Experimentally-induced low flows reveal climate change may shrink trophic niches of mountain stream predators.

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Abstract: Climate change is projected to decrease snowpack and advance snowmelt in mountain ranges globally–including in California's Sierra Nevada, where streamflow in snow-dominated rivers is expected to peak up to 2 months earlier, and remain in baseflow conditions for extended periods of time. Predators may be particularly sensitive to low flows, owing to their larger body sizes, higher metabolic demands, and longer lifespans. Experimental manipulations can help understand mechanistic links between future hydroclimates and stream predator persistence, fitness, or behavior–allowing us to anticipate how whole food webs are likely to respond to snow droughts. Here, we experimentally examined how the trophic ecology of predatory macroinvertebrates will respond to extended low flows expected under climate change. To this end, we manipulated flow regimes in a set of outdoor, large-scale artificial streams in the Sierra Nevada to produce a current flow regime and two future regimes that advanced low-flow conditions by three and six weeks, respectively. We sampled and performed stable isotope analysis on the macroinvertebrate community, focusing on three predatory taxa, i.e., Perlidae stoneflies (Plecoptera), *Rhyacophila* caddisflies (Trichoptera), and Turbellaria flatworms, as well as non-predatory invertebrates (n = 310 samples across eight taxa). We examined the isotopic signals ($\delta^{15}N$ and $\delta^{13}C$) of these predators, and quantified how trophic niche areas, trophic positions, and energy sources (i.e., algal *vs.* detrital-derived energy) varied seasonally and across low-flow treatments. We found no change in reliance on algal ('green') *vs.* detrital ('brown') energy pathways following extended low flows. However, low flows did compress the trophic niches of predatory taxa, with variable responses across taxa and treatments. Predatory taxa exhibited changes in niche areas similar in magnitude and direction to other feeding groups, but they were the only group that was severely impacted by the most extreme low-flow treatment (62% niche compression). Further, gut content analysis showed that Perlidae stoneflies had fewer prey items in their guts under extended low flows. Our experiment suggests that climate-driven low flows will likely shift invertebrate predators' diets, and thus food-web structure, in Sierra Nevada streams. However, species-specific dietary changes illustrate the importance of response diversity, and thus the need to preserve diverse alpine stream assemblages in the face of future hydroclimates.

Key words: Climate change, Food webs, Macroinvertebrates, Niche compression, Predators, Stable Isotope Analysis.

INTRODUCTION

Climate change is intensifying the global hydrologic cycle, with associated impacts to river flow regimes (Palmer et al. 2008, Lobanova et al. 2018, Payne et al. 2020). Freshwater ecosystems, and particularly those at high altitudes, are threatened by climate change stressors such as higher maximum temperatures, reduced streamflow arising from reduced snowpack and early snowmelt, and associated flow intermittency (Dobrowski and Parks 2016, Hotaling et al. 2017). These stressors can individually or synergistically alter community structure and disrupt ecosystem functioning (Woodward et al. 2010). While the effects of altered thermal and flow regimes can differ across species that vary in life-history, morphological, and behavioral traits, responses at the food-web level have been more difficult to elucidate (Palmer and Ruhi 2019). Experiments with whole communities under realistic field conditions are needed to understand the effects of climate change on the higher levels of biological organization.

Snowmelt is key to high-mountain streams, but climate change is drastically altering snow hydrology and run-off magnitude and timing (Viviroli et al. 2007, Milner et al. 2010, Hammond et al. 2018). In snow-dominated mountain regions, precipitation typically falls primarily as snow during winter, and melts during spring and summer before rivers return to baseflow conditions. Climate change threatens montane streams by warming air temperatures and causing more precipitation to fall as rain relative to snow, leading to reduced snowpacks and earlier and faster spring snowmelt (McCabe and Clark 2005, Knowles et al. 2006, Hammond et al. 2024). Model projections show that continued warming will further advance snowmelt (Stewart et al. 2005, Maurer et al. 2007). The runoff midpoint, or the day when half of the annual runoff has occurred, is projected to advance by 50 days in the Sierra Nevada by the end of the century under an unmitigated climate change scenario, or by 25 days under a mitigated scenario RCP 4.5 (Reich et al. 2018). The consequences of these novel snowmelt dynamics on mountain stream food webs could be far-reaching but remain largely unstudied (but see Leathers et al. 2024). Climate-induced flow changes in glacier-fed streams have been relatively more studied (Fell et al. 2017). Streams in the Sierra Nevada and other mountain ranges are typically supported by snowmelt, glaciers, and/or springs (Ward 1994). Because glacial melt is higher during summers, low-flow conditions in glacier-fed streams typically occur in winter (unlike in snowmelt-fed streams, which tend to reach baseflow in late summer). Glacier-fed streams may also experience lower summer flows if glaciers are significantly reduced. When glacier-fed streams are exposed to low-flow conditions, sometimes to the point of flow cessation, macroinvertebrate communities show altered community structure and reduced diversity, with long recovery periods and gains for more tolerant taxa (Cauvy-Fraunié et al. 2016, Piano et al. 2019, Drost et al. 2022). While glacier-fed and sowmelt-fed streams differ in many ways, similar ecological responses could be expected under warming climate scenarios.

Earlier snowmelt represents a shift away from the natural flow regime that shaped behavioral, physiological, or life-history adaptations of species in snow-dependent rivers, and changes to low-flow timing or duration likely represent a source of stress (Giersch et al. 2016). Low flows increase maximum stream temperature and the amplitude of diel swings in temperature (due to reduced buffering), decrease dissolved oxygen, and compress habitat (Dewson et al. 2007, Arismendi et al. 2013). Snowmelt-fed streams experience these shifts annually, and thus invertebrate communities are adapted to them (Danks 2007, Milner et al. 2020). However, long low-flow periods can become a source of environmental stress to stream biota via a variety of mechanisms (Bonacina et al. 2022). At the individual level, warmer stream temperatures and reduced dissolved oxygen forces greater metabolic demands, leading to reduced physiological condition and productivity. Low flows can also change the quantity and quality of basal resources- potentially limiting the food available to macroinvertebrates (Suren and Riis 2010, Ferreira and Canhoto 2015); and can often lead to habitat contraction, often intensifying biotic interactions (Dewson et al. 2007). Responses to low flows from early snowmelt can vary by taxa (Leathers et al. 2024), with species more tolerant to warming and hypoxia likely taking advantage of increased production and access to resources.

Predators tend to be particularly sensitive to these changes (Petchey et al. 1999, Voigt et al. 2003, Ledger et al. 2013), owing to their larger body sizes and associated higher metabolic demands, longer lifespans, and bigger home ranges (Woodward et al. 2005, Brose et al. 2017). In addition, predators are more sensitive to changes occurring in the lower trophic levels, such as changes in productivity or in prey composition and size (Petchey et al. 1999, Ledger et al. 2013, Mor et al. 2022). Studies suggest that even if predator abundances increase short-term with low flows (Bogan and Lytle 2007, Stitz et al. 2017), longer, supraseasonal droughts may tend to impact predators more than non-predator taxa (Ledger et al. 2011, Mor et al. 2022).

Because predatory taxa often exert top-down control on food webs, changes in their trophic ecology or abundance can lead to trophic cascades (Estes et al. 2011). If predators are flexible in their diets, they may be able to take advantage of increased density of particular prey, when available (Walters and Post 2011, Ruhí et al. 2016). We refer to this pattern as the *trophic niche expansion hypothesis*, since predators would widen the range of prey sources they rely on. Support for this hypothesis would be reflected as predators increasing the size of their isotopic niche when exposed to extended low flows–holding higher trophic positions, relying on multiple carbon sources, and showing increased niche overlap (Fig. 1). Alternatively, because environmental stress is typically associated with niche compression, or a reduction in prey diversity (Layman et al. 2007, Burdon et al. 2020), *trophic niche compression* would be possible if predators reduced their isotopic niche area when exposed to novel low-flow conditions (Mor et al. 2022). In that case, diet specialization would lead to predators holding lower trophic positions (e.g., due to reduced trophic efficiency; Mor et al. 2022), showing heavier reliance on fewer carbon sources, and lower trophic niche overlap (Fig. 1).

In this study, we sought to understand how low-flow conditions expected under end-of-century climate change scenarios are poised to alter the trophic ecology of benthic macroinvertebrate predators in Sierra Nevada streams. To this end, we manipulated flow regimes of 9 large-scale, outdoor artificial streams in the Sierra Nevada by lengthening the low-flow period by either three or six weeks (Leathers et al. 2024). We then used carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes and Bayesian modeling techniques to examine shifts in trophic niches (e.g., Layman et al. 2007, Layman et al. 2012, Burdon et al. 2020) of predatory Perlidae stoneflies (Plecoptera), *Rhyacophila* caddisflies (Trichoptera), and Turbellaria flatworms. We also analyzed gut contents of the Perlidae stoneflies *Calineuria californica* and *Doroneuria baumanni*, to ground-truth and increase the resolution of diet shifts inferred via stable isotope analysis. Specifically, we asked: 1) Do predators' diets vary seasonally following low flows under the *current* flow regime, in terms of trophic niche area, trophic position, and reliance on algal *vs.* detrital-derived energy? 2) Do these diets change in response to experimentally-induced extended low flows representative of expected flow regimes under climate change? 3) Are predators more sensitive to extended low flow conditions compared to the rest of the community, as it has been generally reported (Petchey et al. 1999, Mor et al. 2022)?

We expected that: 1) Predators' diets would vary over the season, mostly due to expected short-term increases in their abundance (Bogan and Lytle 2007, Stitz et al. 2017) and associated increases in resource competition. Additionally, we expected that 2) under the extended low-flow treatments, predators' trophic niches would shrink (i.e., *trophic niche compression hypothesis*, Fig. 1), due to increased pressure on predators to meet metabolic demands (as in Burdon et al. 2020, Mor et al. 2022). Lastly, we expected that 3) predators' diets would contract more than other major feeding groups because they should be disproportionately affected by changes in the broader food web, and more vulnerable to environmental stress (Petchey et al. 1999, Ledger et al. 2013). Determining how the trophic ecology of predators changes under seasonal and extended low-flow conditions may help understand how predators, and stream communities as a whole, will respond to projected climate change in snow-dominated rivers.

METHODS

Study site and experimental design

We performed the experiment at the Sierra Nevada Aquatic Research Laboratory (SNARL), located on the eastern slope of the Sierra Nevada mountain range in Mono County, California, USA (2150 m.a.s.l., Fig. S1). The landscape is dominated by sagebrush steppe, and its climate is semiarid with most precipitation occurring as snow in the winter. SNARL features a large-scale, outdoor artificial stream system with 9 identical channels, each 50 m long and 1 m wide (Fig. 2D). Each channel has a meandering path with 6 pool-riffle sequences. The channels have natural substrates composed of pebbles, fine sediment, and larger cobbles. No riparian vegetation or canopy cover is present near the channels, mimicking nearby zero-order and first-order streams. The channels are flow-through and fed by Convict Creek, an adjacent perennial stream that provides the channels with sediment and organic matter, as well as with algal and invertebrate propagules. We controlled channel flow from the inlet channels with sluice gates (see below). Fish were excluded from the experimental channels throughout the experiment to mimic high-elevation streams in the Eastern Sierra that are naturally fishless. We installed fine 1.25-cm mesh screens at channel inlets and outlets to avoid fish colonization, and we electrofished at the beginning of the experiment to ensure their absence. Results from the same experiment, but focusing on invertebrate phenology and ecosystem processes, have been published elsewhere (Leathers et al. 2024). This large-scale experimental system has been used in the past to test questions around the ecology and behavior of stream invertebrates (Albertson et al. 2019, Saffarinia et al. 2022). Kennedy et al. (1995) tested colonization of separate experimental stream sections (before the construction of the artificial stream channels used in this study) at SNARL and found similar macroinvertebrate composition and life stages to the feeder natural stream, Convict Creek.

By controlling the sluice gates at the top of each channel, we simulated 3 flow regimes: one based on historical average conditions, and two flow regimes based on climate change scenarios that will advance snowmelt to different extents, by 3 and 6 weeks respectively (Fig. 2, Reich et al. 2018). Following a block design, we assigned the 3 treatments to the channels, based on when the falling limb of the hydrograph (after peak snowmelt) shifts to baseflow. The treatments were: *current* (reaching low-flow conditions in early August), *three weeks early* (reaching low-flow conditions in mid-July; mitigated climate change scenario or RCP 4.5), and *six weeks early* (reaching low-flow conditions in late June; unmitigated climate change scenario or RCP 8.5). For the *current* treatment, we controlled channel flow to mimic a typical flow regime based on 15 years of historical flow data from Convict Creek (Fig. S1). In turn, channels assigned to the future flow regime treatments experienced the same high discharge in June as the *current* treatment but returned to low flows 3 weeks and 6 weeks earlier, to represent the mitigated and unmitigated climate change scenarios described in Reich et al. (2018). Discharge varied from ~15 L/s at high-flow conditions to 1.5 L/s at low-flow conditions, an order of magnitude change that has been commonly reported in Sierra Nevada headwater streams (Hunsaker and Neary 2012). Low-flow conditions lasted for at least 3 weeks until the experiment finished at the end of August.

We visited and inspected the channels daily. To track changes in environmental variables in the channels, we deployed HOBO U20L-04 pressure transducers that also measure water temperature, placed in the fifth downstream pool of each channel; measurements were recorded every 5 minutes. Two emerged sensors were placed on land to account for fluctuations in atmospheric pressure, and we calculated water level (i.e., pool depth) throughout the experiment duration. We subsequently transformed water level into discharge via channel-specific rating curves. In order to develop rating curves for each channel, we manually estimated discharge using channel depth and velocity measurements, taken with a Marsh-McBirney Flo-Mate 2000 current meter, 17-26 times per channel throughout the summer. Additionally, because low-flow conditions are often associated with lower dissolved oxygen (DO) levels, particularly at night, we monitored DO every 5 minutes using one HOBO U26-001 logger in each channel. As expected, temperature and dissolved oxygen were found to increase ($F_{8,14} = 120.3$, $P < 0.001$) and decrease ($F_{8,13} = 14.18$, $P < 0.001$) respectively, as reported in Leathers et al. 2024 (Fig. S2, S3). Values <2mg/L were never detected, and 99.6% of readings were above 5 mg/L (a threshold used to assess performance of coldwater Ephemeroptera and Plecoptera; Nebeker 1972).

Macroinvertebrate sampling, stable isotope and gut content processing

We collected macroinvertebrates from all channels between 12 May 2019 and 6 June 2019, at the start of the experiment; and again between 21 August 2019 and 25 August 2019 once all channels returned to low-flow conditions (Fig. 2). To sample macroinvertebrates, we visually searched entire channel lengths, flipping cobbles from the shore, and using fine tweezers and trays to pick out individuals. We then confirmed identifications under dissecting microscopes in a wet lab on-site. After identification, we sorted individuals into vials, typically at the genus level. We aimed to collect enough individuals of each taxon to fill at least three 1.5 mL Eppendorf tubes per channel. As such, each sample represents 1 to ~20 individuals (depending on the taxon). Collected samples were placed in Eppendorf tubes with stream water, and we held them for 24 hours in a refrigerator at 10°C to allow gut contents to evacuate. We then froze the specimens (-20°C).

To prepare the samples for stable isotope analysis, we thawed the specimens at room temperature, and removed shells of mollusks and digestive tracts of large individuals (>1 cm in length). We dried samples at 50°C for at least 48 hours, or until they reached constant dry weight. We then ground them into fine powder, and weighed approximately 2 mg of dry material into tin capsules. Several individuals were combined in a single sample when necessary to meet the minimum requisite weight. We performed stable isotope analysis on all taxa that had enough samples to be represented consistently across sampling dates and treatments (n = 310 total samples). Stable isotope analysis was performed at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley, to determine isotopic ratios of carbon and nitrogen. Values were reported in permil (‰), such that $\delta = [(R_{sample} / R_{standard}) - 1] / 1000$, where δ ($\delta^{13}C$ or $\delta^{15}N$) is the difference between the sample values in permil (‰) relative to the standard values, and R is the ratio of the heavy (^{13}C or ^{15}N) to light isotope (^{12}C or ^{14}N) in the sample or standard (Table S1, Table S2).

We focused our analyses on three predacious benthic taxa that were present throughout the experiment: Turbellaria flatworms, *Rhyacophila* caddisflies, and Perlidae stoneflies. Turbellaria are non-parasitic, free-living flatworms (Platyhelminthes) that possess a variety of pharyngeal morphologies that allow them to ingest whole prey or extract prey tissues (Noreña et al. 2015). In contrast, *Rhyacophila* (Trichoptera) and Perlidae (Plecoptera) are semi-aquatic insects and active engulfing predators that may also feed on detritus and algae (DeWalt et al. 2010). *Rhyacophila* and Perlidae have very low tolerance to environmental stress, unlike Turbellaria (Herbst et al. 2018). All focal taxa exhibited low levels of relative abundances within communities, each accounting for less than 2% of the entire population across treatments and sampling dates (Table S3). Turbellaria had small-medium body size; while *Rhyacophila* and Perlidae were among the largest individuals in any given sample (Table S3). None of the taxa exhibited seasonal changes in average size.

Finally, we performed gut content analysis on the Perlidae collected throughout the experiment, represented by *Calineuria californica* and *Doroneuria baumanni*. Gut content analysis allows for finer taxonomic resolution of prey items, and can help confirm reliance on primary consumers that have similar isotopic signatures. We took gut contents from at least 4 individuals (as abundance allowed) every 3 weeks of the experiment for the *current* and *six weeks early* treatments, using published methods (Rosi-Marshall et al. 2016). We then used micro-dissecting scissors to remove each gut, which was placed on a microscope slide with a drop of glycerol, and then shaken to remove gut contents from tubing. We examined contents under a stereoscope to ensure all Chironomidae cephalic capsules were facing up (for ventral view). All invertebrates were counted and identified to the highest resolution possible (mostly genus) with the aid of reference slides we made for each potential prey.

Data analysis

For data analysis, we grouped the isotopic values of taxa based on sampling period and flow treatment. Samples collected in June at the start of the experiment (i.e., after increased discharge due to snowmelt but before any treatment differences) were considered a single baseline group reflecting the trophic ecology of taxa at peak runoff. This group is hereafter referred to as the *peak runoff* sample. Samples collected in August at the end of the experiment were grouped according to the flow treatment they experienced: *current*, *three weeks early*, or *six weeks early*. We examined seasonal variation by comparing *peak runoff* values to values after the *current* treatment. We evaluated effects of low-flow timing and duration by comparing *three weeks early* and *six weeks early* values to *current* treatment values, focusing on isotopic niche area, resource competition, trophic pathways, and omnivory (see below). We also assessed the effect of extended low flows on gut contents of the two Perlidae species. Finally, we compared how isotopic niche areas varied across major feeding groups (i.e., algivores, detritivores, generalists, and predators). All statistical analysis was conducted in R (version 4.3.1; R Project for Statistical Computing, Vienna, Austria).

Isotopic niche areas–To assess the effect of treatment on predators' trophic niche, we quantified isotopic niches of predators using the Bayesian estimate of the standard ellipse area (SEA). We calculated niche areas using the *SIBER* package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). *SIBER* calculates the SEA by generating posterior distributions of the covariance matrices for each group, using Markov chains. We used Monte Carlo simulations for 10^4 iterations, informed by likelihoods calculated from the provided data and purposefully vague prior distributions. The SEA is calculated for each iteration, to obtain a Bayesian SEA (SEA_b). From the posterior distribution, we calculated the SEA_b mode and 95% credible intervals (Hespanhol et al. 2019). The SEAb provides a measure of isotopic space (i.e., 40% of the isotopic niche) that is robust at low sample sizes and comparable across communities (i.e., across treatments in this study). When comparing SEA_b distributions, we considered differences to be statistically significant when neither mode was within the 95% credible interval of the other.

Niche overlap–To estimate potential resource competition between predators, we examined overlap in their isotopic niches. Niche overlap indicates that two taxa are feeding on similar resources and may therefore compete (Guzzo et al. 2013, Cucherousset et al. 2020). We estimated *absolute niche overlap* as the isotopic area occupied by both ellipses at the same time, and *proportion of niche overlap* as the percent of the total niche area of a predator that overlapped with the niche of another predator.

Trophic pathways–To examine shifts in predators' reliance on specific trophic pathways, we used mixing models that estimate reliance on different energy sources, using the *simmr* package (version 0.5.1.216; Parnell et al. 2010, Parnell et al. 2013). Predators' reliance on a particular carbon source may be direct, from consuming that basal resource; or indirect, by consuming primary consumers reliant on that basal resource. We used isotopic values of 2 obligate primary consumers to reflect the isotopic signatures of key basal resources, and determine whether predators relied mostly on algal-derived or detritus-derived energy (i.e., ‘green’ or ‘brown’ pathways respectively). Due to our inability to capture isotopic signatures from all basal resource types, we used primary consumers with known functional feeding strategies as endpoints representing the “green” and “brown” trophic pathways. We then verified these assumptions via our own d13C data (see Fig. S4). Because Heptageniidae primarily graze on benthic algae and biofilm, we chose their isotopic values to reflect the isotopic signature of algal-derived or ‘green’ energy (Merritt et al. 2017). In turn, Oligochaeta are primarily detritivores and were used to represent the isotopic signature of ‘brown’ energy (Usseglio-Polatera et al. 2000). Reliance was estimated with contemporary $\delta^{13}C$ values (i.e., from the same treatment and sampling period) of Heptageniidae and Oligochaeta, such that seasonal change in basal resource $\delta^{13}C$ would not bias dietary proportion estimates of predators. Like *SIBER*, *simmr* uses a Bayesian approach to generate a posterior distribution of dietary proportions. The model requires the raw stable isotope values of the predators, the mean and standard deviation of the raw stable isotope values of each carbon source (here, represented by Heptageniidae and Oligochaeta), and a prior distribution postulating that predators consume all sources equally. We ran the model across treatments and sampling dates. From the posterior distributions, we then calculated dietary proportion modes and 95% credible intervals.

Omnivory–To identify changes in the degree of omnivory of predators, we calculated trophic positions using a two member-mixing equation based on the dietary proportions estimated from *simmr*:

$$TP_{predator} = TP_{prey} + [\delta^{15}N_{predator} - (\delta^{15}N_{prey1} \times Proportion_{prey1} + \delta^{15}N_{prey2} \times Proportion_{prey2})] \,/\, \Delta, (Eq. 1),$$

where $TP_{predator}$ is the unknown trophic position of an individual predator, and TP_{prey} is the trophic position of the prey (Heptageniidae or Oligochaeta), $\delta^{15}N_{predator}$ is the average δ^{15}N value of predator individuals and $\delta^{15}N_{prey}$ is the average δ^{15}N value of Heptageniidae or Oligochaeta individuals. $Proportion_{prey}$ is the estimated dietary proportion of Heptageniidae or Oligochaeta in the predators' diet, i.e., the dietary proportions estimated earlier using the mixing model. Δ is a trophic enrichment factor, assumed here to be 3.4‰ (Cabana and Rasmussen 1996, Post 2002), although other enrichment factors were also examined (as in Ruhí et al. 2016). As primary consumers, Heptageniidae and Oligochaeta were assumed to maintain a trophic position of 2. Because we compared δ^{15}N of predators to contemporary δ^{15}N of Heptageniidae and Oligochaeta, a change in δ^{15}N at the base of the food web would not bias estimated trophic positions of predators. We used one-way ANOVA and Tukey's HSD to examine treatment effects on trophic position.

Perlidae gut contents–To ground-truth predators' diet changes, and further examine if aspects of the diet (e.g., richness and abundance of different items) responded to low flows, we performed gut content analyses of Perlidae individuals from two different species: *C. californica* and *D. baumanni*. Using ANOVA, we then tested whether variation in gut contents were explained by Perlidae species, Perlidae size, and a factor (*period-treatment*) that combined treatment and the time period of the experiment (i.e., start, middle, and end). Because there were no significant differences in the number ($F_{1,40}$ = 1.602; $P > 0.05$) or richness of prey ($F_{1,40}$ = 0.821; $P > 0.05$) consumed between Perlidae species, we pooled their data together for subsequent analyses.

***Responses by feeding group*–**Finally, to test the sensitivity of the predator assemblage relative to the rest of the community, we compared changes in their niche areas. To this end, we combined isotope values from all three predators (*Rhyacophila*, Perlidae, Turbellaria) into a 'Predator' group, and we grouped the remaining taxa based on their feeding strategy and predominant energy reliance. We designated 'algivores' as any scraper/grazer taxa feeding primarily on algae (e.g., Baetidae and Heptageniidae). We considered any taxa that feed on both algae and particulate organic matter to be 'generalists' (e.g., Lymnaeidae). We grouped shredder, collector-gatherer, and collector-filterer taxa that feed primarily on particulate organic matter into 'detritivores' (e.g., Oligochaeta and non-predatory Chironomidae). We assigned taxa to feeding strategies based on the literature (Usseglio-Polatera et al. 2000, Poff et al. 2006, Merritt et al. 2017). We then calculated SEA_b modes and 95% credible intervals for each of the four categories using the same Bayesian methods described above.

RESULTS

Seasonal changes in predator trophic niches

Some, but not all predators shifted their diets as low-flow conditions advanced seasonally under the *current* flow regime, e.g. by increasing their niche area (for Perlidae) or their trophic position (for Turbellaria). Specifically, Perlidae expanded their niche area by 153% by the end of the season relative to the peak runoff period (Fig. 3). Resource competition did not seem to change over time, as no predator experienced statistically significant niche overlap with other predators before or after *current* low flow conditions (Table 1). There was also no evidence of seasonal variation in basal resource reliance in any of the predators (Fig. 4A). Turbellaria and Perlidae relied mostly on 'brown' energy throughout the experiment, while Rhyacophila relied equally on 'brown' and 'green' energy pathways. However, Turbellaria trophic position increased over time under the *current* treatment (3.04 ± 0.12), by >0.25 levels above levels observed during peak runoff (2.77 ± 0.14), illustrating that this taxon became more carnivorous and held the highest trophic position among the studied predators (Fig. 4B). Perlidae and Rhyacophila also both experienced slight increases in trophic position, but these differences were not statistically significant.

Seasonal shifts in Perlidae consumption, based on gut contents, depended on flow regime treatment. Period-treatment explained statistically significant variation in the total number of prey consumed ($F_{5,40} = 3.191$; $P = 0.016$), with Perlidae consuming 11-fold more prey items at the end of the *current* treatment relative to at the beginning of the experiment. Body size had a positive relationship with the number of prey consumed ($F_{1,40} = 4.867$, $P = 0.0332$), with larger individuals being associated with higher numbers and diversity of prey following the *current* treatment (Fig. 5). Overall, our results supported our hypothesis that diet would vary seasonally.

Effects of experimental low flows on predators

Extended low flows simulating an end-of-century climate change scenario caused niche compression for select taxa and treatments (Fig. 3). *Rhyacophila* experienced statistically significant niche compression after the *three weeks early* treatment, with a niche area of 0.202‰^{2} (0.093 to 4.38 credible interval), or 71% smaller than after the *current* treatment; but an 85% expansion after the *six weeks early* treatment. Perlidae showed similar niche areas across treatments. In turn, Turbellaria underwent statistically significant niche compression following the *six weeks early* treatment, with a niche area of 0.191‰^{2} (0.096 to 0.483 credible interval).

This value was 78% and 64% smaller than its niche after the *current* treatment and the *three weeks early* treatment, respectively (Fig. 3B).

We did not observe niche overlap between any of the predators after any length of low-flow treatment (Table 1). Extended low flows were also not associated with a change in dietary proportions of basal resources (Fig. 4A), or in trophic positions (Fig. 4B). When examining energy sources, we found that *Rhyacophila* continued to rely on both ‘green’ and ‘brown’ energy: the proportion of ‘green’ energy in their diet only decreased from 53% (0.143 to 0.851 credible interval) following the *current* treatment to 49% (0.226 to 0.735 credible interval) after the *three weeks early* treatment, and to 38% (0.064 to 0.793 credible interval) after the *six weeks early* treatment. Perlidae relied mostly on ‘brown’ energy, with about 18% reliance on ‘green’ across all treatments. However, Turbellaria incorporated three times less ‘green’ energy into their diet after the *six weeks early* treatment (i.e., 5% [0.009 to 0.133 credible interval]) relative to *peak runoff* (i.e., 16% [0.064 to 0.275 credible interval]; Fig. 4A).

Gut content analysis showed that Perlidae had fewer prey items in their guts under extended low flows relative to the *current* treatment ($F_{5,40} = 3.191$; $P = 0.016$, Fig. 5). The average number of prey consumed increased from the middle to the end of the experiment in the *current* and the *six weeks early* treatments (by 1,120% and 757% respectively). However, this increase was only statistically significant in the *current* treatment, potentially reflecting a delayed effect of low flow. Following both low-flow treatments, Perlidae diets were still dominated by more than 75% *Chironomidae*, largely due to *Apedilum*, *Chironomini*, *Corynoneura*, and *Cricotopus-Orthcladius*. This pattern aligns with the stable isotope results showing that Perlidae continued to rely heavily on “brown” energy throughout the experiment, as most of their diet is composed of collector-gatherer Chironomidae.

Overall, all predatory taxa showed some dimension of niche compression or reduced prey consumption in response to extended low flows–even if specific responses varied across taxa and the specific endpoint being measured.

Comparing predator to non-predator responses

The trophic niche area of predators shrank the most among dietary groups after low-flow conditions were extended by *six weeks*, by 62% relative to *current* low-flow conditions (Fig. 6). This pattern was unique in that it had the opposite direction than that observed in algivores and generalists, and the same direction but much larger magnitude (80-fold) than that observed in detritivores. Notably, their niche area expanded (relative to after the *current* treatment) after the *three weeks early* treatment–a pattern that was shared with all other groups. Overall, these results support our hypothesis that predators' diets would disproportionately contract under extended low flows compared to other functional groups, although this response was only apparent past a certain stress threshold (i.e., a 6-week but not a 3-week advance in low flows).

DISCUSSION

Climate change is altering snow hydrology globally, with potential far-reaching consequences for mountain stream species, biotic interactions, and whole food-web structure (Stewart 2009, Herbst et al. 2019, Leathers et al. 2024). However, our mechanistic understanding of these effects is incomplete, and multi-trophic experiments under realistic field conditions remain rare (Perkins et al. 2010, Cameron et al. 2019). Here, we ran an experiment in outdoor, artificial channels to study trophic responses to climate change-induced extended low flows, and found that longer low-flow conditions altered the diets of predaceous macroinvertebrates.

Extended low flows reduced diet diversity for *Rhyacophila* and Turbellaria following the *three weeks* and *six weeks early* treatments, respectively. These changes were not accompanied by a change in their trophic positions or in the reliance on ‘green’ *vs.* ‘brown’ energy pathways. Although results varied among taxa, predators were generally more sensitive to low flows than the rest of the community, and the only dietary group to have their niche area compressed by the extreme low-flow treatment in a statistically significant way. Gut content analysis on one of the groups (Perlidae stoneflies) offered additional evidence of low-flow induced diet shifts (i.e., fewer prey items under extended low-flow conditions). Similar, and sometimes overlapping isotopic signatures of the primary consumers can make it difficult to differentiate between taxa present in the diets of predatory taxa. However gut content analysis supported that Perlidae continued to consume Chironomidae rather than switching to consuming other taxa, such as Oligochaeta, a pattern that would not have been revealed by isotopic analysis alone. Reduced overall predators’ niche area during extended low flows supports the *trophic niche compression* hypothesis, suggesting that under environmental stress, energy may flow through a reduced number of links (Burdon et al. 2020; Mor et al. 2022). However, the observed diversity of responses to the same stressor across species (*response diversity*, sensu Chapin et al. 1997) suggests that alpine food webs could remain relatively stable under novel low-flow conditions if community diversity across the different trophic levels is maintained.

Novel low flows tend to compress predator niches

Extended low flows produced taxon-specific responses in niche area, such that each predator either experienced a constant or smaller niche, the latter supporting the *trophic niche compression* hypothesis (as in Layman 2007, Mor et al. 2022) (Fig. 1B). A decreased niche area reflects reduced prey diversity stemming from reduced diet breadth or increased specialization, and has been typically associated with environmental stress–either via direct effects on prey, or by limiting the ability of consumers to prey on diverse taxa (Layman et al. 2007).

Along these lines, Mor et al. (2022) found that predator extirpation following a disturbance was due to a combination of the sensitivity of the predator, food limitation, and weakened trophic efficiency. We expected food resources to increase with extended low flows due to increased algal and grazer production during low-flow conditions (Palmer and Ruhi 2019, Cauvy-Franié et al. 2016, Lowman et al. 2024). Prey density and access may also increase due to reduced habitat availability and complexity (Rolls et al. 2012). While we did not measure primary production over the experiment, Leathers et al. (2024) found that 6-week extended low flows did not alter cumulative (community-wide) secondary production or biomass, but increased warming-tolerant Chironomini density by over 150%. Given this result, and that predators' diets were mostly derived from "brown" energy, we are confident that prey availability to individual predators increased with the low flow treatments. If the total pool of available resources likely increased, as did predators' access to the prey, we contend that reduced niche areas likely stemmed from physiological stress reducing predator fitness in non-trophic ways (e.g., Mor et al. 2022). This inference is further supported by the reduced number and diversity of prey items in Perlidae gut content following the 6 weeks early treatment, despite larger Perlidae individuals and consistent community production (see Leathers et al. 2024). Along these lines, when examining predators' trophic niches under climate change warming, Bestion et al. (2019) found that diet shifts and niche compression of predators (lizards) subjected to warming arose from the direct effects of climate on the lizards rather than from indirect changes in the prey community. In our case, larger body sizes of Perlidae suggest that water warming did not push these sensitive predators beyond their thermal maxima, despite impacts on their diets that likely stemmed from increased physiological stress and reduced hunting ability.

Extended low flows reduced prey diversity in some taxa. For *Rhyacophila* and Turbellaria, which experienced niche compression, less variation in their diet suggests that individuals relied on more similar prey items. This may lead to increased conspecific competition, but likely not interspecific competition, since our results suggest limited diet overlap among taxa regardless of flow conditions. This was true even though both Turbellaria and Perlidae strongly relied on 'brown' energy (i.e., detrital-derived, rather than algal-derived). The nonexistent overlap despite similar diets may be indicative of them consuming different detritivorous primary consumers. Low flows may present short-term benefits to predators in terms of higher prey density, but at longer timescales stress may differentially impact the larger individuals. As a carnivorous predator with the highest trophic position, Turbellaria may have already been feeding at the highest trophic level the food web could support (Fig. 4B). In contrast, *Rhyacophila* and Perlidae have more omnivorous diets, and therefore greater flexibility to consume higher proportions of invertebrates to meet the higher metabolic demands brought by extended low flows (*omnivory mechanisms*; Post and Takimoto 2007, Ruhí et al. 2016).

Predators continued to rely on the same energy pathway regardless of low-flow duration (Fig. 4A). Perlidae and Turbellaria showed strong reliance on 'brown' energy, likely consuming collectors and shredders (with some detritus) based on their high trophic positions. Because detrital subsidies are typically a key source of energy in headwater streams (Moore et al. 2004, Di Cugno and Robinson 2017), we expected top predators to be at least partly reliant on detrital-derived energy. However, allochthony can be highly variable across consumer groups and over time (Allen et al. 2024), making it unclear how much our predators' diets would be supported by energy derived from riparian vegetation from upstream reaches. For example, *Rhyacophila* exhibited a lower trophic position and consumed a greater proportion of ‘green’ energy relative to Perlidae or Turbellaria, likely because most *Rhyacophila* species transition from phytophagy in early instars to carnivory later (Céréghino 2002).

Seasonality altered the trophic ecology of the studied invertebrate predators. Under the *current* flow regime, Perlidae tended to consume slightly more diverse prey, and Turbelleria exhibited higher trophic positions at the end relative to the start of the experiment. Regarding the expanded niche area of Perlidae, it is worth noting that the ‘green’ energy base of the food web seasonally shifted to higher δ^{13}C and lower δ^{15}N values (Table S2). As such, the isotopic signature of ‘green’ energy shifted closer to that of ‘brown’ energy, which could reduce the isotopic niche area for Perlidae. However, the niche area of Perlidae expanded–suggesting their seasonal diet shift is real and not merely a result of tracking shifts in basal resources. Omnivorous macroinvertebrates elsewhere have shown seasonally variable trophic positions, switching from omnivorous to carnivorous, likely due to seasonal fluctuations in prey availability (Hellmann et al. 2013). The taxa in our study that experienced a seasonal change in a certain metric (i.e., Perlidae, with an increased niche area; and Turbellaria, with a higher trophic position) did not respond to extended low flows based on those metrics. This observation suggests that predators adapted to low flows via dietary plasticity may be more resilient to novel low-flow conditions. This pattern may be similar to organisms that present high acclimation capacity (e.g. to thermal conditions posed by climate change) due to living in highly-fluctuating environments that have shaped physiological and behavioral plasticity (Riddell et al. 2018).

Consequences of predator sensitivity to extended low flows

Our results support the notion that predators are disproportionately sensitive to drought-induced stress–a pattern that was expected based on past studies. For instance, Voight et al. (2003) found that taxa in higher trophic positions experienced greater population declines in response to climate change. Similarly, Petchey et al. (1999) found that climate-induced extinction risk increases with species trophic position. This differential sensitivity may be realized both directly, via a decrease in the fitness of predators; and indirectly, via prey responses that lead to food limitation to the higher trophic levels (Mor et al. 2022).

Trophic niche compression has been often associated with reduced resilience of a food web against disturbance (Rooney et al. 2006). In an experiment similar to ours, drought altered trophic interactions of predators and decreased their abundance such that top-down control was reduced, with effects that cascaded down the food chain (Amundrud and Srivastava 2016). However, in our experiment the relative abundance of the focal predatory taxa did not change over time, nor did the abundance or density of any predatory or omnivorous taxa (Leathers et al. 2024). Changes in top-down control, if they were to occur, could have profound implications for ecosystem functioning, and ecosystem-level consequences of disrupted predator-prey interactions have often been reported (Chassot et al. 2005, Koltz et al. 2018). Thus, we contend that altered trophic ecology of predators may not only alter community structure, but could also dictate how consumer-mediated ecosystem processes are likely to respond to new hydroclimatic regimes (Woodward et al. 2010).

Our results also illustrate that species diversity in a given trophic guild can be a stabilizing force (akin to the ‘portfolio effect’; Schindler et al. 2015) due to the ability of different species to respond in different ways to the same stressor (i.e., response diversity, Chapin et al. 1997). In our case, the three predator taxa all responded differently to the same stressor (extended low flows), and these unique responses did not lead to their diets converging—illustrated by the lack of overlap among their niches. Our results are consistent with theory showing the importance of taxonomic and functional diversity for stabilizing ecological communities (Petchey et al. 1999). However, trophic niche compression was experienced by predators more severely than by other functional groups, showing that portfolio effects may weaken when risk is concentrated on taxa of a particular trophic level.

Caveats and future directions

The experimental design of our study took advantage of a unique mesocosm system that allows us to examine responses of realistic, complex communities to flow regime alteration. However, our approach is not without limitations. First, our relatively low sample size resulted in large credible intervals, which limits inferences on trends. This limitation arises from the fact that, despite searching channels for individuals for stable isotope analysis, our focal predatory taxa combined account for less than 5% of the total population in any treatment and sampling period. We note, however, that our actual sample size (in terms of individuals that entered analysis) is larger than the reported number of independent samples, as each sample contained ~1-5 individuals depending on size and taxa. Second, our study did not examine interannual, cumulative effects of low flows, as the experiment occurred during a single spring and summer, unlike other studies that examining predator responses to stressors over multiple years, such as Ledger et al. (2011). Unmeasured, intergenerational effects may occur if the fecundity of univoltine taxa is reduced by advanced low flows and rising temperatures (Bonacina et al. 2023). Third, we evaluated the effects of climate change-induced extended low flows, but alpine streams will be vulnerable to additional abiotic stress and disturbance. During the wet season in alpine regions, flows will likely become flashier, with more frequent rain-on-snow events and more severe floods (Safeeq et al. 2016). Climate change may also further reduce baseflow in addition to lengthening low-flow duration (our focus in this study), increasing the likelihood of novel stream intermittency (Reynolds et al. 2015, Paillex et al. 2020). Further, projected air warming in the Sierra could raise stream water temperatures, in addition to the temperature increase associated with reduced thermal buffering during low flows (Null et al. 2013, Leathers et al. 2023). Future studies could examine how these other abiotic changes affect food web dynamics independently and in combination with extended low flows. Fourth, stable isotopes are a useful tool to examine time-integrated energy flow in the food web, but they do not directly reveal prey identities, and inferences can be uncertain–particularly when source signals overlap. Here we examined Perlidae gut contents to ground-truth predator-prey links, but more work on the other predatory taxa would better reveal the mechanisms driving diet shifts. Fifth, fish were excluded from this study to represent naturally fishless high-elevation streams of the Sierra Nevada. However, the region has been stocked with non-native fish, such as the brown trout (*Salmo trutta*), which is known to exert top-down control on macroinvertebrate communities (Herbst et al. 2009). The impacts of non-native predators on Sierra stream food webs will likely intensify as invasive fishes continue to spread into previously fishless streams, and are exposed to increasingly stressful conditions arising from climate change and extended low flow conditions (Rahel et al. 1996, Hari et al. 2006). More studies focusing on whole-community responses will enable testing the generalizability of the reported patterns to mountain ranges in other geographies and ecological contexts.

Conclusions

Climate change disproportionately threatens freshwater biodiversity (Bowler et al. 2017), particularly predators (Petchey et al. 1999). Even when predators that persist under extended low-flow conditions may experience sublethal changes in their foraging behavior and nutritional needs. Our experiment revealed significant changes to the trophic niches of three stream macroinvertebrate predatory taxa following extended low flows, including niche compression and higher trophic positions, and a shrinking of the niche space occupied by the predator assemblage as a whole. However, responses varied by taxa, illustrating that food-web stability requires community diversity–particularly, if predators target compartmentalized prey, and respond differently to common stressors (McCann 2000, Cardinale et al. 2006). Given expected changes in mountain range hydroclimates globally (Stewart 2009) and the elevated vulnerability of high-elevation freshwater habitats to novel climates (Hotaling et al. 2017), further research is needed to understand how climate change will impact the higher levels of biological organization.

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FIGURE CAPTIONS

Fig. 1. Hypothesized shift types in the trophic niches of predaceous macroinvertebrates following extended low flow periods. The left panel depicts hypothesized trophic (isotopic) niches under the current flow regime of the three predator taxa: Perlidae stoneflies (yellow), *Rhyacophila* caddisflies (purple), and Turbellaria flatworms (teal) (A). The right panel depicts different hypothesized shift types in predator isotopic niche and trophic position, indicated by ellipse outlines (B). Under the null hypothesis, predators would not change their trophic niche or position after being exposed to extended low-flow conditions. Under the *trophic niche expansion hypothesis*, predators would exhibit larger niches, higher trophic positions, and greater niche overlap relative to current conditions. Alternatively, under the *trophic niche compression hypothesis*, predators exhibit smaller niches, lower trophic positions, and less overlap relative to current conditions, likely relying on prey that in turn feed on a narrow range of basal resources (illustrated by the narrow range of $\delta^{13}C$ values). [Organism silhouettes credit: PhyloPic.org].

Fig. 2. Experimental setup of flow treatments and channels in the Sierra Nevada Aquatic Research Laboratory (SNARL) experimental stream array. Hydrographs of each treatment flow regime are shown with solid lines to indicate average discharge and a shaded error region (± standard deviation) (A-C). The two sampling dates, during peak flow or low flow, are noted with arrows. Peak runoff (PR) sampling occurred between May 12th 2019 and June 6th 2019. Sampling following low-flow conditions occurred between the 21st and 25th of August. We reduced discharge to achieve low-flow

conditions on August 3rd for the *current* treatment, on July 13th for the *three weeks early* treatment, and on June 22nd for the *six weeks early* treatment. These dates are noted with vertical dashed lines. The experimental stream complex features 9 artificial stream channels (D). Treatments were applied in a block design, with each block containing a channel under the *current* (C), *three weeks early* (+3), and *six weeks early* (+6) treatment. Photo credit: Carol Blanchette.

Fig. 3. Isotopic niche ellipses and areas of the studied predaceous invertebrates, under *current* and experimental low-flow conditions. The isotopic niches of *Rhyacophila*, Perlidae, and Turbellaria across treatments are visualized as sample size-corrected standard ellipses in the $\delta^{13}C$-$\delta^{15}N$ isotopic space (A). Signatures of individuals are represented as semi-transparent icons. Niche areas were calculated as SEA_b values of *Rhyacophila*, Perlidae, and Turbellaria within each treatment (B). SEA_b modes (icons) and 95% credible intervals (vertical lines) were calculated from each posterior distribution (violin plots). Lowercase letters indicate statistically significant differences between treatments for each predator based on credible intervals, within a given taxon. In all plots, PR denotes *peak runoff* (start of the experiment), C denotes end of the experiment for the *current* low-flow treatment (i.e., ‘control’ treatment), +3 denotes end of the experiment under the *three weeks early* low-flow treatment, and +6 denotes end of the experiment under the *six weeks early* low-flow treatment.

Fig. 4. Variation in reliance on ‘green’ *vs.* ‘brown’ energy, and in trophic positions, of the studied predators across treatments. Colors denote *peak runoff* (PR; start of the

experiment) and end of the experiment for the *current* low-flow treatment (C), the *three weeks early* low-flow treatment (+3), and the *six weeks early* low-flow treatment (+6). Reliance is represented as autochthony, or reliance on 'green' energy, estimated in the diets of predators via Bayesian mixing models. Dietary proportion modes are shown as icons and 95% credible intervals as vertical lines; both were calculated from posterior distributions, depicted here as violin plots (A). Lowercase letters indicate statistically significant differences between treatments within each predator. Trophic positions of individuals (semi-transparent symbols) were calculated in comparison to basal consumers, Heptageniidae and Oligochaeta (B). Individual trophic positions were averaged (solid symbols) and standard errors were calculated (vertical lines). A trophic position of 2 would indicate a primary consumer feeding mostly on basal resources, while trophic positions of 3 or above indicate carnivorous diets, and non-integer positions reflect omnivory. Lowercase letters indicate statistically significant differences between treatments within each predator, based on ANOVA and Tukey's HSD tests.

Fig. 5. Variation in Perlidae diet (*Calineuria californica* and *Doroneuria baumanni*) throughout the experiment and across treatments, studied via gut content analysis. The heatmap represents average gut contents for Perlidae individuals every three weeks. The total number of prey consumed increased seasonally for the *current* but not the *six weeks early* treatment (see *Results* for details). Lowercase letters indicate statistically significant differences in post-hoc comparisons of gut content prey abundance. Chironomidae (primarily *Apedilum*, the *Cricotopus-Orthocladius* group, and the *Micropsectra-Tanytarsus* group) were the most common prey.

Fig. 6. Isotopic niche areas of major feeding groups by treatment. Colors denote treatment: *peak runoff* (PR, when the experiment started) and at the end of the experiment for the *current* low-flow treatment (C), the *three weeks early* low-flow treatment (+3), and the *six weeks early* low-flow treatment (+6). This community-level analysis grouped taxa by feeding strategy and energy source reliance. SEA_b modes (icons) and 95% credible intervals (vertical lines) were calculated from each posterior distribution (violin plots). Lowercase letters indicate statistically significant differences between treatments for each dietary group based on non-overlapping credible intervals (letters are not comparable across groups).

Table 1. Absolute niche area overlap (‰^{2}) and proportion of niche area overlap (%) between predators. Overlap was calculated based on SEA$_b$ posterior distributions, and is presented as the total area shared between the two niches (top value), or the percentage of the niche (in the row) that overlaps with another niche (in the column) (with 95% credible intervals, bottom row). The percentage of overlap represents is 0 when there is no overlap (as the ellipses share no space), and 1 when the two ellipses are identical in size and position (and therefore overlap fully). None of the overlap values were statistically significant based on their credible intervals, despite a high overlap percentage between Turbelleria and Rhyacophlia under the current treatment. All overlapped areas were below 1‰^{2} with most under 0.01‰^{2}, and all credible intervals included 0% or 0.00‰^{2}, indicating no significant overlap among predator niches at any point in the experiment.

Treatment	Overlapping taxa	*Rhyacophila*	Perlidae	Turbellaria
Peak runoff	*Rhyacophila*	---	0.009‰^{2} <1% (0% - 23%)	<0.001‰^{2} <1% (0% - <1%)
	Perlidae	0.009‰^{2} 3% (0% - 65%)	---	0.000‰^{2} 0% (0% - <1%)
	Turbellaria	<0.001‰^{2} <1% (0% - <1%)	0.000‰^{2} 0% (0% - <1%)	---
Current	*Rhyacophila*	---	0.000‰^{2} 0% (0% - <1%)	0.159‰^{2} 20% (0% - 76%)
	Perlidae	0.000‰^{2} 0% (0% - <1%)	---	0.000‰^{2} 0% (0% - <1%)
	Turbellaria	0.159‰^{2} 11% (0% - 57%)	0.000‰^{2} 0% (0% - <1%)	---
Three weeks early	*Rhyacophila*	---	0.000‰^{2} 0% (0% - <1%)	0.000‰^{2} 0% (0% - <1%)
	Perlidae	0.000‰^{2} 0% (0% - 31%)	---	<0.001‰^{2} <1% (0% - 17%)
	Turbellaria	0.000‰^{2} 0% (0% - <1%)	<0.001‰^{2} <1% (0% - 17%)	---
Six weeks early	*Rhyacophila*	---	<0.001‰^{2} <1% (0% - 17%)	0.000‰^{2} 0% (0% - <1%)
	Perlidae	<0.001‰^{2} <1% (0% - 29%)	---	<0.001‰^{2} <1% (0% - 17%)
	Turbellaria	0.000‰^{2} 0% (0% - <1%)	<0.001‰^{2} <1% (0% - 17%)	---

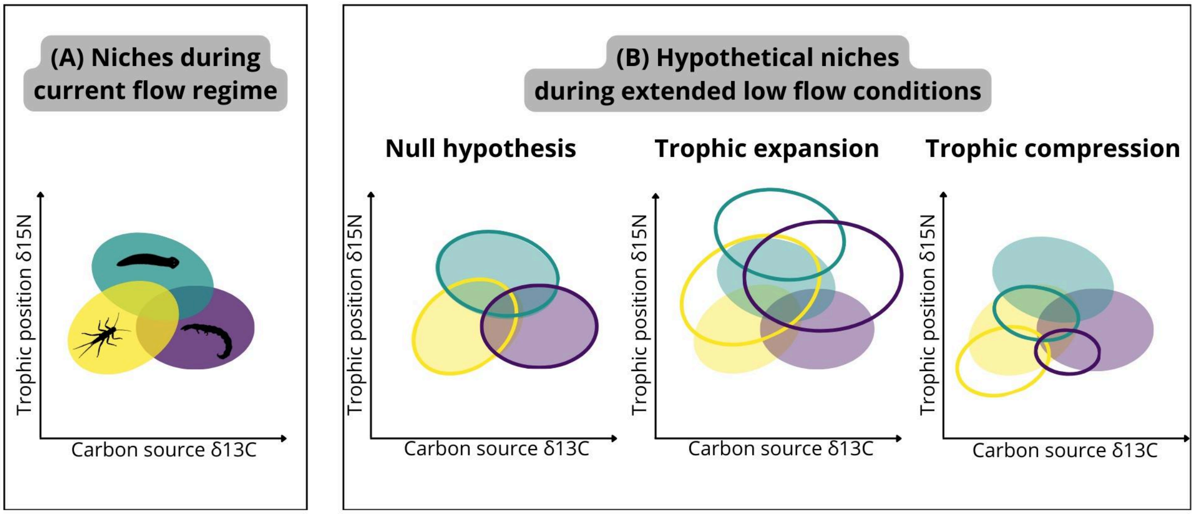

(A) Niches during current flow regime
Trophic position δ15N
Carbon source δ13C
(B) Hypothetical niches during extended low flow conditions
Null hypothesis
Trophic expansion
Trophic compression
Trophic position δ15N
Carbon source δ13C
Trophic position δ15N
Carbon source δ13C
Trophic position δ15N
Carbon source δ13C

Figure 1.

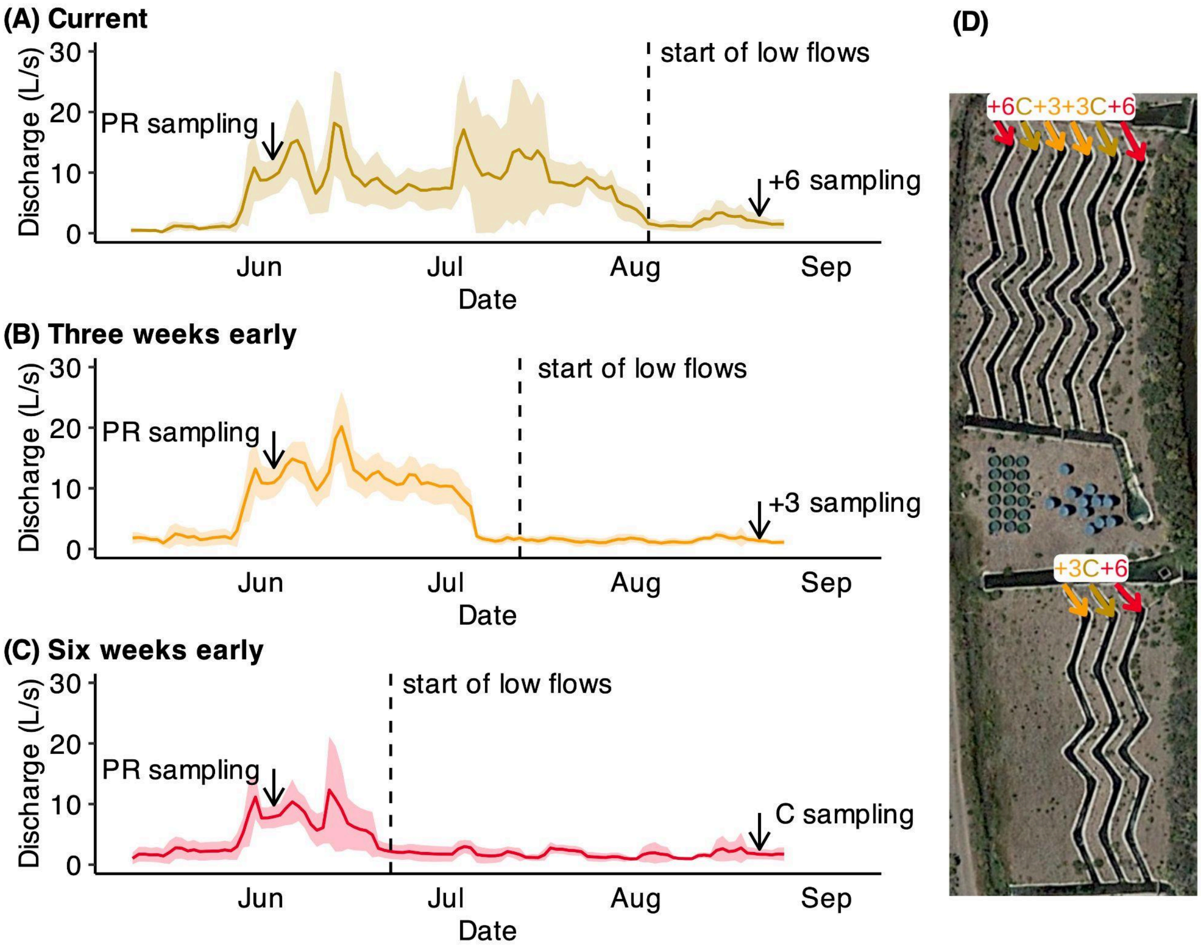

(A) Current
Discharge (L/s)
30
20
10
0
PR sampling
start of low flows
+6 sampling
Jun
Jul
Aug
Sep
Date
(B) Three weeks early
Discharge (L/s)
30
20
10
0
PR sampling
start of low flows
+3 sampling
Jun
Jul
Aug
Sep
Date
(C) Six weeks early
Discharge (L/s)
30
20
10
0
PR sampling
start of low flows
C sampling
Jun
Jul
Aug
Sep
Date
(D)
+6C+3+3C+6
+3C+6

Figure 2.

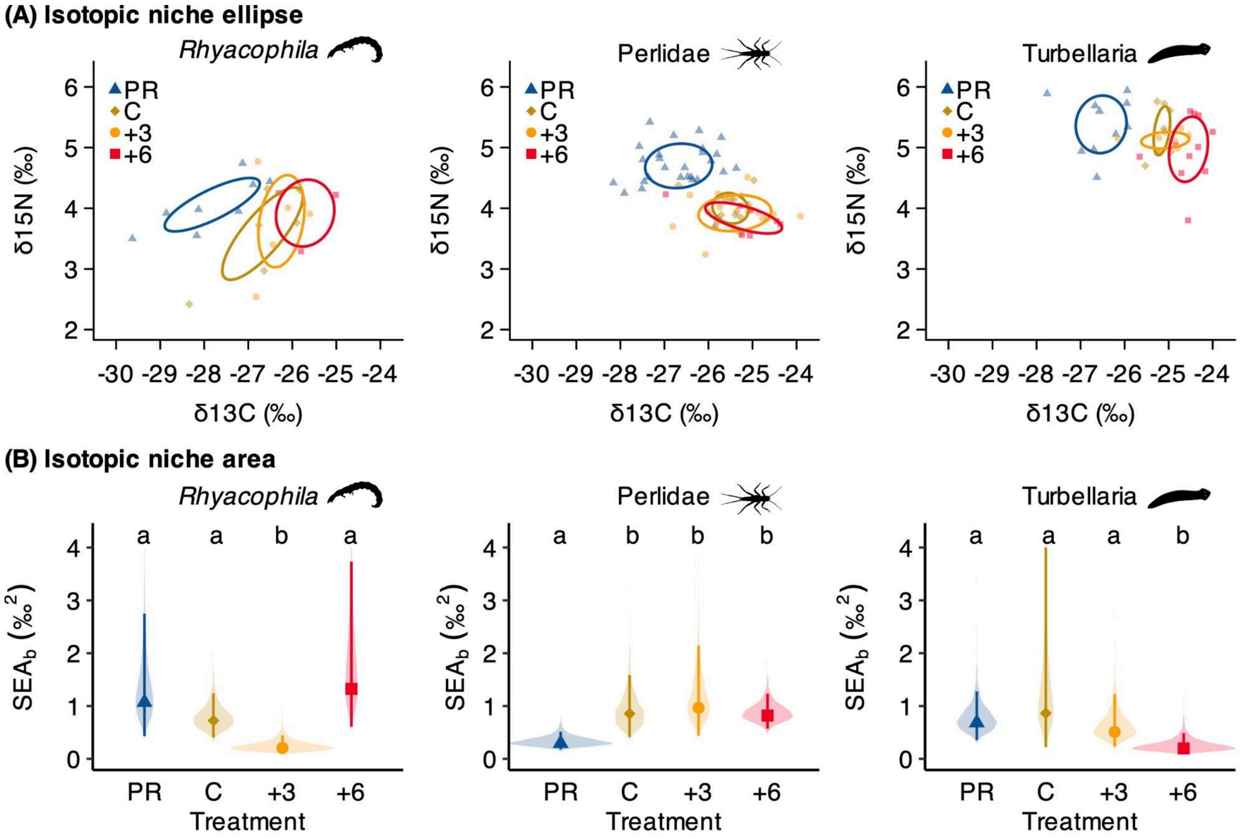
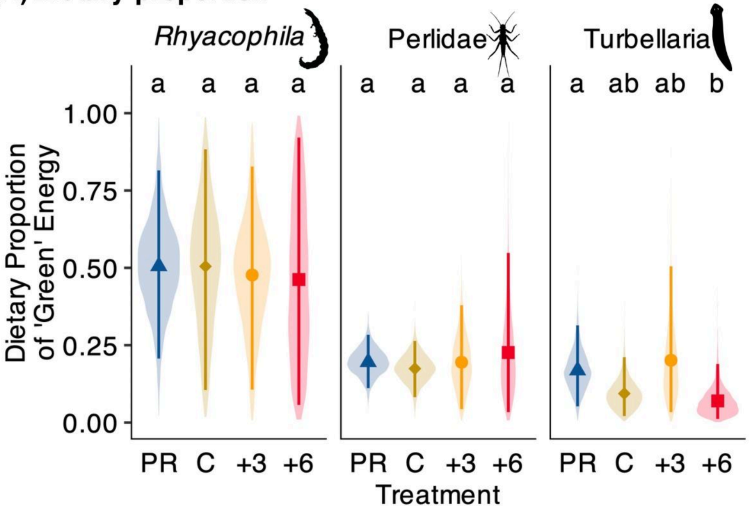

(A) Isotopic niche ellipse
Rhyacophila
Perlidae
Turbellaria
PR
C
+3
+6
δ15N (‰)
δ13C (‰)
-30 -29 -28 -27 -26 -25 -24
2 3 4 5 6
(B) Isotopic niche area
Rhyacophila
a a b a
Perlidae
a b b b
Turbellaria
a a a b
SEA_b (‰²)
0 1 2 3 4
PR C +3 +6
Treatment

Figure 3.

(A) Dietary proportion



(B) Trophic position

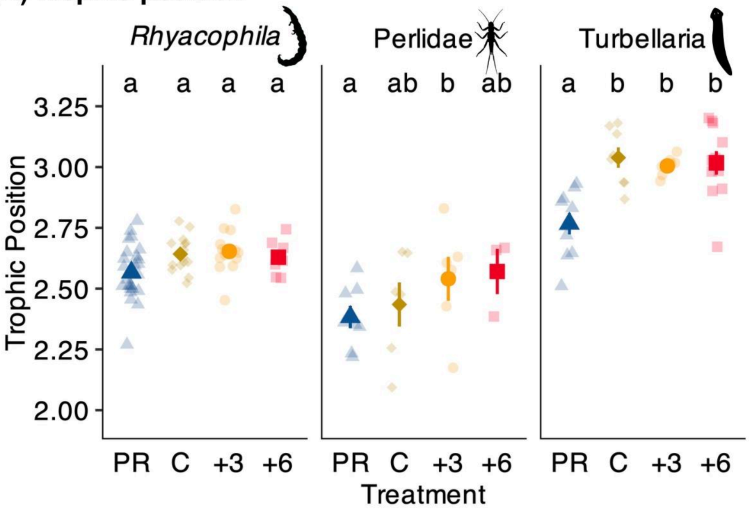
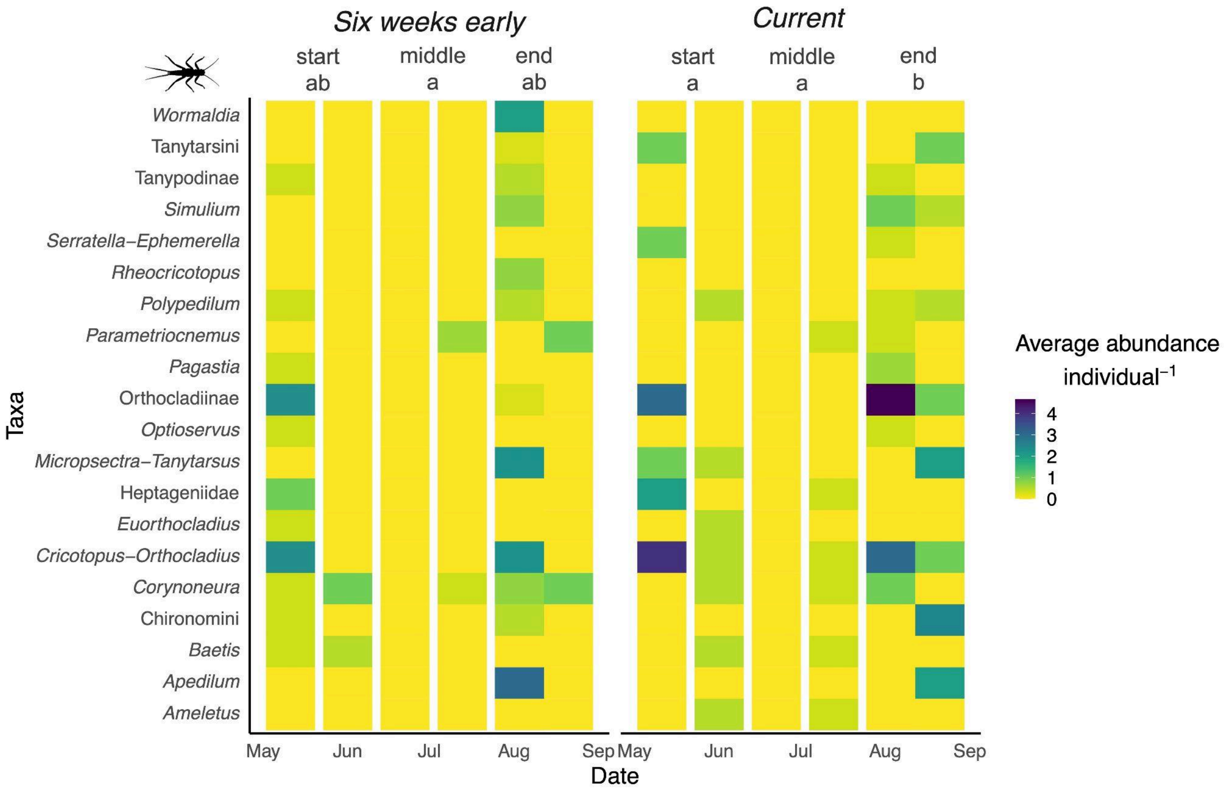


Figure 4.



Six weeks early
start
ab
middle
a
end
ab
Current
start
a
middle
a
end
b
Taxa
Wormaldia
Tanytarsini
Tanypodinae
Simulium
Serratella–Ephemerella
Rheocricotopus
Polypedilum
Parametriocnemus
Pagastia
Orthocladiinae
Optioservus
Micropsectra–Tanytarsus
Heptageniidae
Euorthocladius
Cricotopus–Orthocladius
Corynoneura
Chironomini
Baetis
Apedilum
Ameletus
May
Jun
Jul
Aug
Sep
May
Jun
Jul
Aug
Sep
Date
Average abundance individual⁻¹
4
3
2
1
0

Figure 5.

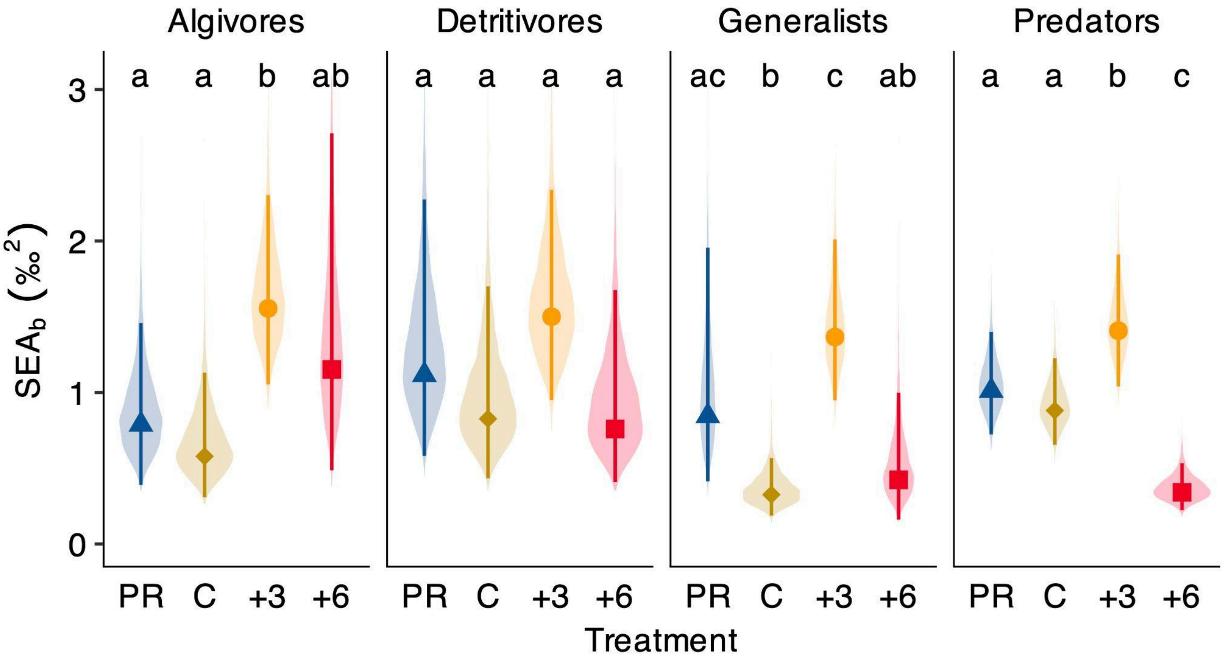

Algivores
Detritivores
Generalists
Predators
a a b ab
a a a a
ac b c ab
a a b c
$\mathrm{SEA_b}$ (‰^{2})
0
1
2
3
PR C +3 +6
PR C +3 +6
PR C +3 +6
PR C +3 +6
Treatment

Figure 6.

Supplementary Material

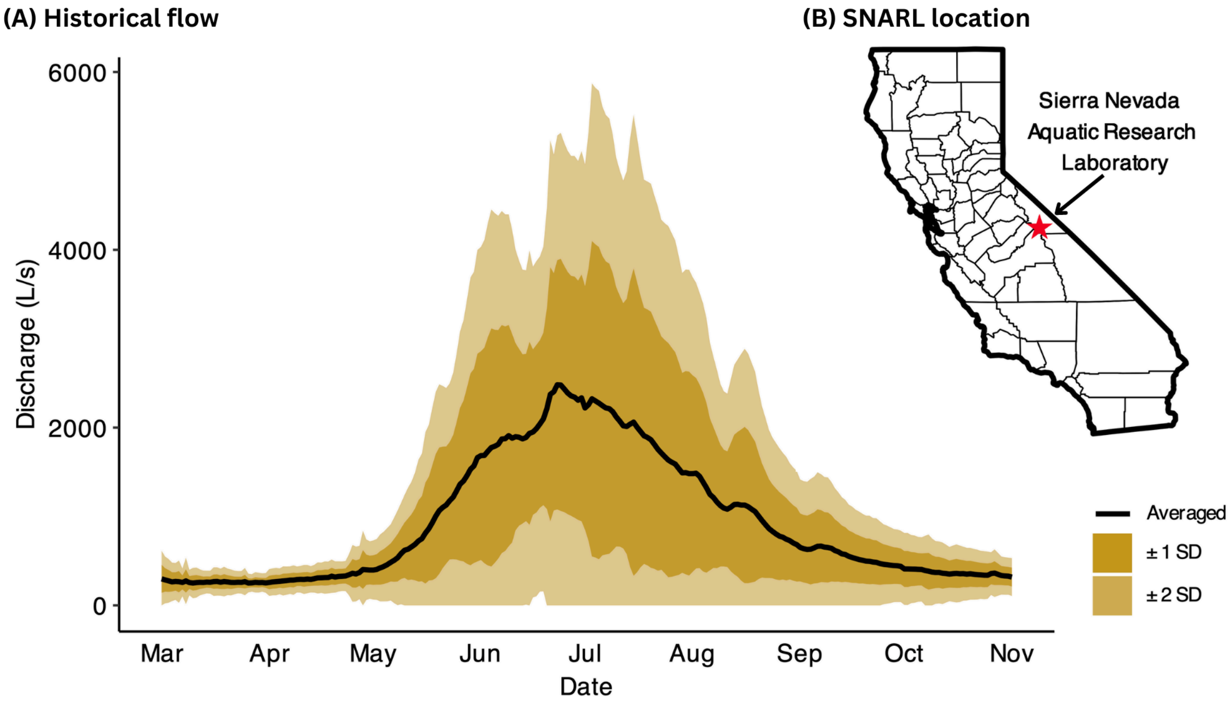


Figure S1. Convict Creek historical flow regime informing the *current* treatment. (a) We downloaded daily discharge in Convict Creek from March to November each year from 1960 to 1974, as measured by the US Geological Survey streamgage 10265200. We then averaged the 15 years of streamflow data to create a daily mean value (black line), with ± one (darker region) and ± two (lighter region) standard deviations. We used this averaged flow regime as the basis for the *current* treatment flow regime, and advanced the start of low-flow conditions by *three weeks* or *six weeks* in our early low-flow treatments. **(b)** Location of the Sierra Nevada Aquatic Research Laboratory (SNARL) in the Eastern Sierra Nevada (Mammoth Lakes, California, U.S.A).

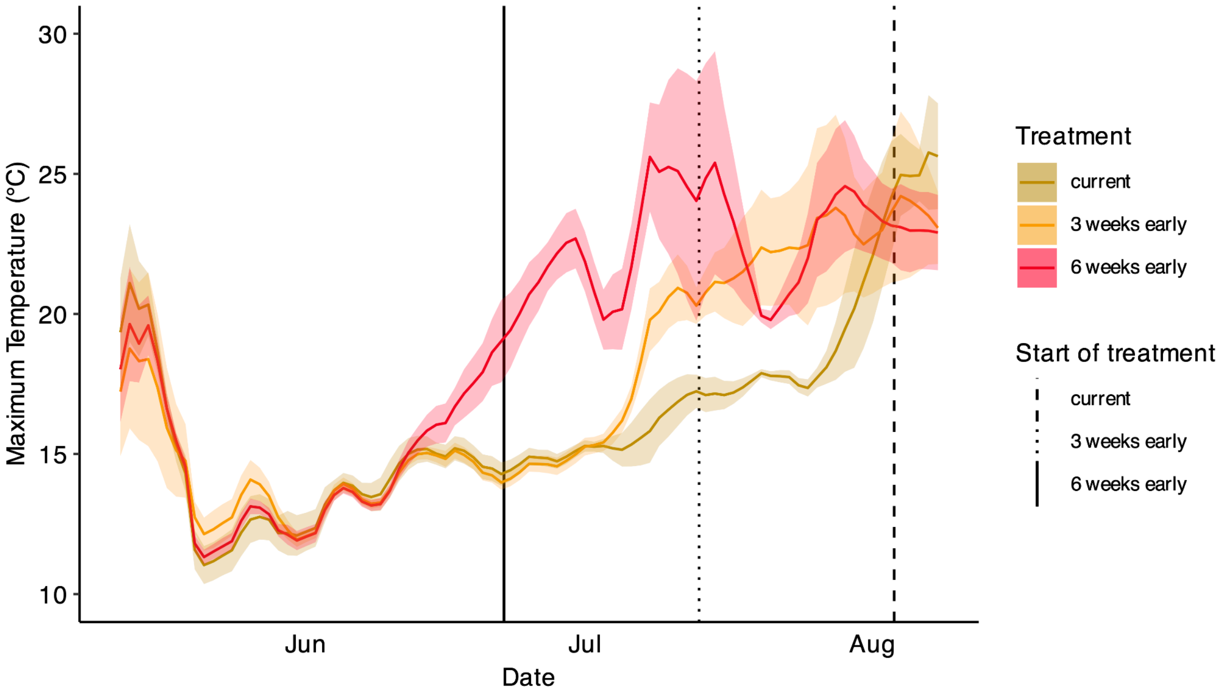


Figure S2. Temperature throughout the experiment, by treatment. We monitored water temperature every 5 minutes throughout the experiment using HOBO U20L-04 loggers. We averaged the maximum observed temperature across channels experiencing the same treatment, and smoothed the resulting time series using a 5-day moving average.

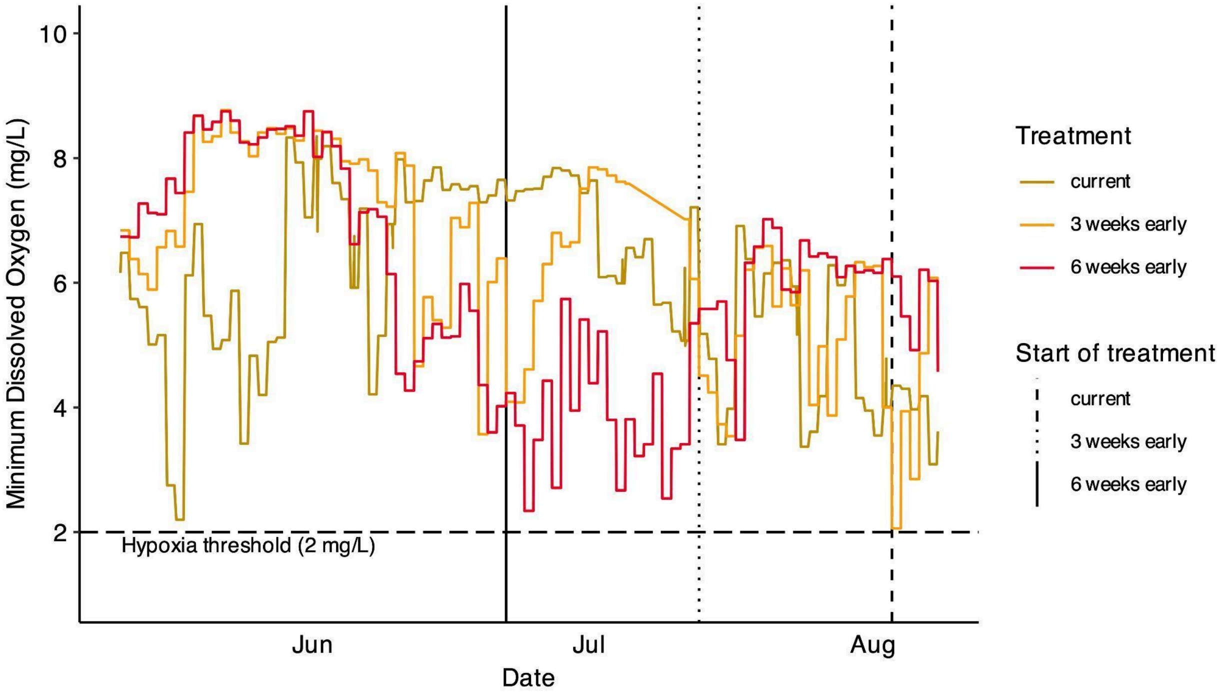


Figure S3. Dissolved oxygen values throughout the experiment, by treatment. We monitored dissolved oxygen every 5 minutes throughout the experiment using HOBO U20L-04 loggers. We averaged values across channels experiencing the same treatment, and smoothed the resulting time series using a 5-day moving average. A hypoxia threshold of 2 mg/L is noted with a horizontal dashed line.

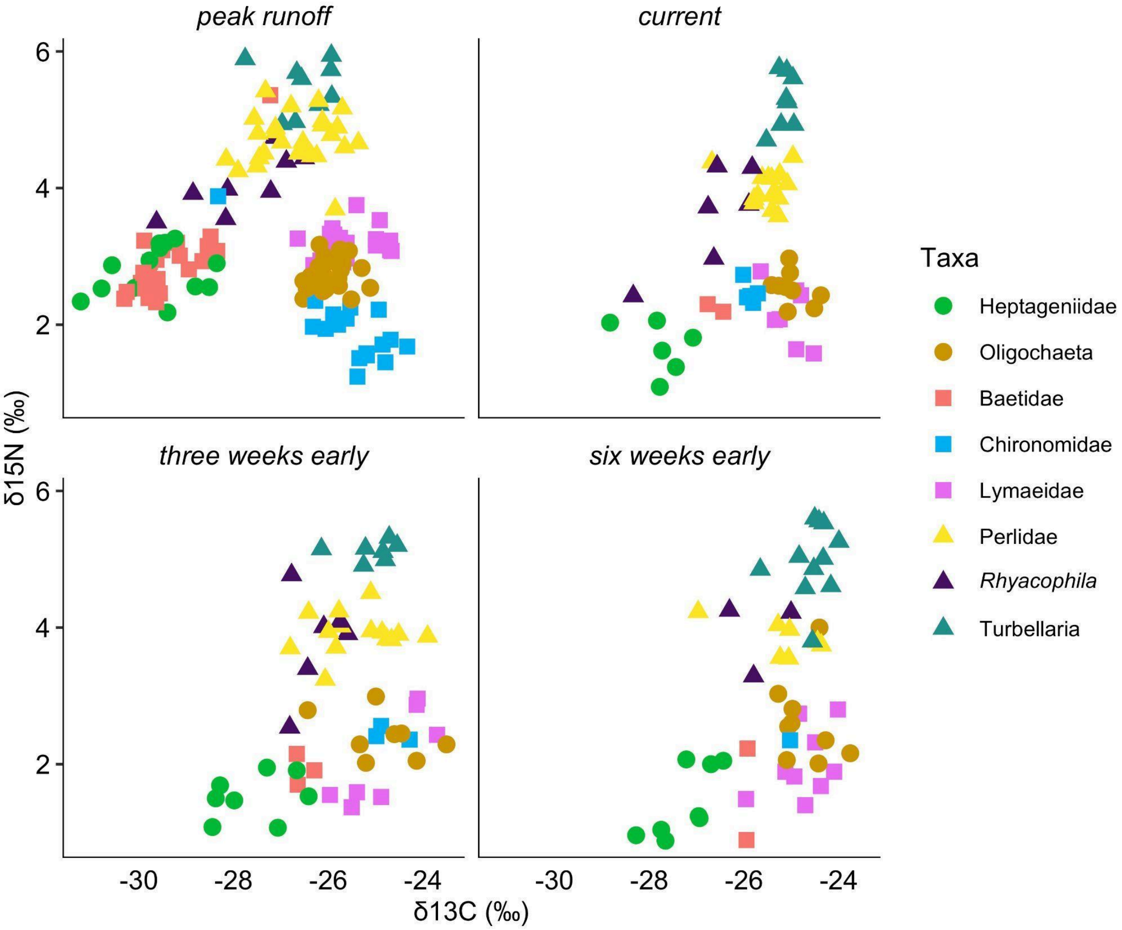


Figure S4. Isotopic biplot of the community (taxa by taxa) across treatments. Each point represents the isotopic signature of a sample, which consists of a carbon (δ13C) and nitrogen (δ15N) value. The isotopic signatures of our three focal predators, Perlidae, Rhyacophila, and Turbellaria, are shown as triangles. The isotopic signatures of obligate primary consumers, Oligochaeta and Heptageniidae, are shown as circles. We use Oligochaeta and Heptageniidae to represent "brown" and "green" energy pathways, respectively, as expected from the literature and confirmed by our stable isotope data. Heptageniidae displayed the lowest d13C values of any species, while Oligochaeta displayed some of the highest values, creating a split between the "greener" and "browner" energy pathways. The rest of the community (generalist primary consumers) are shown as squares.

Table S1. Sample sizes and mean isotopic values.

Dietary Group	**Taxon**	**Treatment**	**Sample Size**	**Average $\delta^{13}C$ (‰)**	**Average $\delta^{15}N$ (‰)**
Predators	*Rhyacophila*	Peak runoff	8	-27.82	4.06
		Current	6	-26.67	3.58
		3 weeks early	6	-26.25	3.79
		6 weeks early	3	-25.71	3.92
	Perlidae	Peak runoff	27	-26.68	4.70
		Current	15	-25.50	4.00
		3 weeks early	14	-25.40	3.92
		6 weeks early	7	-25.20	3.84
	Turbellaria	Peak runoff	10	-26.53	5.39
		Current	8	-25.15	5.28
		3 weeks early	7	-25.08	5.12
		6 weeks early	11	-24.55	4.97
Algivores	Baetidae	Peak runoff	24	-29.35	2.91
		Current	2	-26.60	2.24
		3 weeks early	3	-26.54	1.92
		6 weeks early	2	-25.94	1.56
	Heptageniidae	Peak runoff	13	-29.64	2.78

		Current	6	-27.79	1.66
		3 weeks early	8	-27.57	1.53
		6 weeks early	8	-27.24	1.43
Detritivores	Oligochaeta	Peak runoff	23	-25.96	2.73
		Current	9	-24.98	2.53
		3 weeks early	8	-24.84	2.42
		6 weeks early	9	-24.70	2.62
	Chironomidae (non-predatory)	Peak runoff	18	-25.58	1.97
		Current	5	-25.87	2.47
		3 weeks early	3	-24.72	2.44
		6 weeks early	1	-25.03	2.35
Generalists	Lymnaeidae	Peak runoff	23	-25.62	3.17
		Current	7	-25.05	2.15
		3 weeks early	7	-24.82	2.04
		6 weeks early	9	-24.73	2.00

Note- We collected abundant taxa from channels to fill at least three 1.5 mL Eppendorf tubes per channel. We performed stable isotope analysis on the same to determine the isotopic ratios of carbon and nitrogen, with values reported in permil (‰), such that $\delta = [(Rsample / Rstandard) - 1] / 1000$.

Table S2. Abundance and size of focal predators.

Taxon	Treatment	Abundance (%)	Mean size (mm)		Size range (mm)
Rhyacophila	Peak runoff	0.39	13.09	a	12.72 - 13.47
	Current	0.19	11.29	a	10.92 - 11.67
	6 weeks early	1.92	6.07	b	5.34 - 6.80
Perlidae	Peak runoff	0.24	7.47	a	7.34 - 7.59
	Current	0.29	6.33	a	5.72 - 6.93
	6 weeks early	0.19	8.76	b	8.58 - 8.94
Turbellaria	Peak runoff	2.13	3.46	a	3.38 - 3.55
	Current	1.14	3.55	a	3.14 - 3.96
	6 weeks early	1.92	3.44	a	3.32 - 3.56

Note- We sampled and identified the macroinvertebrate communities present in the channels at *peak runoff* and during low flows. We sampled channels during peak flow between 5/11/2019 and 6/1/2019 and during possible low flow conditions between 6/22/2019 and 8/21/2019. We only sampled channels assigned to the *current* or *six weeks early* treatment for benthic macroinvertebrates. Abundance was calculated as the percent of the total abundance comprising the target taxa within the treatment and sampling period. Size range represents ± one standard deviation from the mean size. There was no seasonal effect on size of any of the taxa, but Rhyacophila ($F2,63 = 42.09$; $P < .001$) and Perlidae ($F2,46 = 16.89$; $P < .001$) experienced lower sizes on average following the 6 weeks early treatment compared to after the current treatment. Lowercase letters indicate significant differences between treatments for each predaotry taxa based on ANOVA and Tukey's HSD test results. Letters are not comparable across taxa.

Table S3. Mean isotopic values and distribution ratios of energy sources.

Energy Source	**Treatment**	**Average d13C (‰)**		**Average d15N (‰)**	
Heptageniidae	Peak runoff	-29.64	a	2.78	a
	Current	-27.78	b	1.67	b
	3 weeks early	-27.78	b	1.53	b
	6 weeks early	-27.24	b	1.43	b
Oligochaeta	Peak runoff	-25.96	a	2.73	a
	Current	-24.98	a	2.53	a
	3 weeks early	-24.84	a	2.42	a
	6 weeks early	-24.70	a	2.62	a

Note- We measured the quality of energy source with the C:N ratios of obligate primary consumers, Heptageniidae (‘green’ energy) and Oligochaeta (‘brown’ energy). There was a significant effect of seasonal low flow conditions on the carbon and nitrogen values of ‘green’ energy ($F_{3,45} = 0.875$; *P* = 0.461), but not those of ‘brown’ energy (($F_{3,31} = 0.744$; *P* = 0.534). Lowercase letters indicate significant differences between treatments for each energy source based on ANOVA and Tukey’s HSD test results. Letters are not comparable across energy sources.