

A COMPARISON OF COMMUNITY STRUCTURE IN REGULATED AND
UNREGULATED REACHES IN THE UPPER EEL RIVER, CALIFORNIA

By

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ABSTRACT

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Flow regulation of rivers by impoundments and diversions can reduce hydrological variability. As a result, densities of algae and benthic macroinvertebrates often increase, but many sensitive taxa are lost, causing shifts across the food web. In Northern California, dams that reduce winter peak floods can result in the primary consumer community becoming dominated by grazers that are relatively invulnerable to predation, which can reduce the amount of energy transferred up the trophic levels. The steeper slope of the spring hydrograph recession limb downstream of a dam can also greatly impact instream diversity of periphyton, invertebrates and fish. The dam and diversion system on the upper Mainstem Eel River in Northern California has direct impacts on endangered salmon populations, but the effects of the dams on the greater ecosystem are not well understood. This study compared the seasonal algal and benthic macroinvertebrate communities from the Mainstem Eel River below Cape Horn Dam to that of the unregulated Middle Fork Eel River. The 2017 water year had above average rainfall, with several bankfull flows observed in the winter as well as elevated base flows in the summer in both rivers. Despite the wet water year in 2017, the regulation of flows by the dams still likely produced a shorter spring recession limb and, more importantly, a

delay in peak summer temperatures in the Mainstem relative to the Middle Fork.

Although the abundance and diversity of invertebrates were not notably different between the regulated and unregulated rivers, there did appear to be a variation in the food webs.

By mid-summer, the unregulated Middle Fork developed into an ecosystem predominated by *Cladophora* and its epiphytes with numerous invertebrate grazers. Yet the Mainstem, especially immediately below the dam with the encroachment of vegetation, had less growth of the filamentous green algae ($t(20)=4.61$, $p=0.0002$) with lower mid-summer algal richness ($t(20)=2.53$, $p=0.020$), resulting in an invertebrate community more reliant on filtering fine organic matter with far fewer grazers ($p<0.01$).

Macroinvertebrate drift densities in June, when Chinook outmigration occurs, were significantly lower in the Mainstem relative to the Middle Fork ($p<0.02$). The altered flow regime of the regulated reach may be impacting the growth of *Cladophora* as well as the abundance and development of some key macroinvertebrate taxa, such as midges and small minnow mayflies relative to an unregulated reach. As the Middle Fork is an inherently warmer system, future studies are needed across a longitudinal gradient of the Mainstem over multiple water years to capture interannual variation and to ultimately determine the influence of the dams on riverine ecosystems.

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INTRODUCTION

Rivers and streams are heavily impaired ecosystems throughout the world, as anthropogenic development has extensively altered the hydrologic regime through irrigation, impoundments and interbasin diversions (Poff et al. 1997; Nilsson et al. 2000). River channels below dam diversions in Mediterranean climates often have lower winter peak flows and a faster spring recession limb of the hydrograph, therefore the rise in stream temperature and decrease in channel connectivity occurs earlier in the summer and often to a greater degree (Poff et al. 1997). The ramifications of these flow alterations on species of concern such as anadromous salmonids are well-documented; they include reduced suitable habitat availability and subsequent loss in population sizes (Liermann et al. 2012; Sheer & Steel 2006). Although these direct impacts of dams on salmonids are important, flow management can also have indirect impacts on salmonids through effects on the food web (Nilsson et al. 2000; Power et al. 1996). For example, the thermal tolerances of salmon, especially in juveniles, can be reduced with declines in the abundance and energy density of prey (Beauchamp 2009). Therefore, the recovery of these key species in part depends on an ecosystem-level approach that can account for shifts throughout the trophic levels.

Regulated flow effects on algal communities

Regulated flow regimes have been associated with distinct shifts in the composition and productivity of benthic algae relative to unregulated reaches (Bunn and

Arthington 2002; Wu et al. 2008; Ponsati et al. 2015). The dampening of bed-mobilizing floods and reduction in seasonal variability of flow often allows for higher primary production in the summer with more homogenous and denser growth of periphyton and reduced turnover (Munn and Brosven 2004; Aristi et al. 2014; Ponsanti et al. 2015). While stabilization of flow can increase gross production: community respiration (P/R) ratios and the abundance of certain algal groups such as green algae communities in regulated rivers often have fewer algal taxa represented overall (Growthns and Growthns 2001; Munn and Brosven 2004; Smolar-Zvanat and Mikos 2014). Reductions and shifts in the diversity of epiphytic algae are likely due to shifts in traits such as size and morphology, which may also explain taxonomic inconsistencies across watersheds; however, few studies have taken a trait-based approach to flow regime effects (Growthns and Growthns 2001; Wu et al. 2008; Wu et al. 2017). Additionally, seasonal variation in the algal community can be altered in regulated rivers. If regulation maintains lower base flows relative to unregulated reaches, then warming water temperatures in combination with stagnant backwater can cause green algae, a major basal resource, to senesce earlier in the season, potentially shifting to a community dominated by cyanobacteria (Power et al. 2008; 2015). High standing stock of algal biomass may also be short-lived if the abundance of predator-resistant grazers increases, readily consuming a significant portion of the algae (Wootton et al. 1996). Yet the top-down effects of grazers on primary producers are often highly variable, especially in the presence of strong environmental disturbances (Lamberti and Feminella 1996).

Regulated flow effects on benthic macroinvertebrate communities

The long-term response of the benthic macroinvertebrate (BMI) community to flow regulation is often a decline in diversity with more tolerant taxa (Munn et al. 1991; Cortes et al. 2002; Lobera et al. 2016). Through elevated or reduced hydrologic variability, dams can directly impact BMIs by disrupting life cycles, which can be temperature and flow dependent (Munn et al. 1991; Wallace 1996; Nelson & Lieberman 2002; Kennedy et al. 2016). In rivers where dam regulation stabilizes and reduces both peak and base flows, favored taxa are often multivoltine as well as aquatic migrators, creating a community with higher Dipteran richness and lower EPT (Ephemeroptera, Plecoptera and Trichoptera) richness (Cortes et al. 2002; Lobera et al. 2016; Steele et al. 2017). In addition, the reduction of bed mobilizing floods can create a grazing community dominated by large invertebrates invulnerable to predation such as the heavily-cased caddisfly *Dicosmoecus*, which are usually flushed out by the floods in unregulated rivers (Wootton et al. 1996). Peak flows are critical for creating habitat heterogeneity and seasonal flow variability can be a highly significant factor in maximizing macroinvertebrate diversity (Cortes et al. 2002; Lobera et al. 2016; Lusardi et al. 2016). The response of the invertebrate communities to flow regulation in terms of specific taxa is variable and remains an area of emerging information (Lobera et al. 2016).

Regulated flow effects on the aquatic food web

River food webs are sensitive to hydrologic alterations, which can cause drastic changes within and across trophic levels (Power et al. 1996; Nilsson et al. 2000; Bunn and Arthington 2002). The aquatic communities of Mediterranean-climate watersheds in particular are well-adapted to the seasonal variability in annual precipitation, and therefore when regulation reduces flow variation, certain taxa are favored (Wootton et al. 1996; Power et al. 2015). Regulated flows can lower the photosynthetic efficiency of periphyton and limit its availability to invertebrate grazers, which in turn can reduce grazer diversity and density (Ponsati et al. 2015; Llobrera et al. 2016). Therefore, even in cases where primary production increases under a regulated flow regime, there is not necessarily an equivalent increase in grazers and their predators (Ponsati et al. 2015). Similarly, when large invulnerable grazers dominate algal consumption in regulated reaches, less energy is transferred to higher trophic levels, most notably predatory fish, and therefore the composition of the food web is significantly altered (Fig 1; Wootton et al. 1996). In addition, if the system shifts to a cyanobacteria-dominated algal community due to low, warm base flows, then the energy moving through the food web is further reduced into the summer (Figure 1; Power et al. 2008, 2015). The presence of cyanobacteria toxins can also be potentially lethal to macroinvertebrates and vertebrates?, reducing the abundance of sensitive taxa (Bridge unpublished data 2016). As regulation of flow by dams can impact all levels of the food web, the productivity of an ecosystem has the potential to be significantly reduced.

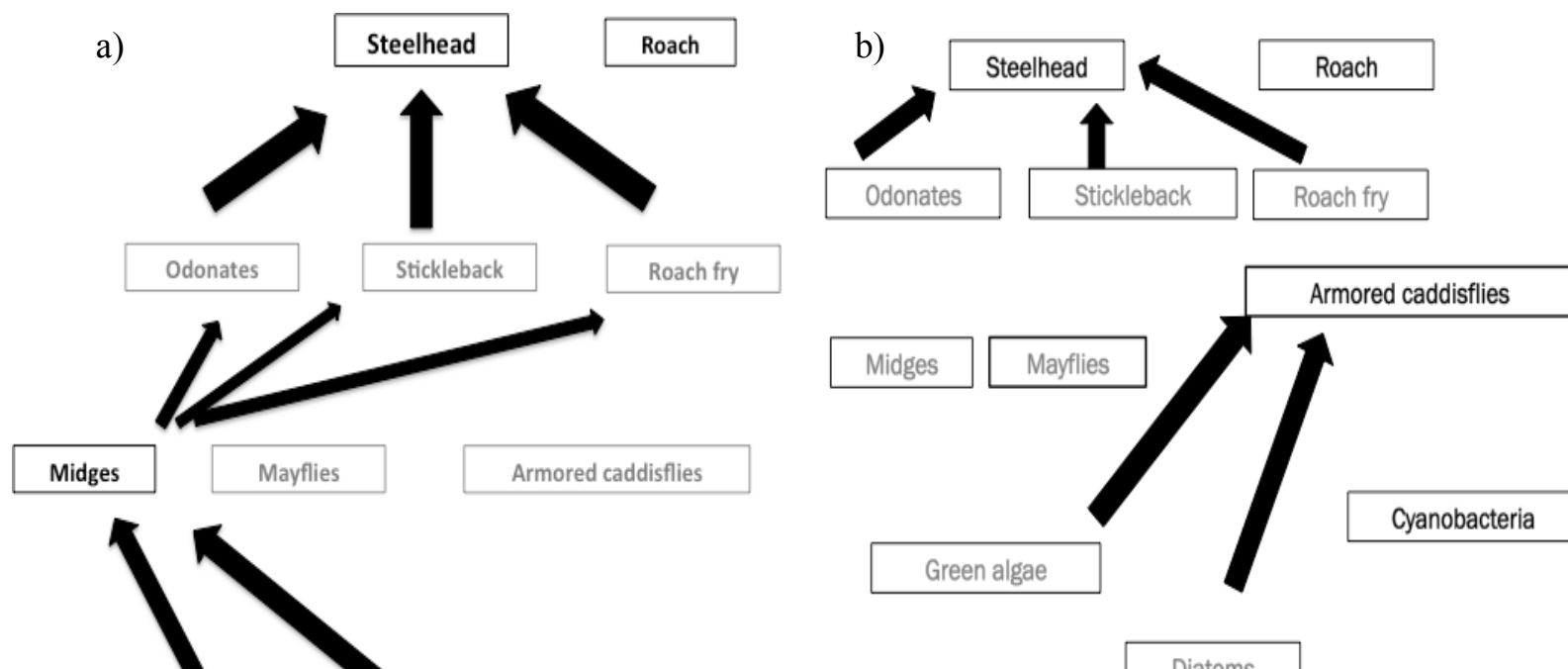


Figure 1. Simplified diagrams representing the food web of a Mediterranean stream under a) normal/unregulated conditions with winter scouring floods and b) drought/regulated conditions with no scouring floods and low base flows. Groups suppressed by predation are in gray type. Taxa at each level indicate the key groups; such as mayflies representing mobile grazers. Thick arrows only represent strong linkages, and thin arrows represent weak linkages in the presence of larger roach and steelhead. While other interactions exist, they are assumed not significant under either normal or drought conditions. Figure adapted from Power et al. 2008.

Background & Relevance

The Eel River watershed in Northern California has been the subject of many broad-scale food web studies in part to assist with the recovery of its anadromous salmonids, but specific ecological effects due to large-scale flow regulation on the Eel River remain unexamined (Wootton et al. 1996; Yoshiyama & Moyle 2010). The Eel River watershed historically supported large anadromous salmonid populations such as spring-run and fall-run Chinook (*Oncorhynchus tshawytscha*) and Coho salmon (*O. kisutch*) as well as steelhead (*O. mykiss*), which has both a winter and summer run (Yoshiyama & Moyle 2010). In the upper Mainstem Eel River, the dams of the Potter Valley Project (PVP) divert a portion of the Eel River flow (on average of 197,356,800 m³ per year) into the Russian River watershed for agricultural and municipal use with the highest withdrawals occurring during the summer months (Figure 2; NMFS 2002; Higgins 2010). The current flow releases from Scott Dam are insufficient in terms of temperature and passage for federally-listed Chinook and Coho salmon as well as steelhead (Asarian 2016; O'Dowd & Trush 2016). Yet the extent to which the PVP dams may limit production of BMI salmonid prey is not known. In addition, the Eel River watershed faces increasing toxic cyanobacteria blooms that pose health risks both to the ecosystem and the public (Havens 2008; Power et al. 2015; Bridge unpublished data 2016). Due to thermal stratification and increased water clarity that is often found downstream of dams, cyanobacteria can often persist at high abundances, increasing the frequency of blooms relative to unregulated rivers (Huisman et al. 2004; Mitrovic et al. 2011). Based upon

previous work in the Eel River Watershed, I designed a study on the regulated Upper Eel Mainstem that tests for the predicted trophic shifts (Wootton et al. 1996; Power et al. 2008). As a food-web study, I set out to examine impacts on both the algal primary producers and invertebrate consumers, which has a greater application in describing how the dam system has altered the ecosystem as a whole.



Figure 2. Map of the Eel River watershed with the major tributaries such as the Middle and South Fork as well as the Potter Valley Project dams (source: USGS).

Despite efforts to ameliorate dam impacts, including a 2002 Biological Opinion by National Marine Fisheries Service (NMFS) that requires the PVP to release flows for

salmon migration, modeling of the unimpaired Eel River flow regime indicates that spring and often winter flows in the Upper Mainstem Eel River (hereafter-Mainstem) are notably reduced due to the PVP (Asarian 2015). Therefore, further study on the impacts of the dams is needed as the PVP dams come up for relicensing in 2022. An examination of the downstream effects below the PVP diversion on the mainstem Eel in comparison to an unregulated reach could reveal the magnitude and extent of these flow alterations on the stream ecosystem. As the survival of threatened salmonids remains tenuous, it is important to identify possible factors currently limiting prey availability and overall habitat suitability. Data on the seasonal shifts in the food web, which influences the overall productivity and health of the ecosystem, can inform management on the extent of downstream alteration.

The characterization of the changing abiotic and biotic community can contribute information to provide a more holistic view of the impairments on the Mainstem. As the relicensing process of the PVP begins, a thorough understanding of how current regulation impacts the flow and thermal regimes as well as the physical channel can improve models of flow management alternatives. Collection of algal data not only for primary production estimates, but also the abundance of cyanobacteria is critical as toxic blooms have become more prevalent in the watershed (Power et al. 2015). Measures of BMI composition and abundance can offer information on possible constraints on salmonid growth as well as the overall resiliency of the ecosystem, functioning as key intermediate trophic levels. Although the data of a wet year (2017) may not show the full impacts by the PVP dams, in context with existing data on the watershed from dry years

it can offer a baseline for future comparison. The project, taken in context with prior ecological data from the Eel River, ultimately expands on the current understanding of this significant coastal river ecosystem.

Research Objectives

The research objectives of this study were to assess the impacts of the PVP on the downstream aquatic ecosystem by examining the algal and invertebrate community seasonal assemblage on the Mainstem Eel River below Cape Horn Dam relative to the unregulated Middle Fork from early summer to early fall. I expected aspects of the flow regime known to disturb the biological communities (e.g., bankfull flows) to be key predictors of community-level differences even in the presence of other altered abiotic factors such as temperature. I expected that reduced peak flows, reduced overall daily variation, as well as a shortened spring recession limb will result in lower diversity and abundance across the two trophic levels in the Mainstem relative to the Middle Fork. I also expected reduced algal biomass in the Mainstem in the summer due in part to the early senescence of algae will correlate specifically to lower diversity and abundance of grazing invertebrate taxa, which are often an important food resource for salmonids.

METHODS

Site Background

The Eel River watershed drains 9,541 square kilometers with 315 river kilometers as the third largest river entirely in California. The headwaters of the Eel River are located in southern Mendocino and Lake Counties and then runs north with its outlet into the Pacific Ocean in central Humboldt County (Figure 2). The watershed has been impacted by heavy commercial logging in the late 19th century and throughout the 20th century as well as overfishing of its salmonids in the late 19th to early 20th century, causing over a 90% decline in most populations (Yoshiyama & Moyle 2010). This project involved field surveys on the Mainstem and the Middle Fork Eel River (hereafter ‘Middle Fork’) from early summer (June) to early fall (September) 2017. Consultation with local professionals as well as spatial analysis suggested the adjacent Middle Fork, which has no major dams or diversions, serves as a natural comparison with the regulated Mainstem due to similar geology and climate in both watersheds (Table 1). The regulated reach for this study was on the Mainstem from Cape Horn Dam downstream to the confluence with the Middle Fork, encompassing 54.7 river-kms (Figure 3). I compared this regulated study reach with an unregulated reach of similar length (48.2 river-kms) on the Middle Fork (Figure 3). Flow releases at Cape Horn Dam during the spring typically exhibit a steeper receding limb relative to the unregulated Middle Fork (CDEC 2016). Modeled unimpaired flows that estimate the discharge at Cape Horn Dam in the absence of dams

show a more gradual slope in the spring recession limb and higher base flows in the summer (Asarian 2015, O'Dowd & Trush 2016). There is also a steep thermal gradient in this section of the Mainstem downstream of Cape Horn Dam, with summer high water temperatures ranging from 23°C at Van Arsdale Reservoir to over 27°C at the Outlet Creek confluence, usually peaking in late July (Asarian 2016). Throughout the study section of the Middle Fork, summer high water temperatures vary little, averaging around 27°C (Asarian 2016).

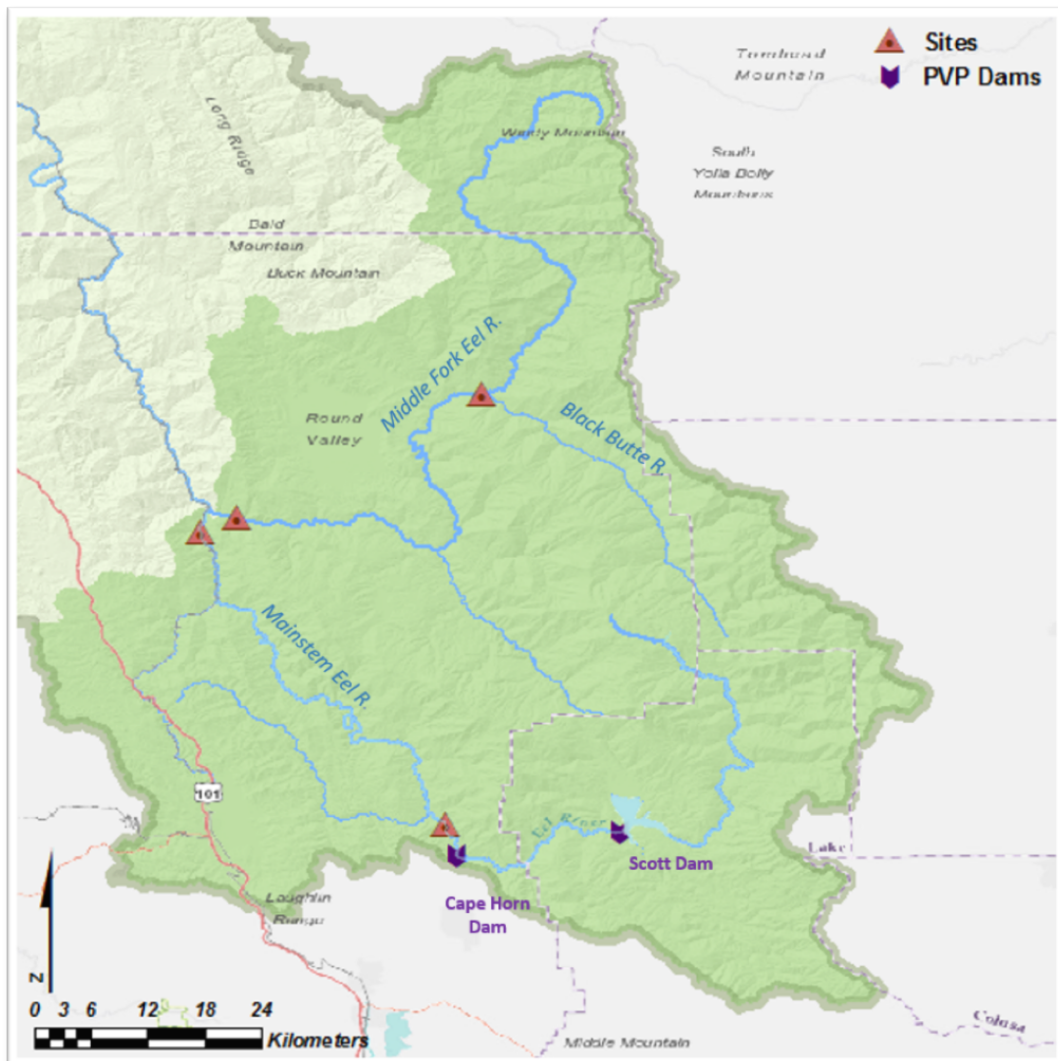


Figure 3. Map of the study sites in the upper section of the Eel River watershed, including the major tributaries of each river and the Potter Valley Project (PVP) (source: USGS 2014).

Table 1. Drainage area and parameters of the Mainstem and Middle Fork Eel River at their confluence derived from existing spatial data (digital elevation model and modeled climate data from 1980-2010). Source: USGS 2014, PRISM 2016.

<i>Physical Parameters</i>	Mainstem Eel River	Middle Fork Eel River
<i>Drainage area (ha)</i>	183,330	194,474
<i>Mean elevation (m)</i>	866.6	1,117
<i>Max elevation (m)</i>	2,140	2,305
<i>Min elevation (m)</i>	263.2	263.2
<i>Annual precipitation (cm)</i>	141	143
<i>Mean air temperature (°C)</i>	12.8	12.0
<i>Max air temperature (°C)</i>	22.4	23.3
<i>Min air temperature (°C)</i>	2.85	1.37
<i>Dominant geology</i>	Franciscan	Franciscan

In order to capture the downstream effects of the dam, this study consisted of a sampling reach on the Mainstem directly below Cape Horn Dam and a sampling reach on the Mainstem directly upstream of the confluence with the Middle Fork. On the Middle Fork, one sampling reach was located at a similar distance upstream from the confluence with the Mainstem and another sampling reach further upstream at a location with a similar upstream watershed area as the Cape Horn Dam site (Fig 3). Sampling took place three times in 2017: in June (11th-23rd), July (12th-25th) and September (8th-17th). This time of year is the critical period when dam releases are reduced as water diversions occur and temperature rises, and salmonids and other aquatic organisms are placed under potentially stressful conditions (O'Dowd & Trush 2016).

Long-term Flow & Thermal Regime Trends

I examined summer thermal regimes of the Mainstem and Middle Fork, using continuous monitoring data from 2010 to 2014 (Asarian 2016). Temperature loggers were located in the upstream reaches in riffles, directly downstream of Cape Horn Dam on the

Mainstem collected by Pacific Gas & Electric and directly downstream of the confluence with the Black Butte River on the Middle Fork collected by the Eel River Recovery Project (Asarian 2016). I examined flow regimes of the Mainstem and Middle Fork using long-term gage station data from 2010-2017 (Mainstem USGS # 11471500 Eel R A Van Arsdale Dam Nr Potter Valley CA; Middle Fork: USGS # 11473900 MF Eel R Nr Dos Rios, CA) (CDEC; USGS 2017). In addition, I measured flow during each sampling period with a Swiffer 2100 current velocity meter at each sampling site. Gages for long-term flow data were located directly below Cape Horn Dam on the Mainstem (CEDEC 2016) and above the Mainstem confluence on the Middle Fork with estimates made for each sampling site using basin size and sample flow data. I used these long-term flow data to calculate the frequency and magnitude of scouring or bankfull floods (1.5yr recurrence interval). The beginning of the spring recession period was based upon the last scouring flood and defined as the first day when daily discharge declined by less than 2% per day (Steel et al. 2017).

Field Methods

Water Chemistry and Channel Morphology

At the first sampling date for each designated study reach, I characterized the morphology of three adjacent riffles with channel profiles. Cross sections within the sampling reach included measurements of wetted and bankfull width, substrate size (pebble count within the wetted channel, n=100 particles), depth, and slope of the channel. At each sampling date prior to disturbing the wetted area, I took spot

measurements of water temperature and chemistry at each of three riffles within the study reach. Conductivity [S/m] was determined to the nearest hundredth of a unit using EXTECH ExStik meters. Dissolved oxygen as a percentage of air saturation was measured using a YSI Pro20 meter.

Algae sampling

I collected representative samples of algal community composition and abundance at each study reach. I tracked changes in macro-algae at each reach by setting up nine transects: three at each riffle (Figure 4; Power & Stewart 1987). Transect sites were selected on the first sampling date directly adjacent to the BMI sampling sites and were placed approximately 30-50m apart, depending on the riffle length (Power & Stewart 1987). Along each transect, I measured percentage algal cover, algal conditions and height of major algal groups within a 10 X 10cm quadrat every 0.5-1m (Power & Stewart 1987; Grimm & Fisher 1989). To improve the degree of precision and accuracy, I collected voucher samples and stored on ice for transport back to the laboratory (Power et al. 2009). Algal samples for each transect consisted of scrapings from five bed substrate particles that were selected haphazardly and composited into a single jar kept on ice for microscopic identification as well as for filtration on Whatman glass filters for chlorophyll-a analysis.

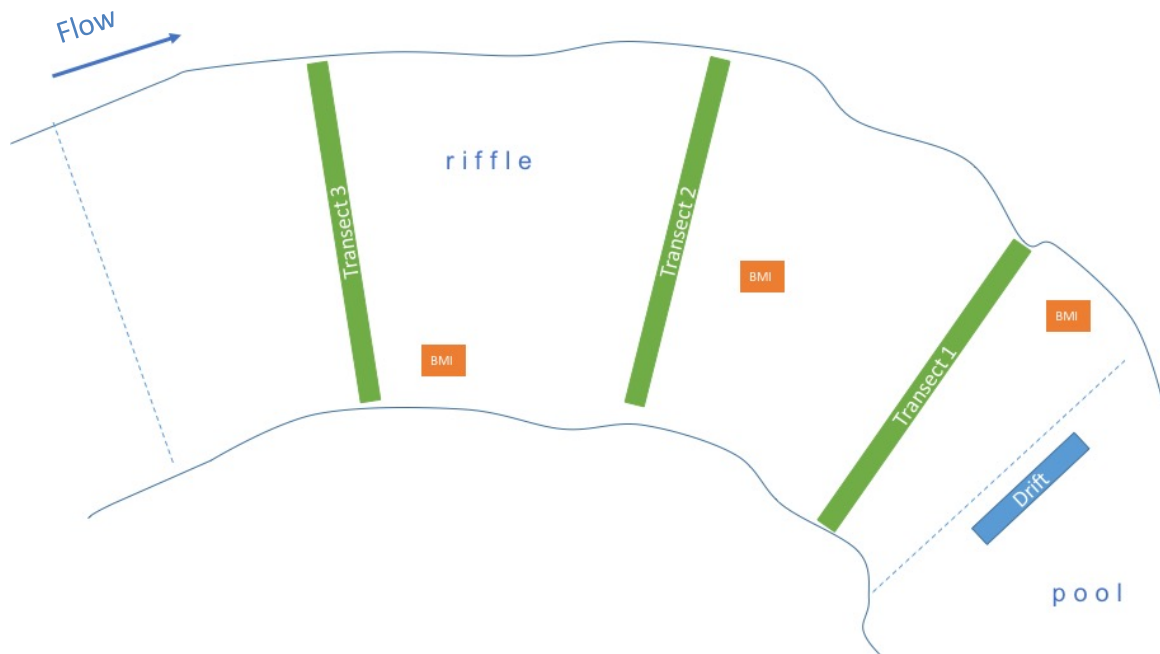


Figure 4. Sampling scheme within each riffle with transect (thick bands), kick-net (squares), and drift net (rectangle) locations approximated with direction of flow defined by the arrow.

Benthic macroinvertebrate sampling

Benthic macroinvertebrate (BMI) sampling occurred one meter downstream of each algal transect within the four study reaches. Three benthic samples were collected in each riffle, composited and preserved in 95% ethanol for laboratory analysis. At each riffle benthic sampling point, a hand-held 500micron mesh D-frame net was placed at the stream bottom facing upstream and the benthic substrate directly upstream in a 30 x 30 cm area was agitated for one minute in order to dislodge benthic macroinvertebrates (Hoffman 2009). The three sampling points were composited at each riffle. Thirty-six benthic samples were to be collected over the duration of the study (3 months x 3 riffles x

2 rivers x 2 reaches= 36 benthic samples); however, in June only two riffles per reach were sampled.

In addition to the BMI benthic samples, drift samples were collected in June 2017, during Chinook outmigration, at the downstream end of each riffle, which is a typical feeding location for juvenile salmonids (Harvey et al. 2005). A drift net with a 30 x 60 cm openings and 500micron mesh was positioned vertically in the water column at 0.1m above the bed with velocity measured with a Swiffer 2100 current velocity meter at the beginning and end of the drift sampling period (Shearer et al. 2002). BMI drift was measured at least two hours after benthic sampling, starting one hour before sunset and ending one hour after sunset to capture the daytime and nocturnal peak for drifting invertebrates and thus, can be somewhat representative of the complete diel composition, yet with more active drifting taxa present (Harvey et al. 2005; Flecker 1992). Twelve BMI drift samples were collected over the duration of the study (1 month x 3 replicates x 2 rivers X 2 reaches=12 drift samples).

Lab Methods

Algae identification and chlorophyll-a

Preserved algal voucher samples were examined under a compound microscope at 400X to identify the major groups: green algae, diatoms and cyanobacteria to the Genus level. A minimum of 400 cells were examined to capture a sufficient sample size of the algal community within each transect. For spectrophotometric measurements of chlorophyll-a, a modified approach of the Environmental Protection Agency's Rapid

Bioassessment Protocols (RBPs) for Streams and Wadeable Rivers was used (Barbour et al. 1999). After a 24-hour extraction in 95% ethanol, the concentration of chlorophyll *a* per unit area ($\mu\text{g}/\text{cm}^2$) in each transect sample was measured with dichromatic readings of the 665nm and 750nm chromatic bands on a spectrophotometer before and after acidification with 0.1 mol HCl to correct for phaeo-pigments densities (Lorenzen 1967). The three transect readings per riffle were averaged to produce riffle chlorophyll *a* values.

Macroinvertebrate Identification and Biomass

In the laboratory, each BMI sample was filtered through stacked 5mm and 500micron mesh to sort larger and smaller material. Macroinvertebrates were identified under a dissecting microscope (up to 40X) to the most relevant and practical taxonomic level (typically Genus for aquatic insect groups, Subfamily for Chironomidae; Family for terrestrial groups and Class for non-insects). In order to estimate drift biomass, the body length of each individual was measured to be used in taxa-specific length weight regressions (Benke et al. 1999; Sabo et al. 2002; Cummins et al. unpublished; Wisseman et al. unpublished). Each taxon was assigned the primary level of functional feeding group according to the Southwest Association of Freshwater Invertebrate Taxonomists (SAFIT) List of Californian Macroinvertebrate Taxa and Standard Taxonomic Effort (CDFG 2011) and An Introduction to Aquatic Insects of North America (4th Edition; Merritt, Cummins and Berg 2008).

Statistical Analysis

The maximum daily mean temperature was found for each year and differences among rivers and years were examined using a two-way ANOVA from the long-term continuous data from 2010-2014. Spot water chemistry measurements were averaged by riffle to reduce diel variation in readings. Then differences in spot water chemistry measurements among rivers, months and sites were tested using three-way ANOVAs with log or square root transformations applied when needed to fit normal distribution, using estimated marginal means for post-hoc comparisons with the “emmeans” function that was developed for linear and generalized linear models with data like this study that have an unbalanced design (Lenth 2018).

Differences between rivers, months and sites in chlorophyll *a* density, *Cladophora* cover, filament length as well as algal genus richness were tested through a three way- ANOVAs with the averages of each riffle at each date. *Cladophora* cover and richness was square root transformed to fit a normal distribution. Post hoc tests of pairwise comparisons were conducted, using estimated marginal means with the “emmeans” function.

General differences in algal/macroinvertebrate composition of each riffle within and across sites, months and rivers were characterized through nonmetric multidimensional scaling (NMDS) ordinations using the R *vegan* package. Continuous

environmental variables were correlated to NMDS axes to examine possible relationships with community composition. Permutational multivariate analyses of variance (PERMANOVA) were used to test for potential differences in community assemblages between rivers, months and sites. When significant interactions between rivers and sites were found, additional PERMANOVAs were run separated by site location to examine differences between rivers over time. Significant associations of specific taxa with certain rivers and sites were tested through indicator species analysis with the R *indicspecies* package, which reveals if certain taxa are driving community differences (De Cáceres 2016).

Differences between rivers, months and sites in taxa richness and Shannon diversity index of benthic macroinvertebrates were tested through three way ANOVAs with square root transformation applied for diversity to fit a normal distribution. Variation in total abundance between rivers, months and sites was tested through a generalized linear model with a negative binomial distribution, which is commonly used for count data. Distinctiveness was also tested through variation between rivers, months and sites in abundances of BMI functional feeding groups using generalized linear models with negative binomial distributions. Variation in abundances of the dominant taxa of each functional feeding group were also tested through generalized linear models with negative binomial distributions. Post hoc tests of pairwise comparisons were conducted, using estimated marginal means with the “emmeans” function.

Differences between rivers, months and sites in drift biomass and density of benthic macroinvertebrates were tested through three way ANOVAs with square root

transformation applied to fit a normal distribution. Post hoc tests of pairwise comparisons were conducted, using Tukey Honest Significant Differences.

RESULTS

Thermal Regimes and Physical Habitats

Differences in seasonal thermal trends were observed between the Middle Fork and Mainstem Eel rivers in summer temperature data from 2010-2014 (Asarian 2016). Peak temperatures on average were 5°C higher and occurred 22 days earlier on the Middle Fork relative to the Mainstem (Figure 5). In addition, temperatures in the Mainstem declined later in the season, suggesting a consistent delay in the summer thermal regime relative to the Middle Fork (Figure 5). The magnitude of variation in temperature over the low flow period was smaller in the Mainstem relative to the Middle Fork across all years.

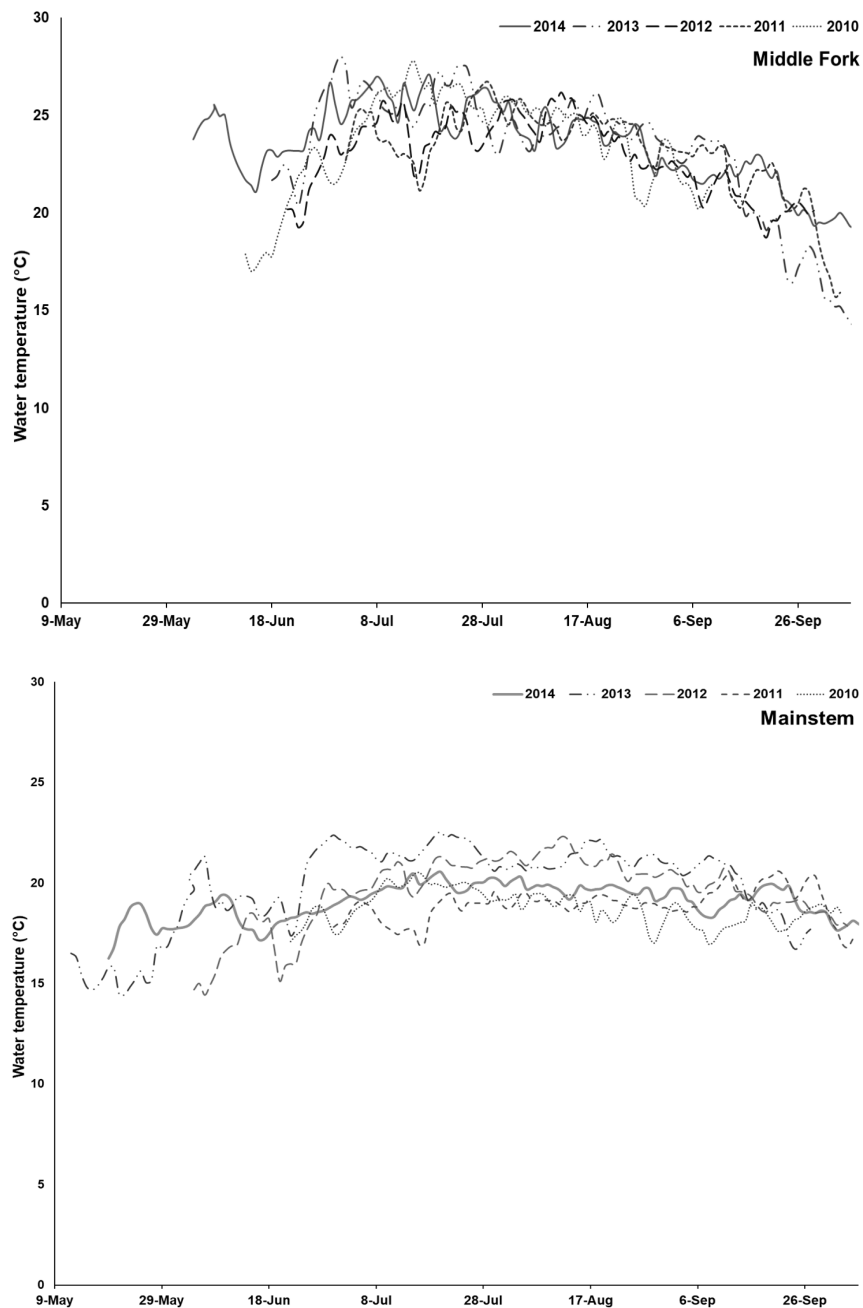


Figure 5. Mean daily temperatures near the upstream sites during the low flow season from 2010 to 2014 for the Middle Fork Eel River below the Black Butte confluence (top) and Mainstem Upper Eel River below Van Arsdale Reservoir (bottom).

In terms of spot water chemistry measurements from this study, the Mainstem and Middle Fork varied in multiple parameters across sites throughout the summer of 2017.

Water temperatures were higher at the downstream sites of both rivers across all sampling months (Table 2: $F(1,68)=20.21$, $p>0.0001$). Based upon pairwise comparisons of estimated marginal means by river, sites and time, June temperatures were lower in the Mainstem compared to the Middle Fork; 11.2°C lower at the downstream sites and 9.2°C lower at the upstream sites ($t(68)=3.15$, $p=0.002$, Table 3,3). River temperatures increased from June to July at all sites, but the Mainstem remained cooler than the Middle Fork by $2\text{-}3^{\circ}\text{C}$. However, in September the Middle Fork was significantly cooler at least at the downstream site by 4°C ($t(68)=-2.52$, $p=0.014$, Table 3). Dissolved oxygen was higher in the cooler Mainstem in June relative to the Middle Fork ($t(68)=-2.56$, $p=0.01$), but by July dissolved oxygen was only significantly higher at the upstream sites ($t(68)=-2.49$, $p=0.015$, Table 3). In September, dissolved oxygen was significantly higher in the Middle Fork compared to the Mainstem ($t(68)=4.31$, $p=0.001$, Table 3). In June, conductivity was higher at the upstream sites on the Mainstem relative to the Middle Fork ($t(68)=7.37$, $p<0.0001$, Table 3). In July, conductivity dropped in the Mainstem and remained lower than the Middle Fork into September ($t_{\text{july}}(68)=5.42$, $p<0.0001$, $t_{\text{sept}}(68)=13.71$, $p<0.0001$).

Table 2. F and p-values from the average spot water chemistry measurements with degrees of freedom of two-way ANOVA analyses of river and sites (upstream: downstream) and time (months) on temperature (Celsius), conductivity ($\mu\text{S}/\text{cm}$) and dissolved oxygen (mg/L) with the degrees of freedom (df), mean squares (MS), and p-value (P). Significant factors are indicated in bold and by asterisk, “*” indicates $p=0.05$, “**” indicates $p<0.005$

<i>Temperature</i>				
	Df	MS	F	P
Time	2	153.9	18.60	<0.0001**
River	1	31.07	3.75	0.070
Site	1	167.2	20.21	<0.0001**
Time X River	2	121.7	14.71	<0.0001**
Time X Site	2	17.86	2.156	0.124
River X Site	1	11.00	1.330	0.253
Time X River X Site	2	4.45	0.537	0.587
<i>Conductivity</i>				
Time	2	23.67	114.7	<0.0001**
River	1	90.41	438.1	<0.0001**
Site	1	14.35	69.56	<0.0001**
Time X River	2	23.04	111.7	<0.0001**
Time X Site	2	8.338	40.40	<0.0001**
River X Site	1	2.534	12.28	0.0008**
Time X River X Site	2	6.616	32.06	<0.0001**
<i>Dissolved Oxygen(mg/L)</i>				
Time	2	128,557	14.24	<0.0001**
River	1	131,473	14.56	0.0002**
Site	1	45,892	5.082	0.027*
Time X River	2	362,103	40.10	<0.0001**
Time X Site	2	38,995	4.318	0.017*
River X Site	1	47.00	0.005	0.943
Time X River X Site	2	53,265	5.899	0.004**

Table 3. Spot water quality measurements (n=3 for each site) on the Middle Fork and Mainstem Eel River in June, July and September 2017. Values in table are mean (\pm standard deviation). Asterisk indicates significant difference between downstream sites and upstream sites of the two rivers with * indicates $p \leq 0.05$ and ** indicates $p \leq 0.005$.

- Water Chemistry Parameters						
Middle Fork	June	Upstream July	- September	- June	- Downstream July	- September
Temperature ($^{\circ}\text{C}$)	24.4 (± 3.2)*	26.8 (± 2.9)*	22.6 (± 3.8)	28.4 (± 3.2)*	29.9 (± 3.1)*	22.9 (± 3.1)**
Dissolved Oxygen (mg/L)	8.29 (± 0.34)*	8.74 (± 0.18)*	9.84 (± 0.68)	8.06 (± 0.20)*	8.57 (± 0.11)	9.59 (± 0.65)
Conductivity ($\mu\text{S}/\text{cm}$)	83.1 (± 8.0)*	126.1 (± 2.8)*	153.8 (± 3.3)*	235 (± 11.3)	123.4 (± 18.9)*	151.3 (± 6.5)*
Discharge (cfs)	89.9	21.5	6.2	184	43.9	12.7
Canopy Cover		0-10%**			10-15%	
Dominant/ Sub-dominant Substrate		Boulder/Cobble			Boulder/Cobble	
Mainstem		-Upstream			Downstream	
Temperature ($^{\circ}\text{C}$)	15.2 (± 0.2)*	23.2 (± 1.6)*	23.1 (± 2.1)*	17.2 (± 1.2)*	27.6 (± 3.2)*	26.3 (± 2.3)**
Dissolved Oxygen (mg/L)	9.72 (± 0.5)*	9.21 (± 0.08)*	8.38 (± 0.78)	9.66 (± 0.03)*	8.36 (± 0.27)	8.49 (± 0.44)
Conductivity ($\mu\text{S}/\text{cm}$)	155 (± 1.5)*	65.9 (± 2.8)*	82.1 (± 2.1)*	190 (± 0.28)	93.7 (± 4.3)*	87.7 (± 3.1)*
Discharge (cfs)	94	52	39	191	44.7	34
Canopy Cover		60-70%**			10-15%	
Dominant/ Sub-dominant Substrate		Cobble/Boulder			Cobble/Boulder	

Substrate composition was similar between the rivers, yet canopy cover was higher at the Mainstem site directly downstream of Cape Horn Dam. The substrate at all four sites was predominately cobble and boulder in the riffles (Table 3). Canopy cover was higher at the Mainstem upstream site (Table 3) relative to the Middle Fork sites likely due in part to encroachment of riparian vegetation downstream of Cape Horn Dam, which has been frequently observed below dams (Gordon and Meentemeyer 2006).

In the 2010-2015 water years, the Mainstem experienced fewer large winter floods relative to the Middle Fork with less gradual spring recessions (Figure 6). The 2017 water year was marked by precipitation that was 134% of the historic average (CDEC 2018), and the two study rivers experienced multiple bankfull or bed-scouring floods as defined by a peak discharge with a 1.5 year recurrence interval (Figure 6). However, the flows of the Mainstem dropped earlier relative to the Middle Fork in the spring as diversions by the PVP began and the duration of its spring recession was approximately 40 days shorter than the Middle Fork (Figure 6). It should be noted that a pulse release flow occurred on the Mainstem in late May 2017 as directed by NMFS and CDFW to facilitate juvenile Chinook outmigration (Figure 7). Sampling for this study began at the end of the recession limb of the pulse flow (early June) (Figure 7).

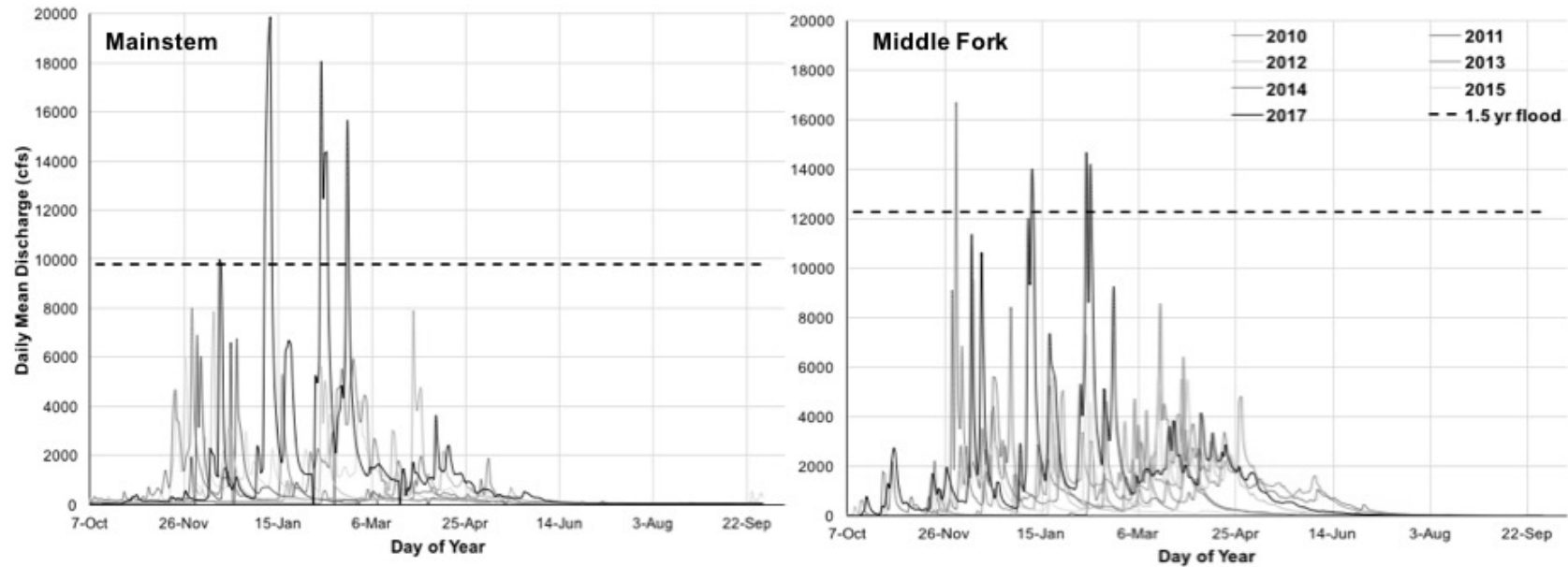


Figure 6. Hydrographs of the 2010-2015 (gray lines), 2017 (black lines) water years for the Upper Mainstem (left) and Middle Fork (right) Eel Rivers at similar drainage areas in the watersheds with the 1.5-year recurrence interval of each river delineated by dashed lines. These hydrographs were constructed from gage data on the Mainstem directly below the Van Arsdale Dam (USGS # 11471500) and estimated using related gage data for the Middle Fork below the confluence with the Black Butte River (USGS # 11473900).

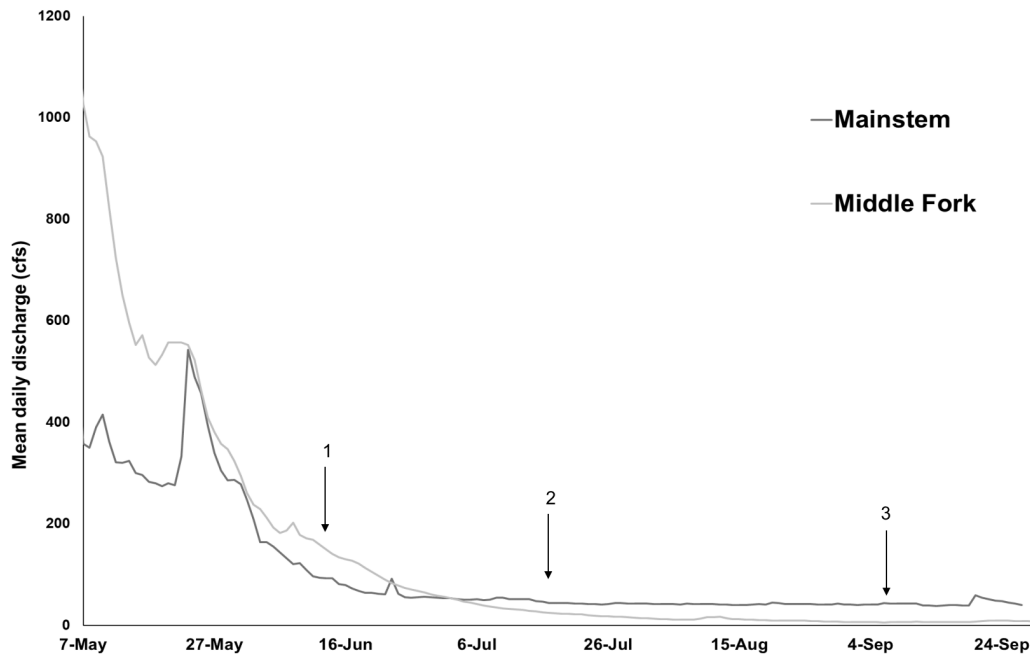


Figure 7. Hydrographs of the spring-summer recession for the 2017 water year for the Upper Mainstem (black line) and Middle Fork (gray line) during which sampling occurred with each date denoted by a numbered arrow. These hydrographs were constructed from gage data on the Mainstem directly below the Van Arsdale Dam (USGS # 11471500) and estimated using related gage data for the Middle Fork above the Mainstem confluence (USGS #11473900).

Algae abundance and composition

Percentage cover of *Cladophora* increased and remained fairly constant throughout the summer across rivers with the exception of the upstream site on the Mainstem (Figure 8). There were no significant differences among sites or rivers in June with similar levels of *Cladophora* observed in both rivers (Figure 8, Table 4). Based upon pairwise comparison of months, an increase of mean cover of *Cladophora* was observed from June to July on the Middle Fork ($t(20)=3.04$, $p=0.008$, Figure 8). In July,

Cladophora cover was higher in the Middle Fork relative to the Mainstem between the downstream ($t(20)=2.74$, $p=0.013$) and upstream sites ($t(20)=4.61$, $p=0.0002$, Figure 8). There were no significant changes in *Cladophora* cover between July and September at either site. In September, there was no significant variation in *Cladophora* cover among rivers and sites (Table 4). On average, based upon pairwise comparisons of months, filament lengths of *Cladophora* grew significantly from June to July on the Middle Fork ($t(20)=-2.62$, $p=0.041$), but this trend was not observed on the Mainstem (Figure 8). In June, the rivers had similar lengths of *Cladophora* while longer at the upstream sites (Figure 8, Table 4). In July, filaments were longer on the Middle Fork relative to the Mainstem at upstream sites ($t(20)=4.87$, $p=0.0001$) and downstream sites (Figure 8, $t(20)=3.71$, $p=0.0014$). From July to September, average filament length of *Cladophora* decreased only on the Middle Fork upstream ($t(20)=3.24$, $p=0.011$) and downstream sites (Figure 8, $t(20)=4.13$, $p=0.0014$). There was no significant variation in lengths of *Cladophora* filaments across river or sites in September.

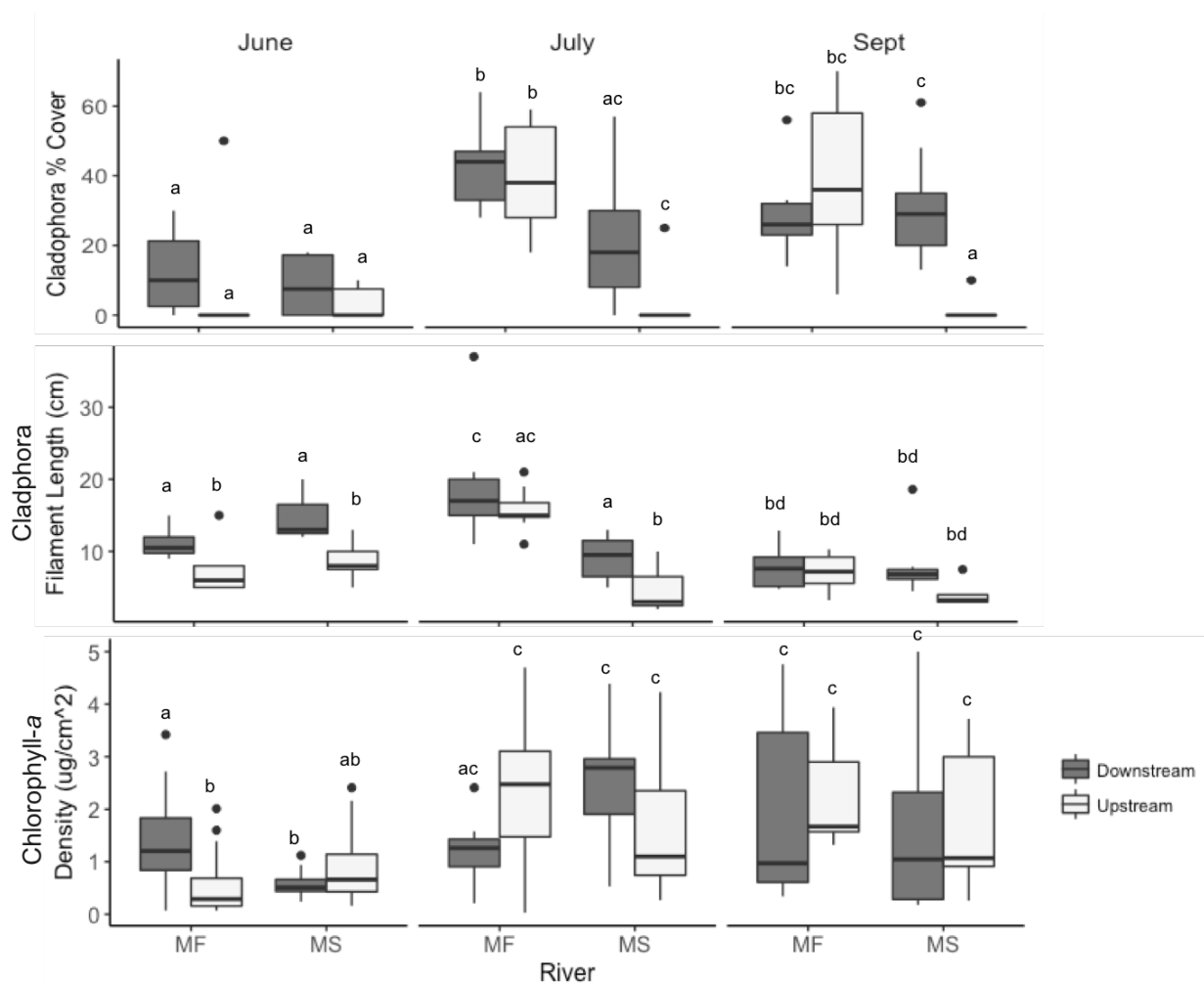


Figure 8. Boxplots of *Cladophora* percentage cover (top), and *Cladophora* filament length in centimeters (middle), and Chlorophyll-a density in micrograms per cubic centimeter (bottom) by river (MF-Middle Fork, MS-Mainstem) and site location (dark grey=downstream, light grey=upstream). Points delineate outliers and letters denote significant differences between sites and months ($\alpha = 0.05$).

Table 4. Analyses of variance in algal growth parameters from June to September in 2017. The F-values and p-values for 3-way ANOVAs by River (Mainstem vs. Middle Fork), Site (downstream vs. upstream), and Time (months). Values significant at the $p \leq 0.05$ level are indicated in bold.

<i>Cladophora</i> % coverage				
	Df	MS	F	P
Time	2	910.4	9.415	0.001
River	1	2775	28.70	<0.0001
Site	1	600.9	6.214	0.0216
Time X River	2	380.1	3.93	0.0363
Time X Site	2	21.79	0.225	0.8002
River X Site	1	868.1	8.977	0.007
Time X River X Site	2	247.3	2.557	0.1026
<i>Cladophora</i> filament length				
Time	2	77.08	7.409	0.004
River	1	217.9	20.95	0.0002
Site	1	66.81	6.422	0.020
Time X River	2	89.71	8.624	0.002
Time X Site	2	7.924	0.762	0.480
River X Site	1	4.985	0.479	0.500
Time X River X Site	2	14.42	1.386	0.273
Chlorophyll- <i>a</i> density				
Time	2	2.679	3.295	0.058
River	1	0.112	0.138	0.714
Site	1	0.002	0.002	0.962
Time X River	2	0.585	0.720	0.499
Time X Site	2	0.350	0.430	0.656
River X Site	1	0.202	0.249	0.623
Time X River X Site	2	3.989	2.453	0.111

There was an overall trend of chlorophyll-*a* densities increasing from June to July with the exception of the downstream sites on the Middle Fork (Figure 8). Average chlorophyll-*a* densities in July were highest at the downstream site on the Mainstem, although not significantly greater than on the Middle Fork sites (Figure 8). However, there were no significant differences among any of the sites from June to September in chlorophyll-*a* densities. In September, there was a high variability in chlorophyll-*a* across all sites (Figure 8).

Based upon the Non-metric Multidimensional Scaling (NMDS) ordinations of the benthic algal communities, taxa shifted across sites over the summer with time of sampling being a key factor, but it was only clear between the downstream sites (Figure 9 & 10, Table 5). The algal communities of the upstream sites on the Middle Fork were different from the upstream sites on the Mainstem (Table 5 : $p=0.005$). In relation to the upstream seasonal trend of algal community assembly, mean flow had relatively high correlation ($R^2=0.469$, $p=0.017$). Canopy cover was the most significant vector ($R^2=0.634$, $p=0.001$), suggesting the differences in algal communities is driven partly by riparian vegetation. At the downstream sites, the composition of benthic algae taxa became relatively similar between the Middle Fork and Mainstem from June to July, but in September the two rivers diverged with the ordination also showing large taxonomic variation within the Middle Fork riffles (Figure 10). The significant vector of mean conductivity ($R^2=0.597$, $p=0.002$) possibly suggests the variation in flow over summer, which was less in the Mainstem, likely plays a more important role where canopy cover varied less so between the two river reaches (Figure 10).

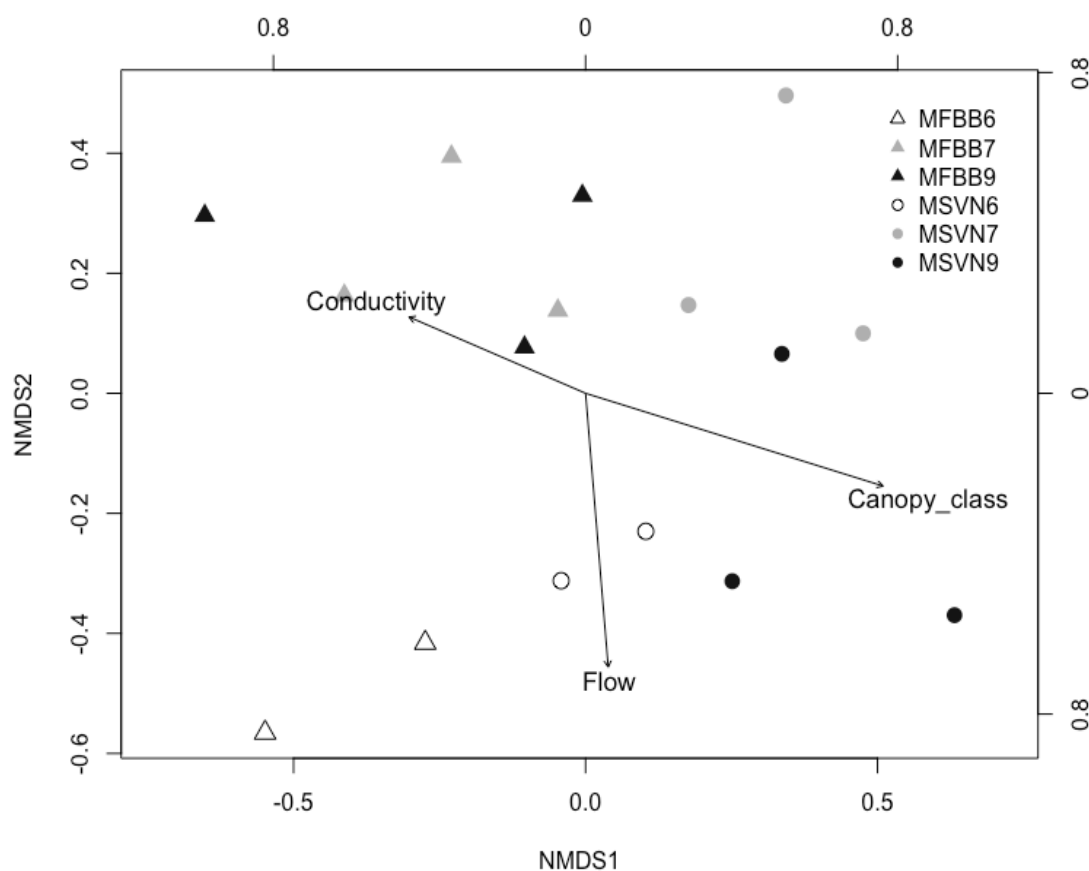


Figure 9. Ordination diagrams for Non-metric Multidimensional Scaling (NMDS) analyses of benthic algal communities of upstream sites in the Middle Fork (triangle) and Mainstem (circle). Numbers and colors refer to the sampling months-June (6-white), July (7-gray), and September (9-black). Environmental variables are overlaid as vectors (R^2 threshold was 0.350) with length and direction indicating the correlation with the ordination. Environmental vectors are: the mean conductivity in microsiemens per centimeter (Conductivity), amount of canopy cover (Canopy_class), and mean discharge in cubic feet per second (Flow). Final stress value was 0.076.

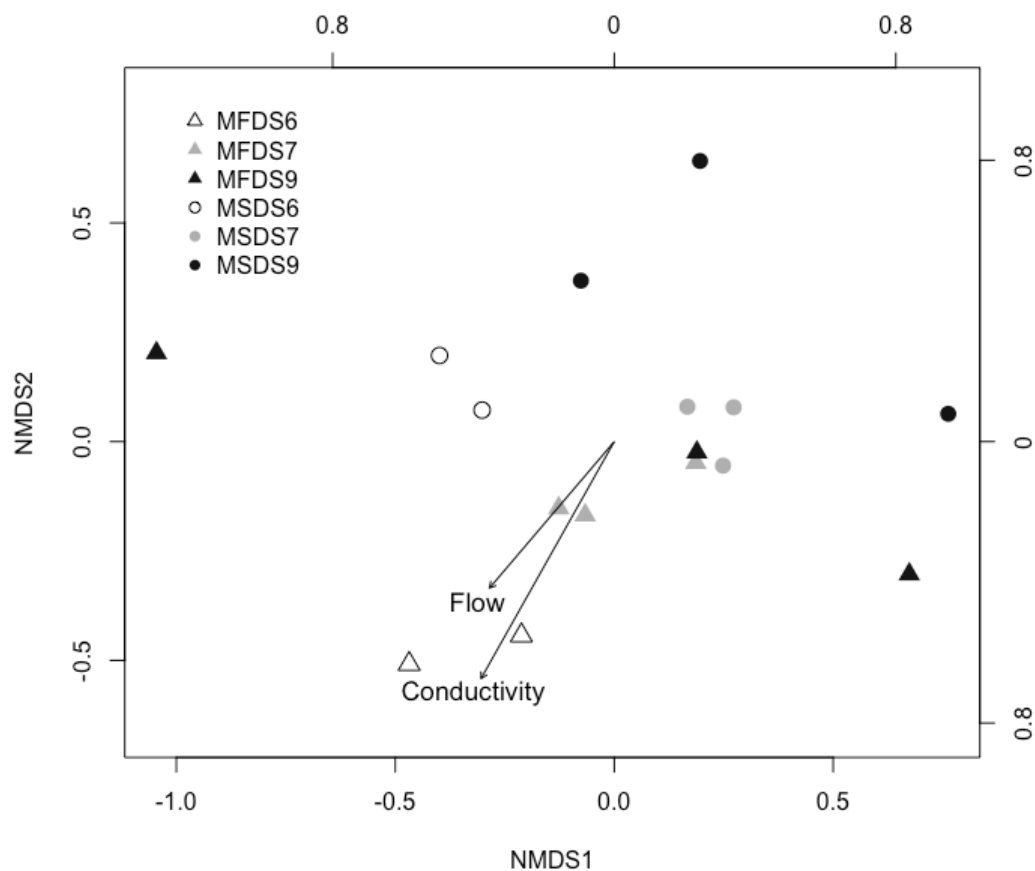


Figure 10. Ordination diagrams for Non-metric Multidimensional Scaling (NMDS) analyses of benthic algal communities of downstream sites in the Middle Fork (triangle) and Mainstem (circle). Numbers and colors refer to the sampling months-June (6-white), July (7-gray), and September (9-black). Environmental variables are overlaid as vectors (R^2 threshold was 0.350) with length and direction indicating the correlation with the ordination. Environmental vectors are: the mean discharge in cubic feet per second (Flow) and mean conductivity in microsiemens per centimeter (Conductivity). Final stress value was 0.065.

Table 5. Results of the PERMANOVA analyses for the benthic algal communities comparing rivers, sampling month and the interaction of the two are the downstream and upstream sites separately with the degrees of freedom(df), mean squares (MS), and permutation significance (P). Significant effects are in bold.

Source of variation	<i>Downstream</i>				<i>Upstream</i>			
	Df	MS	Pseudo-F	P(perm)	Df	MS	Pseudo-F	P(perm)
River	1	0.204	2.07	0.054.	1	0.391	4.85	0.005
Time	1	0.291	2.97	0.035	1	0.228	2.82	0.010
River x Time	1	0.102	1.037	0.473	1	0.	1.64	0.164

Although an increase in algal richness was observed in both rivers from June to July, the Middle Fork had more genera on average in July relative to the Mainstem (Figure 11, $t(20)=2.53$, $p=0.020$). By September, the rivers were similar in algal richness with a slight decline in the Middle Fork (Figure 11). No clear differences in the richness of diatoms, green algae and cyanobacteria was observed between the rivers over the sampling period (Table 7 & 8). However, in July more genera of diatoms and green alga were found in the Middle Fork on average, but the lack of significance was possibly due to limitations of microscopic resolution with small taxa likely under counted.

Table 6. Analysis of variance in algal richness from early to late summer in 2017. The F-values and p-values for a 3-way ANOVA by River (Mainstem vs. Middle Fork), Site (downstream vs. upstream), and Time (months). Values significant at the $p \leq 0.05$ level are indicated in bold.

<i>Genus Richness</i>				
	df	MS	F	P
Time	2	1.493	17.55	<0.0001
River	1	0.428	5.035	0.036
Site	1	0.017	0.202	0.658
Time X River	2	0.097	1.416	0.339
Time X Site	2	0.060	0.704	0.506
River X Site	1	0.059	0.699	0.413
Time X River X Site	2	0.044	0.523	0.601

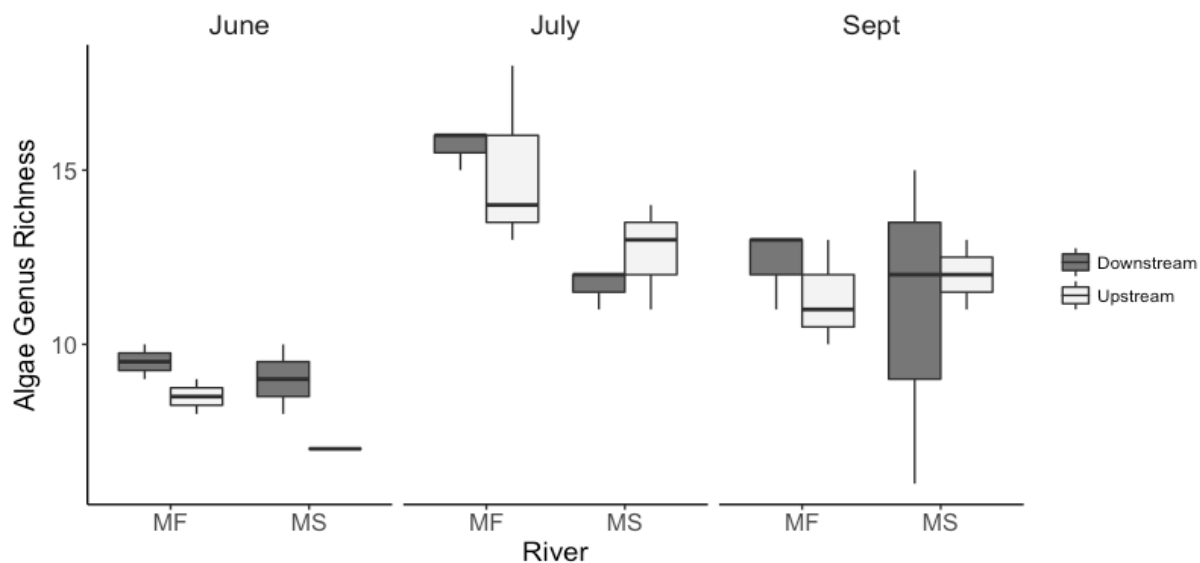


Figure 11. Algae genus richness by rivers (MF-Middle Fork, MS-Mainstem) and sites (Downstream-dark gray, Upstream-light gray) in June, July, and September 2017.

Table 7. Genera of algae (listed in alphabetical order) organized by major algal divisions and by sites and months for the Middle Fork Eel River.

Middle Fork	Downstream			Upstream		
	Month			Month		
	June	July	September	June	July	September
Chlorophyta	<i>Cladophora</i>	<i>Cladophora</i> <i>Pediastrum</i> <i>Scenedesmus</i> <i>Spirogyra</i> <i>Staurastrum</i>	<i>Cladophora</i> <i>Gloeocystis</i> <i>Pediastrum</i> <i>Scenedesmus</i> <i>Spirogyra</i> <i>Stigeoclonium</i>	<i>Cladophora</i>	<i>Ankistrodesmus</i> <i>Cladophora</i> <i>Pandorina</i> <i>Pediastrum</i> <i>Scenedesmus</i> <i>Spirogyra</i> <i>Zygnema</i>	<i>Ankistrodesmus</i> <i>Cladophora</i> <i>Mougetia</i> <i>Pandorina</i> <i>Spirogyra</i> <i>Stigeoclonium</i>
Bacillariophyta	<i>Cocconeis</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Cosmarium</i> <i>Diatoma</i> <i>Epithemia</i> <i>Fragilaria</i> <i>Gomphoneis</i> <i>Gomphonema</i> <i>Melosira</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Cosmarium</i> <i>Cymbella</i> <i>Diatoma</i> <i>Epithemia</i> <i>Fragilaria</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Melosira</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>
Cyanobacteria	<i>Calothrix</i> <i>Nostoc</i>	<i>Anabaena</i> <i>Calothrix</i>	<i>Calothrix</i>	<i>Calothrix</i>	<i>Anabaena</i> <i>Calothrix</i> <i>Nostoc</i>	<i>Calothrix</i>

Table 8. Genera of algae (in alphabetical order) organized by major algal divisions and by sites and months for the Mainstem Upper Eel River.

Mainstem	Downstream			Upstream		
	Month			Month		
	June	July	September	June	July	September
Chlorophyta	<i>Cladophora</i>	<i>Cladophora</i> <i>Closterium</i> <i>Mougetia</i> <i>Scenedesmus</i> <i>Spirogyra</i>	<i>Ankistrodesmus</i> <i>Cladophora</i> <i>Pediastrum</i> <i>Scenedesmus</i>	<i>Cladophora</i>	<i>Cladophora</i> <i>Stigeoclonium</i>	<i>Cladophora</i> <i>Scenedesmus</i> <i>Spirogyra</i> <i>Stigeoclonium</i>
Bacillariophyta	<i>Cocconeis</i> <i>Cymbella</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Cosmarium</i> <i>Cymatopleura</i> <i>Cymbella</i> <i>Diatoma</i> <i>Epithemia</i> <i>Fragilaria</i> <i>Gomphoneis</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Cymbella</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Diatoma</i> <i>Epithemia</i> <i>Fragilaria</i> <i>Gomphoneis</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>	<i>Cocconeis</i> <i>Cymbella</i> <i>Diatoma</i> <i>Epithemia</i> <i>Gomphoneis</i> <i>Gomphonema</i> <i>Navicula</i> <i>Rhoicosphenia</i> <i>Rhopalodia</i> <i>Synedra</i>
Cyanobacteria	<i>Lyngba</i> <i>Nostoc</i>	<i>Anabaena</i> <i>Calothrix</i> <i>Nostoc</i>	<i>Anabaena</i> <i>Calothrix</i>		<i>Anabaena</i> <i>Calothrix</i> <i>Lyngba</i> <i>Phormidium</i>	<i>Anabaena</i> <i>Calothrix</i> <i>Lyngba</i> <i>Nostoc</i>

Macroinvertebrate Abundance and Composition

The abundance and composition of the BMI community differed between rivers from early summer to early fall (Figure 12 & 13, Table 9). The BMI communities of the upstream sites on the two rivers differed throughout the summer (Figure 12, Table 9: $p=0.005$). The community in the Middle Fork in mid-summer was somewhat similar to Mainstem community in early fall (Figure 12). The seasonal shift of the upstream communities was correlated with mean flow (Figure 12, $R^2=0.849$, $p=0.001$). The relative amount of canopy cover, which was notably higher on the Mainstem sites directly below the dam, was also correlated (Figure 12, $R^2=0.593$, $p=0.008$). At the downstream sites, the composition of invertebrates was only different in June and then became more similar in July and September (Figure 13). However, in July there was an outlier from the Mainstem that was riffle with only ten individuals. The only significant vector for the downstream sites was mean flow (Figure 13, $R^2=0.607$, $p=0.006$).

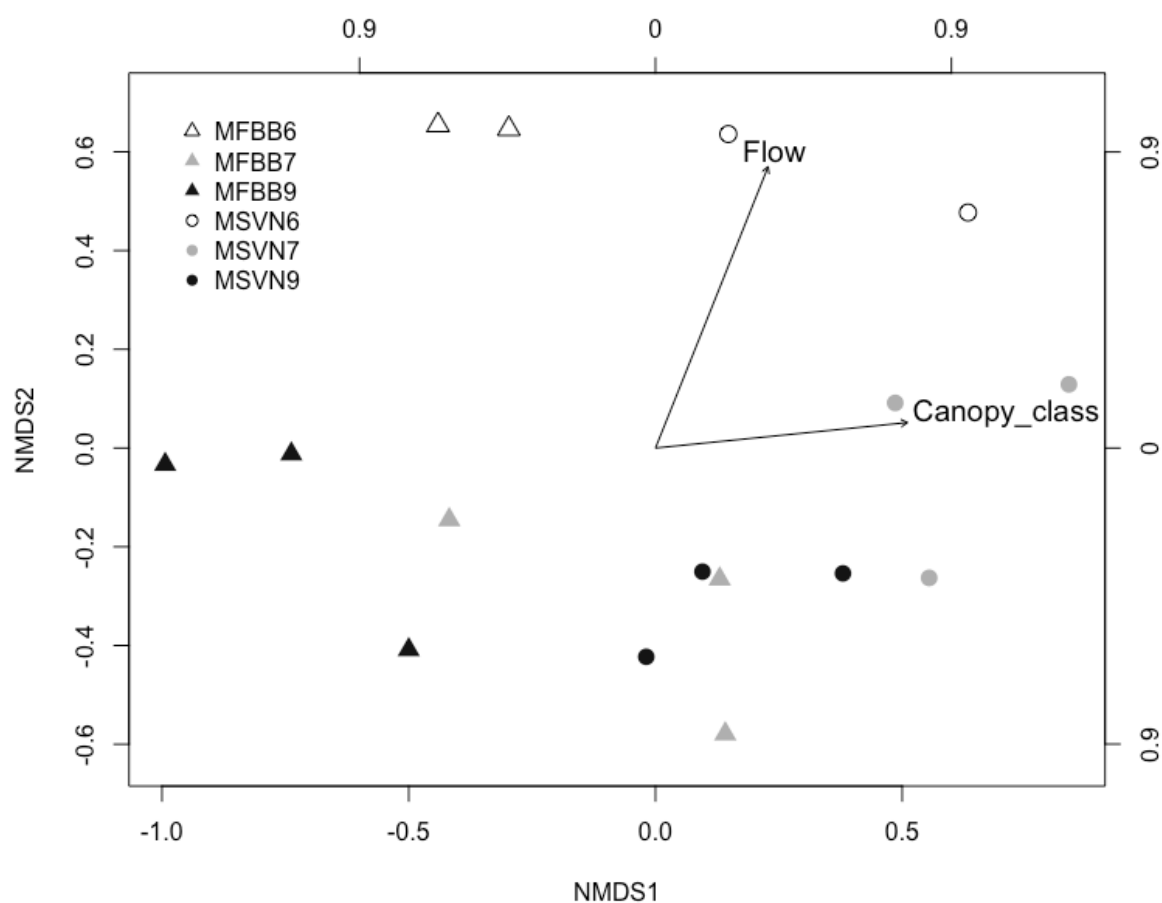


Figure 12. Ordination diagrams for Non-metric Multidimensional Scaling (NMDS) analyses of benthic macroinvertebrate communities, using total abundances of upstream sites in the Middle Fork (triangle) and Mainstem (circle). Numbers and colors refer to the sampling months: June (6-white), July (7-gray), and September (9-black). Environmental variables are overlaid as vectors (R^2 threshold = 0.350) with length and direction indicating the correlation with the ordination. Environmental vectors are: the amount of canopy cover (Canopy class) and mean discharge in cubic feet per second (Flow). Final stress value was 0.103.

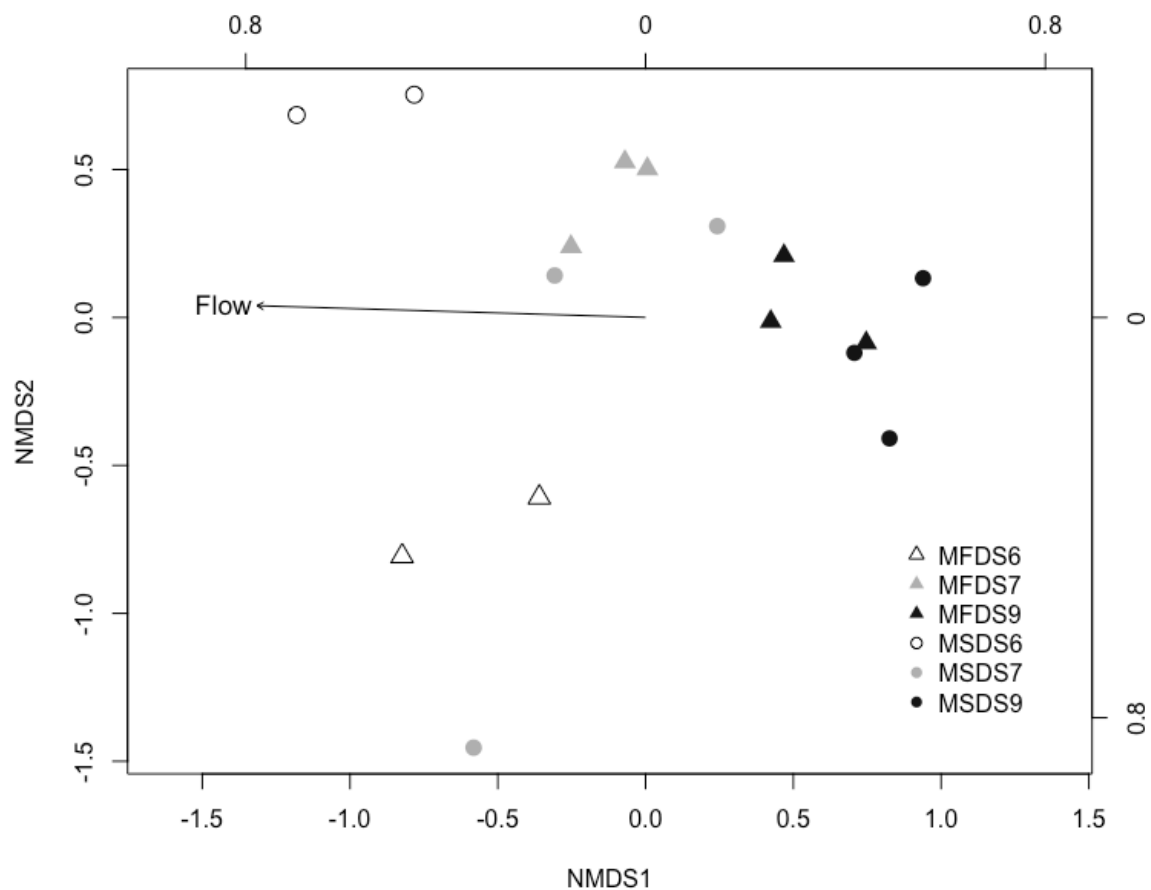


Figure 13. Ordination diagrams for Non-metric Multidimensional Scaling (NMDS) analyses of benthic macroinvertebrate communities using total abundances of downstream sites in the Middle Fork (triangle) and Mainstem (circle). Number and color refer to the sampling months-June (6-white), July (7-gray), and September (9-black). Environmental variables are overlaid as vectors (R^2 threshold = 0.350) with length and direction indicating the correlation with the ordination. Environmental vector is mean discharge in cubic feet per second (Flow). Final stress value was 0.103.

Table 9. Results of the PERMANOVA analyses for the benthic macroinvertebrate communities comparing rivers, sampling month and the interaction for the downstream and upstream sites separately with the degrees of freedom(df), mean squares (MS), permutation significance (P), Significant effects are in bold.

Total Abundance		<i>Downstream</i>			<i>Upstream</i>			
Source of variation	Df	MS	Pseudo-F	P(perm)	Df	MS	Psuedo-F	P(perm)
River	1	0.418	1.20	0.179	1	0.633	2.63	0.005
Time	2	0.720	2.07	0.005	2	0.570	2.37	0.005
River x Time	2	0.422	1.21	0.134	2	0.334	1.39	0.051
Presence-Absence								
River	1	0.220	1.10	0.313	1	0.628	4.09	0.005
Time	2	0.537	2.69	0.005	2	0.414	2.70	0.005
River x Time	2	0.264	1.32	0.134	2	0.231	1.51	0.03
Relative Abundance								
River	1	0.418	1.55	0.059.	1	0.718	3.76	0.005
Time	2	0.649	2.42	0.005	2	0.568	2.97	0.005
River x Time	2	0.352	1.31	0.138	2	0.307	1.61	0.02

Abundance, richness and diversity of macroinvertebrates varied over the summer with a general positive trend (Table 10). Based upon the pairwise comparisons of sites and months, the BMI communities in the Middle Fork and Mainstem increased in total abundance of all taxa from June to July at the downstream sites (Figure 14, Middle Fork- $t(20)=2.62$, $p=0.024$; Mainstem- $t(20)=2.50$, $p=0.033$). BMI abundance was greater in September relative to June in the Mainstem upstream site ($t(20)=4.16$, $p=0.0001$). Based on pairwise comparisons of rivers and months, from June to September BMI taxa richness only increased in the Mainstem downstream site (Figure 14; $t(20)=3.81$, $p=0.003$). There appeared to be a general positive trend in diversity overall, yet similarly in pairwise comparisons of months and sites the only clear increase was observed from June to September at the Mainstem downstream site ($t(20)=-4.13$, $p=0.0014$). The greatest variation in abundance and diversity within a single site was in the Mainstem downstream riffles in July, where only ten specimens were collected from one of the three riffles.

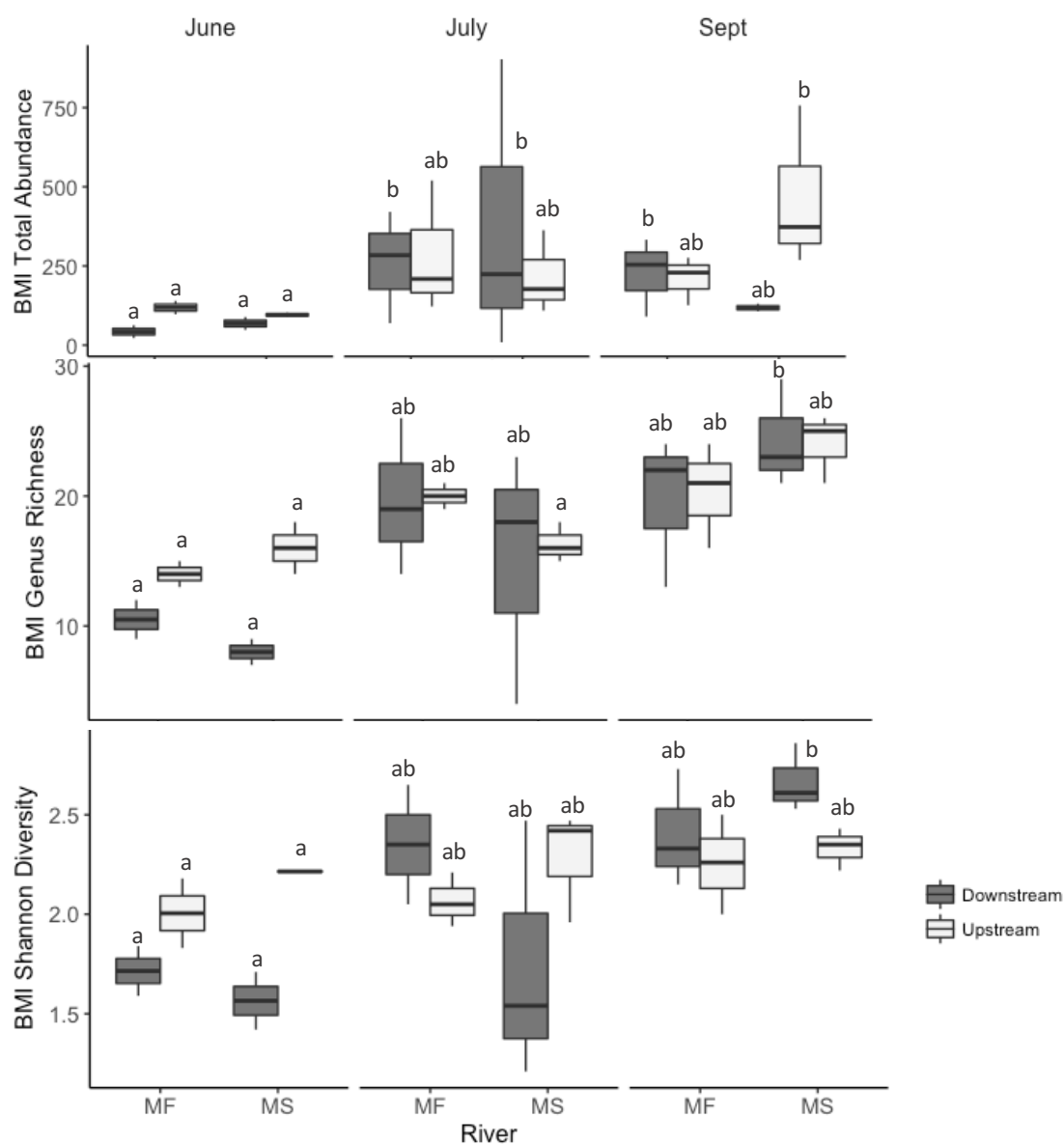


Figure 14. Univariate BMI community metrics of total abundance, genus richness, and Shannon Diversity Index by river (MF-Middle Fork, MS-Mainstem) and site (Downstream-dark gray, Upstream-light gray) over the summer of 2017. Points delineate outliers and letters denote significant differences between sites and months ($\alpha = 0.05$).

Table 10. Analyses of variance in BMI total abundance, richness and Shannon Diversity Index from early to late summer in 2017. The F-values and p-values for 3-way ANOVAs by River (Mainstem vs. Middle Fork), Site (downstream vs. upstream), and Time (months). Values significant at the $p \leq 0.05$ level are indicated in bold.

<i>Total Abundance</i>				
	Df	MS	F	P
Time	2	4.980	6.159	0.021
River	1	0.016	0.019	0.089
Site	1	2.385	2.950	0.099
Time X River	2	0.0004	0.0005	0.982
Time X Site	2	0.003	0.004	0.951
River X Site	1	0.307	0.379	0.543
Time X River X Site	2	1.246	1.541	0.226
<i>Taxa Richness</i>				
Time	2	473.8	21.84	<0.0001
River	1	0.030	0.001	0.970
Site	1	26.28	1.211	0.282
Time X River	2	35.00	1.613	0.216
Time X Site	2	33.67	1.552	0.225
River X Site	1	2.530	0.117	0.736
Time X River X Site	2	8.830	0.407	0.530
<i>Shannon Diversity Index</i>				
Time	2	25.97	16.66	0.0004
River	1	0.097	0.062	0.805
Site	1	0.106	0.068	0.797
Time X River	1	0.791	0.508	0.483
Time X Site	2	10.74	6.892	0.014
River X Site	1	2.852	1.830	0.189
Time X River X Site	1	2.349	1.507	0.231

Functional Feeding Groups

Across major functional feeding groups, the rivers varied in seasonal trends in both the downstream and upstream sites (Figure 15 & Figure 16). Based on pairwise comparisons by site and month, in June more filtering collector individuals ($t(20)=-3.02$, $p=0.002$) were in the Mainstem compared to the Middle Fork at the downstream site, but with the development of the BMI community into the summer, filterer collectors became

more abundant in both rivers (Figure 15). However, by September, the Mainstem had higher abundances of filterer collectors in the upstream site relative to the Middle Fork (Figure 15, $t(20)=-2.08$, $p=0.038$). From pairwise comparisons by sites and months, the Middle Fork had more scraper individuals than in the Mainstem downstream sites in June (Figure 15, $t(20)=2.59$, $p=0.01$). Scrapers increased in the downstream sites from June to July in both rivers. The Mainstem upstream sites had more scraper individuals in July ($t(20)=-3.32$, $p=0.009$) and September (Figure 15, $t(20)=-2.04$, $p=0.041$). The abundance of gathering collectors increased from June to July with the exception of the upstream sites on the Mainstem with fewer gathering collector individuals than on the Middle Fork based on pairwise comparisons (Figure 15, $t(20)=1.98$, $p=0.048$). Gathering collector abundance decreased in the downstream sites of the Mainstem, and became less abundant relative to the Middle Fork in September (Figure 16, $t(20)=2.70$, $p=0.007$). Predators increased in abundance through the summer, except in the Middle Fork upstream sites (Figure 16). Based on pairwise comparisons by months and sites, the Middle Fork had higher abundances of predators in the downstream sites relative to the Mainstem in July (Figure 16, $t(20)=2.72$, $p=0.007$). The Mainstem had higher abundances of predators in the upstream sites than on the Middle Fork in July as well in September (Figure 16, July- $t(20)=-2.28$, $p=0.022$; September- $t(20)=-4.63$, $p<0.0001$). Based upon the functional feeding groups ratio of predator to all other functional groups with a threshold of 0.10, the BMI community of the Mainstem immediately below the dams (0.12) is the only one that appears to be under top-down control by invertebrate predators (other sites ≤ 0.08) (Merritt et al. 2002). No clear differences were found across the other functional group

ratios. Shredders were in relatively low abundance in June and July, but the Middle Fork downstream site had higher shredder abundances in September relative to the Mainstem based on pairwise comparisons ($t(20)=2.87$, $p=0.0041$).

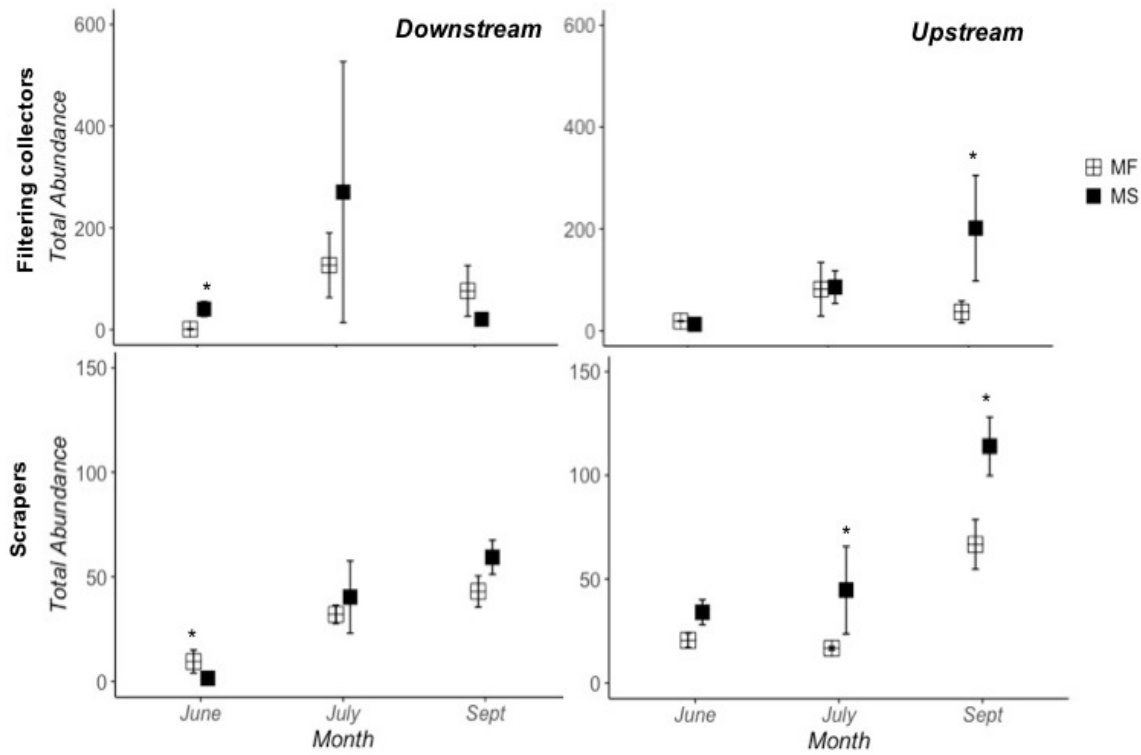


Figure 15. Interaction plots of sampling month and rivers (MF-Middle Fork, MS-Mainstem) by downstream (left) and upstream (right) sites for Filtering Collectors (top) and Scrapers (bottom). Total abundance is the number of individuals ± 1 standard error. Asterisk denote significant differences between rivers within months. * p-value ≤ 0.05).

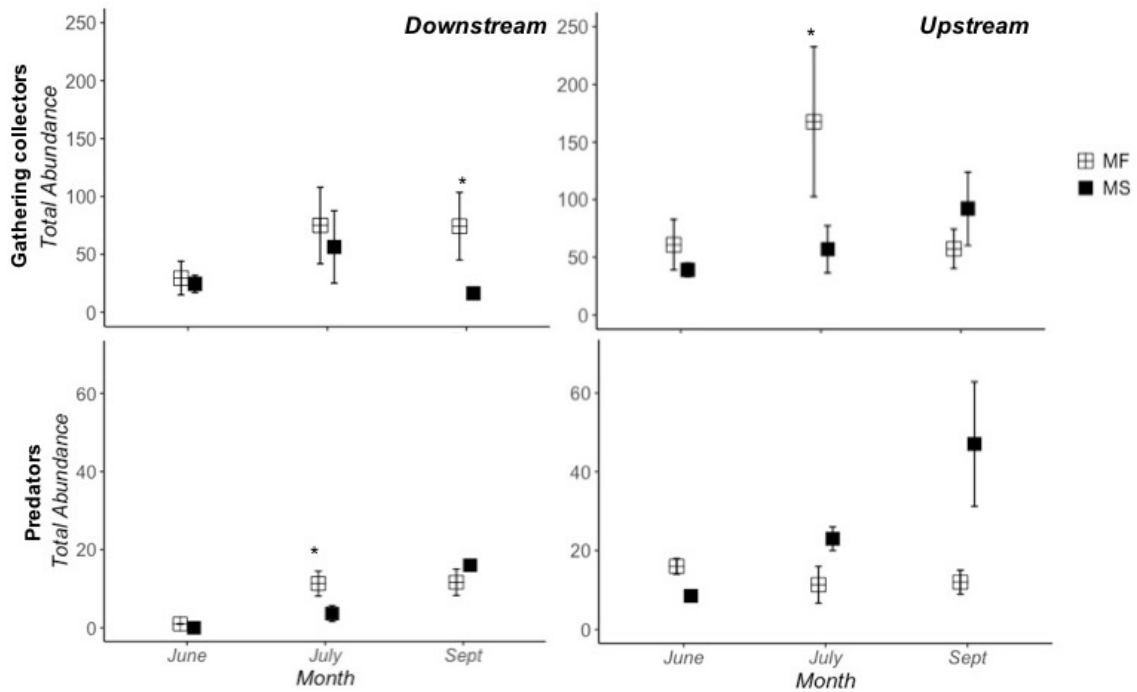


Figure 16. Interaction plots of sampling month and rivers (MF-Middle Fork, MS-Mainstem) by downstream (left) and upstream (right) sites for Gathering Collectors (top) and Predators (bottom). Total abundance is the number of individuals \pm 1 standard error. Asterisk denote significant differences between rivers within months. * p-value \leq 0.05).

Indicator taxa analysis

Significant associations of specific genera among sites and rivers were tested using the R package-“indicspecies.” Larval *Marilia* (Odontoceridae, Trichoptera), a caddisfly genus known to be a generalist collector was found to be significantly associated with the Middle Fork sites ($p=0.004$). *Isonychia* (Isonychidae, Ephemeroptera), a brushfoot mayfly known as a filtering collector was significantly associated with the Mainstem sites ($p=0.034$). The free-living predatory caddisfly,

Rhyacophila (Rhyacophilidae, Trichoptera) was significantly associated with upstream sites on the Mainstem ($p_r=0.001$).

Common taxa of the functional feeding groups

In order to test if specific taxa were influencing the observed differences in the communities and functional feeding groups, the abundance of most common taxa of each functional feeding group was examined from benthic kick samples. *Cheumatopsyche* (Hydropsychidae, Trichoptera), a filtering collector was observed to be more abundant in the Mainstem than the Middle Fork in the upstream sites in September ($p=0.0039$). Yet *Hydropsyche*, another common hydropsychid filtering collector genus was not found to significantly differ in abundance between the rivers during the sampling period. *Zaitzevia* (Elmidae, Coleoptera), a scraper that was most abundant in the early summer, was found at significantly higher abundances in the Middle Fork in June ($p=0.028$). *Baetis* (Baetidae, Ephemeroptera), a common mayfly gathering collector occurred at significantly higher abundances on the upstream sites ($p=0.0015$), but did not significantly vary among rivers or time. *Chironominae*, a sub-family of Chironomidae (Diptera) made of mostly gathering collectors, became increasingly more abundant over the summer (Merritt and Cummins 2009, Fig 17). In July, there were significantly higher abundances of *Chironominae* in the Middle Fork in upstream ($p=0.0016$) and downstream sites (Fig 17, $p=0.018$). Abundances of *Chironominae* remained significantly higher in the downstream sites in the Middle Fork into September relative to the Mainstem (Fig 17, $p=0.0013$). *Calineuria* (Perlidae, Plecoptera), a predatory stonefly

increased in abundance as the summer progressed and was found significantly more so in the upstream sites of the Middle Fork than in the Mainstem (Fig 17, $p=0.038$).

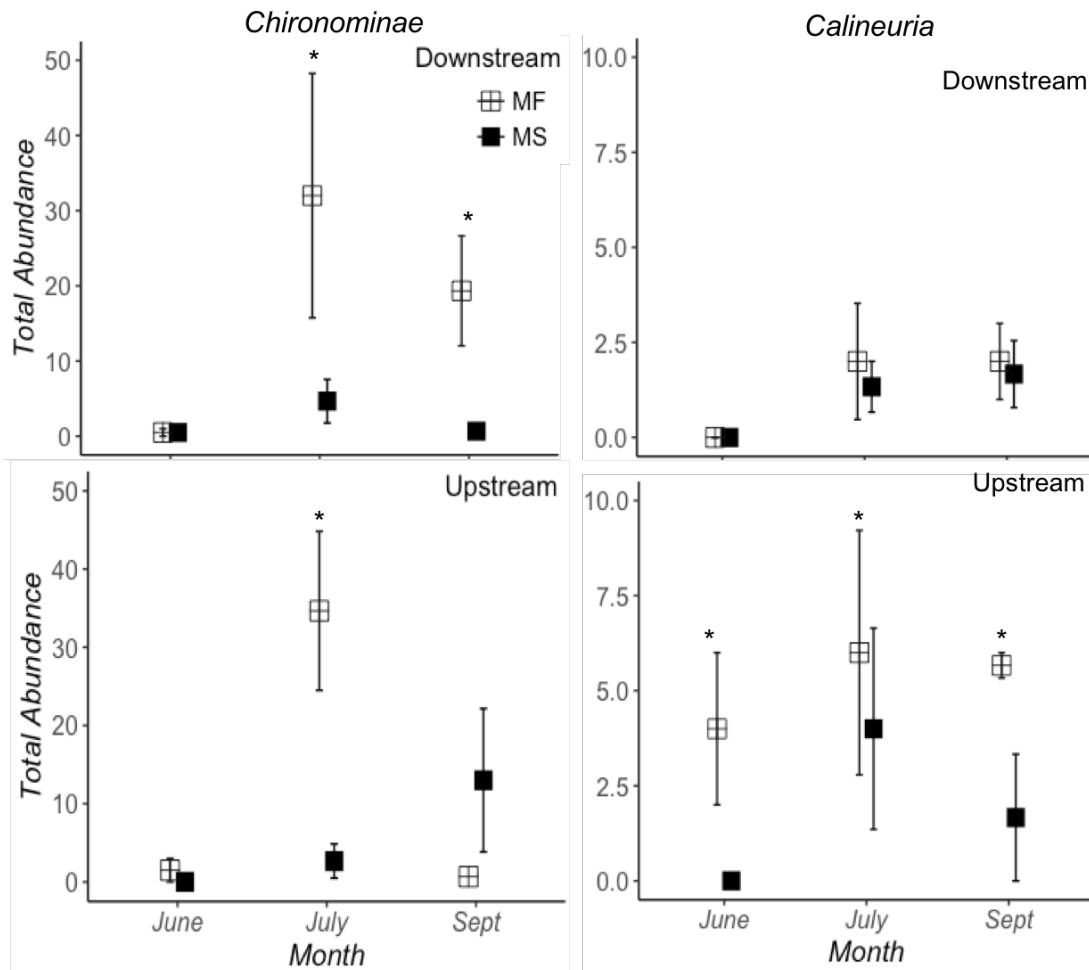


Figure 17. Interaction plots of sampling month and rivers (MF-Middle Fork, MS-Mainstem) by downstream (top) and upstream (bottom) sites for *Chironominae* (left) and *Calineuria* (right). Total abundance is the number of individuals ± 1 standard error.

Grazers of *Cladophora*

A subset of taxa was created based upon previous literature to test if there were differences in the abundances of taxa directly associated with *Cladophora* as either a grazer or shredder of senesced material (Dodds 1990, Dodds & Gudder 1994, Feminella et al. 1998, and Power et al. 2008). The five most abundant taxa that made up this functional group were *Petrophila*, *Ochrotrichia*, *Tricorythodes*, *Baetis* and Chironominae. Based on pairwise comparisons of sites and months there was only one clear difference; in September with higher abundances in the downstream sites of the Middle Fork relative to the Mainstem (Figure 18, $t(20)=2.09$, $p=0.036$). When *Baetis*, a common generalist taxa that did not differ between rivers, was removed from the dataset it revealed more distinct patterns (Figure 18). Based on pairwise comparisons of the downstream sites and months, the Middle Fork had significantly higher grazer abundances in July (Figure 18, $t(20)=1.91$, $p=0.05$). At the upstream sites, the Middle Fork experienced a large increase from June to July that resulted in significantly higher abundances than the Mainstem in July (Figure 18, $t(20)=3.14$, $p=0.002$). However, in September there was clear drop in grazer abundances in the upstream sites of the Middle Fork (Figure 18).

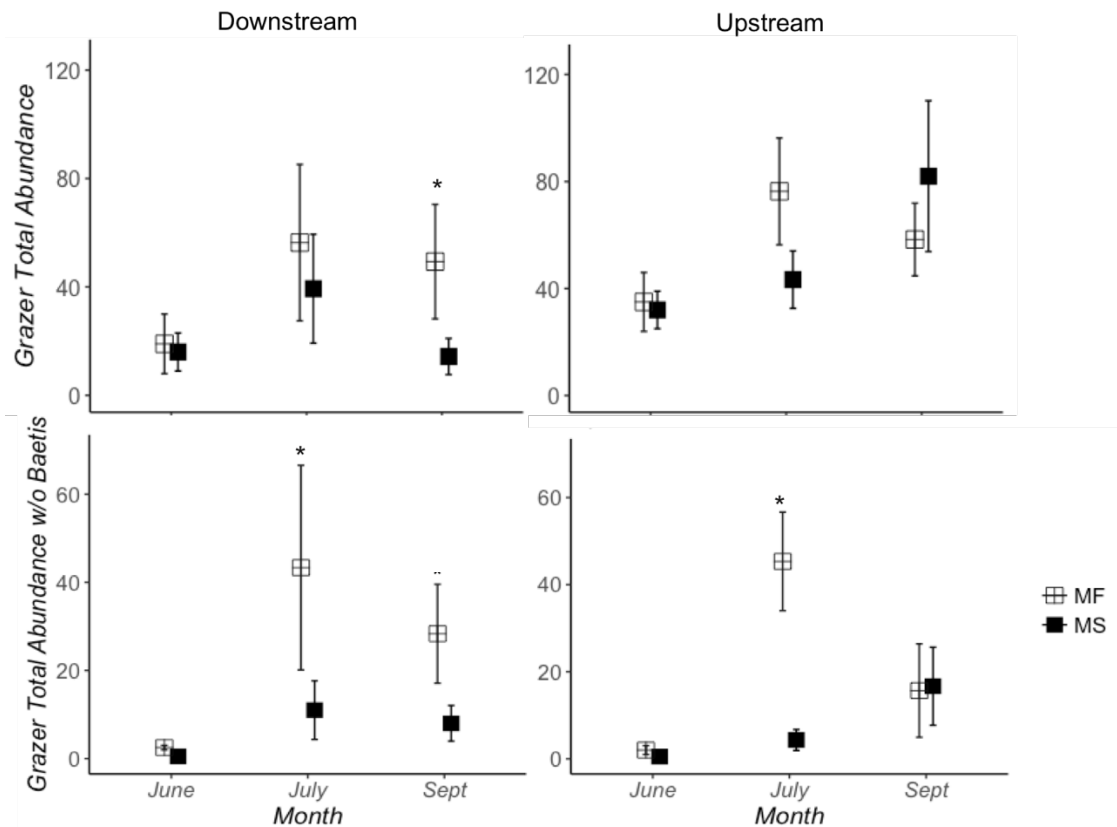


Figure 18. Interaction plots of sampling month and rivers (MF-Middle Fork, MS-Mainstem) by downstream (left) and upstream (right) sites for *Cladophora* grazers with *Baetis* (top) and without *Baetis* (bottom). Total abundance is the number of individuals ± 1 standard error. Asterisk denote significant differences between rivers within months. (* p-value ≤ 0.05).

Drift density and biomass of benthic macroinvertebrates

Macroinvertebrate drift in June differed among the rivers and sites in terms of abundance and composition. As the densities of terrestrial invertebrates that do not have an aquatic life stage are often not related to the densities of the benthic macroinvertebrates, they were removed from the analyses (Shearer 2003). Terrestrial invertebrates were also only a small proportion, making up on average 5% of the drift in the Middle Fork and 1% in the Mainstem. BMI drift biomass (mg/m^3) varied between rivers and sites (Table 11) as based on pairwise comparisons of sites and months, the

Middle Fork downstream site having significantly higher drift biomass than the Mainstem (Tukey HSD: Upstream- $p=0.02$, Downstream- $p=0.004$). Drift density (number of individuals/m³) also varied ($F_{1,8}=38$, $p=0.003$) between rivers with slightly lower densities at the upstream site at the Middle Fork (Table 11, Figure 19). Drift density was greater in the Middle Fork downstream site relative to the Mainstem (Figure 19, Tukey HSD: $p=0.002$). The Middle Fork upstream site also had significantly higher densities than the upstream Mainstem site (Tukey HSD: $p=0.017$). Based on pairwise comparisons by sites, the number and biomass of emerging adult aquatic invertebrates was significantly higher at the Middle Fork downstream sites relative to the Mainstem sites (Tukey HSD: Upstream- $p=0.017$, downstream- $p=0.002$). With aquatic adults excluded in pairwise comparisons of sites, the biomass was still significantly higher in the Middle Fork than the Mainstem (Tukey HSD: $p=0.005$). The most common order found across all samples was Ephemeroptera, a generally highly mobile order and largely made up of *Baetis* (Radar 1997). Yet the Middle Fork sites had significantly greater densities and biomass of Ephemeroptera relative to the Mainstem sites based on pairwise comparisons (Figure 20, Tukey HSD: biomass- $p=0.003$, density- $p=0.0002$). Therefore, the density and biomass of aquatic dipterans did not significantly vary between the two rivers, but dipterans did make up a greater proportion of the Mainstem drift relative to the Middle Fork sites with and without the inclusion of emerging adults (Figure 20).

Table 11. F and p-values from the June 2017 drift sampling with degrees of freedom of two-way ANOVA analyses of river and sites (upstream: downstream) on BMI drift biomass (mg/m^3) and drift density (no of individuals/ m^3) with the degrees of freedom(df), mean squares (MS), and p-value (P). Significant factors are indicated by asterisk, “*” $p=0.05$

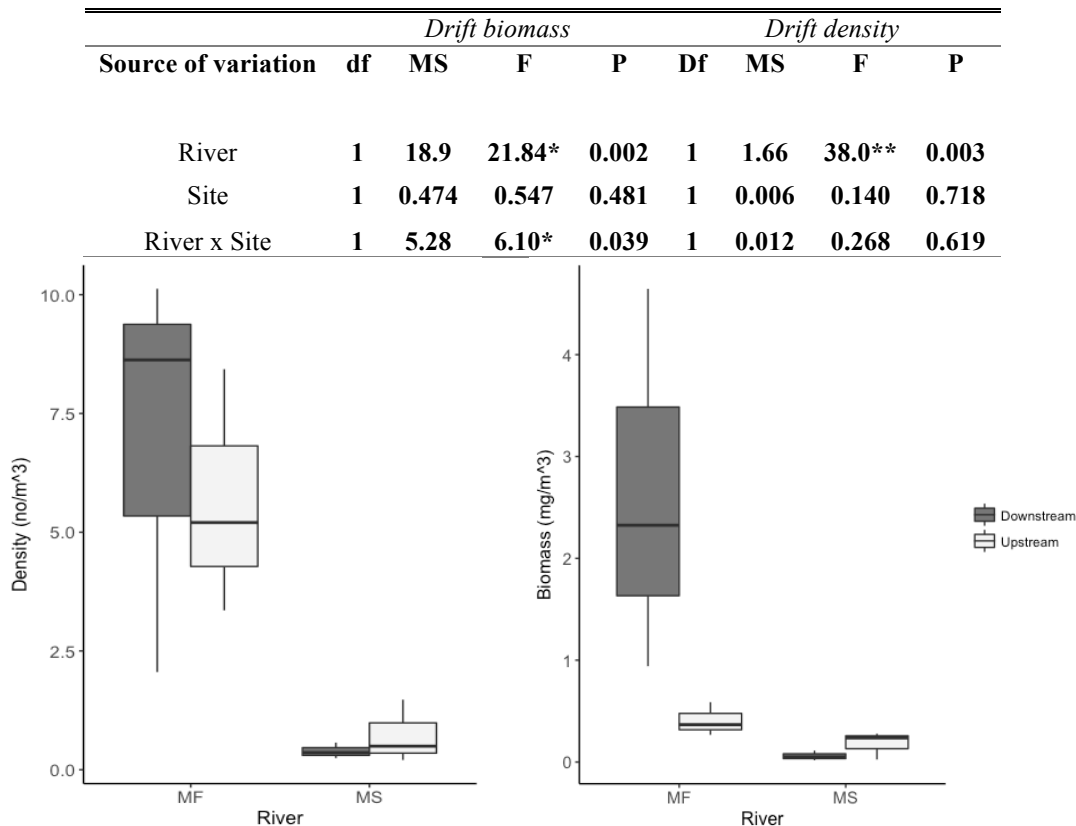


Figure 19. BMI metrics from the June 2017 drift sampling. Left: Mean density of BMIs per unit volume (no. of individuals/ m^3). Right: Mean biomass of drifting benthic macroinvertebrates per unit volume (mg/m^3) across rivers (MF-Middle Fork, MS-Mainstem) and sites (US-Upstream, DS-Downstream). Only adults of aquatic origin were included as terrestrial invertebrates were excluded.

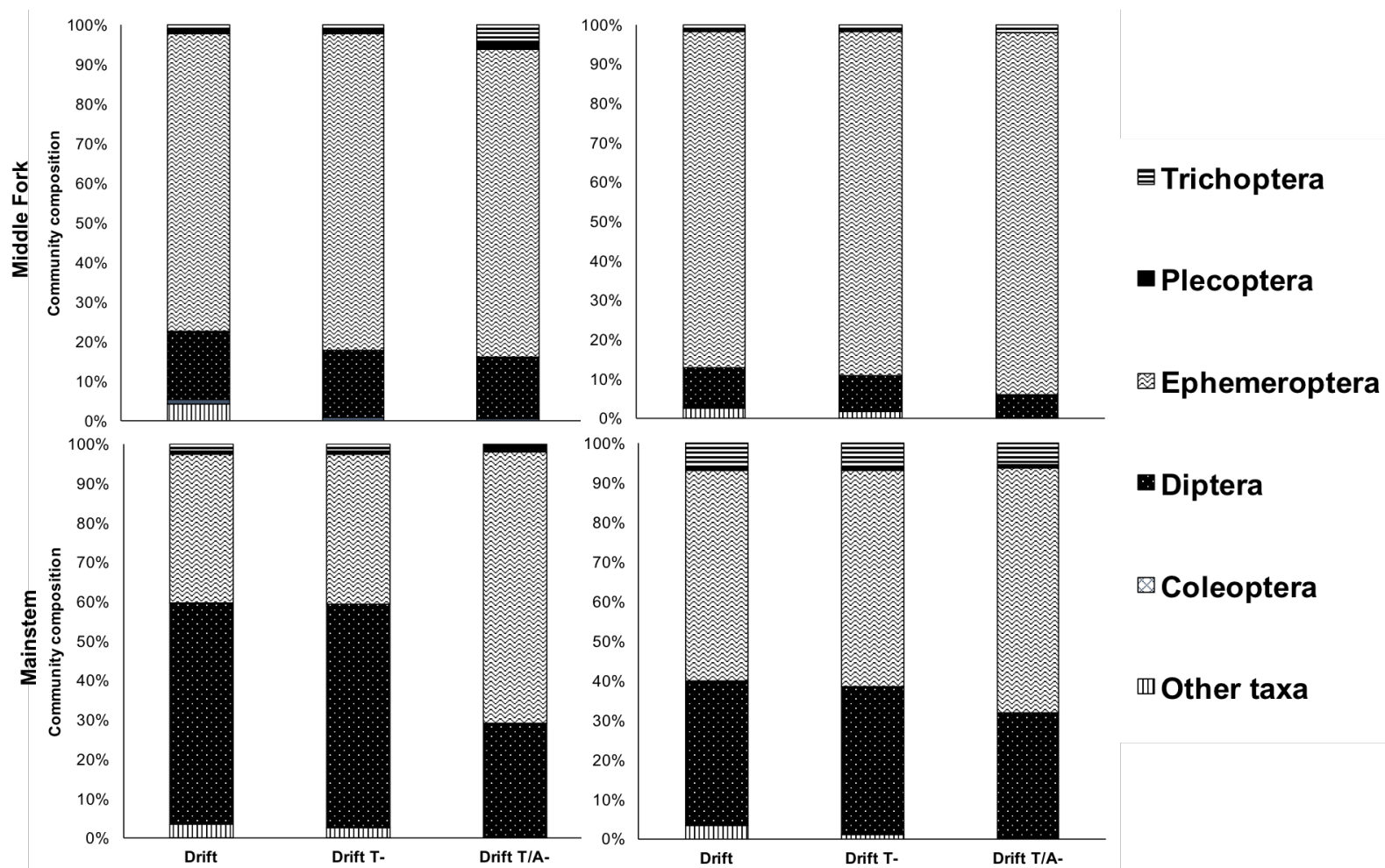


Figure 20. Percentage composition of drift of the Middle Fork (top) and Mainstem (bottom) by sites (downstream-left, upstream-right). (T-, terrestrials excluded, TA-, terrestrials and emergent adults of aquatic insects excluded).

DISCUSSION

Long term trends in flow and temperature

The Middle Fork Eel River is inherently a warmer river system than the Upper Mainstem Eel with greater sun exposure due to its predominantly western aspect. In contrast, the Upper Mainstem Eel River is relatively cooler because of its southern aspect and more canopy cover especially at the study reach directly downstream of Cape Horn Dam. Moreover, the seasonal variability of river temperatures also differs between the two rivers with the timing of peak temperatures and rate of change over the summer being greater in the Middle Fork, appearing to have a somewhat bell shape (Asarian 2016; Figure 5). Large dam systems like Scott Dam that typically release water at the bottom (CDFG 1976) can often shift the timing of maximum water temperatures to later in the summer and can keep temperatures artificially cooler for great distances downstream when tributary and groundwater influences are minimal (Olden & Naiman 2010; Preece and Jones 2002). River temperature monitoring in 2015-2016 on the Mainstem above Scott Dam found maximum water temperatures occurred around mid-July, about 20 days earlier than the 2010-2014 average downstream of Van Arsdale Dam (Native Fish Society 2017). Based upon the spot water quality measurements in 2017, the Middle Fork was warmer on average, but cooled down in the early fall, which was not observed on the Mainstem (Table 2). The constant release of Mainstem summer base flows resulted in higher flows in the Mainstem in the late summer relative to the Middle

Fork; therefore, water temperatures in the Mainstem were less sensitive to cooling air temperatures in the early fall due to higher thermal capacity. Reservoirs can reduce the annual and daily temperature fluctuations downstream, causing a more stable thermal regime (Ward and Stanford 1983; Olden & Naiman 2010). Lake Pillsbury, the large reservoir (811 ha) above Scott Dam is stratified with a longer residence time compared to the smaller and shallower Van Arsdale Reservoir. The cold bottom water release from Scott Dam has been shown to be a significant thermal disturbance on Chinook juvenile migration (CDFG 1976; NMFS 2002). While some warming by solar radiation occurs in the 19.3km of river between Lake Pillsbury and Van Arsdale reservoir it is unlikely to be sufficient to remove the thermal depression created by Scott Dam. Therefore, the low seasonal variability observed downstream on the Mainstem relative to the Middle Fork is probably due in part to the PVP regulated flows.

During the above average water year of 2017, the Eel River experienced 34% greater rainfall than the historical average, which allowed the PVP dams to spill to such a degree that scouring floods occurred downstream. In 2010-2015, the Mainstem had a shorter spring recession limb, resulting in an earlier drop to base flows relative to the Middle Fork (Figure 6). Yet in 2017 a spring pulse release extended the recession, reducing the difference in the recession limbs between the Mainstem and Middle Fork. Dam diversions have been shown to create steeper and shorter recessions with more stable base flows, which can result in lower heterogeneity in the downstream channel conditions (Yarnell et al. 2010). Although Mediterranean watersheds experience a large range of interannual climate variability, causing inherent variability in the timing and

duration of the recession limb, the flow regime of the Mainstem shows a consistently steeper spring recession regardless of water year relative to the Middle Fork (Yarnell et al. 2010). Modeled unregulated flows on the Mainstem show a longer and relatively later spring recession limb (Asarian 2015). In addition, the consistent flow magnitude of the summer dam release and elevated late summer base flows observed on the Mainstem typify a regulated river, which can result in artificially higher abundances of invertebrates, but with more tolerant taxa (Bunn and Arthington 2002). This alteration of the spring and summer flows by the dams on the Mainstem can disrupt the life cycles of sensitive invertebrates and fish, which are adapted to natural flow fluctuations (Bunn and Arthington 2002).

Water chemistry

In June, at the end of the spring recession, specific conductivity was higher with the increased turbidity as flows changed rapidly at all sites with the exception of the Middle Fork upstream sites. As specific conductivity has been shown to be inversely related to flow, the stable and higher summer flows likely also reduced conductivity on the Mainstem from mid- to late-summer relative to the Middle Fork (Allan and Castillo 2007). Some regulated rivers have only a slight drop in total dissolved solids while others showed a rise (Ward & Stanford 1983; Byren & Davies 1989). As the Mainstem and Middle Fork rivers are of similar geology and climate, it is unlikely another external factor is having a greater effect than flow. Cooler temperatures on the Mainstem in the early summer likely influenced the higher levels of dissolved oxygen compared to the

Middle Fork, where dissolved oxygen increased into the later summer likely in part due to increasing primary production and cooler temperatures by September (Allan and Castillo 2007). Yet as diel and short-term variation can be significant, continuous monitoring is needed to accurately describe the physicochemical trends of these two rivers (Nimick et al. 2011).

Algal community

The algal community composition shifted over the summer of 2017 in both rivers. For example, *Cladophora*, a common and key genus of green alga was less prevalent in the Mainstem in July with fewer epiphytic genera (Tables 5 & 6). The development of *Cladophora* was delayed in the Mainstem relative to the Middle Fork as slightly greater *Cladophora* cover and diatom diversity was observed by September on Mainstem near the confluence. *Cladophora* is a warm water alga, so significant increases in growth are often observed as temperatures climb with peak growth of some strains occurring at 27°C or greater (Dodds & Gudder 1994). Therefore, later peak summer and overall cooler temperatures on the Mainstem likely contributed to a later and smaller peak extent of *Cladophora* growth. As many of the diatom genera found in the Eel Rivers are epiphytic in nature, the later *Cladophora* growth likely delayed their rise in abundance (Power 1990a; Furey 2012). Lower coverage of *Cladophora* has implications for the rest of the Eel River food web, as the growth of many invertebrate taxa has been linked to the growth of *Cladophora* (Power et al. 2008). Although other regulated rivers have increased periphyton including green algae, fewer other green algae were present on the

Mainstem directly downstream of the dams, which is likely due to the higher canopy cover from encroached riparian vegetation that reduced light availability (Sze 1998; Smolar-Zvana & Mikos 2014). In combination, this resulted in distinct communities between the two rivers at the upstream sites, growing more different over the summer with more cyanobacteria genera in the Mainstem immediately below the dam. If the Mainstem, like other regulated rivers, has increased water clarity near the dam, this could partially influence the algal community composition as cyanobacteria prevalence often increases with decreasing turbidity (Huisman et al. 2004). In dry years, when baseflows begin earlier and are lower as a result of dam regulation, these community-level differences could be even greater as the Mainstem tilts more to a cyanobacteria-dominated system (Power et al. 2015).

Benthic macroinvertebrate metrics

Although lower benthic macroinvertebrate (BMI) richness and abundance have been observed in regulated systems relative to unregulated reaches (Munn et al. 1991, Steel et al. 2017), there was no notable variation in BMI richness and abundance between the Mainstem and Middle Fork Eel Rivers observed in this study. As both rivers experienced bankfull winter floods in the 2017 above average water year, the BMI communities of both rivers showed similar patterns of abundance and richness from summer into the early fall (Figure 14) with increasing time since the last floods and increasing primary production (Power et al. 2008). The BMI communities of Mediterranean climates are adapted to a naturally variable flow regime as diversity can

be even higher following large winter floods (Power et al. 2008; Lobera et al. 2016). This inherent resilience has likely allowed the core community of BMIs to persist across both rivers even with varying flow and temperature conditions (Allan and Castillo 2007). As the BMI taxa have the capacity for aerial dispersal and are relatively small bodied (midges in the family Chironomidae and minnow mayflies in the genus *Baetis*) dispersal limitation of the regional species pool is likely low (Bie et al. 2012). Dam regulation in other river systems has not always resulted in reduced BMI richness, but instead shifts in BMI composition (Lobera et al. 2016).

Although most of the dominant BMI taxa were fairly consistent among sites, there were differences in abundance of some BMI taxa between rivers, with the BMI community immediately below Cape Horn Dam on Mainstem being the most distinct. Some regulated rivers vary in the composition of major BMI orders between regulated to unregulated reaches, with shifts in channel narrowing, riparian encroachment, flow and temperature (Ward and Stanford 1979; Lobera 2016). In particular, the diversity and abundance of caddisflies can change or decline notably below impoundments (Ward and Stanford 1979; Munn et al. 1991). The caddisfly genus *Rhyacophila* was found in far greater numbers immediately below Cape Horn Dam on the Mainstem, which may be due in part because this free-living caddisfly prefers cooler temperatures (Wiggins 1990). Yet some small caddisfly genera such as *Marilia* and *Helicopsyche* (Helicopsychidae, Trichoptera) that were found in the Middle Fork were nearly absent in the Mainstem (Wiggins 1990). Stoneflies that are amongst the most sensitive BMIs varied somewhat, with *Pteronarcys* (Pteronarcyidae, Plecoptera) a shredder of decaying leaves, as the most

common in the shaded reach below Cape Horn Dam while *Calineuria*, a taxa negatively associated with regulated rivers, was less abundant in the dammed Mainstem relative to the unimpounded upstream sites of the Middle Fork (Ward 1992; Steel et al. 2017). The composition of Ephemeroptera at all sites was fairly similar with the exception of *Isonychia* (Isonychiidae), which is a genus known to be sensitive to water chemistry, which was more common on the Mainstem, perhaps due to cooler temperatures and lower ionic concentrations (Echols 2010). In general, the regulated flows in this study did not appear to consistently reduce the number of sensitive taxa in the Mainstem compared to the Middle Fork. Instead, select taxa drove the differences in BMI community structure in the regulated and unregulated rivers in this study.

Benthic Macroinvertebrate Functional Feeding Groups

Over the summer, collectors became the most prevalent functional feeding group (FFG) followed by scrapers, with gathering collectors predominantly in the Middle Fork and filtering collectors more so in the Mainstem (Cummins & Klug 1979). These patterns were driven in part by the Mainstem caddisflies being more dominated by Hydropsychidae in the later summer with greater numbers of the more tolerant genus *Cheumatopsyche* below the dam, which has been associated with regulated rivers (Wiggins 1990; Munn et al. 1991; Steel et al. 2017). Although other studies have found certain gathering collectors like the midges of the sub-family Orthocladinae more common downstream of dams, Orthocladinae, and more so Chironominae, were more abundant in the Middle Fork (Munn et al. 1991; Steel et al. 2017). This difference in

collectors suggests the Middle Fork has higher levels of benthic organic matter like macro-algae and lower levels of suspended organic matters with declining flows like fine particle detritus relative to the Mainstem (Cummins & Klug 1979). Scrapers also increased in abundance, and even though no differences in benthic chlorophyll-*a* between rivers were observed, scrapers grew more common by July in the Mainstem immediately below the dam than in the upstream Middle Fork sites (Figure 15). While scrapers are commonly associated with benthic algae, these groups can also subsist on detritus (Cummins & Klug 1979). In addition, scrapers cannot fully represent the broad range of grazers especially when filamentous algae are highly prevalent, which scrapers do not readily feed upon (Sze 1998). Previous stable isotope analyses in another tributary of the Eel River showed gathering collectors, a group that was less common in the Mainstem, also derived most of their diet from algae (Finlay 2002).

There were no consistent differences in BMI predator abundances at the confluence, but immediately below the dam there were higher numbers of predators relative to the Middle Fork by late summer (Figures 16 & 17). Based upon the functional group ratio of predators to all other functional groups, with a range of 0.10-0.20 developed by Merritt and others (2002), there potentially is a greater influence of top-down forcing than bottom-up on the BMI community below Cape Horn Dam with an average ratio of 0.12 for predators to all other FFGs compared to the other study reaches (≤ 0.08). Therefore based upon the same ratio, net primary production of the other sites may be likely driven more by top-down forces such as grazers (Power 1992). The substantial canopy and riparian vegetation at the upstream Mainstem site below Cape

Horn Dam may be preferred by certain predator taxa such as Odonates (*Agria* and *Ophiogomphus*) for cooler temperatures for nymphs and greater perch selection in the riparian vegetation for adults (Hofmann and Mason 2004). However, differences in trophic interactions can only be made evident through experiments of predator exclusion.

Grazers of *Cladophora*

As a major basal resource of the Eel River food web, *Cladophora* had lower peak summer coverage in the Mainstem, which resulted in fewer of the associated grazers relative to the Middle Fork (Power et al. 2008). The grazing community that subsists either directly on *Cladophora* or on its epiphytes is diverse, ranging from hydroptilid piercers to tuft-weaving midges to the aquatic moth *Petrophila* (Crambidae, Lepidoptera) (Dodds 1990; Dodds & Gudder 1994; Feminella et al. 1998; Power et al. 2008). Although the mayfly genus *Baetis*, which was common throughout both rivers, has been commonly associated with *Cladophora*, it is also a generalist that can readily subsist on detrital matter as well (Dodds & Gudder 1994; Willoughby 1988). Therefore, grazer abundances when examined without *Baetis*, showed a pattern that more reflected the growth of *Cladophora* with the highest abundances observed in July and peak filament lengths of *Cladophora* on the Middle Fork. As Power (2008) and others found previously, in a water year marked by several winter scouring floods, heavily cased caddisflies like *Gumaga* (Sericostomatidae, Trichoptera), which readily grazed down the algal community, were in low abundance. In the Middle Fork, chironomid midges were the most common grazers in July at the peak of *Cladophora* coverage as it also yellowed

with more loosely attached epiphytes such as *Rhopalodia*, a preferred food source (Furey et al. 2012). Although there was a later bloom in *Cladophora* in the Mainstem at the confluence, a consistent increase in grazers, including *Baetis*, was not observed, possibly because it was too late in the season and therefore not aligned with their development. The smaller extent and delay of seasonal *Cladophora* growth appears to support lower abundances of grazers, which can serve as a major resource for higher trophic levels (Power et al. 2008).

Food Availability for Fish

Overall abundance and diversity of benthic macroinvertebrates, including those considered readily available as food to salmonids (Radar 1997) were not significantly higher in the unregulated Middle Fork. However, BMI drift in June was significantly higher in density and biomass in the Middle Fork relative to the Mainstem at similar flow levels. This was driven primarily by significantly higher numbers of the highly mobile *Baetis* in the Middle Fork, which was the single most common taxa in the drift samples among rivers and sites. While BMI population density can be a key factor in drift densities, the abundance of *Baetis* in the June benthos samples was not significantly higher in the Middle Fork compared to the Mainstem, suggesting other variables were influencing this disparity (Pearson & Franklin 1967). Temperature can be an important environmental variable on *Baetis* drift rates, and can result in higher rates of drift with warmer temperatures as those observed in the Middle Fork in summer (Pearson & Franklin 1967). In addition, as the delayed rise in temperatures in the Mainstem likely

slowed the growth of *Cladophora*, the delay and slower rate of change may have slowed the development of *Baetis* (Munn et al. 1991). *Baetis* may have been at an earlier instar in the Mainstem relative to the Middle Fork as they were a millimeter shorter on average. In terms of development, Muller (1966) found that drift densities increased as *Baetis* reached pupation and emergence, and a significant emergence event was observed on the Middle Fork during the sampling period. This has potential repercussions for out-migrating Chinook juveniles, which are moving through the Upper Eel in the early summer and could have reduced tolerance to rising summer temperatures with lower prey availability (Beauchamp 2009). However, further sampling over multiple time points is needed to test if this depression in early summer drift in Mainstem is a consistent pattern.

CONCLUSIONS

In an above average water year, the regulated Mainstem and the unregulated Middle Fork both experienced several winter scouring floods with relatively high summer base flows. These conditions likely improved the overall success of the biota with relatively similar diversity and abundances of primary producers and macroinvertebrates between rivers. However, the Mainstem had a shorter spring recession limb as well as a delayed and reduced rise in water temperature that was likely due to the dam flow regulation. This altered thermal regime in the Mainstem potentially had an effect on the seasonal growth of *Cladophora* and its associated grazers, with lower levels of both *Cladophora* and BMI grazers observed in the regulated Mainstem relative to the unregulated Middle Fork. The Mainstem supported more filter feeders compared to the Middle Fork, especially tolerant taxa such as *Cheumatopsyche* as well as predators including *Rhyacophila* immediately below the dam where temperatures were cooler compared to the Middle Fork. The BMI drift in early summer was notably lower in the Mainstem relative to the Middle Fork, which could suggest food limitation for Chinook juveniles. However, as the assembly of the biotic communities of the Eel River are well known for having a high degree of interannual variability, additional years of sampling are needed to elucidate the ecological impacts of the PVP dam system on the downstream ecosystem (Power et al. 2008). In addition, a greater number of sites along the Mainstem downstream of the dams along with more frequent sampling would provide a more

complete picture of how the community changes longitudinally over the season. The primary aspect of the Mainstem (northwest) and Middle Fork Eel Rivers (southwest) may have a significant influence on water temperature and light availability. Future studies should examine the Mainstem above the PVP dams as well to see if the downstream communities are significantly altered relative to the upstream reaches as there appears to be possible but limited effects of flow regulation, changing the composition of the biotic communities. Relative to an unregulated tributary, dam regulation appears to have a potentially significant impact on *Cladophora* and its associated community of epiphytes and grazers, which are a key component of the Eel River food web. Additional studies are warranted to further elucidate the extent of the dam's impact on the food web of the Upper Mainstem Eel River.

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APPENDIX A

Appendix A: Macroinvertebrate taxa found in the Upper Eel study reaches, grouped for analysis using functional feeding groups (FFGs) and associated grazers in *Cladophora*. Abbreviations of FFGs are provided: scraper (SC), shredder (SH), gathering collector (GC), filtering collector (FC), piercer (PC) and predator (P).

Order	Family	Genus/ Sub-family	FFG	<i>Cladophora</i> grazer
Coleoptera	Elmidae (larvae)	<i>Heterlimnius</i> , <i>Microcylleopus</i> , <i>Narpus</i> , <i>Neolmis</i> , <i>Optioservus</i> , <i>Ordobrevia</i> , <i>Zaitzevia</i>	SC	N
	Elmidae (adult)	<i>Microcylleopus</i> , <i>Narpus</i> , <i>Neolmis</i> , <i>Optioservus</i> , <i>Ordobrevia</i> , <i>Stenelmis</i> , <i>Zaitzevia</i>	SC	N
	Eulichadidae	<i>Stenocolus</i>	SH	N
	Hydrophilidae	-	GC	N
	Psphenidae	<i>Psphenus</i>	SC	N
	Ptiliidae	-	SC	
Diptera	Blephariceridae	<i>Blepharicera</i>	SC	N
	Ceratopogonidae	<i>Bezzia</i> , <i>Palpomyia</i> , <i>Stilobezzia</i>		
	Chironomidae	<i>Chironominae</i> , <i>Orthocladinae</i> <i>Tanypodinae</i>	GC	Y
	Empididae	<i>Oregoeton</i>	P	N
			P	N

Order	Family	Genus/ Sub-family	FFG	<i>Cladophora</i> grazer
Ephemeroptera	Ephydriidae	<i>Ephydra</i>	SH	N
	Simuliidae	<i>Prosimulium</i> , <i>Simulium</i> , <i>Twinnia</i>	FC	N
	Stratiomyiidae	<i>Caloparyphus</i> , <i>Euparyphus</i>	GC	N
	Tipulidae	<i>Hexatoma</i>	P	N
	Baetidae	<i>Acentrella</i> , <i>Baetis</i> , <i>Heterocloeon</i> , <i>Procleon</i>	GC	Y
	Ephemerellidae	<i>Drunella</i>	SC	N
	Heptageniidae	<i>Ephemerella</i> , <i>Serratella</i>	GC	N
		<i>Cinygma</i> , <i>Cinygmula</i> , <i>Ecdyonurus</i> , <i>Epeorus</i> , <i>Ironodes</i> , <i>Nixe</i>	SC	N
	Isonychidae	<i>Isonychia</i>	FC	N
	Leptohyphidae	<i>Asioplax</i> , <i>Tricorythodes</i>	GC	Y
Hemiptera	Leptophlebiidae	<i>Paraleptophlebia</i>	GC	N
	Hebridae	<i>Hebrus</i>	P	N
	Naucoridae	<i>Ambrysus</i>	P	N
	Saldidae	<i>Calacanthia</i>	P	N
	Veliidae	<i>Rhagovelia</i>	P	N
Lepidoptera	Crambidae	<i>Petrophila</i>	SC	Y
Odonata	Coenagrionidae	<i>Argia</i> , <i>Chromagrion</i>	P	N
	Gomphidae	<i>Gomphus</i>	P	N
	Libellulidae	<i>Brechmorhoga</i>	P	N
Plecoptera	Chloroperlidae	<i>Alloperla</i> , <i>Haploperla</i> , <i>Suwalia</i> , <i>Sweltsa</i> , <i>Utaperla</i>	P	N
		<i>Kathroperla</i>	GC	N

Order	Family	Genus/ Sub-family	FFG	<i>Cladophora</i> grazer
Trichoptera	Perlidae	<i>Calineuria</i> , <i>Hesoperoperla</i>	P	N
	Perlodidae	<i>Isoperla</i> , <i>Setvena</i>	P	N
	Pteronarcyidae	<i>Pteronarcys</i>	SH	N
	Brachycentridae	<i>Micrasema</i>	GC	Y
	Glossosomatidae	<i>Glossosoma</i>	SC	Y
	Helicopsychidae	<i>Helicopsyche</i>	SC	N
	Hydropsychidae	<i>Cheumatopsyche</i> , <i>Hydropsyche</i>	FC	N
	Hydroptilidae	<i>Hydroptila</i> , <i>Leucotrichia</i> , <i>Metrichia</i> , <i>Neotrichia</i> , <i>Ochrotrichia</i>	PC	Y
	Odontoceridae	<i>Marilia</i>	SH/GC	N
	Philopotamidae	<i>Chimarra</i> , <i>Dolophilodes</i> , <i>Wormaldia</i>	GC	N
	Polycentropodidae	<i>Polycentropus</i>	FC	N
	Rhyacophilidae	<i>Rhyacophila</i>	P	N
	Sericostomatidae	<i>Gumaga</i>	SH	Y
Non-insect class:				
Arachnida	Sub-class: Acari		P	
Amphipoda			GC	N
Gastropoda	Physidae		SC	Y
Oligochaeta			GC	N
Tricladida	Planariidae		P	N
Hirudinea			P	N

APPENDIX B

Appendix B: Taxa specific coefficients for length-weight regressions ($BW = A(L)^B$) to calculate body weight (BW) derived from previously established equations (Benke et al. 1999; Sabo et al. 2002; Cummins et al. unpublished; Wisseman et al. unpublished).

		Body Length (BL)		Head Width (HW)			
Aquatic	Family	A	B	R^2	a	B	R^2
Acari		0.03714	2.366				
	Hydrachnidia						
Amphipoda							
	TBA	0.0058	3.015				
Coleoptera (adults)							
	Dryopidae						
	Dytiscidae	0.0473	2.611				
	Elmidae	0.0074	2.879		9.564898584	3.5741	0.86
	Haliplidae						
	Psephenidae	0.0123	2.906				
	Hydrophilidae	0.0473	2.611				
	TBA						
Coleoptera (larvae)		0.04736	2.681				
	Elmidae	0.0067	2.879				
	Hydrophilidae	0.0013	3.356				
	Psephenidae	0.0012	2.906				
	Dytiscidae	0.0013	3.356				

		Body Length (BL)		Head Width (HW)			
Collembola		0.0024	3.676				
	Poduridae						
	TBA						
Diptera		0.001135	2.7508	0.922562643	0.9202	0.2	
	Ceratopogonidae	0.0025	2.469				
	Chironomidae	0.0018	2.617	17.13477458	2.6356	0.8	
	Dixidae	0.0027	3.084	0.63			
	Simuliidae	0.002	3.011				
	Stratiomyidae						
	Tipulidae	0.0029	2.681				
	TBA						
Ephemeroptera		0.014	2.49	0.89	0.749236943	2.8402	0.57
	Baetidae	0.0053	2.875				
	Ephemerellidae	0.0103	2.676				
	Heptageniidae	0.0108	2.754				
	Siphonuridae	0.0027	3.446				
	Leptohyphidae	0.0061	3.194				
	TBA						
Gastropoda							
	TBA	0.0269	3.003				
Hemiptera							
	Corixidae	0.0031	2.904				
	Gerridae	0.015	2.596				
	Mesoveliidae						
	Veliidae	0.00126	2.719				
	TBA						

		Body Length (BL)		Head Width (HW)			
Lepidoptera		0.012	2.69	0.82			
	TBA						
Megaloptera							
	Corydalidae	0.0045	2.935				
	Sialidae	0.0037	2.753				
	TBA						
Odonata		0.14	2.27	0.9			
	Coenagrionidae	0.001	2.672	0.9			
Orthoptera		0.03	2.55				
	TBA						
Plecoptera		0.26	1.69	0.95	0.906195693	2.8538	0.89
	Chloroperlidae	0.005	2.732	0.98			
	Nemouridae	0.0056	2.762				
	Perlidae	0.008	2.819	0.98			
	Perlodidae	0.0196	2.742				
	Pteronarcyidae	0.0324	2.573	0.9			
	TBA				(Uncased)		
Trichoptera		0.01	2.9	0.92	1.475504551	2.131	0.57
	Glossosomatidae	0.0082	2.958				
	Hydropsychidae	0.049	2.295	0.96			
	Limnephilidae	0.0034	2.66				
	Lepidostomatidae	0.0079	2.649				
	Philopotamidae	0.005	2.511				
	Polycentropodidae	0.0047	2.705				
	Rhyarophilidae	0.0099	2.48				
	TBA						

		Body Length (BL)		Head Width (HW)			
Terrestrial	Family	A	b	R^2	a	b	R^2
Coleoptera		0.04	2.64	0.95			
	Coccinellidae	0.343	1.5	0.91			
	Curculionidae	0.1281	2.254				
	Staphylinidae	0.001	4.026	0.99			
Hymenoptera		0.04	2.64	0.95			
	Ichneumonidae						
	Formicidae	0.027	2.666	0.93			
Araneae		0.05	2.74	0.98			
	TBA						
Diptera		0.04	2.26	0.67			
Sub-family	Brachycera	0.006	3.05	0.85			
	Nematocera	0.1	1.57	0.9			
Orthoptera		0.03	2.55	0.95			
	TBA						
Psocoptera		0.0425	1.637				
	TBA						
Arachnida		0.03714	2.366				
	TBA						
Trichoptera		0.01765	2.903				