signatures. Items that were collected as potential food  
244 resources but were not observed in the guts of any taxa were excluded from the model (e.g.,  
245 moss). We included an additional resource for two sites. First, we included a filamentous alga  
246 collected at South Fork Teton Creek because an end member representing algae was missing for  
247 this site, and a few strands of this alga were observed in some invertebrate guts at this site.  
248 Second, we included small mammal fecal pellets collected at Grizzly that provided a missing end  
249 member and had caddisfly larvae congregated around them at the site. Sample sizes for different  
250 resources was supplemented by collections in July 2021 for *Hydrurus* at Alaska Basin, Skillet  
251 and Delta, and biofilm at Skillet. Comparison of samples from different sampling events did not  
252 show clear seasonal or annual differences. Source sample sizes ranged from 2 to 14 samples.

253 We decided which taxa and individuals to include in our primary consumer models using  
254 their trophic position (TP) and gut content analysis data. We calculated the trophic position of  
255 each individual from the  $\delta^{15}\text{N}$  values ( $\delta^{15}\text{N}_{\text{consumer}}$ ) using a one-baseline model:  $\text{TP} = 2 +$   
256  $(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta\delta^{15}\text{N}$  (Post 2002). We used the TEF ( $\Delta\delta^{15}\text{N}$ ) of 3.4 ‰ from Post  
257 (2002) to account for predators. Midges (which did not include any predatory Tanyptodinae), or  
258 *Allomyia* caddisflies if midges were insufficiently abundant, were selected as the baseline taxon  
259 ( $\delta^{15}\text{N}_{\text{base}}$ ). Taxa were categorized as predators if animal material was observed in their guts at  
260 any site, and individuals of predatory taxa were excluded from the mixing models if their trophic  
261 position was calculated to be greater than 2.5.

262 We used the diet estimates from our isotope mixing models in additional analyses aimed  
263 to identify cross-site patterns. Prior to these, we combined the model estimates for filamentous

264 algae and biofilm at South Fork Teton Creek, and CPOM and small mammal feces at Grizzly.  
265 We then calculated the average diet composition for each site to avoid pseudoreplication in our  
266 analyses. We also used biomass estimates and modeled diet proportions to calculate the  
267 invertebrate biomass supported by each food resource in each stream as an alternative way to  
268 assess community resource use.

269 We performed principle component analysis (PCA) to visualize diet variation among  
270 sites and environmental variation (e.g., source) using the ‘vegan’ package (Oksanen et al. 2022).  
271 We calculated multivariate metric variances (Pawlowsky-Glahn & Egozcue 2001) using the  
272 package ‘compositions’ (Van den Boogaart & Tolosana-Delgado 2013) to estimate within-site  
273 and among-site variation in the diet compositions. We ran an ANOVA to test whether the within-  
274 site variance in diet compositions of taxa significantly differed among hydrologic sources. To  
275 evaluate whether trophic diversity related to community diversity, we ran linear models using the  
276 lm function to test if the within-site variation in diet compositions increased with increasing  
277 Shannon or Simpson diversity.

278 We used the package ‘DirichletReg’ (Maier 2013) to perform multivariate regression of  
279 relationships between diet composition and environmental variables. This package uses a  
280 Dirichlet distribution to model compositional data and we used the common parameterization.  
281 We modeled the diet composition with the hydrologic source, the first and second principle  
282 components of the environmental PCA, and each separate environmental variable. We also ran  
283 models with multiple environmental variables as explanatory variables and with environmental  
284 variables combined with hydrologic source. However, with our sample size we were not able to  
285 combine all of the environmental variables in a single model. We calculated corrected Akaike  
286 information criterion (AICc) to determine which variables best modeled our observed diet

287 proportions. Using the same methods, we also modeled the percent biomass at each site that was  
288 supported by each resource.

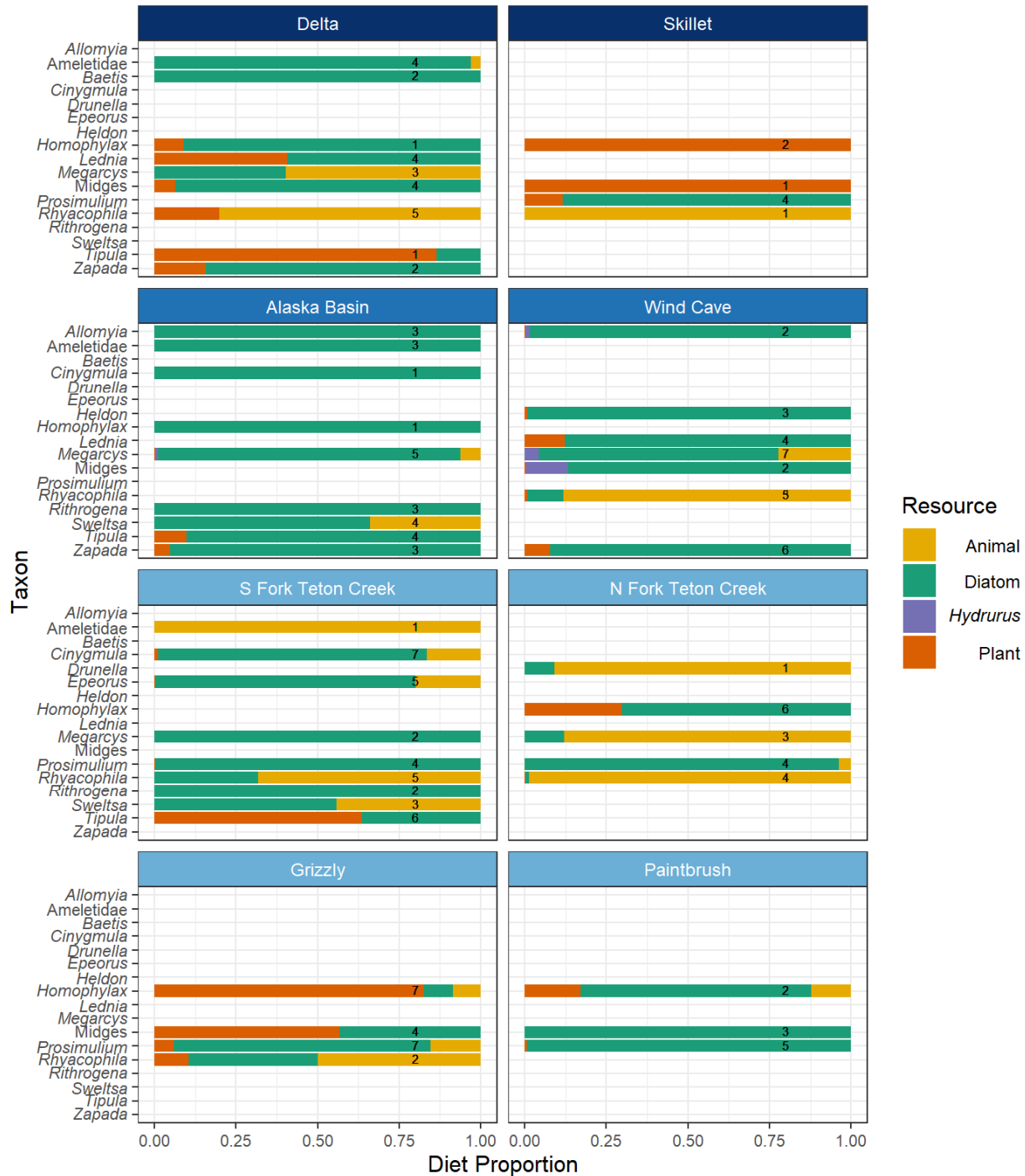
289

290 **Results:**

291 *Food web structure*

292 Gut content analysis revealed high omnivory in many taxa. While functional feeding  
293 group assignments rely on the idea that each taxa has a consistent food source in all  
294 environments, our gut content and stable isotope analyses suggest that the alpine  
295 macroinvertebrate diets in our study vary across sites. We found omnivory that deviated from the  
296 functional feeding groups described by Merritt et al. (2008) for these taxa (Appendix 2, Table  
297 S1). Predatory feeding was common, with over half of all taxa (*Megarcys*, *Rhyacophila*, *Sweltsa*,  
298 *Prosimulium*, *Ameletidae*, *Drunella*, *Homophylax*, *Epeorus*, and *Cinygmula*) had midge larva in  
299 their guts (Figure 2). Two samples of *L. tetonica* at one site (Delta) had especially high trophic  
300 positions (Appendix 2, Figure S1), although we did not see identifiable animal material in their  
301 guts. The only observations of wood—cross sections of tracheids—in any digestive tract were  
302 from *L. tetonica* and *Zapada* sp. at one site (Delta).

303

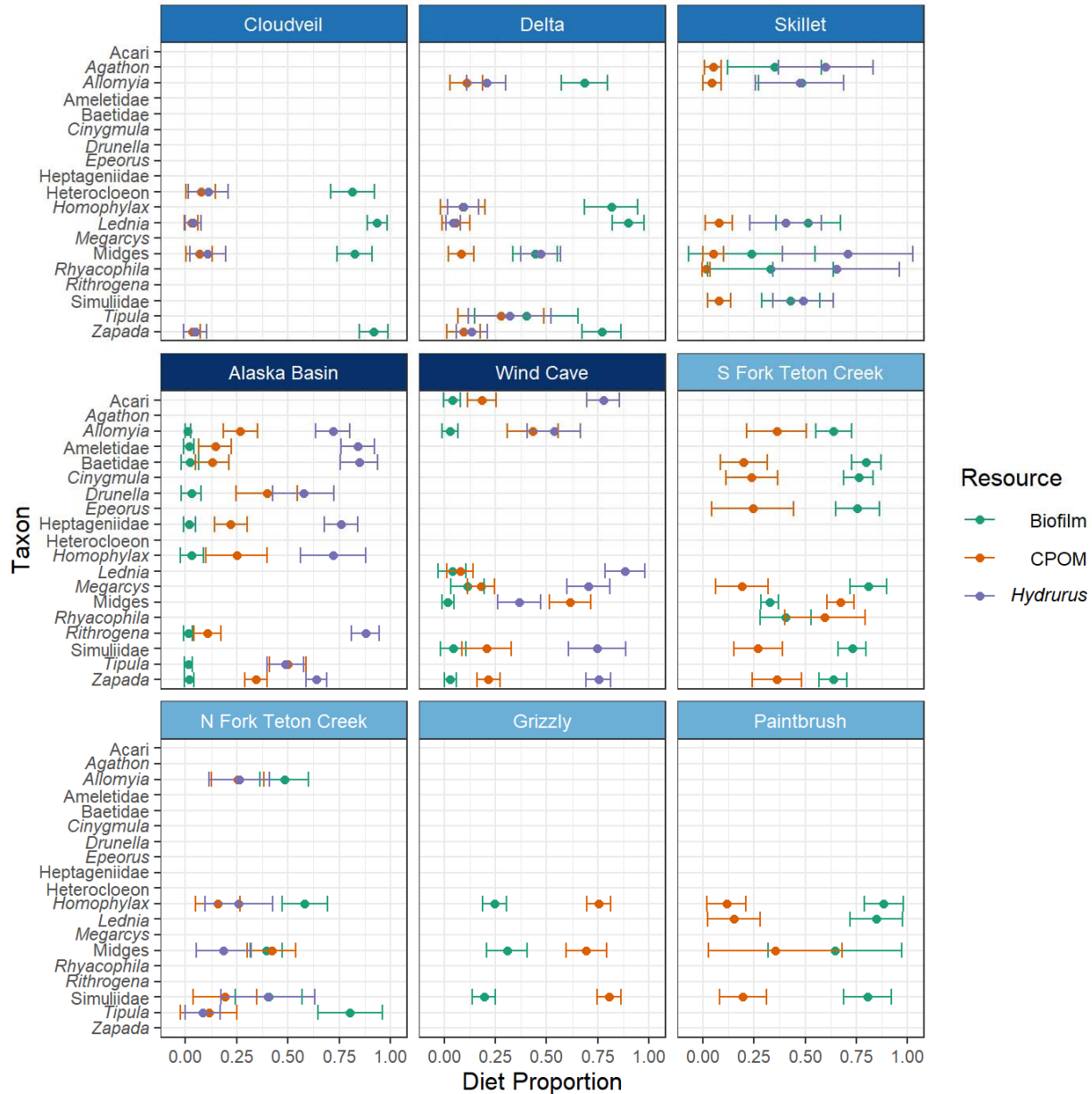


304  
305

306 Figure 2. Diet composition for each taxon estimated using gut content analysis. The numbers on  
307 each bar represent samples size (multiple individuals were pooled for most samples). Site names  
308 are colored by hydrologic source (dark blue = subterranean ice, medium blue = glacier, light blue  
309 = snowmelt). Cloudveil is not shown because no identifiable particles were recovered from  
310 specimen digestive tracts. This is likely due to low diatom abundance at this site. Very small  
311 proportions of a filamentous alga were observed in the guts of *Tipula* and *Prosimulium* at South  
312 Fork Teton Creek.



313 Our results from gut content analysis informed our decisions about which taxa or  
314 individual samples to include in the isotope mixing models as primary consumers. It is possible  
315 that the fragments of exoskeleton found in the guts of *Homophylax*, *Epeorus*, and *Cinygmula*  
316 were devoid of digestible animal material before they were consumed, and we therefore included  
317 all individuals of these taxa in our models. All other taxa observed to contain animal material  
318 had some samples above and below the trophic cutoff (Appendix 2, Figure S1). In these cases,  
319 only the samples below the cutoff were included. *L. tetonica* over the trophic cutoff were also  
320 excluded at Delta. No Turbellaria were included in our model as they were clearly secondary  
321 predators in these streams. The food resources had varying isotopic signatures among sites which  
322 necessitated the use of site-specific source isotope values in the mixing models. The site  $\delta^{13}\text{C}$   
323 mean values of biofilm (-28.9 to -11.6‰) and *Hydrurus* (-34.6 to -22.0‰) were variable across  
324 sites, while CPOM was more consistent (-29.3 to -26.3‰). Plots of isotope values at each site are  
325 included in the Supplementary Materials (Appendix 2, Figures S2-S10).



326

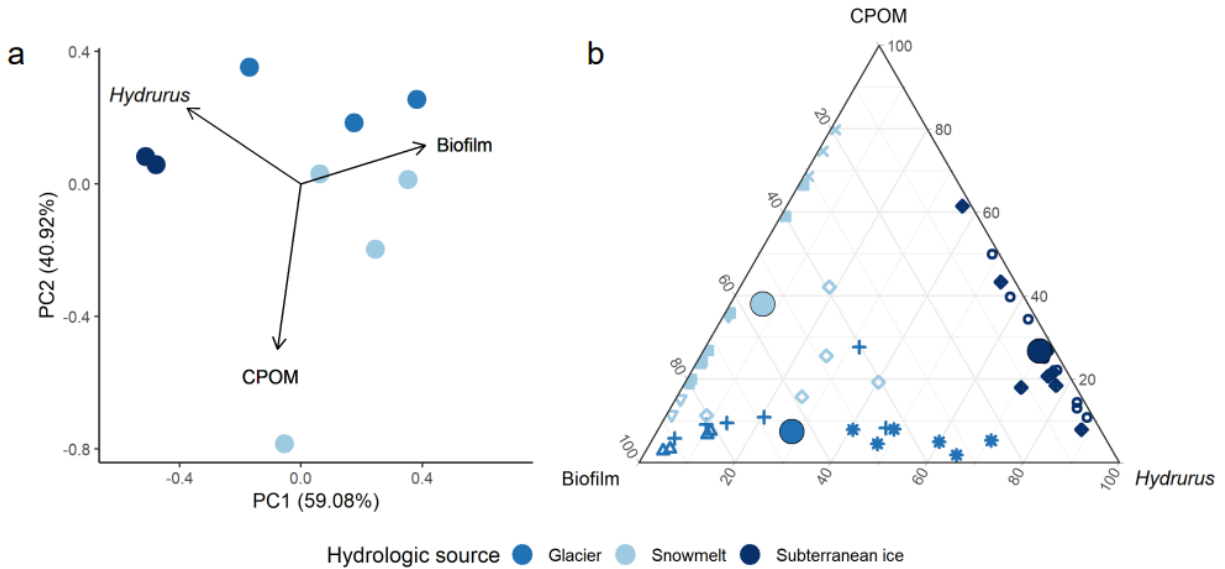
327 Figure 3. Diet proportions for taxa across sites estimated using isotope mixing models. Error bars  
 328 represent standard deviation, and the site names are colored by hydrologic source (dark blue =  
 329 subterranean ice, medium blue = glacier, light blue = snowmelt). Model estimates were  
 330 combined for the filamentous alga and biofilm at South Fork Teton Creek, and small mammal  
 331 feces and CPOM at Grizzly.

332

333 Diet proportions for individual taxa varied widely among sites (Figure 3). PCA showed

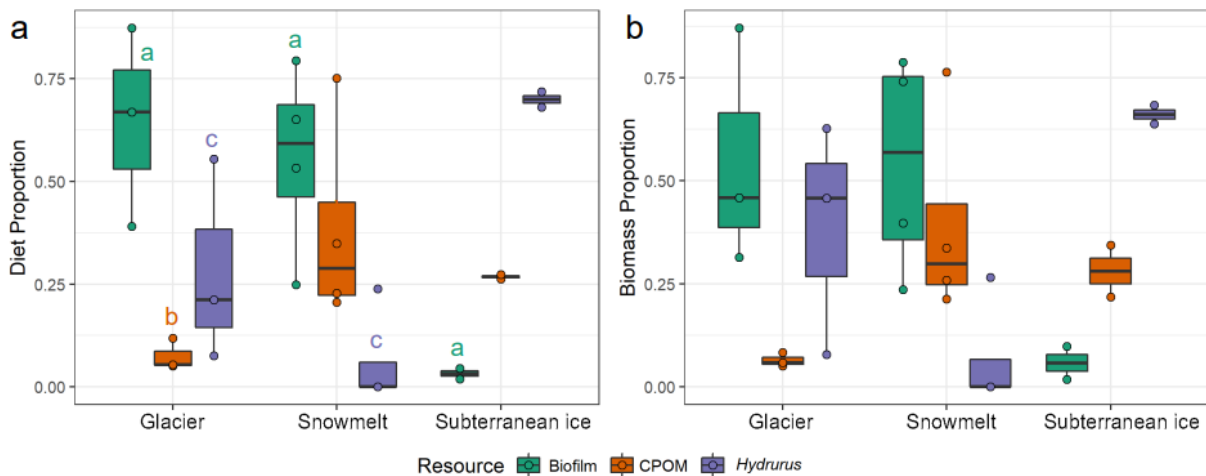
334 that our sites grouped into glacier, snowmelt, and subterranean ice streams by diet compositions

335 (Figure 4a). Site mean diet compositions were significantly different among streams fed by  
336 different hydrologic sources (Figure 5). The diet proportions of biofilm, CPOM and *Hydrurus*  
337 were significantly ( $\alpha = 0.05$ ) different between subterranean ice and both glacier (biofilm:  
338 coefficient = -2.0, p-value = 0.030; CPOM: -coefficient = 4.9, p-value < 0.001; *Hydrurus*:  
339 coefficient = -6.3, p-value < 0.001) and snowmelt streams (biofilm: coefficient: -2.4, p-value =  
340 0.007; CPOM: coefficient = -4.1852, p-value < 0.001; *Hydrurus*: coefficient = -5.1, p-value <  
341 0.001), but glacier and snowmelt streams did not differ significantly in diet proportions (model  
342 results in Appendix 2, Table S2). We observed some differences in the diet compositions of  
343 individual taxa between hydrologic sources. For *Zapada*, the proportions of all resources were  
344 significantly different between glacier and subterranean ice-fed streams (biofilm: coefficient: -  
345 2.6, p-value = 0.009, CPOM: coefficient = 2.2, p-value = 0.032, *Hydrurus*: coefficient = 2.8, p-  
346 value = 0.006). The macroinvertebrate biomass supported by each resource followed similar  
347 trends due to the low diet variability between taxa within each site (Figure 5b). Glacier and  
348 snowmelt-fed streams did not have significantly different biomass contributions, but they both  
349 differed from subterranean ice-fed streams in the proportions of biomass supported by CPOM  
350 (glacier: coefficient = -2.9, p-value = 0.002; snowmelt: coefficient = -1.9, p-value = 0.030) and  
351 *Hydrurus* (glacier: coefficient = -2.8, p-value = 0.003; snowmelt: coefficient = -4.0, p-value <  
352 0.001).



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Figure 4. Sites have low within-site variation and are clustered by hydrologic source. (a) Principle component analyses showing diet variation among sites with different hydrologic sources. (b) Ternary plot of taxa diet compositions. Shapes represent different stream sites and large circles depict the mean of each hydrologic source.



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Figure 5. (a) Boxplot of mean site diet proportions of each food resource grouped by hydrologic source. Points represent site means and letters indicate resource proportions that did not differ significantly. Diet compositions were significantly different among all hydrologic sources. (b) Boxplot of the proportion of macroinvertebrate biomass supported by each resource within different hydrologic source categories. Biomass composition was significantly different between subterranean ice and both snowmelt and glacier-fed streams. Points represent unique sites.

371 The among-site multivariate metric variation was 0.23 and the mean within-site variation  
 372 was 0.04. Within-site variation did not differ significantly between hydrologic sources, and  
 373 among-site variation increased from subterranean ice (0.001), to glacier (0.121), to snowmelt  
 374 (0.132) fed streams. Resource use by *L. tetonica* and *Zapada* ranged from 88% *Hydrurus* and 4%  
 375 biofilm to 4% *Hydrurus* and 94% biofilm, and 75% *Hydrurus* and 3% biofilm to 5% *Hydrurus*  
 376 and 92% biofilm, respectively. The mean diet proportions of CPOM across all sites by *L.*  
 377 *tetonica* and *Zapada* were  $0.08 \pm 0.05$  and  $0.21 \pm 0.15$ . The within-site variation did not have a  
 378 significant linear relationship with the Shannon or Simpson diversity indices.

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Table 1. Site characteristics and environmental variables for alpine stream sites in the Teton Range, Wyoming.

T <sub>max</sub> (°C)	DO (mg/L)	SPC (µS/cm)	TSS (g/L)	pH	Aspect (°)	Slope (°)	Sulfate (µg/L)	Nitrate (µg/L)	Chloride (µg/L)	Fluoride (µg/L)
1.9	10.9	226.0	3.2	7.84	330	3	27962	609	796	399
3.2	11.3	153.8	3.3	8.53	15	25	1600	1100	857	493
7.8	9.7	3.6	5.9	8.86	60	29	1519	502	748	411
3.6	10.5	5.4	4.4	9.6	75	22	707	1004	756	21
3.5	11.3	8.1	12.4	9.43	115	6	860	806	776	398
14.8	8.1	14.5	4.0	8.28	343	6	1766	395	742	478
12.2	8.6	9.8	3.1	7.31	30	2	1003	721	762	398
9.8	9.5	32.3	2.4	8.46	41	9	8801	660	771	410
16.8	7.6	59.0	21.0	7.8	90	3	5241	12	746	403

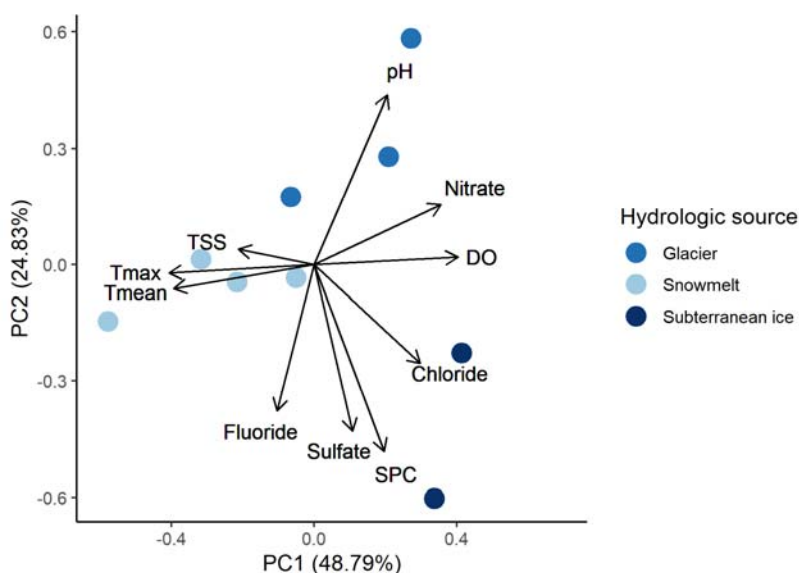
Site	Hydrologic source	Riparian habitat	Elevation (m)	T <sub>mean</sub> (°C)
Alaska Basin	Sub-terranean ice	Alpine tundra	2881	1.6
Wind Cave	Sub-terranean ice	Alpine tundra	2660	2.8
Skillet	Glacier	Boulder field	2733	4.1
Cloudveil	Glacier	Boulder field	2897	2.1
Delta	Glacier	Forested	2755	2
Grizzly	Snowmelt	Alpine tundra	2970	5.6
N Fork Teton Creek	Snowmelt	Alpine tundra	2956	5.9
Paintbrush	Snowmelt	Boulder field	2796	5.4

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419 *Influence of environmental variables*

420 Site characteristics varied among streams (Table 1). Principle component analysis (PCA)  
421 showed that our sites grouped into glacier, snowmelt, and subterranean ice streams by  
422 environmental variables (Figure 6). The first principle component (PC1) was primarily  
423 influenced by mean temperature ( $T_{\text{mean}}$ ), maximum temperature ( $T_{\text{max}}$ ), DO, chloride and nitrate.  
424 The second principle component (PC2) was primarily influenced by SPC, pH, fluoride, and  
425 sulfate.

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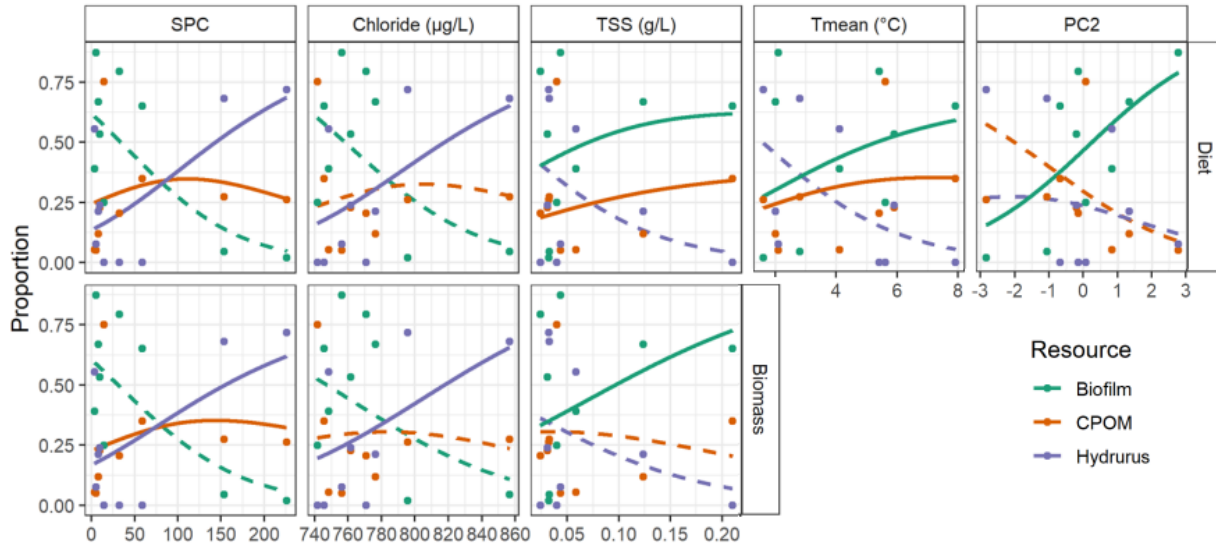
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429 Figure 6. Principle component analyses showing environmental variation among sites with  
430 different hydrologic sources.

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434 Figure 7. Models with significant relationships between diet or biomass proportion and  
435 environmental variables. Solid lines represent significant relationships, while dotted lines were  
436 not significant.

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439 SPC (CPOM: -coefficient = 0.02, p-value = 0.002; *Hydrurus*: coefficient = 0.03, p-value  
440 < 0.001),  $T_{\text{mean}}$  (biofilm: coefficient = 0.47, p-value = 0.028; CPOM: -coefficient = 0.42, p-  
441 value = 0.044), chloride (*Hydrurus*: coefficient = 0.04, p-value = 0.004), and TSS (biofilm:  
442 coefficient = 32.43, p-value = 0.005; CPOM: coefficient = 33.35, p-value = 0.019) all had  
443 significant relationships with diet composition (Figure 7, Appendix 2 Table S2.). PC2 (biofilm:  
444 coefficient = 0.89, p-value = 0.012) also significantly influenced the diet composition and had a  
445 similar AICc value to individual environmental variables, while the model with hydrologic  
446 source had a much lower AICc value (Table 2). Combining environmental variables or  
447 environmental variables and hydrologic source increased the model fit, but the model did not  
448 converge for most combinations and sample size was too low to reliably combine explanatory  
449 variables. The biomass supported by each resource followed similar trends but with fewer  
450 significant relationships. Hydrologic source was still by far the best explanatory variable, with  
451 several individual variables that are known to be related to hydrologic source (Tronstad et al



452 2020) also having significant relationships (Figure 7), including SPC (CPOM: coefficient = 0.02,  
453 p-value = 0.010, *Hydrurus*: coefficient = 0.02, p-value < 0.001), TSS (biofilm: coefficient =  
454 18.93, p-value = 0.034), and chloride (*Hydrurus*: coefficient = 0.04, p-value = 0.007). Examples  
455 of model checks are included in the appendix (Figures S11 and S12).

456

457 Table 2. Model selection using corrected Akaike information criterion (AICc). We observed a  
458 large increase in model fit between single environmental variables or the first PCA component  
459 (PC1) and models that included hydrologic source or multiple variables. Only models with  
460 significant effects are shown.

461

Explanatory variables	AICc
Hydrologic source	-211.5
SPC + Tmean	-200.7
Hydrologic source + Tmax	-107.2
SPC	23.5
Chloride	29.4
PC2	30.1
TSS	31.5
Tmean	31.7

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## 464 **Discussion:**

465 Understanding links between hydrologic source, imperiled taxa, and resource use in  
466 alpine streams strengthens our capacity to predict how climate change will impact these  
467 vulnerable ecosystems. In this study, we show that hydrologic source is a driver of food web  
468 structure, which expands on previous evidence about the important role of hydrology in shaping  
469 alpine diversity and community composition (Fell et al. 2017, Giersch et al. 2017). Overall,  
470 macroinvertebrate communities in alpine streams appear to rely heavily upon autochthonous  
471 resources, but large differences in the assimilation of biofilm and *Hydrurus* exist among

472 hydrologic sources. This was particularly true for streams fed by subterranean ice—which are  
473 predicted to be most resilient to cryosphere recession (Brighenti et al. 2021)—as they exhibited  
474 the highest rates of *Hydrurus* assimilation. While we were not able to distinguish differences in  
475 resource use between snowmelt and glacier-fed streams with our sample size, previous research  
476 has shown that allochthonous diet contribution increases with decreasing environmental  
477 harshness in glacier-fed streams (Niedrist and Füreder 2018). Generally, hydrologic source  
478 explained diet compositions better than other environmental variables. Surprisingly, PCA  
479 components which summarized multiple environmental variables did not explain diet  
480 compositions better than individual variables.

481         Climate change is expected to influence the nutritional quality and availability of basal  
482 resources in alpine streams, which will in turn alter resource use in these communities. For  
483 instance, warmer water temperatures and decreased glacial influence are expected to increase the  
484 quantity of algal biofilms (Mosser & Brock 1976, Cauvy-Fraunié et al. 2016) and litter input is  
485 expected to increase as vegetation increases and shifts uphill (Xu et al. 2020, Emmet et al. 2019).  
486 However, nutrient limitation is an important consideration. Decreased glacier influence will  
487 likely decrease nitrogen availability, which could intensify nutrient limitation for autochthonous  
488 production (Slemmons et al. 2013). Additionally, litter decomposition (which increases  
489 nutritional quality) can also decrease with increasing stream intermittency resulting from reduced  
490 meltwater (Siebers et al. 2019) and nutrient limitation (Robinson & Gessner, 2000). The  
491 availability of *Hydrurus* may decrease in the future as the period when temperatures are too high  
492 for *Hydrurus* growth lengthens (Klaveness 2019, Hieber et al. 2001). As temperatures rise,  
493 currently abundant algae could be outcompeted by filamentous algae with lower nutritional  
494 quality (Oleksy et al. 2021, Brett et al. 1997). Although we lack a complete understanding of

495 how climate change will influence food resources, there is potential for the quality of  
496 allochthonous resources, and the quantity and quality of autochthonous resources for stream  
497 macroinvertebrates to be reduced.

498

499 *Trophic flexibility and the role of Hydrurus in alpine food webs*

500 Trophic flexibility can increase the resilience of organisms and communities to  
501 environmental change (Saint-Béat et al. 2015, Bartley et al. 2019). We observed a prevalence of  
502 trophic flexibility in alpine streams across hydrologic sources, with individual taxa and  
503 communities capitalizing on different resources among sites and seemingly unconstrained by  
504 feeding morphology. The low within-stream variability in resource use demonstrates that  
505 invertebrate communities in the Teton Range are consuming the same food resources instead of  
506 specializing, suggesting low pressure from competition (Mihuc 1997). Thus, it appears that at  
507 present, competition for resources is not an important driver of macroinvertebrate distributions in  
508 Teton alpine streams. Furthermore, community diet variance at a given site did not increase with  
509 taxonomic diversity, indicating that whole communities are targeting the same resources, even in  
510 more diverse snowmelt-fed streams. Trophic flexibility likely helps enable many invertebrate  
511 taxa to maintain populations in diverse alpine stream habitats, as has been seen in other  
512 ecosystems with large environmental gradients (Schalk et al. 2017, Leclerc et al. 2021).

513 Gut content analysis allowed us to observe flexible feeding at a smaller scale, including  
514 predatory behavior in taxa that are usually primary consumers (e.g., black fly larvae, Simuliidae),  
515 potentially due to low quality resources (Diehl 2003). We also observed consumption of algae by  
516 predators, which may result from low prey availability (Coll & Guershon 2002) and could reduce  
517 predation stress on primary consumers. Trophic flexibility by macroinvertebrate communities in

518 alpine streams suggests that these taxa do not conform to traditional functional feeding groups  
519 and that population growth may be limited more by the harsh environment than by food  
520 availability.

521         Despite the benefits of flexible feeding strategies, they may not be sufficient to stabilize  
522 alpine food webs if the degradation of a key resource such as *Hydrurus* occurs. *Hydrurus* is an  
523 especially valuable resource because of its high fatty acid content (Klaveness 2017) and  
524 abundance early in the growing season (Rott et al. 2006). Alterations in the phenology of food  
525 resources due to climate change will have detrimental effects on many consumers worldwide  
526 (Parmesan 2006). If the growth of *Hydrurus* is limited by stream temperatures rising in the  
527 spring (Klaveness 2019, Hieber et al. 2001), taxa may struggle to acquire the nutrients needed  
528 early in the growing season. Thus, even if overall primary productivity increases in alpine  
529 streams, the decreased growth of an alga that is abundant before snow and ice recedes may limit  
530 macroinvertebrate development. We also observed lower consumption of *Hydrurus* in warmer  
531 snowmelt-fed streams when *Hydrurus* may be senescing, suggesting that it may be a lower  
532 quality resource when dying back. The typically distinct carbon isotope signature of *Hydrurus*  
533 provides a valuable opportunity to observe changes in its importance over time or to detect its  
534 food web signature when streams are inaccessible in the spring and *Hydrurus* is most abundant.

535         Because *Hydrurus* appears to be an integral part of alpine stream food webs and changes  
536 in its availability will likely have larger ramifications than other food resources, its presence and  
537 persistence could be relevant for identifying refugia where meltwater biodiversity may persist  
538 under climate change. Rock glaciers, the most common type of subterranean ice, are ~10 times  
539 more abundant than traditional surface glaciers in the contiguous US (Johnson 2018).  
540 Additionally, rock glaciers are predicted to melt slower than glaciers because of the insulation

541 provided by layers of rock and debris (Anderson et al. 2018, Brighenti et al. 2021). Thus, our  
542 finding that macroinvertebrate communities in these streams had the largest assimilation of  
543 *Hydrurus* in August suggests that it may persist longer into the growing season compared to  
544 streams with glacier or snowmelt sources. Subterranean ice-fed streams lack the high turbidity  
545 and scouring of glacier-fed streams which limits algal productivity during the summer (Rott et al.  
546 2006, Hieber et al. 2001, Uehlinger et al. 2009), while still maintaining relatively high nitrogen  
547 (Fegel et al. 2016) and the cold temperatures necessary for *Hydrurus* (Klaveness 2017).  
548 *Hydrurus* may therefore be more stable in subterranean ice-fed streams than those fed by other  
549 hydrologic sources. Given that subterranean ice-fed streams in the Teton Range maintain diverse  
550 macroinvertebrate assemblages relative to other stream types, including rare cold-water taxa  
551 (e.g., *L. tetonica* and *Zapada glacier*, Tronstad et al. 2020), the stability of *Hydrurus* in these  
552 streams may contribute to their long-term potential as high mountain refugia for aquatic  
553 biodiversity. This combination of subterranean ice meltwater and abundance of high-quality  
554 resources may also explain why cold-water biodiversity has been observed persisting in some  
555 reaches of other montane regions long after glaciers have receded (Muhlfeld et al. 2020).

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#### 557 *Implications for vulnerable taxa in the Teton Range*

558 In the Teton Range, two stoneflies—*L. tetonica* and *Z. glacier*—are of conservation and  
559 management interest as they are either ESA-listed (*Z. glacier*) or the close congeneric of another  
560 listed species (*L. tetonica*). However, both species are poorly studied with basic aspects of their  
561 life history largely unknown, including their dietary needs, which makes management planning  
562 difficult. We show that both taxa can switch from biofilm to *Hydrurus* dominated diets, and  
563 *Zapada* consumed more allochthonous resources than *L. tetonica*. These taxa were also the only

564 taxa observed to consume wood at any of our sites. In one glacier-fed stream, our analyses  
565 indicated that *L. tetonica* may exhibit predatory behavior. This finding aligns with a recent study  
566 of its congener—*L. tumana*—which can exhibit cannibalism in captivity (Shah et al. 2022).  
567 These taxa are most abundant in the coldest sections of alpine streams, making shifts to higher  
568 elevations unlikely (Giersch et al. 2017). The high consumption of *Hydrurus* by *L. tetonica*,  
569 *Zapada*, and co-occurring species in our study, including in streams fed by subterranean ice,  
570 further supports the idea that these streams may act as climate refugia (Brighenti et al. 2021). By  
571 pairing prior knowledge of species distributions with their trophic ecology and predictions about  
572 which hydrologic sources will be most resilient to climate change, managers are left with a  
573 clearer picture of what habitats warrant protection for limiting the magnitude of biodiversity loss  
574 as the cryosphere fades.

575

#### 576 *Conclusion*

577 The hydrology of alpine ecosystems is changing rapidly, and the communities within streams fed  
578 by distinct hydrologic sources will likely be impacted by these changes at different rates.  
579 Flexible feeding strategies may allow the persistence of alpine taxa until other impacts of climate  
580 change, including invasive species or stream intermittency, become primary limiting factors. In  
581 addition to many other factors that make them suitable as potential climate refugia, subterranean  
582 ice features also support abundant *Hydrurus* populations, a key food resource for many taxa  
583 including vulnerable species. Further study is necessary to test these results in additional  
584 mountain ranges and geographic regions with different seasonal resource dynamics, and over  
585 broader spatial scales. This study advances our understanding of how alpine stream ecosystems

586 function across different hydrologic sources and provides baseline data for further exploring  
587 what the future may hold for these imperiled communities.

588

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599

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