The Diversity and Distribution of Macroinvertebrate Assemblages in Two California Streams

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ABSTRACT

Mediterranean stream systems are characterized by seasonal cycles of hydrologic flow recession, which plays a major role in structuring macroinvertebrate communities. The contrasting flow regimes of intermittent and perennial streams contribute to differences hydrology, and therefore, macroinvertebrate assemblage composition. The intermittency of streams and rivers is expected to increase with climate change, and a better understanding of the linkage between hydrology and phenology is necessary. In this study, we analyzed the density, diversity, functional feeding group composition, and taxonomic composition of benthic macroinvertebrate communities within a perennial stream (Elder Creek) and a intermittent stream (Porter Creek) in Northern California throughout the summer (from May – August). We found that the densities of macroinvertebrates were similar between the streams, but the composition and distribution of organisms differed. Density and diversity metrics fluctuated more throughout the summer in the intermittent stream, due to habitat heterogeneity and transiency throughout the summer. Pools did not serve as a refuge from stream desiccation in either stream, as organisms did not seem to migrate to pools throughout the summer. The streams were taxonomically similar; but there were differences between the densities of taxa in each stream. The densities and compositions of functional feeding groups were generally dissimilar, although certain groups (shredders) were highly similar between streams.

KEYWORDS

community composition, hydrology, intermittent, perennial, density, Shannon diversity index, family richness, functional feeding group

INTRODUCTION

Many environmental factors affect the distribution of organisms in stream systems, including substrate type (García-Roger et al. 2011), thermal regimes (Ward and Stanford 1982), inter-annual hydrologic variation (Gasith and Resh 1999, Beche 2005), and food availability (Cummins and Merritt 1996, Hawkins and Sedell 1981). The pressure of hydrology however, plays a dominant role in structuring macroinvertebrate communities (Gasith and Resh 1999, Boulton 1989, Giam et al. 2017). In Mediterranean regions, stream hydrology is largely driven by climate seasonality; rainy winters characterized by periods of stochastic flooding and increased streamflow are followed by dry summers with receding flows (Gasith and Resh 1999). Seasonal conditions in Mediterranean climates, particularly periods of summertime drought, will likely become more extreme with climate change (Larned et al. 2010). The intermittency of rivers and streams is also expected to increase, yet not enough is known about the effect of intermittency on macroinvertebrate assemblage distributions in California's streams (see Bogan et al. 2013, Datry et al. 2014). Thus, to understand the consequences of a changing climate on macroinvertebrates in Mediterranean streams, a better understanding of the linkage between stream hydrology and macroinvertebrate assemblages is needed. Additionally, the effect of flow intermittence on functional feeding group compositions of macroinvertebrate communities has not been studied extensively (Belmar et al. 2019), especially within California Mediterranean stream systems.

The seasonality of flow regimes in streams is a function of climate, lithology, storage capacity, land use, soil, canopy cover, and topography (Canning et al. 2019, Gutiérrez-Jurado et al. 2019, Costigan et al. 2015, Fortesa et al. 2021). During the summer season in perennial streams, groundwater inflows maintain connectivity between pools (Datry et al. 2014). In contrast, flow in intermittent streams is not maintained throughout the summer; riffles dry up which results in disconnectivity between remaining pools (Gasith and Resh 1999). Water quality in intermittent streams also deteriorates throughout the summer; water temperature increases and dissolved oxygen and flow velocity decline (Boutlon 1989, Gasith and Resh 1999).

Flow regime is a primary control of macroinvertebrate community composition (Datry 2012, Bogan et al. 2013, Gasith and Resh 1999, Boulton 1989), and therefore the composition of invertebrate communities between perennial and intermittent streams may become more dissimilar through the summer season, as water conditions diverge (Bogan et al. 2013). In comparison to their perennial counterparts, intermittent streams host less abundant (del Rosario and Resh 2000, Beche et. al 2005) and less diverse (Giam et al. 2017, del Rosario and Resh 2000, Datry 2012, Beche et al. 2005, Arscott et al. 2010) macroinvertebrate communities, which has been attributed to the inability of certain taxa to withstand poor water quality and drought conditions (Sarremejane 2021, Belmar 2019). Community composition in perennial streams is also generally less variable throughout the summer, as a result of habitat stability, and stream flow retention (Giam et al. 2017). Past research has largely focused on these community differences between stream type, but there are also similarities between assemblages; some studies have supported a hypothesis of nestedness, where taxa present in intermittent streams are a tolerant subset of the taxa found in similar perennial streams (Arscott et al. 2010, Datry 2012, Sarremejane et al. 2021).

The objective of this study is to examine the effect of summer seasonality on the diversity of macroinvertebrate assemblages between a perennial and an intermittent California freshwater stream. We hypothesized that:

1. Invertebrate density in the perennial stream will be higher than in the intermittent stream, and less variable throughout the summer, due to the stability and quality of habitat;
2. Invertebrate density in pools in both streams will be higher than riffles, as pools will serve as refuges from desiccation;
3. Invertebrate diversity (as measured by family richness and Shannon diversity) will be higher and fluctuate less throughout the summer in the perennial stream due to the stability of habitat; and,
4. The density of functional feeding groups and families will be dissimilar between streams, and the taxa of the intermittent stream will be a nested subset of the taxa in the perennial stream, due to the dissimilarity of the hydrology of each stream.

METHODS

Study Site

In order to compare macroinvertebrate diversity and distribution between stream types, two stream systems were sampled (Figure 1). Both are located in Northern California, and experience Mediterranean climates, but differ in local topology, riparian corridor vegetation, and hydrologic regime. The intermittent stream, Porter Creek (drainage area 19.4 km2), is located in Sonoma County, California (Figure 1). It is a second order stream, and a tributary to the Russian river. Porter Creek's geology is primarily composed of central belt Franciscan melange (Jennings 1977, California Geological Survey, Geologic Data Map No. 2), which has limited water storage capacity resulting in stream intermittency in the summer months. Stream substrate is primarily composed of gravel bedrock. Porter Creek is 11.4 km in length, from headwaters to the Russian River, and our study site was located ~4.5 km upstream of the confluence.

We also sampled macroinvertebrates from Elder Creek (drainage area 16.7 km2), a third order perennial stream. It is a tributary to the South Fork of the Eel River, and is located in Mendocino County (Figure 1). The stream's bedrock is primarily composed of coastal belt shales (Lovill et al. 2018), and its substrate is primarily cobble and gravel. Elder Creek's thick layer of fractured bedrock (up to 30meters) allows for substantial groundwater storage, and results in perennial streamflow. The Elder Creek study site is located 2 km from its confluence with the South Fork of the Eel River.

Sampling Method

Benthic macroinvertebrates from both streams were collected during four sampling events in the summer of 2018, from April to August. Invertebrates were sampled from 6 sites in total, and 3 sites per stream, where each site was composed of an upstream riffle and its downstream pool. 90 cobbles were sampled from Elder Creek and 81 cobbles were sampled from Porter Creek (8 cobbles were not sampled in Porter due to riffle desiccation in August).

At each site, macroinvertebrates were sampled from benthic cobbles; cobbles were collected from the stream bed, using the step-toe procedure (Harrelson et al. 1994). Aquarium nets were held downstream of the cobble, to capture dislodged macroinvertebrates. The dimensions (a-axes and b-axes) of each cobble were recorded, and the exposed surface area was computed. The invertebrate samples were elutriated through a 500-μm mesh, and preserved in 80% ethanol. Macroinvertebrates were identified to family or genus under a dissecting scope with 10X magnification, and then measured to the nearest 0.5 mm.

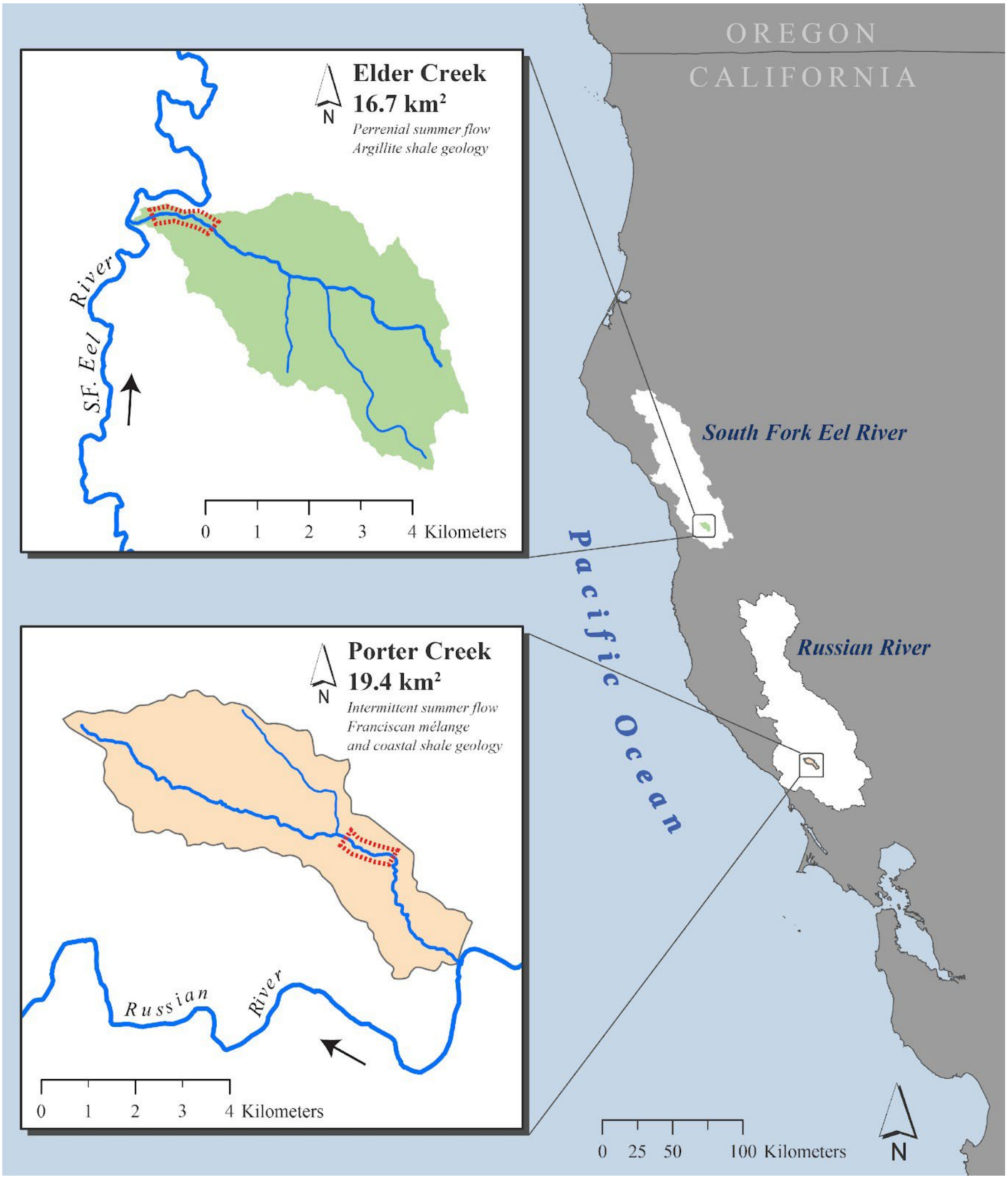

Figure 1. Map of study streams and study stream watersheds. Elder Creek is a perennial tributary to the South Fork of the Eel, and Porter Creek is an intermittent tributary to the Russian River. The stream reaches containing study sites are shown in red. The map was sourced, and used with permission, from Rossi (2020) dissertation.

Data Analysis

The dataset for this study was sourced from Rossi 2020 unpublished data (Rossi 2020). From this raw data, we computed the following metrics of macroinvertebrate community composition: density, Shannon diversity, family richness, and functional feeding group composition. Density was calculated by dividing total macroinvertebrate abundance by the total surface area of sampled cobbles (measured in m^2). Total density was computed for each site and sampling date.

Both family-level richness and the Shannon diversity index were used as metrics of diversity. Shannon diversity ($H = -\sum[(p_i) * \log(p_i)]$ where p_i is the proportion of individuals of a family) was calculated for each site and sampling date. The Shannon diversity index accounts for both richness and evenness, and was calculated using family level data. Richness was also calculated at the family level for each site and sampling date.

Macroinvertebrates are assigned to functional feeding groups (FFGs) based on their dominant food acquisition strategies, and the densities of FFGs were used to understand trophic dynamics. We assigned macroinvertebrates to seven functional feeding groups (collector-gatherer, collector-filterer, predator, shredder, scraper, macrophyte herbivore, piercer herbivore and omnivore) based on classes defined by Cummins and Meritt (1996). Functional feeding groups were assigned based on family level identification (or genus/species level identification, when possible). Trends in FFG presence and density by stream, habitat type, and sampling date, were compared using summary statistics. All data manipulation, statistical summaries and plots were procured using the statistical program R(version 4.1.1) and packages lubridate and tidyverse.

RESULTS

Density

The density of benthic macroinvertebrates (abundance per cobble surface area (m^2)) was similar, but slightly higher in the intermittent stream, Porter (mean = 0.2873, sd = 0.338) than in the perennial stream, Elder (mean = 0.269, sd = 0.201), and density in Porter varied more by site than density in Elder. Density also fluctuated more throughout the summer in Porter than in Elder, where coefficients of variation were 1.77 and 0.747, respectively. Elder experienced in

increase in density (both in riffles and pools) in August at the lowest streamflows (Figure 2).

In Elder, there was very little difference in the density of benthic macroinvertebrates in riffles (mean = 0.282, sd = 0.205) and in pools (mean = 0.256, sd = 0.203) (Figure 2). Riffles were more dense in Porter (mean = 0.436, sd = 0.468) than pools (mean = 0.170, sd = 0.0963). Although riffles had higher densities than pools in both streams, the difference between density by habitat type was larger in Porter than Elder (Figure 2).

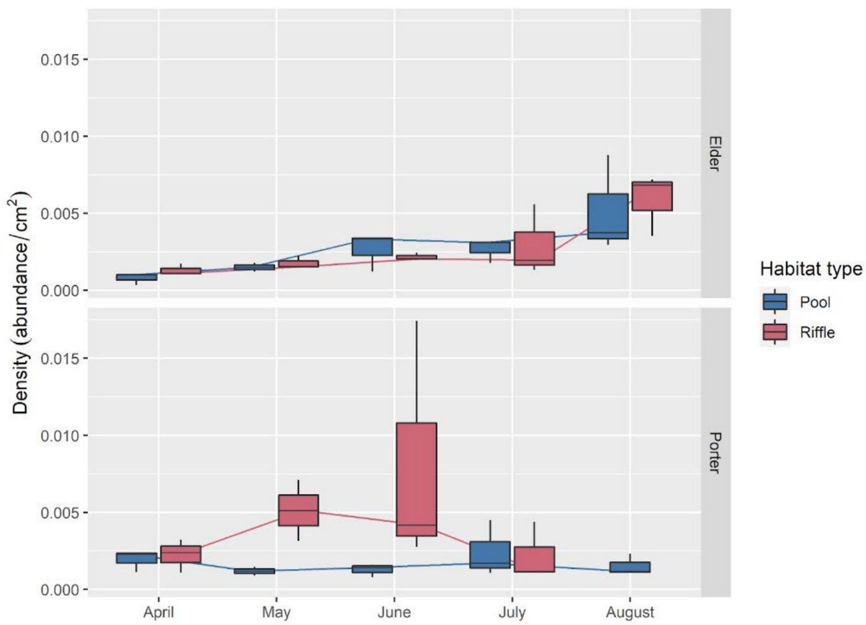

Figure 2. Density of benthic macroinvertebrates. Color represents habitat type, and density is shown by stream. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in the summer of 2018.

Diversity

Richness

Porter and Elder were similar in macroinvertebrate family level richness and composition; 41 families were present in Porter, 37 families were present in Elder, and 32 families were common to both streams. Family richness was similar between streams, but slightly higher in Elder (mean = 11.70, sd = 3.52) than in Porter (mean = 11.33, sd = 4.53). The number of families fluctuated more throughout the summer in Elder (cv = 3.36) than in Porter (2.50). Richness was more similar across sites in Elder and more variable across sites in Porter (Figure 3). Family richness was more consistent across habitat type in Elder than in Porter. In Porter, more families were present in riffles (mean = 13.08, sd = 3.50) than in pools (mean = 9.93, sd = 4.88). In Elder, family richness was higher in pools (mean = 12.20, sd = 4.16) than in riffles (mean = 11.20, sd = 2.70), although the difference between the habitat types was smaller than in Porter (Figure 3).

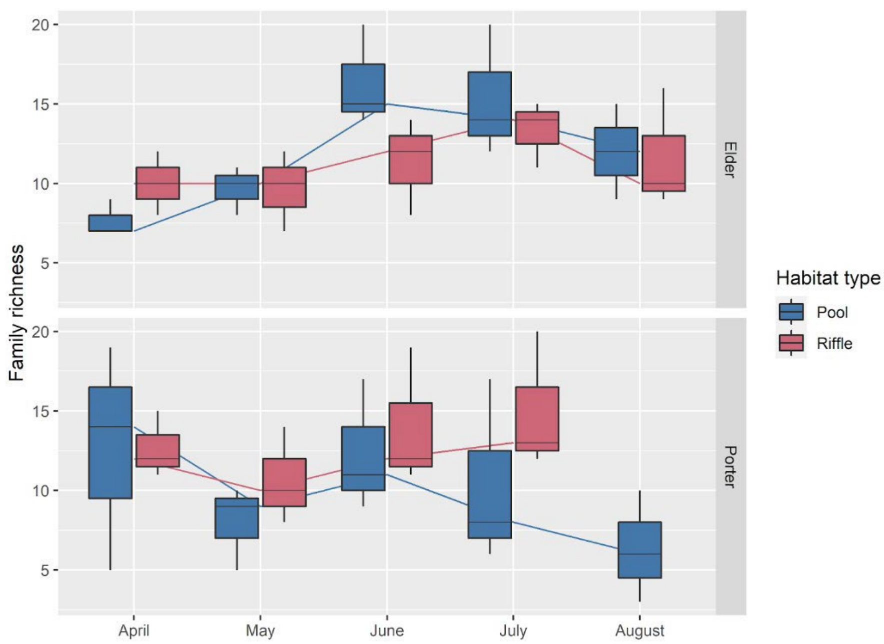

Figure 3. Family richness of benthic macroinvertebrates. Color represents habitat type, and richness is shown by stream. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in the summer of 2018. Overall, 41 families were present in Porter, 37 families were present in Elder.

Shannon Diversity

The Shannon diversity index values were similar between Elder (mean = 1.69, sd = 0.256) and Porter (mean = 1.67, sd = 0.41) (Figure 4). Shannon diversity was more variable across sites in Porter than Elder (Figure 4). Shannon diversity also fluctuated more throughout the summer in Porter (cv = 0.25) than in Elder (cv = 0.15). Riffles in Porter experienced the most fluctuation in diversity (cv = .27), while riffles in Elder experienced the least (cv = .12). In Elder, pools (mean = 1.77, sd = 0.29) were more diverse than riffles (mean = 1.61, sd = 0.20), but in Porter riffles (mean = 1.72 sd = 0.47) were more diverse than pools (mean = 1.63, sd = 0.37). The high diversity of riffles in Porter can be partially attributed to the peak in diversity in July (mean = 1.973881 sd = 0.5184951).

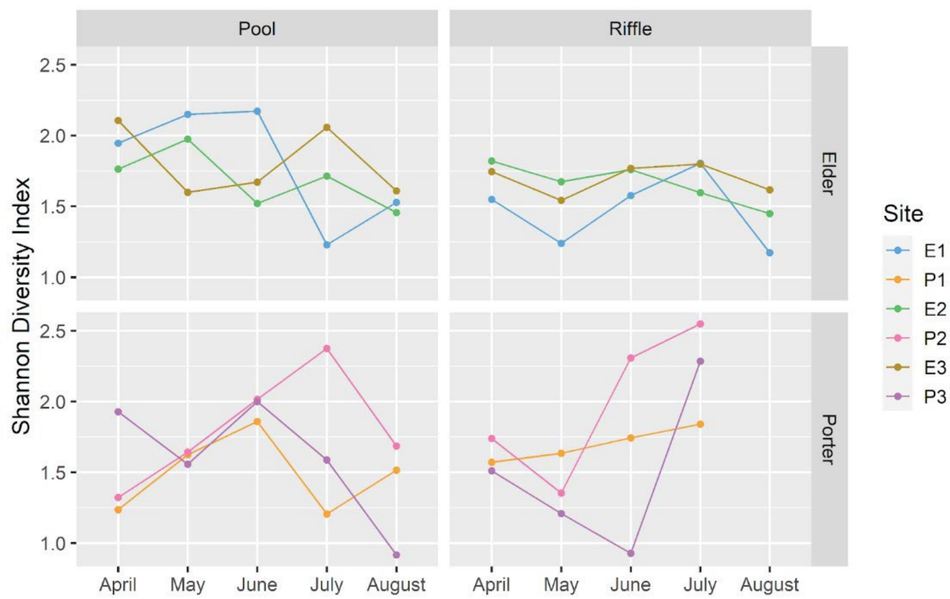

Figure 4. Shannon diversity of benthic macroinvertebrates. Shannon diversity was calculated at the family level, and macroinvertebrate samples were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in the summer of 2018. Color depicts sampling site (three riffle and three pool sites per stream).

Functional Feeding Groups

Benthic macroinvertebrate families were categorized into functional feeding groups (FFGs); all eight groups were present in both streams, but densities and family compositions of each group varied between streams (Figure 5 and Figure 6). The number of FFGs was higher in Elder (mean = 6.60, sd = 0.97) than in Porter (mean = 5.22, sd = 1.09).

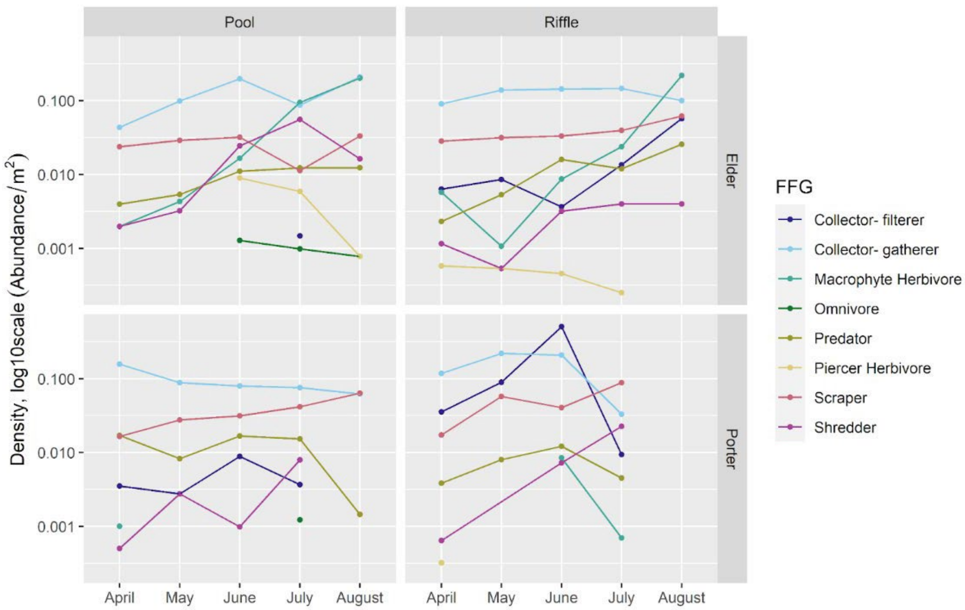

Figure 5. Functional Feeding Group (FFG) densities of benthic macroinvertebrates. Color represents FFG, and density is shown by habitat type and stream. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in the summer of 2018, and FFGs were assigned based on family level data.

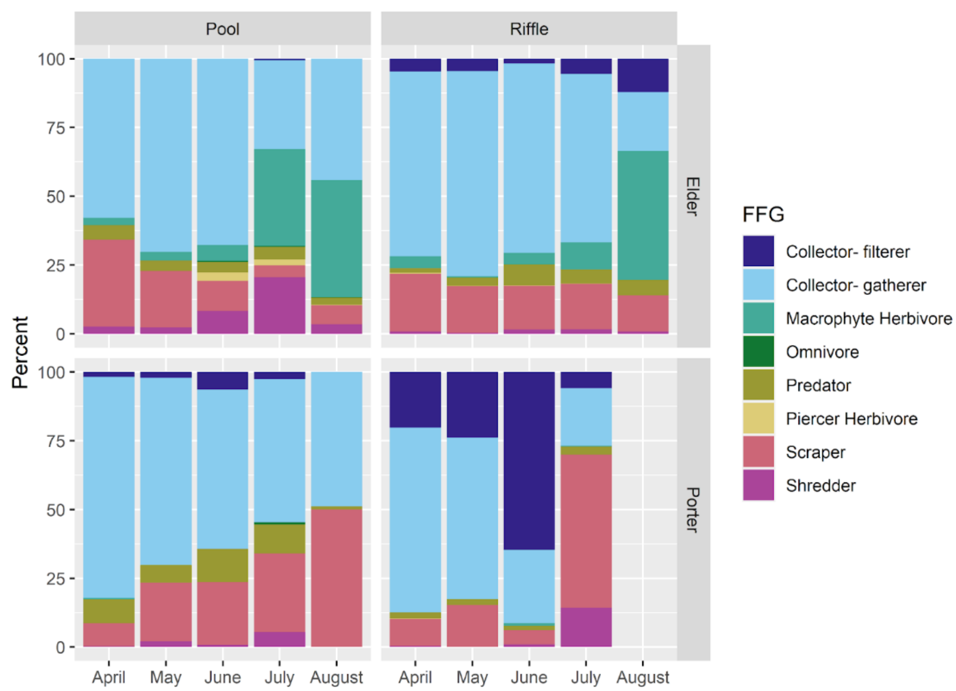

Figure 6. Percent contributions of benthic macroinvertebrate functional feeding group (FFG) densities. Color represents FFG. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in the summer of 2018, and FFGs were assigned based on family level data.

Collector-filterer (CF)

Three families, Hydropsychidae, Philopotamidae, and Simuliidae, represented the collector-filterer group, and the density of Simuliids was highest in both streams (Figure 7). The family Simuliidae made the largest contribution to collector-filterer density in Porter in June, where they accounted for 88% of density (Figure 6). The density of collector-filterers was higher in Porter than Elder for every month (excluding August when riffles in Porter were dry and could not be sampled). Collector-filterers were the most dense FFG in Porter (mean = 0.14, sd = 0.34), and third densest FFG in Elder (mean = 0.05, sd = 0.14) (Figure 4). The density of collector-filterers was higher in riffles than pools for both streams; in Elder they were present in pools only in July (Figure 5). Collector-filterer density was highest in Porter riffles in June, where they accounted for 66% of overall density (Figure 6).

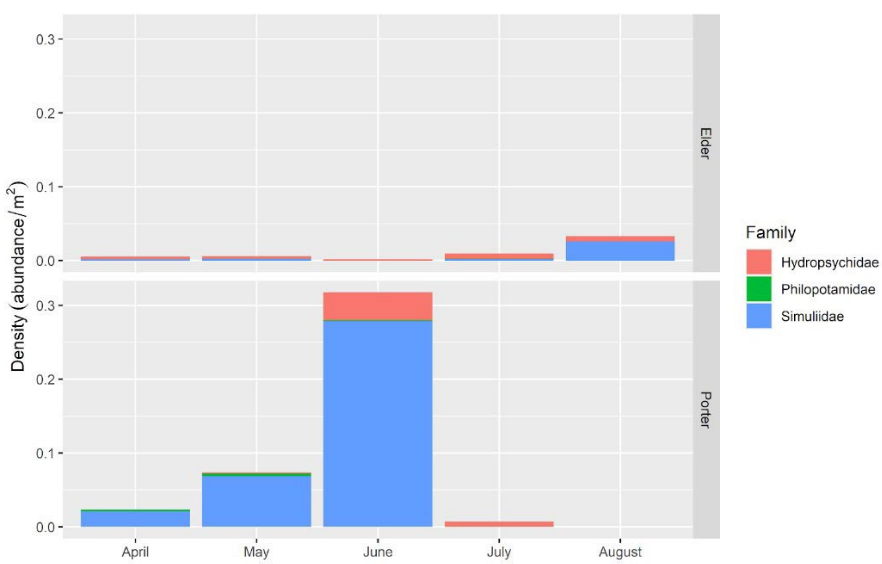

Figure 7. Densities of families within the collector-filterer functional feeding group. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in 2018.

Collector-gatherer (CG)

Collector-gatherer families included Ameletidae, Baetidae, Chironomidae, Ephemerellidae, Leptohyphidae, and Leptophlebiidae. Chironomid density was highest amongst the collector-gatherer group in both Elder (mean = 0.34, sd = 0.17), and Porter (mean = 0.24, sd = 0.14) (Figure 8). Baetids were the second densest family in both streams. The overall density and composition of the collector-gatherer group was similar between streams. Collector-gatherers had the highest density of all FFGs in Elder (mean = 0.13, sd = 0.08), and they were the second densest FFG in Porter (mean = 0.12, sd = .08) (Figure 8). Collector-gatherers were present throughout the summer in both streams and both habitat types; density was slightly higher in riffles in Porter and slightly higher in pools in Elder (Figure 5). Collector-gatherer density was less variable in Elder, but declined continuously from May to August in Porter (Figure 8).

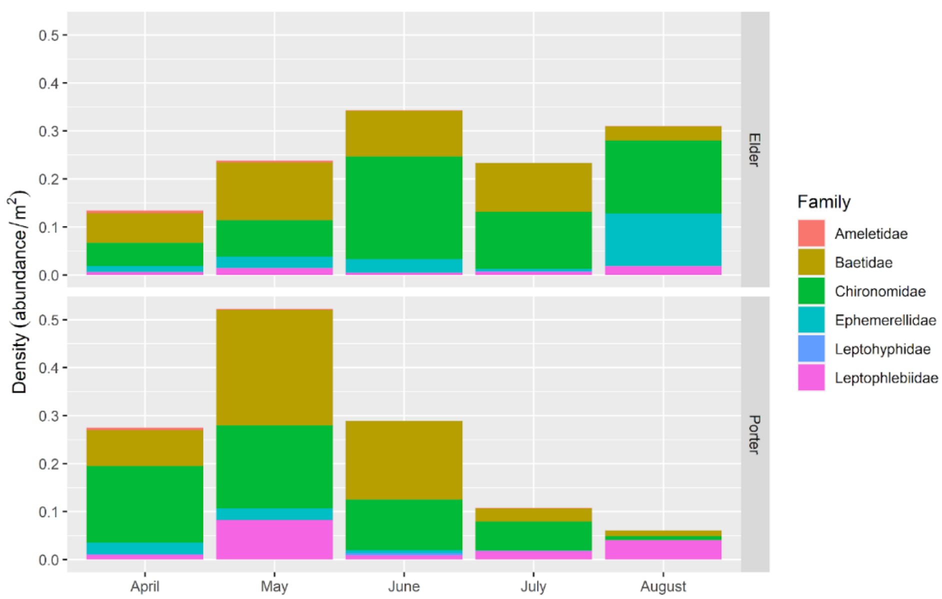

Figure 8. Densities of families within the collector-gatherer functional feeding group. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in 2018.

Macrophyte Herbivore (M)

The macrophyte herbivore group was only composed of one family, Brachycnetridae. The density of macrophyte herbivores was higher in Elder (mean = 0.058, sd = 0.085) than in Porter (mean = 0.003, sd = 0.003). Macrophyte herbivores were only present in pools in Porter for two months, but were present throughout the summer in both habitat types in Elder (Figure

5). In Elder, the density of macrophyte herbivores was slightly higher in pools (mean = 0.064, sd = 0.086) than in riffles (mean = 0.052, sd = 0.094) (Figure 5).

Predator (P)

Family richness was highest in the predator functional feeding group, where 16 families were represented. In Porter, the highest density families were Dytiscidae (mean = 0.006, sd = 0.005) and Chloroperlidae (mean = 0.004, sd = 0.003), whereas in Elder, the predator group was dominated by Rhyacopilidae (mean = 0.003, sd = 0.003) and Perlidae (mean = 0.003, sd = 0.002) (Figure 9). The families Perlodidae and Polycentropodidae were present in Porter only in the beginning of the summer (April and May), but were present throughout the summer in Elder. The density of predators was higher in Elder (mean = 0.052, sd = 0.094), than in Porter (mean = 0.010, sd = .006), and the number of families was higher in Elder than Porter throughout most of the summer (May-August) (Figure 9). Predators were present in both streams and habitat types throughout the summer (Figure 5). Predator density was higher in pools in Porter, but higher in riffles in Elder (Figure 5). In Porter, density peaked in May, and then declined throughout the summer (Figure 9).

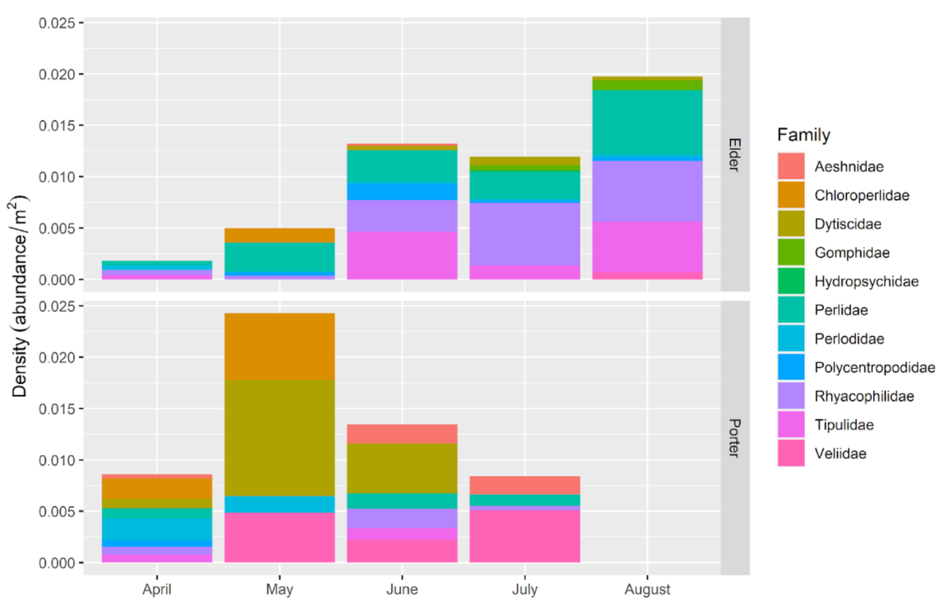

Figure 9. Densities of families within the predator functional feeding group. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in 2018.

Scraper (S)

Scraper family richness was higher in Porter (8 families) than in Elder (5 families). The family composition of the scraper group in Elder was dominated by two families: Glossosomatidae (mean = 0.015, sd = 0.015) and Heptageniidae (mean = 0.013, sd = 0.008), but the increase in scrapers in August can be largely attributed to the increase in density of Psephenids (Figure 10). The densities of families were also more variable in Porter than in Elder. The density of scrapers was higher in Porter (mean = 0.043, sd = 0.023) than in Elder (mean = 0.032, sd = 0.013), and fluctuated more throughout the summer in Porter (cv = 0.550) than in Elder (cv = 0.394) (Figure 5). In both streams, the density of scrapers was higher in riffles than in pools. The relative density of scrapers increased in Porter throughout the summer, and scrapers accounted for 50% of density in pools in August, and 55% of density in riffles in July (where July is the last summer month with flow over riffles) (Figure 6). In Porter, the family richness of scrapers was highest in June and July, where 8 families were present. Density of scrapers in Porter increased from June to July, but the increase in density was not attributed to a large increase in a single family (Figure 10).

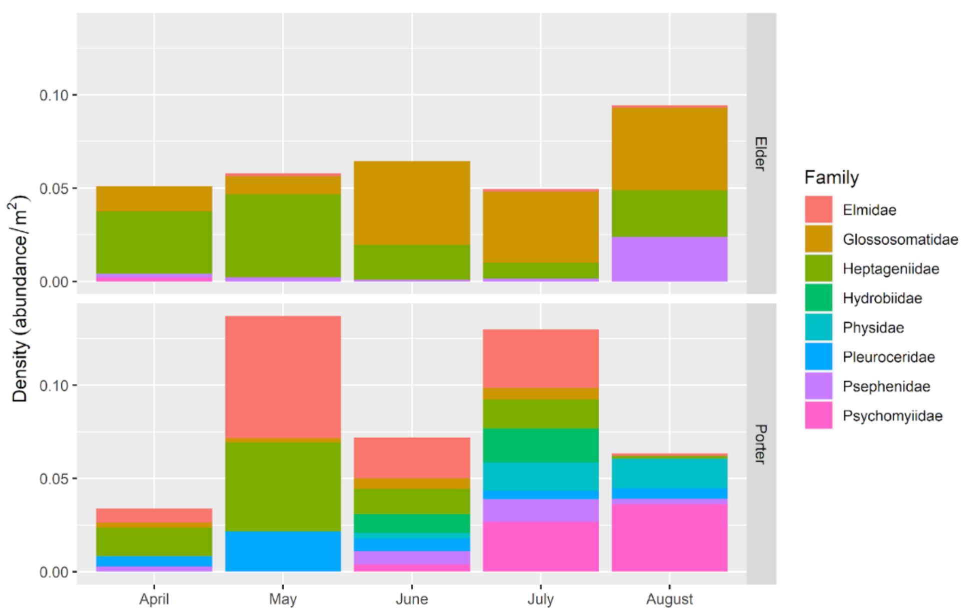

Figure 10. Densities of families within the scraper functional feeding group. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in 2018.

Shredder (SH)

The Shredder group was composed of four families (Lepidostomatidae, Limnephilidae, Nemouridae, Sericostomatidae), and all families were present in both streams (Figure 11). Lepidostomatidae was the highest density family in both Elder (mean = .00006, sd = .00005), and Porter (mean = .00004, sd = .00007). The family Sericosomatidae was not abundant in either stream, but density peaked notably in Elder in July (Figure 11). Shredder density was higher in Elder (mean = 0.011, sd = 0.017) than in Porter (mean = 0.006, sd = 0.008) (Figure 11). In Porter, the density of shredders was higher in riffles, but in Elder, shredder density was higher in pools (Figure 5). Temporal trends in shredder density were similar between streams; density was low in April and May, and peaked in July.

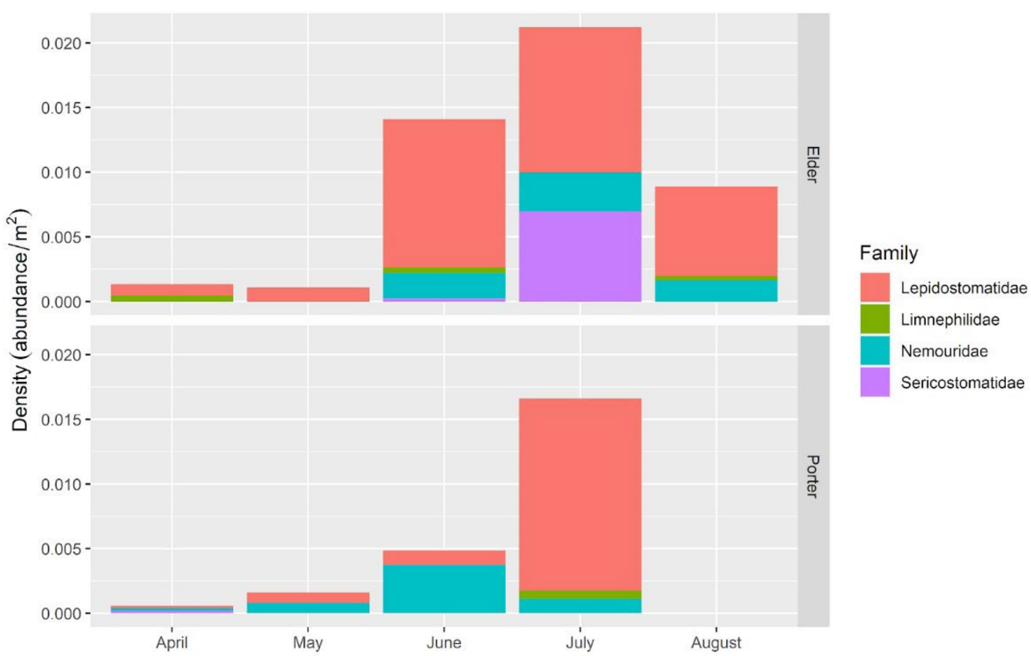

Figure 11. Densities of families within the shredder functional feeding group. Macroinvertebrates were collected from benthic cobbles in Elder Creek (perennial) and Porter Creek (intermittent) in 2018.

DISCUSSION

In this study, we compared the summer macroinvertebrate assemblages of two California streams with differing flow regimes. Contrary to expectations based on literature review, certain elements of macroinvertebrate community composition were surprisingly similar between the streams, including overall density, taxonomic diversity, and Shannon diversity. However, we also found that macroinvertebrate densities within families and functional feeding groups were dissimilar between the two streams, and that the distribution of macroinvertebrates within these groups also differed by habitat type and month. Notably, the composition of certain functional feeding groups that relied on autochthonous food resources (scrapers and predators) were more dissimilar between streams than the compositions of other groups (shredders) which rely on allochthonous food availability.

Density and Diversity

Contrary to our predictions, we found that the density of macroinvertebrates was not higher in the perennial stream than the intermittent. The overall densities of the streams were surprisingly similar across all summer months, and stream type did not appear to be a determinant of overall invertebrate density (FIG). Some studies have found higher densities of macroinvertebrates in perennial streams (del Rosario and Resh 2000, Giam et al. 2017), which has been attributed to the stability of habitat through the summer (Gasith and Resh 1999, Giam et al. 2017, Beche et al. 2005), or a lack of drought tolerance adaptations in intermittent streams (del Rosario and Resh 2000). Other studies have found higher densities in intermittent streams, which has been explained by the concentration of organisms during summertime habitat contraction (Smith and Pearson 1987), and the persistence of taxa with behavioral or physiological drought avoidance strategies (Williams and Hynes 1977, Leigh and Datry 2017, Sarremejane et al. 2021). We did not find that density increased continuously throughout the summer in the intermittent stream, which suggests that habitat constriction did not play a role in consolidating organisms. The surprisingly high average density of invertebrates in the intermittent stream across all summer months can be partially attributed to a peak in density in riffles during May and June. High riffle density may be associated with higher food availability or better habitat quality than pools. Low flows in the intermittent stream may also make riffle-dwelling macroinvertebrates less available to larger predators like salmonids, as passage between pools and riffles becomes more difficult.

Density and diversity fluctuated more in the intermittent stream than the perennial across all sampled months, as we predicted. Macroinvertebrate communities are largely shaped by hydrologic features (Gasith and Resh 1999, Boulton 1989), and so communities may vary more in response to environmental change associated with seasonal intermittency (Leigh and Datry 2017, del Rosario and Resh 2000, Bonada et al. 2006). Fluctuations in density in the intermittent stream did not indicate directional movement from one habitat type to another as density did not increase in pools and decline in riffles. This suggests that pools are not acting as a refuge from flow constriction. Past studies have identified riffle-pool migration as a resilience strategy (Boulton 1989, Saffarinia et al. 2021), but our findings suggest that other strategies are more important in defining macroinvertebrate communities.

In addition to a greater fluctuation in diversity across the summer, the diversities of sites within the intermittent stream were also more variable (Figure 4). In the perennial stream, the diversities of sites may have been more similar due to the effect of flow permanence on the consistency of habitat throughout the stream. In intermittent streams, flow recession and subsequent pool isolation may act to limit organismal migration and resource flow (Smith and Pearson 1987, Hawkins and Sedell 1981). Therefore, the heterogeneity of habitat throughout the intermittent stream may have been greater, resulting in the divergence of macroinvertebrate assemblages throughout the stream (Smith and Pearson 1987).

Functional Feeding Groups (FFGs)

The taxonomic compositions and densities of functional feeding groups showed both similarities and differences between stream types. Although all eight groups were present in both streams, there were differences in the relative contributions of each group to total stream density, as well as seasonal contributions of families to the densities of each FFG (Figure 6). Past studies have found that the composition of FFGs within communities is dependent on food resource availability (Hawkins and Sedell 1981), and trends in FFG densities indicate both similarities and differences between streams.

The collector-filterer and collector-gatherer FFGs were taxonomically similar between streams, but differed in terms of density and seasonality (Figure 5 and Figure 6). The family Simuliidae was the most common taxa in both streams, and accounted for the majority of collector-filter density in the intermittent stream. Collector-filterers were nearly absent from the perennial stream, but made significant contributions to overall density in the intermittent stream, especially in June (Figure 7). Collector-filterers, like Simuliids, feed through passive filtration (Adler and McCreadie 2019), and past research has associated high densities of collector-filterers to organic enrichment of water (Rosenberg and Resh 1993). In the intermittent stream, a higher concentration of organic particulate matter may contribute to higher densities of collector-filterers. In both streams, the density of collector-filterers was higher in riffles than pools (Figure 5), which indicates the importance of habitat type in defining macroinvertebrate communities.Higher flow velocity in riffles facilitates the transport of organic particulate matter, contributing to the higher density of collector-filterers. The peak in density in June may be attributed to a decrease in predation following low stream flow in riffles, or the decline in habitat quality in pools.

The taxonomic composition of the collector-gatherer FFG was also highly similar between streams, and both the communities of both streams were largely composed of Chirnomidae and Baetidae (Figure 8). In the intermittent stream, the density of collector-filterers declined from May to August, whereas overall density was relatively stable in the perennial stream. Similarly to collector-filterers, collector-gatherers feed on organic particulate matter (Meritt et al. 2017), and the decline in density throughout the summer could suggest a decline in organic detritus, or an increase in predation. The dominant families, Chironomidae and Baetidae, both rely largely on predator avoidance strategies (swimming or drifting) rather than on morphological defenses (body-armoring or other appendages) (Lancaster 1990), and so predation pressures on accessible prey may have increased as habitat constricted throughout the summer.

The shredder group was similar between streams, in terms of both density and taxonomy. Although the overall density of shredders was lower in the intermittent stream, trends in density were similar between streams; density was low in the beginning of the season, and peaked in July in both streams (Figure 11). Shredders primarily consume leaf litter (Meritt et al. 2017), and the increase in density in late summer may be indicative of the accumulation of organic matter, resulting from declining stream flow. Shredders are the only FFG (in this study) whose density and distribution is closely related to terrestrial inputs (Meritt et al. 2017, Hawkins and Sedell 1981). The similarity between the taxonomy and density of shredders in the two streams may reflect the similarities of allochthonous contributions, as well as the role that terrestrial components play in structuring macroinvertebrate communities.

In contrast to shredders, the taxonomic composition and densities of the predator group and scraper group were different between the two streams, in terms of both density and taxonomic composition. Within the predator group, the taxa present in the intermittent stream seemed to be a subset of taxa in the perennial stream in the later summer months (Figure 10). Across all taxa, we found that the taxonomic composition of the intermittent stream was not a nested subset of the perennial stream, however there was a pattern of nestedness in the predator group; family richness was lower in the intermittent stream, particularly in the later months, and families that are sensitive to water quality conditions, like Rhyacophilidae, Perlidae, and Tipulidae (Ode 2003) were abundant in the perennial stream, but nearly absent from the intermittent stream. Boulton and Lake (1992) suggested that as flows decline, the population of predators will increase due to habitat constriction and resource competition. Conversely, we found that the density of predators in the intermittent stream declined throughout the summer and the remaining taxa were highly tolerant, which suggests that tolerance plays a large role in structuring the compositions of intermittent streams in the summer. This is corroborated by previous studies which have found that perennial and intermittent streams host taxonomically similar macroinvertebrate communities (Beche et al. 2005), but as flows recede throughout the summer, taxa richness in the intermittent stream declines to exclude organisms that are intolerant of drought or poor water quality (Leigh et al. 2019, Arscott et al. 2010, Datry 2012, Boulton and Lake 1992).

The scraper group also differed between the two streams, but taxa in the intermittent stream were not a subset of taxa in the perennial stream. In contrast to the idea of nestedness, some studies have found that summertime conditions in intermittent streams favor desiccation resistant specialists, which are absent from perennial streams (Arscott et al. 2010, Sarremejane et al. 2021). Specialist taxa in the intermittent stream were not common in any FFG, except for the scraper group. Family richness was higher in the intermittent stream, and this can be attributed to the presence of snail families (Hydrobiidae, Physidae, Pleuroceridae) which were absent from the perennial stream. Past studies have shown that there is a relationship between scraper abundance and the presence of diatoms and algae (Hawkins and Sedell 1981), and so the higher diversity and density of scrapers may suggest greater food availability in the intermittent stream.

Additionally, snails may be less vulnerable to predation, and may be able to persist throughout the summer despite predator pressure. Therefore, the combination of food availability and resistance strategies may contribute to the presence of unique taxa in the scraper groups of the intermittent stream.

In this study, two streams with contrasting flow regimes hosted dissimilar communities of macroinvertebrates; distribution, diversity, and composition of the assemblages indicate that intermittency and hydrologic seasonality are drivers of community structure. To better understand the intricacies of these interactions, future studies could investigate the relationship between predictor variables (stream flow, dissolved oxygen, inputs of terrestrial organic matter, algal density, terrestrial and aquatic predator pressures etc.) and macroinvertebrate distributions. The differences that we found between the intermittent and perennial stream indicates the importance of hydrology as a driver of the distributions of stream organisms.

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