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FACTORS INFLUENCING CLADOPHORA BIOMASS ABUNDANCE IN THE UPPER
CLARK FORK RIVER, MONTANA.

By

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Bachelors of Science, The University of Montana, 2015

Thesis

presented in partial fulfillment of the requirements

for the degree of

Master of Science
Systems Ecology

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Dedication

To Mom, for taking me *Up North*.

To Ed Love (WDET) and John Jackson (KBGA), for ‘Young Rabbits’.

To D. Rickles, for laughs when needed most.

To J. Douglas, for motivation to get back up.

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Introduction

At the ecosystem scale, both exogenous and endogenous factors influence the abundance and character of benthic organic matter (BOM) in lotic ecosystems. In many streams, BOM standing crops are linked to riverine food webs (e.g., Power 1990) that depend on the energy provided by autochthonous carbon (C) supplied by extant algal communities (Finlay 2001, Power et al. 2015).

Periphyton, mainly as attached algae, are the dominant primary producers in most temperate stream ecosystems (Biggs 1995). Algae and other primary producers (e.g., bryophytes, macrophytes, cyanobacteria) collectively form autochthonous organic matter (OM) standing crops, accumulations of organic material that influence stream ecosystem structure and function in a variety of ways. Autochthonous BOM has been shown to provide colonization surfaces for epiphytic diatoms (Dodds 1991b, Dodds and Gudder 1992), algae that comprise a basal component of many riverine food webs (Power et al. 2015). Furthermore, stream benthos may rely on energy derived from OM detritus sourced from crops of BOM (Wallace et al. 1982, Fisher and Gray 1983, Jackson and Fisher 1986), and this material has been shown to fuel heterotrophic components (bacteria, fungi) of riverine food webs (Hall and Meyer 1998) as well.

Blooms of filamentous green algae and associated BOM can alter biogeochemical conditions in aquatic ecosystems with potential consequences for in-stream communities and processes. BOM accumulation potentially influences a range of biogeochemical processes such as respiratory demand for dissolved oxygen (DO) at night when photosynthesis is not occurring (Watson 1989, Stevenson et al. 2012, Valett et al. 2017), liberation of metabolic byproducts (e.g., ammonium, Peckol and Rivers 1995), or hydrogen sulfide (Gubelit and Berezina 2010) during

decomposition, effects with implications for the structure and function of lotic ecosystems and their goods and services (Suplee et al. 2009, Stevenson et al. 2012).

In this thesis, I investigate the distribution and abundance of the common green alga *Cladophora glomerata* (*C. glomerata*) in the Upper Clark Fork River (UCFR) Montana (MT) where it frequently generates nuisance blooms (Dodds et al. 1997, Suplee et al. 2012) to address seasonal change in algal standing crops and discuss implications for trophic dynamics within the river. I first provide an overview of the role of periphyton in streams, then specify how *C. glomerata* influences benthic conditions before describing the experimental design and approach.

Factors influencing stream algae — Many factors influence seasonal patterns of autochthonous BOM accrual and loss, including both exogenous and endogenous features. Exogenous abiotic factors include stream power (Power and Stewart 1987), chemical properties of stream water like dissolved nutrient concentrations (Dodds et al. 1997) and their speciation (Fisher et al. 1982), physicochemical conditions including insolation and irradiance (Hill and Boston 1991, Finlay et al. 2011), and stream thermal regimes (Entwisle 1989, Dodds 1991). At the same time, endogenous factors, i.e., the biologic and metabolic character of in situ BOM itself, influences the timing and rate of biomass change (Bothwell et al. 1989, Higgins et al. 1998).

Flow and disturbance — Streamflow is considered to be the master variable (sensu Poff 1997) governing the biotic template of lotic ecosystems. Attributes of the annual hydrograph (e.g., magnitude, timing, frequency) influence the nature of BOM abundance (Biggs 1995, Biggs 1996) over varying spatiotemporal scales, and serve as a fundamental part of a stream ecosystems' disturbance regime (Pedersen and Stevenson 1992) to which BOM responds (Power and Stewart 1987, Stevenson 1990). Increased discharge caused by flooding can reduce BOM

standing crops by scouring surfaces upon which periphyton grow, partially or wholly removing attached algae (Fisher et al. 1982, Power and Stewart 1987, Flinders and Hart 2009) which is then subject to transport (Blinn et al. 1995, Shannon et al. 1996, Biggs et al. 2005).

Transport of OM in streams plays a critical role in stream metabolism and energy budgets (Vannote et al. 1980, Golladay 1997). In addition, transport can export OM (Fisher et al. 1982, Ng 2012, Power et al. 2015), alter resource availability (Valett et al. 1994), reduce foraging success of fish (Nördstrom and Booth 2007). Suspended material may also be the dominant form of algal OM in some systems. For example, Gubelit and Bezerina (2010) found that in the Neva Estuary (Russia), drifting algae represented an OM pool nine times greater than that of attached, benthic algal biomass. In stream ecosystems, detached algae may function as viable floating mats (e.g., Power 1990), but may also become stranded on shore and decompose. Power (1990) noted enhanced insect secondary production in floating algal mats of the Eel River, California (CA), and this material has been shown to release nutrients that can fuel cyanobacteria algal blooms (Power et al. 2015) during algal succession. Lateral exports of algae from the stream's wetted channel to perched gravel bars or banks may account for a significant portion of total organic material loss at the reach-scale (Fisher et al. 1982).

Sustained periods of relatively stable low-flow can influence the overall character of BOM crops. During these periods, characterized by low-stage, low-turbidity flows, and increased temperatures, biomass may accrue rapidly, in part because losses resulting from scour are minimal. In this scenario, stream biota may be constrained by the chemical and biogeochemical characteristics of the river ecosystem. Biggs (2000) noted that stream ecosystems with prolonged periods of stable flow over the course of the year may respond differently to nutrient loading or limitation than streams with frequent flushing by high flows, especially when nutrient

enrichment influences algal primary productivity. Similarly, Chételat et al. (1999) argued the effect of nutrients on algal standing crops would be more pronounced in the absence of flow disturbance.

Physicochemical attributes — Physicochemical attributes of stream ecosystems can affect BOM abundance and character. Variables such as stream temperature and irradiance are exogenous factors that act to regulate algal metabolism (Whitton 1970, Entwisle 1989, Hill and Boston 1991, Higgins et al. 1998). In the broadest sense, growth of benthic autotrophs such as algae is largely constrained by water temperature, since algal metabolism (i.e., growth rates, nutrient uptake rates) is ultimately a function of this factor. Most genera that comprise autochthonous BOM crops in streams have an optimal window of temperatures that fosters new growth, while temperatures outside of this range may have inhibitory effects (Whitton 1970). Solar insolation is strongly linked to autotrophic activity in lotic ecosystems (Minshall 1978), and is one of the primary factors responsible for governing stream ecosystem thermal regimes (Cassie 2006, Finlay et al. 2011). For example, Warnaaars et al. (2007) found that as channels widened, solar inputs and temperatures increased, and river ecosystem metabolism became more influenced by algal production.

Biogeochemistry — Among biogeochemical factors, plant-available nitrogen (N) and phosphorus (P) influence the abundance and character of BOM through bottom-up regulation of ecosystem productivity. Redfield (1958) quantified the extant elemental C:N:P ratio for oceanic phytoplankton, and that ratio has been used by freshwater ecologists to evaluate putative nutrient limitation to primary productivity in streams. Ammonium-nitrogen ($\text{NH}_4\text{-N}$), nitrate-nitrogen ($\text{NO}_3\text{-N}$) and forms of P such as soluble reactive phosphorus (SRP) and their relative abundance may govern primary productivity (Sterner and Elser 2002). Stoichiometric relationships for

freshwater algae typically indicate that P serves as the primary limiting nutrient (Hill et al. 2009), however, evidence suggests that N (Grimm 1987) or P (Pitcarin and Hawkes 1973, Hill et al. 2009), or both N and P (co-limitation, Francouer et al. 1999, Bracken et al. 2015) may limit primary productivity. Increased abundance of plant-available nutrients in aquatic ecosystems (i.e., eutrophication) is a recognized driver of enhanced rates of primary production (Schindler 1974). In streams, the positive relationship between nutrient enrichment and primary productivity, represented as Chlorophyll *a* (Chl *a*) standing crops, is well documented (Dodds 1991, Chételat et al. 1999, Biggs 2000, Dodds et al. 2002, Stevenson et al. 2012). Enrichment has been shown to fuel algal proliferations that can reach nuisance levels (Dodds and Smith 1995, Biggs 2000). Nutrient enrichment is also associated with growth of particular taxa (Stevenson et al. 2012), including filamentous green algae such as *C. glomerata* (Wharfe et al. 1984, Freeman 1986, Entwisle 1989).

Role of endogenous factors in BOM accrual — Condition of autotrophic BOM may be determined by a combination of exogenous factors that influence the abiotic template and the endogenous conditions of the algal community (Bothwell et al. 1989, Higgins et al. 1998). Coupling of endogenous response of algal mats to exogenous factors may determine the viability of algae at any point in time, and in stream ecosystems this relationship influences autochthonous OM dynamics over varying spatiotemporal scales. Interactions between primary producers and their surrounding environment may be especially important given the short window of intense biological activity characterizing the summer growing season in temperate stream ecosystems (Power et al. 2015). Processes like nutrient uptake rates (Stream Solute Workshop 1990) that have been shown to affect algal growth are affected by stream flow (Borchardt 1996), light delivery to benthic environment (Hill and Boston 1991), temperature

(DeNicola 1996), and the amount of biomass present, among other factors. Growth form of certain taxa can dictate light delivery to basal portions of rupicolous algae (Hill 1996). For instance, Higgins et al. (1998) explained seasonal collapses in biomass of *C. glomerata* in Lake Huron (Great Lakes) by invoking a density-dependent self-shading mechanism, with losses driven by population-level responses. Filaments attached to rock surfaces received a fraction of the light delivered to the uppermost portions of thick benthic algal mats, causing reduced tensile strength at basal attachment sites and eventual sloughing. Dodds (1991) posited that that oxygen bubbles formed by photosynthesis could buoy algal filaments in streams, causing distal filaments to receive greater irradiance than portions below. These lines of evidence support the notion that processes occurring at the habitat-scale may directly affect those responsible for accrual and loss such as endogenous sloughing. Overall, the complexity of physical, chemical and biological interactions is great and likely will be of increasing importance in the face of predicted climate-induced changes to aquatic ecosystems of the interior mountain west (Pedersen et al. 2007, Whitlock et al. 2017).

Algal periphyton and the Upper Clark Fork River — The UCFR drains 57,000 km² of the western slope of the continental divide above the river's confluence with the Blackfoot River, and is Montana's largest river system by flow at the point where it meets the Idaho border. A century of fluvial ecosystem degradation occurred as a result of mining practices for high-grade ore deposits near Butte, MT (Moore and Langner 2012), resulting in accumulation of mining and smelting wastes (Andrews 1987) in the UCFR headwaters and throughout the fluvial corridor. As a result of flooding at the turn of the 20th century, the UCFR was inundated with toxic sediments such that elevated concentrations of metals are now found throughout its floodplain (Moore and Langner 2012), river channel bed sediments (Poulton et al. 1995), benthos (Hornberger et al.

2009), resident salmonids (Leon et al. 2014), and predator birds such as osprey (Langner et al. 2012) at levels that exceed EPA toxicity criteria.

Following legal settlement with The Atlantic-Richfield Corporation, the State of Montana Department of Justice and US EPA designated approximately 200 km of UCFR fluvial corridor and floodplain ecosystem as an impaired Superfund site, where restoration is ongoing. Beginning roughly 132 km below the headwaters confluence, near the town of Drummond, MT, 60-km of stream corridor is designated as 'Reach C' (Natural Resources Damage Program 2012). Throughout this reach, poor conditions for riverine biota during summer low-flow are thought to be linked to *C. glomerata* abundance and threatening to native and introduced trout populations (Naughton 2015). Trout abundance in this reach of UCFR is greatly suppressed (Leon et al. 2014). Recurring nuisance algal blooms, as key organizers of ecosystem structure, may prove problematic for successful recovery of fish populations in this reach of UCFR. The Montana Department of Justice Natural Resources Damage Program spearheaded a collaborative effort with ecologists at the University of Montana to investigate these relationships.

Proliferations of benthic algae in the UCFR were documented as early as the mid-1970s by Braico (1973), and recur with regularity during summer (Watson 1989, Suplee et al. 2009). Summertime nuisance blooms of *C. glomerata* (defined as benthic Chl *a* in excess of 100 mg/m², or BOM in excess of 50 g/m², Welch et al. 1988) manifest as abundant autochthonous BOM crops throughout the growing season, and have been shown by several workers (Tri-State Water Quality Council 2009, Valett et al. 2017) to dominate the benthic periphyton assemblage.

Nuisance BOM may alter environmental conditions (Dodds 1991, Peckol and Rivers 1995, Power et al. 2015) with potential adverse effects on aquatic biota. For example, Power et al. (2015) found that mats of stranded algae were significantly warmer than in surrounding water

due to altered albedo (Power et al. 2015), exhibiting temperatures exceeding thresholds of tolerance for cold-water salmonids. Additionally, enhanced respiratory demand driven by algal biomass accumulations, associated detrital stocks (Hall and Meyer 1998), and extant microbial biomass (Parker et al. 2007), can induce hypoxia (Watson 1989, Quinn and McFarlane 1989, Stevenson et al. 2012). Occurrence of anoxic zones in streambeds, indicative of reducing environments (e.g., Brick and Moore 1996), partly support the notion that BOM accumulation may facilitate hotspots (McClain et al. 2003) of biogeochemical activity.

In some MT streams, biogeochemical phenomena affecting ecosystem structure and function may be recurring during years with abundant algal biomass and low-flow, with implications for the fate of nutrients, physicochemical conditions, and functioning of food webs. Watson (1989), documented substantial reductions in nighttime DO content of UCFR stream water during summer base flow, attributing declines to respiratory demand by abundant *C. glomerata*. These studies, in addition to foundational work by Dodds (1991) and Lohman and Priscu (1992), help elucidate the role of *C. glomerata* in this river ecosystem and other MT streams with nuisance growth, but perspectives offering broader spatial and temporal resolution of nuisance algal seasonal cycles and their effect on riverine ecosystems are lacking.

Attributes of the UCFR promoting algal growth — Exogenous factors such as solar insolation, water clarity and chemistry, and regional land use may fuel autotrophic production within this system. Much of the UCFR is wide and shallow, lacks significant riparian canopy to inhibit light delivery to the benthic environment, and low water column turbidity enhances solar insolation for benthic autotrophs (Hill 1996, Wilson et al. 1999). In addition, *C. glomerata* flourishes in hard water with elevated concentrations of divalent cations and high alkalinity (Whitton 1970), both of which are characteristic of the UCFR (Lynch et al. 2010).

As for other unregulated stream ecosystems of this physiographic region, annual streamflow in the UCFR reflects a snowmelt-fed system (Whitlock et al. 2017), with peak discharge occurring in late-spring and early summer. However, the UCFR hydrograph likely reflects basin-scale alterations as well. Stream power in the UCFR is attenuated below the headwaters' confluence, in part due to liming ponds constructed between 1911 –1958 to buffer acid-mine runoff (Phillips and Lipton 1995, Brick and Moore 1996). In addition, however, human extraction of water to meet needs of surrounding agricultural communities occurs broadly throughout the upper basin, promoting seasonal dewatering (Watson 1989) that may reduce intensity of the snowmelt-pulse and its influences on the river ecosystem. The combination of holding ponds and human extraction of water from the UCFR may decrease the magnitude and prolong the duration of summer low-flow during some years. Perhaps as much as 70 % of the historical discharge volume is removed from the UCFR on an annual basis (pers. comm., B. Anderson, WGM Group, Missoula, MT).

Summertime conditions promote high rates of primary production in the benthic environment, as evidenced by rapid accrual of *C. glomerata* biomass. As snowmelt-fed flows transition to seasonal low-flow characterized by lack of flood disturbance, water temperatures (13 – 17 °C) foster lush *C. glomerata* growth (Graham et al. 1982, Dodds 1991). Prolonged warming may result in water temperatures greater than 24 °C that exceed the threshold for *C. glomerata* growth (Wong et al. 1978) later in the year.

In the UCFR, dissolved nutrient concentrations change seasonally, in part reflecting autotrophic demand (Valett et al. 2017), but broader scale nutrient dynamics in the basin reflect both regional geologic character and history of land use practice. P-rich sedimentary rocks occur throughout the watershed of the upper river (Pardee 1917, Priscu 1986) possibly contributing to

the high background concentrations of SRP (20 – 50 µg/L) throughout the year. Low to undetectable NO₃-N (2 – 6 µg/L) characterizes most of the summer growing season with greater concentrations during fall and winter (Valett et al. 2017, Peipoch and Valett, in review). Diffuse runoff from agricultural land may contribute a significant source of dissolved inorganic N (DIN) to the river ecosystem (Peipoch and Valett, in review).

Given the link between nutrient enrichment and primary productivity described above, nutrient reduction was proposed as a viable step to reduce summertime nuisance blooms of *C. glomerata* in the UCFR. The Voluntary Nutrient Reduction Program was implemented in the mid-1990s by stakeholders and scientists from the Tri-State Water Quality Council to reduce nutrient loading to the upper river in effort to curb nuisance algal growths. Despite nutrient reduction efforts (Tri-State Water Quality Council 2009), summertime benthic algal standing crops in the UCFR often exceed nuisance levels (Suplee et al. 2009, Suplee et al. 2012).

Relatively few studies have addressed structural features of BOM abundance and composition during the seasonal progression of a *C. glomerata* bloom. The investigation addressed herein focuses on the temporal evolution of nuisance algae in ‘Reach C’ of the UCFR and is of value locally to stream ecologists, river managers, and more broadly considering the globally recognized (Zulkify et al. 2013) role that this alga has in modifying its surrounding environment and influencing river food webs. I examined the filamentous green alga *C. glomerata* as autochthonous BOM in the UCFR and factors potentially influencing its distribution and abundance during the progression of the 2016 summer growing season. Documenting changes in biomass form and abundance at the reach scale over the period of summer low-flow enhances understanding of autotrophic BOM crops, and their central role in governing seasonal attributes within the UCFR ecosystem. The purpose of this study was to

assess which factors influence BOM, and how in-stream physicochemical, biogeochemical, and benthic conditions change temporally in this critical segment of UCFR. My objective was to discern which factors most contribute to the abundance and character of BOM standing crops during the summer growing season.

Methods

Study Sites — Over the course of the summer growing season of 2016, I characterized the seasonal progression of *C. glomerata* as autochthonous BOM along approximately 60 km of the UCFR corresponding to ‘Reach C’, as designated by US Environmental Protection Agency and MT Department of Justice Natural Resource Damage Program (NRDP 2012). From the origin of the UCFR near Warm Springs, MT, study sites 1, 2, and 3 were located at downstream distances of 132 km, 155 km and 180 km, respectively (Table 1). Two principal Clark Fork River tributaries, Flint Creek (upstream), and Rock Creek (downstream), bracket ‘Reach C’ (Figure 1). The stream channel was predominantly single-thread, composed mostly of small cobbles and gravel, and moderately entrenched into Quaternary alluvium valley fill. Within the study reach, the river was approximately 30 – 40 m wide and exhibited alternating pool-riffle morphology, with little riparian cover shading the main-stem channel. Average water column depth during base flow was 0.25 m – 0.75 m. Five transects across the stream were delineated at each site along 250 – 300 m of channel and spaced 20 – 25 m apart. Samples of BOM, water for chemical analyses, and metered physicochemical assessment occurred in 0.40

Table 1. UCFR study site characteristics. River km is distance downstream from headwaters' confluence, and reach km is longitudinal distance in 'Reach C' (see text for description).

Site	River km	Reach km	Latitude	Longitude	Length (m)	Width (m)
1	132	1	46°39'41.08" N	113°08'55.82" W	225	34.7 ± 0.4
2	155	18	46°42'42.89" N	113°19'50.81" W	260	40.3 ± 1.2
3	180	41	46°43'18.59" N	46°43'18.59" N	290	26.6 ± 4.2

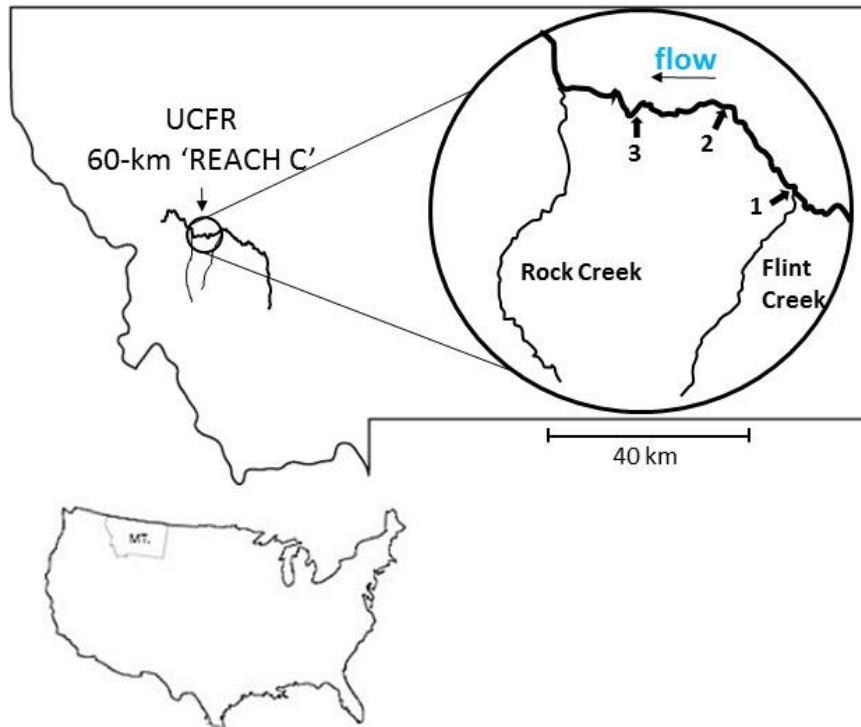


Figure 1. Map showing Montana, USA, the 'Reach C' segment of UCFR and location of two principal tributaries that bracket the study reach. Small black numbered (1-3) arrows indicate approximate location of study sites along approximately 60 km stream channel. Scale bar is for inset area.

m² study plots randomly located along each transect, resulting in five observations for each site for each sampling date.

Hydrologic Properties — Discharge among sites is gauged by United States Geological Survey (USGS) streamflow gaging station no. 12331800 ‘Clark Fork near Drummond’, reflecting an upstream drainage area of 4049 km². The annual hydrograph for this reach of the UCFR (Figure 2A) is typical of Rocky Mountain streams, with an early summer snowmelt-fed peak discharge that occurs on June 11 based on the mean annual flow record; streamflow then declines rapidly to base flow discharge, remaining relatively stable until autumn rains increase river stage and flow variability (Figure 2A, B). Peak streamflow during the 2016 study season occurred on 28 May, which was roughly three weeks earlier and approximately 66 % of the volume compared to historic discharge for the period of record.

Sampling commenced when the river was low enough to wade and always occurred during daylight hours, typically midday or thereafter. By the beginning of the study in mid-June when conditions allowed for sampling, streamflow was clear (i.e., low suspended sediment), and averaged 21.2 m³/s in mid-June, but declined to 9.2 m³/s by the end of the month. Two of eight samplings (I & II, Figure 2B) made over the course of the growing season occurred during this period on the recessional limb of the hydrograph. Samplings III-V occurred as discharge transitioned to base flow, when flow averaged 10.0 m³/s. On July 10–11, 2016, a weather system moved through the region, causing rains that increased streamflow in the UCFR study reach from 9.3 to 15.5 m³/s over 24-hours (Figure 2B). Following this event, streamflow varied little throughout base flow (samplings VI-VII), until mid-September and the onset of increased magnitude and variability in flow that lasted through the end of the study period (sampling VIII).

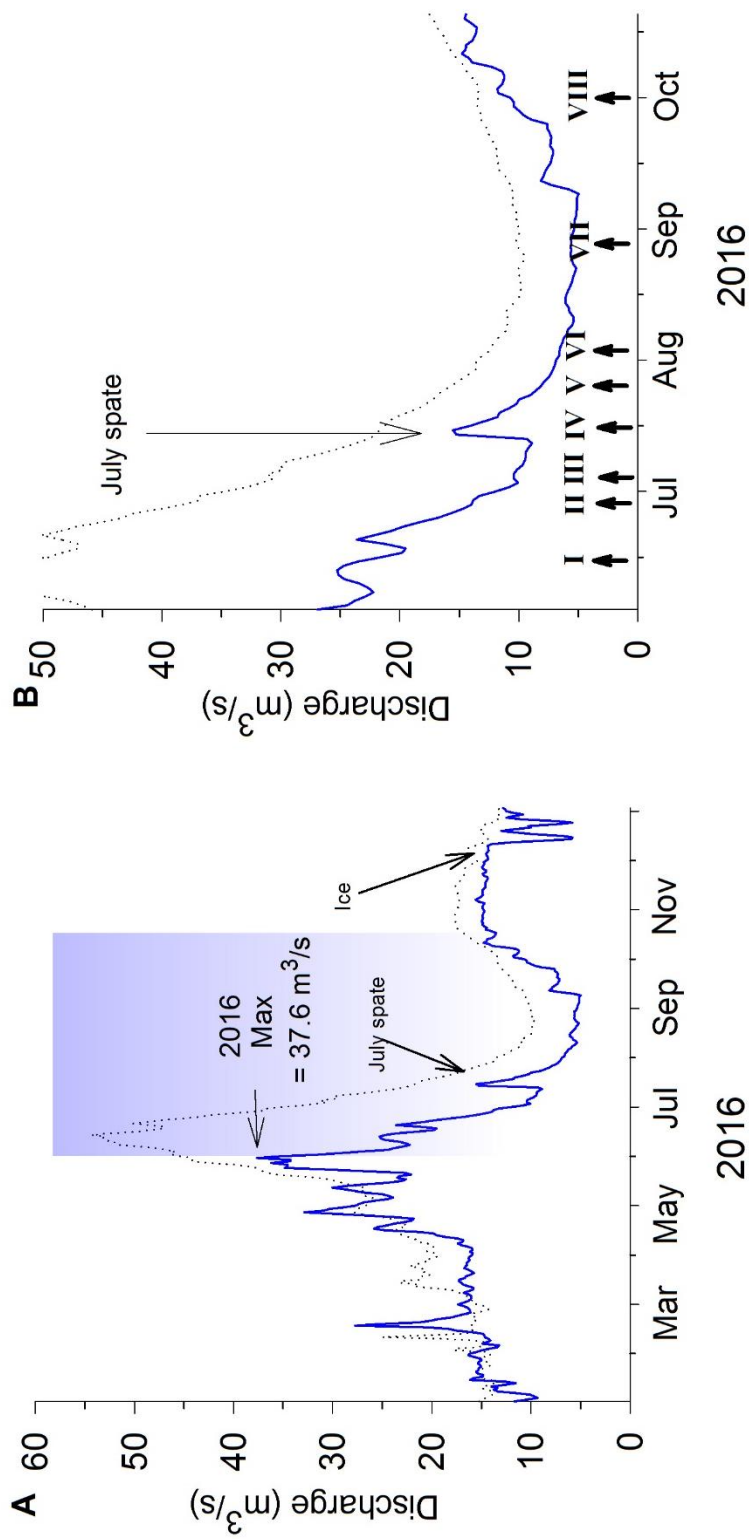


Figure 2. UCFR hydrograph characteristics during the study period. (A) Discharge (m^3/s) for the 2016 calendar year, where shaded box indicates period of observation in this study and (B) discharge (m^3/s) during the summer 2016 growing season (June 1 – October 15). Thin dotted line in both panels shows the mean daily flow for 24-year period of record (1993 – 2016), while thick blue line shows mean daily flow for 2016. Roman numerals above thick arrows in (B) indicate samplings (I-VIII), thin downward arrow in (B) indicates the occurrence of spate event described in text.

Ice coverage was observed throughout much of the UCFR by the end of November, 2016 (Figure 2A).

Biogeochemical and physicochemical conditions — I used a handheld meter (YSI Incorporated, Yellow Springs, OH) to assay in situ physicochemical conditions at each site. Variables measured included DO concentration (mg/L), DO % saturation, specific electrical conductivity ($\mu\text{S}/\text{cm}$) and water temperature ($^{\circ}\text{C}$). The probe was placed at mid-depth in the water column and allowed to equilibrate for 30 seconds before each data point was recorded. Dissolved stream water nutrient ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, SRP) dissolved organic carbon (DOC) concentrations were determined analytically on samples that were collected from the UCFR water column using a 60-mL acid-rinsed syringe. Samples were filtered through a 0.45- μm glass fiber filter (Whatman GF/F, Kent, UK) into duplicate 15-mL Falcon Tubes or 60-mL glass vials for DOC analysis, stored on ice in the field, then frozen in the laboratory until analyzed. DOC was determined using an Aurora 1030w TOC Analyzer (Oceanographic International, College Station, TX) by heated-persulfate oxidation methods (Menzel and Vocaro 1964). Concentrations of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ (as nitrate plus nitrite) and SRP were determined by microsegmented flow analysis using an Astoria 2 Analyzer (Astoria-Pacific Inc., Clackamas, OR), following standard methods (APHA 2006). DIN represents the sum of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, while SRP represents plant-available P.

Benthic Organic Matter — Standing crops of autochthonous BOM were collected to represent attached *C. glomerata* (herein, coarse benthic organic matter, CBOM) or detrital material derived from *C. glomerata* (i.e., fine benthic organic matter, FBOM). Organic material of evident terrestrial origin was very rare, and while other autotrophs (i.e., macrophytes, and bryophytes) co-exist with filamentous algae (pers. obs.), proportional abundance of these

taxonomic groups was very low compared to that of *C. glomerata*. By treating all forms of BOM in this manner, this investigation identifies BOM crops as predominantly autochthonous, and driven by the algal dynamics that characterize the seasonal bloom of *C. glomerata*.

A large-river benthic-sampler (i.e., stovepipe corer) was used to assess BOM standing crops. The benthic-sampler was a hollow cylinder (36.5 cm diameter, area = 0.40 m²) inserted a few centimeters into the streambed. Coarse substrate within the sampler was picked up and shaken gently into the interior of the cylinder to dislodge excessive inorganic debris (i.e., sediments) from algal material. Following this mild elutriation, algae was detached from cobble surfaces with scissors or razor blades into collection pans. Remaining CBOM filaments within the stovepipe were then collected using a 4-mm sieve. To reduce water content, algae samples were drained in the field before being stored on ice for transport to the laboratory.

To assay crops of FBOM either already present as streambed deposits, or loosed from crops of attached algae during CBOM collection, contents of the benthic-sampler was stirred to entrain FBOM and a sample of water and suspended material was collected in a 125-ml HDPE bottle. Water depth (cm) in the cylinder was measured prior to FBOM sampling to allow conversion from volumetric to areal units. FBOM subsamples were stored on ice until laboratory analysis, when a measured volume was filtered over a pre-weighed 0.45- μ m filter. To obtain dry mass, CBOM subsamples were dried to constant weight for at least 48 hours at 60 °C. Dry mass of FBOM was derived following drying of filters for at least 24 hours at 60 °C. I analyzed Ash-Free Dry Mass (AFDM), calculated as the difference between dry and ash weight after combustion at 500 °C, and determined percent organic matter content (% OM) for both CBOM and FBOM. In order to assess the character of the total BOM pool (TOM = CBOM + FBOM), I

summed standing crop abundance (g/m^2) and determined % OM for all autochthonous BOM using a mass-weighted approach.

To characterize the autotrophic component of BOM, I determined standing crops of Chl *a* (mg/m^2) following methods of Steinman et al. (2006). Upon thawing, subsamples of CBOM were extracted in 90 % acetone solution for 24 hours. Following centrifuging for 10 minutes at 10 °C, algae was analyzed for phytopigment content at 664, 665, and 750 nm using a V-550 UV/VIS spectrophotometer (Jasco Incorporated, MD) before and after acidification to correct for phaeopigments. Additionally, I calculated the Chlorophyll *a*: biomass ratio (Chl *a*:AFDM) following Valett et al. (1994), in order to assess the relative contributions of autochthonous forms to the overall character of BOM standing crops.

Suspended Organic Matter — To evaluate transport of suspended algal organic matter (SOM) in the UCFR study reach, I measured the drift density (g/m^3) of entrained *C. glomerata* transported in streamflow at each site. To catch drifting algae, three stationary 500- μm mesh drift nets (area = 0.109 m^2) were deployed roughly equidistant across the wetted channel and positioned in the water column at mid-depth. Occasionally during base flow, stream water depth was not great enough to fully submerge the drift net, in which case, net area was adjusted according to depth. I used an acoustic Doppler current profiler (Son-Tek FlowTracker®, San Diego, CA) to measure the local velocity field ($n = 15$) directly in front of each drift net. The product of net area, sampling duration and mean stream water velocity provided the volume of water (m^3) sampled per deployment interval. Net contents were cleaned of any terrestrial material and the remaining material was retained in collection vessels. Drift samples were stored on ice before processing in the laboratory, where they were subsampled for AFDM and Chl *a* by methods described above.

Statistical Analysis — All observations for OM response variables, physicochemical variables, and dissolved nutrient concentrations from the three sites ($n = 12 - 15$ per site, due to occasional sample loss) were compiled for a given sampling round and pooled to generate river-scale means. Changes in river-scale means ($n = 8$) over the study period are presented as temporal trajectories of UCFR ecosystem physicochemical, biogeochemical, and biological attributes during the 2016 summer growing season. Variability around means is presented as standard error (SE) of the mean, and as the coefficient of variation (CV, where $CV = \text{standard deviation} / \text{mean}$, given as a percentage). Relationships among variables were examined using Spearman Rank Correlation and paired t -tests were used to compare means of some variables. In some cases, *a priori* causality was expected between variables, and regression analyses were employed. For each instance where curves are fit to data, statistical parameters of the relationship are provided. Stepwise multiple linear regression (MLR) analyses were used to assess which explanatory variables contribute to the overall character of BOM in the UCFR during the summer growing season. Because benthic algal standing crops already attained appreciable quantities by the time sampling began, statistical assessment of factors influencing accrual was quantitatively unreasonable. Accordingly, regression analyses were performed on the data set corresponding to the time frame including and following peak biomass. MLRs for BOM response metrics were performed using non-transformed and transformed variables to accommodate needs for normal distributions. Types of transformation performed on dependent and independent factors are given in parenthesis next to each variable in the MLR table (see below). Not all factors were used in each regression analyses since many variables were not independent of one another. The variable time represents days from June 1, 2016. In addition to BOM, stepwise MLRs were performed on SOM response variables to understand the role of

drifting OM in the seasonal progression of *C. glomerata*. Relationships derived from regressions between response and explanatory variables may not lead to the ability to “predict” the character of BOM crops in the UCFR, but are potentially fruitful in exploring overall patterns among factors driving the general progression of the *C. glomerata* bloom. All statistical analyses and curve fitting was performed using SigmaPlot v. 12.3 (Systat Software, San Jose, CA).

Results

Dissolved Oxygen, Temperature and Conductivity— Over the course of the summer, the UCFR water column was supersaturated with respect to DO during daytime hours. Daytime observations reflected a range from 129 – 153 %, and DO concentrations were not greatly variable across all samplings (CV = 5 %, Table 2). Percent saturation of DO exceeded 150% by the end of June, concomitant with the most abundant standing crops of CBOM, and these variables were positively correlated ($r = 0.22$, $p < 0.05$, data not shown). Opposite to relationships expected from physicochemistry alone, DO % saturation was also positively correlated to water temperature ($r = 0.48$, $p < 0.001$, data not shown). Minimum mean water temperature (14.1 ± 0.3 °C) for the study reach was observed during the recessional hydrograph period of mid-June, when discharge was maximal. By the end of the month, mean stream water temperature had risen to 21.4 ± 0.4 °C. Seasonal temperature maximum (22.6 ± 0.4 °C) was observed at base flow (Table 2). Mean water temperature dropped below 20 °C with decreased photoperiod and increased autumnal flow variability, and by October, steam water temperature was 16.05 ± 0.1 °C. Specific electrical conductance (Table 2) in the UCFR study reach increased steadily throughout most of the growing season from 359 $\mu\text{S}/\text{cm}$ during snowmelt recession (sampling I) to a maximum of 525 $\mu\text{S}/\text{cm}$ in late September (Table 2). Conductivity declined to 458 $\mu\text{S}/\text{cm}$ in October as discharge increased.

Table 2. Physicochemical and biogeochemical characteristics in the UCFR during the summer growing season. Data are means (\pm SE).

Sampling #	Date	Q (m ³ /s)	DO (mg/L)	DO (%)	Conductivity (μ S/cm)	Temp. (°C)	NH ₄ -N (μ g/L)	NO ₃ -N (μ g/L)	SRP (μ g/L)	DOC (mg/L)
I	6/15	21.2	11.6 \pm 0.1	129.5 \pm 2.2	359.0 \pm 3.8	14.2 \pm 0.3	15.6 \pm 4.6	1.29 \pm 0.21	52.4 \pm 0.56	4.2 \pm 0.1
II	6/30	9.2	11.7 \pm 0.1	153.4 \pm 2.3	408.1 \pm 9.7	21.4 \pm 0.4	7.53 \pm 1.2	0.61 \pm 0.20	14.1 \pm 1.7	4.2 \pm 0.1
III	7/03	9.7	11.4 \pm 0.2	136.1 \pm 3.3	383.1 \pm 2.8	19.6 \pm 0.1	7.95 \pm 2.0	0.83 \pm 0.09	23.1 \pm 2.0	6.1 \pm 0.3
IV	7/14	10.2	11.4 \pm 0.1	144.9 \pm 1.9	396.9 \pm 7.2	20.0 \pm 0.4	73.0 \pm 7.9	1.65 \pm 0.46	32.9 \pm 1.0	3.9 \pm 0.1
V	7/23	10.2	10.5 \pm 0.1	134.9 \pm 3.9	443.5 \pm 13.8	22.6 \pm 0.4	99.2 \pm 18.0	1.63 \pm 0.70	28.4 \pm 2.2	4.1 \pm 0.2
VI	8/1	6.3	11.4 \pm 0.1	142.2 \pm 1.0	442.4 \pm 3.6	20.3 \pm 0.2	25.2 \pm 12.6	2.11 \pm 0.68	32.8 \pm 3.0	4.0 \pm 0.2
VII	8/25	5.5	11.6 \pm 0.1	142.2 \pm 0.8	525.8 \pm 23.4	18.7 \pm 0.2	85.6 \pm 30.5	2.87 \pm 0.88	47.1 \pm 3.6	14.5 \pm 1.5
VIII	10/1	11.2	11.5 \pm 0.1	134.6 \pm 2.5	458.7 \pm 5.8	16.1 \pm 0.1	8.60 \pm 0.9	0.74 \pm 0.25	36.0 \pm 3.1	9.4 \pm 0.4

Dissolved Nutrient and Biogeochemical Conditions — *DIN*: $\text{NH}_4\text{-N}$ comprised most of DIN on all sampling dates. For the entire growing season, average $\text{NH}_4\text{-N}$ was $41.4 \pm 5.0 \mu\text{g/L}$ (CV = 131 %). Concentrations of $\text{NH}_4\text{-N}$ in the UCFR during the study period (Figure 3A) were initially low and relatively invariant (CV = 43%), with mean values of 5 – 15 $\mu\text{g/L}$ as the growing season progressed into July. Elevated $\text{NH}_4\text{-N}$ concentrations during July and August were considerably more variable (CV = 70 – 85 %) than observed earlier. Substantial fluctuation in mean $\text{NH}_4\text{-N}$ levels occurred during the final four samplings (Figure 3A), with mean values ranging from 8.6 to 99.2 $\mu\text{g/L}$. Growing season mean concentration of $\text{NO}_3\text{-N}$ was $1.42 \pm 0.17 \mu\text{g/L}$ and concentrations were always low during daytime hours over the course of the summer growing season (Figure 3A).

SRP and DOC — SRP was abundant throughout the UCFR study reach on all dates (growing season mean = 34.7 ± 1.3 ; CV = 41%, Figure 3B). Maximum mean SRP concentrations ($52.6 \pm 0.56 \mu\text{g/L}$) occurred at the start of the study in mid-June, but mean values declined to growing season minimum by the next sampling round. Concentrations of SRP then generally increased throughout base flow to $47.1 \pm 3.6 \mu\text{g/L}$, but decreased during the last sampling (VIII). DOC remained relatively stable (Figure 3C) over most of the samplings (growing season mean = $6.4 \pm .04$), but beginning in early autumn, mean DOC concentration increased sharply to $14.5 \pm 1.5 \text{mg/L}$, and continued to remain elevated, marked by considerable variation from background DOC observed earlier the study period (growing season CV = 66 %). Over the course of the entire study period, concentrations of DOC were positively related to CBOM standing crops ($r = 0.21$, $p = 0.02$, data not shown).

BOM crops and organic matter content — BOM increased initially and then decreased over the course of the study. During the recessional limb of the hydrograph, standing crops of

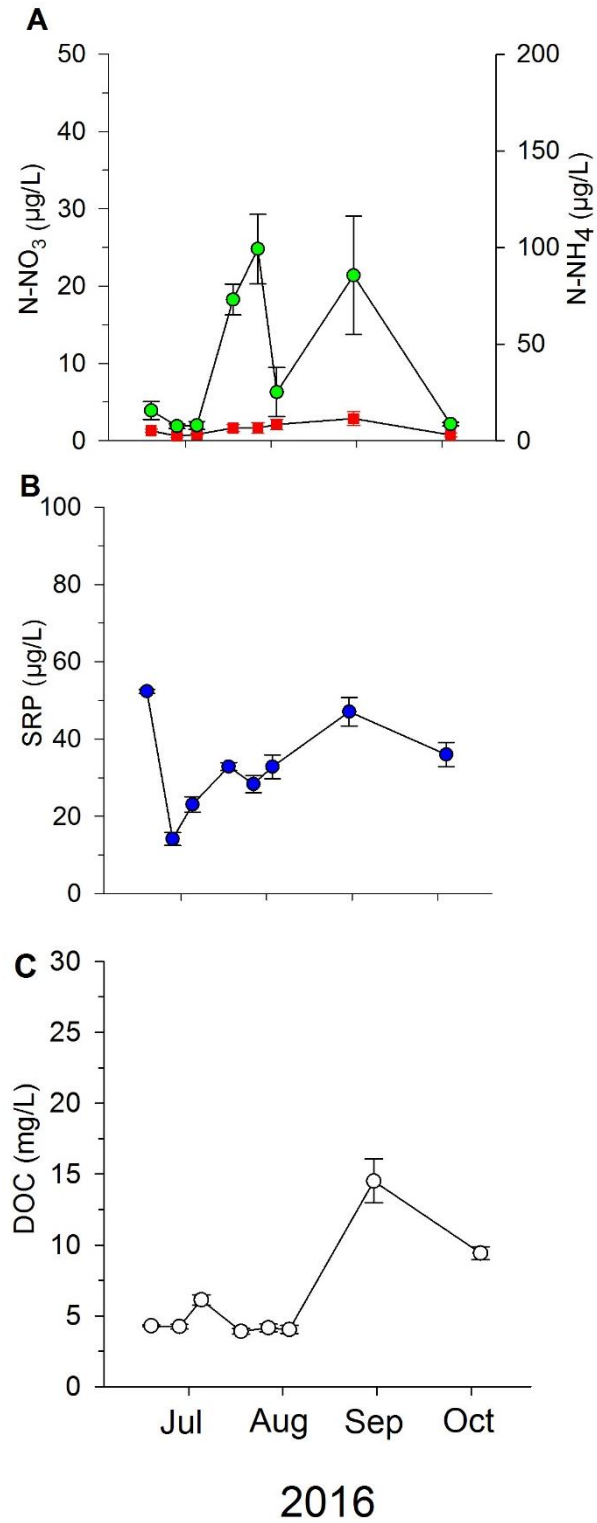


Figure 3. Dissolved nutrient concentrations for (A) nitrate-N (squares) and ammonium-N (circles), (B) SRP, and (D) DOC. Data are means ± SE.

CBOM (Figure 4A) were $92.8 \pm 14.9 \text{ g/m}^2$, and represented 99.8% of the autochthonous TOM pool (Figure 4B). CBOM seasonal maximum ($168.9 \pm 32.3 \text{ g/m}^2$) occurred during the second sampling (late-June), and crops declined exponentially ($r^2 = 0.86$, $p = 0.002$) over the remainder of the study period to seasonal minimum of $10.5 \pm 3.4 \text{ g/m}^2$ (Figure 4A). Standing crops of FBOM were minimal during the first sampling of the study period ($1.82 \pm .17 \text{ g/m}^2$) and increased to seasonal maximum ($6.7 \pm 2.1 \text{ g/m}^2$) in early July, one sampling after the observed peak in CBOM. FBOM then declined more than 2.5-fold, mirroring earlier declines in CBOM abundance. Throughout the remainder of the growing season (samplings IV-VIII), mean FBOM abundance varied by only 1.0 g/m^2 (CV = 15 %). While abundance fluctuated for both size fractions, CBOM comprised greater than 80% of the total BOM pool for seven out of eight samplings (Figure 4B). Overall, however, proportional abundance of the coarse fraction declined over the course of the study period, concomitant with a linear increase in the proportion of the fine fraction with time since initiation of the study. By autumn, FBOM comprised as much as 30 % of autochthonous BOM in the UCFR. In a multiple regression model SRP, DO % saturation and depth accounted for a considerable proportion of the variation in \log_{10} transformed FBOM (Table 3). In this model, SRP was negatively related to FBOM abundance and accounted for 20 % of variation (coefficient = -0.0128). DO % saturation was also negatively related to FBOM (coefficient = -0.0122), but explained only 3.8 % of variation. Inclusion of depth improved the model by about 6.6 %, to explain a total of 30.4 % of FBOM variation.

Mean % OM of CBOM over the growing season was $21.2 \pm 1.3 \%$ (Figure 5A), a value noticeably lower than expected for typical autotrophic algal mats despite

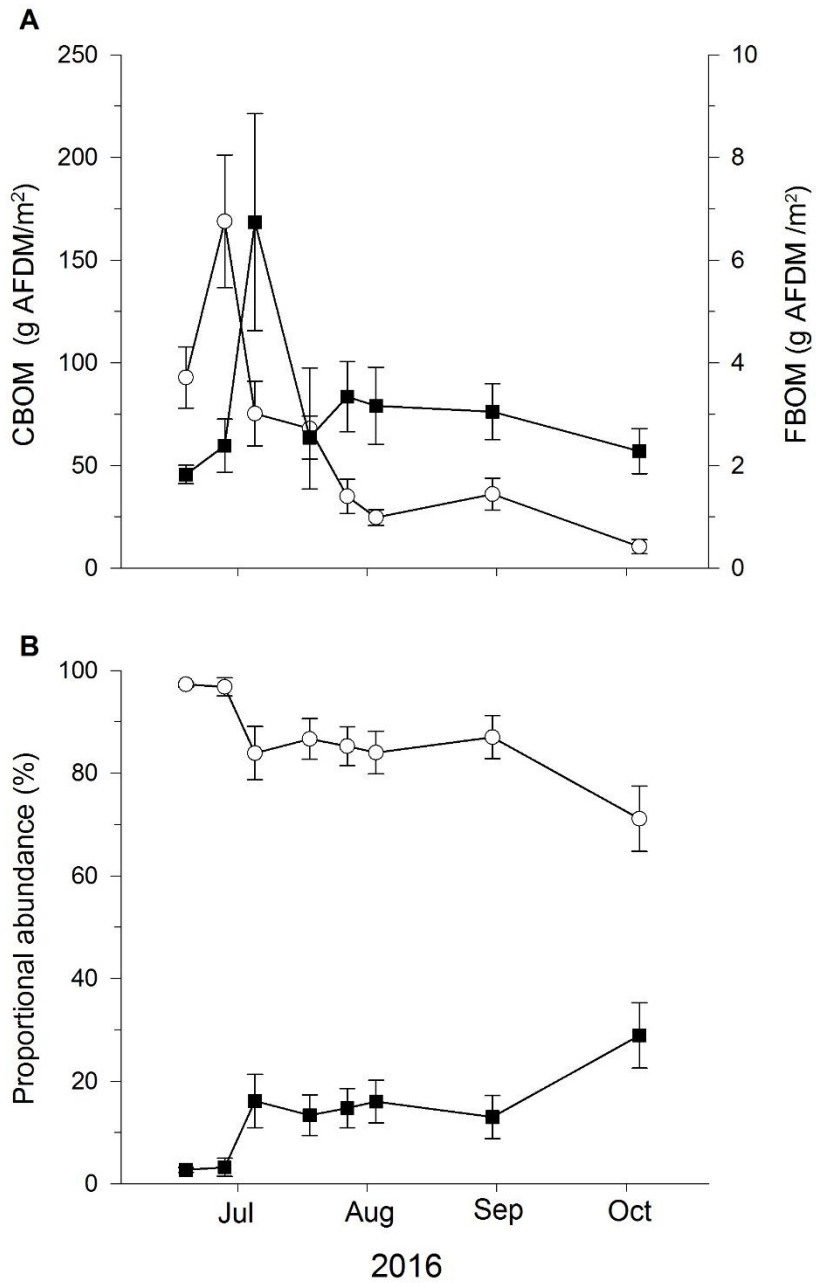


Figure 4. Standing crops of CBOM (open circles) and FBOM (filled squares) and (B) proportional abundance of each size fraction of autochthonous benthic organic matter. Data are means \pm SE.

Table 3. Results of stepwise multiple regression analyses. Types of transformations performed on variables are indicated in parentheses.

Dependent variables	Independent variables	Coefficient	Model r^2	P
FBOM (\log_{10})	SRP	-0.0128	0.200	0.002
	DO %	-0.0122	0.238	0.007
	Depth	0.0108	0.304	0.010
TOM (\log_{10})	Chl a ($\log_{10} x$)	0.214	0.198	0.012
	Drift Chl a ($-1/x$)	0.00601	0.241	0.029
Chl a (\log_{10})	Time (\sqrt{x})	-0.173	0.306	<0.001
	NH ₄ -N ($\log_{10} x$)	0.314	0.375	0.003
	TOM ($\log_{10} x$)	0.613	0.436	<0.001
	CB % OM (\sqrt{x})	-0.114	0.477	0.018
SOM (\log_{10})	Q (x^3)	1.596	0.561	<0.001
	Time (\sqrt{x})	-0.186	0.923	<0.001
Chl a drift ($-1/x$)	Time (\sqrt{x})	-12.601	0.930	<0.001
	Q (x^3)	-13.611	0.945	<0.001

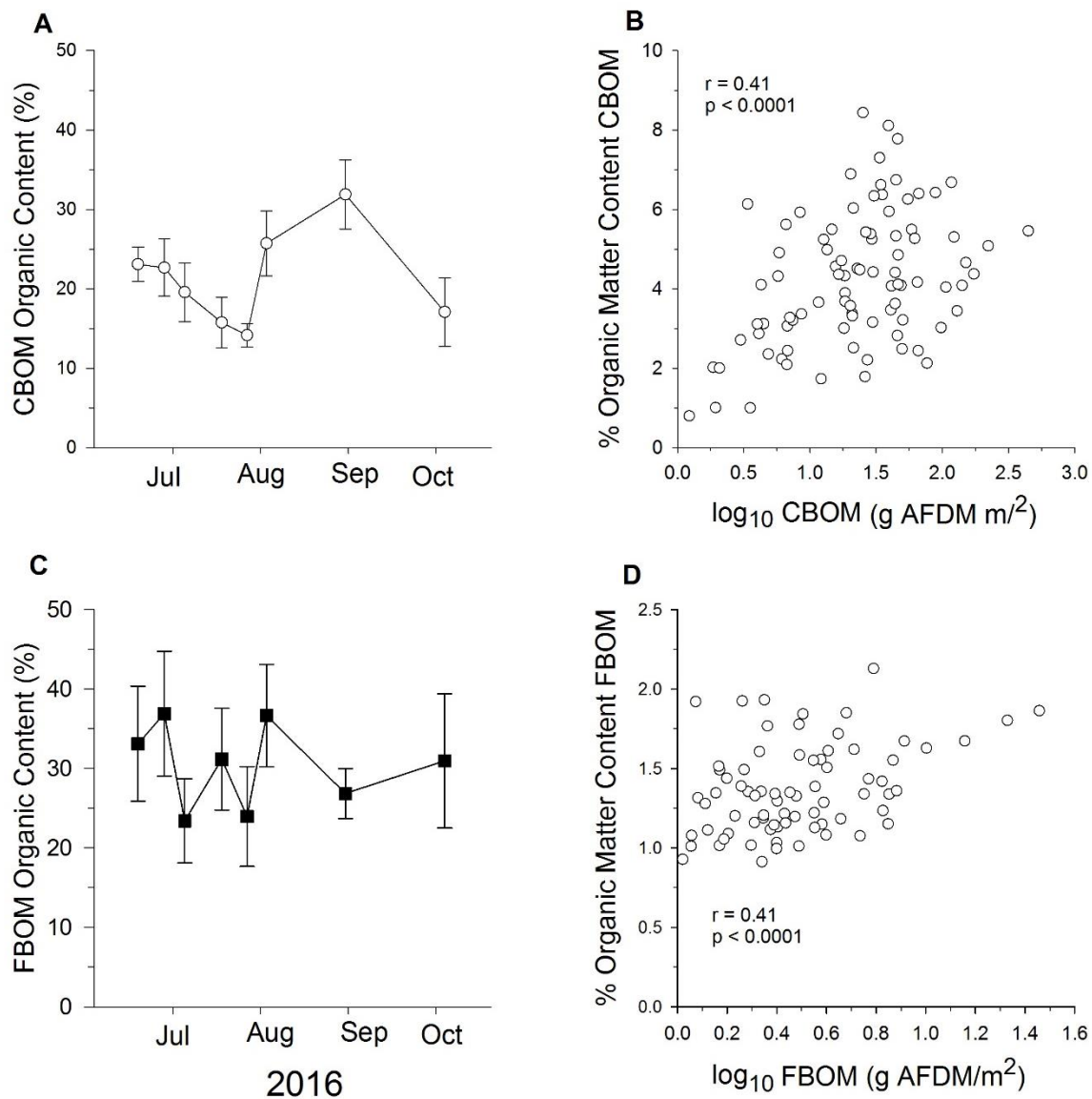


Figure 5. Percent organic matter content for (A) CBOM and (C) FBOM, and the relationship between \log_{10} -transformed standing crops and % organic matter content for (C) FBOM and (D) CBOM. Data are means \pm SE.

elutriation during sampling. The latter part of June and all of July were marked by a period of decline in % OM content from 22.6 % to 14.1 %, followed by a recovery period that increased % OM of CBOM to seasonal maximum of 31.8 %. Percent OM content in the coarse fraction was significantly positively related to standing crop abundance ($r = 0.41$, $p < 0.001$, Figure 5B). Mean % OM content for FBOM for the study period was 30.3 ± 2.3 %, but patterns in FBOM % OM were more variable for a given sampling and fluctuated more erratically over the growing season (Figure 5C) compared to CBOM. Percent OM content in FBOM also varied with abundance ($r = 0.41$, $p < 0.001$, Figure 5D). Overall, the % OM of FBOM was significantly greater than the % OM content of CBOM (t -test, $p < 0.001$, data not shown).

Patterns of TOM abundance over the growing season closely resembled those of the coarse fraction (Figure 4A, Figure 6A). Maximum TOM (187.3 ± 35.4 g/m²) occurred as CBOM peaked (Figure 6A). An exponential decline ($r^2 = 0.79$, $p < 0.05$, regression line not shown) in abundance of TOM occurred following seasonal maximum levels observed in mid-June, and standing crops approached a minimum of 12.8 ± 3.3 g/m² by the end of the study period, a value about 15-times lower than peak TOM. Average % OM content for TOM across the growing season was 23.7 ± 1.2 %. Percent OM content of TOM (Figure 6B) generally reflected trends in CBOM composition (Figure 5A), and these variables were positively correlated ($r = 0.81$, $p < 0.0001$, data not shown). Multiple regression analysis showed that \log_{10} TOM was positively related to benthic Chl *a* (coefficient = 0.214) which explained 19.8 % of the variation in TOM. Inclusion of Chl *a* drift, when negative-reciprocal transformed (coefficient = 0.00601) improved the model of TOM by 4.3 %, to explain a total of 24.1 % of the variation in TOM standing crop (Table 3).

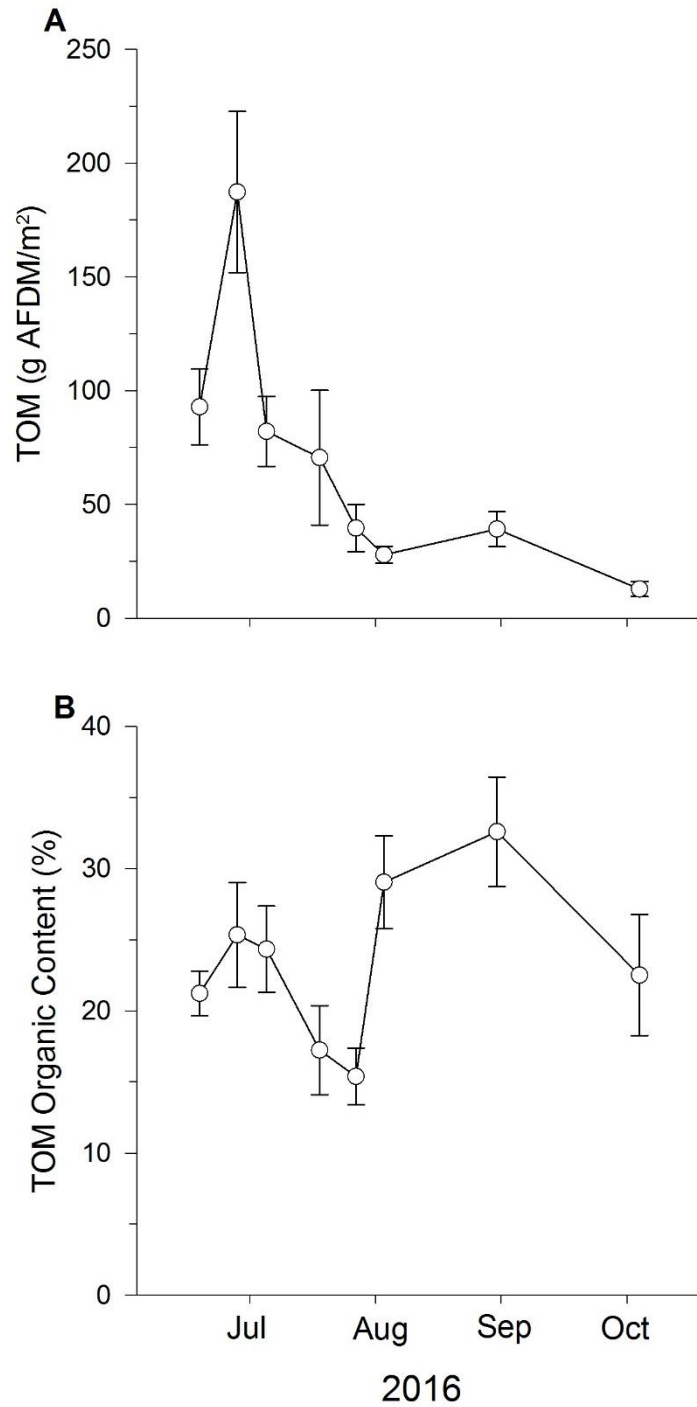


Figure 6. Total benthic organic matter (A) AFDM standing crops (g/m²) and (B) percent organic matter content during the summer growing season. Data are means \pm SE.

Chlorophyll a standing crops and Chl a:AFDM ratio — Standing crops of benthic Chl *a* co-varied over the growing season with CBOM, and these variables were significantly related in log-log space ($r^2 = 0.32$, $p < 0.001$, Figure 7B). Maximum Chl *a* (89.9 ± 22.0 mg/m²) was observed during the first sampling round in mid-June (Figure 7A), and an exponential decline in benthic biomass abundance as Chl *a* occurred over time ($r^2 = 0.92$, $p = 0.0001$) as streamflow in UCFR receded to base flow. By July, Chl *a* standing crop had declined by roughly 75 % and continued decreasing to a mean of only 1.1 ± 0.2 mg/m². Values for the Chl *a*:AFDM during samplings I & II were elevated compared to later samplings, and the quotient was at a seasonal maximum level of 1.0 ± 0.6 during the second round of sampling (Figure 7C). The Chl *a*:AFDM ratio then declined exponentially ($r^2 = 0.52$, $p < 0.05$) over time as both Chl *a* (Figure 7A) and TOM (Figure 6A) standing crops declined to mean values two orders of magnitude lower than observed at seasonal maximum. A noticeable increase in the Chl *a*:AFDM ratio occurred during the final sampling in October, concomitant with an increase in Chl *a* standing crops (Figure 7A). Multiple regression analysis indicated that when square-root transformed time was negatively related to Chl *a* (coefficient = -0.173) and explained 30.6 % of the variation in benthic Chl *a*, an expected relationship given the high coefficient of determination ($r^2 = 0.92$) associated with the exponential decline in Chl *a* with time since peak abundance (Figure 7A). Regression analyses indicated NH₄-N was positively related to Chl *a* (coefficient = 0.314) and inclusion of NH₄-N as an independent variable improved the prediction of Chl *a* by 6.9 %. Regression analyses indicated that when square-root-transformed, % OM of CBOM was negatively related to Chl *a* (coefficient = -0.114), and when log₁₀-transformed, TOM was positively related (coefficient = 0.613) to Chl *a*. Inclusion of these BOM variables improved the regression model by 10.2 %, explaining 47 % of the variation in Chl *a* (Table 3).

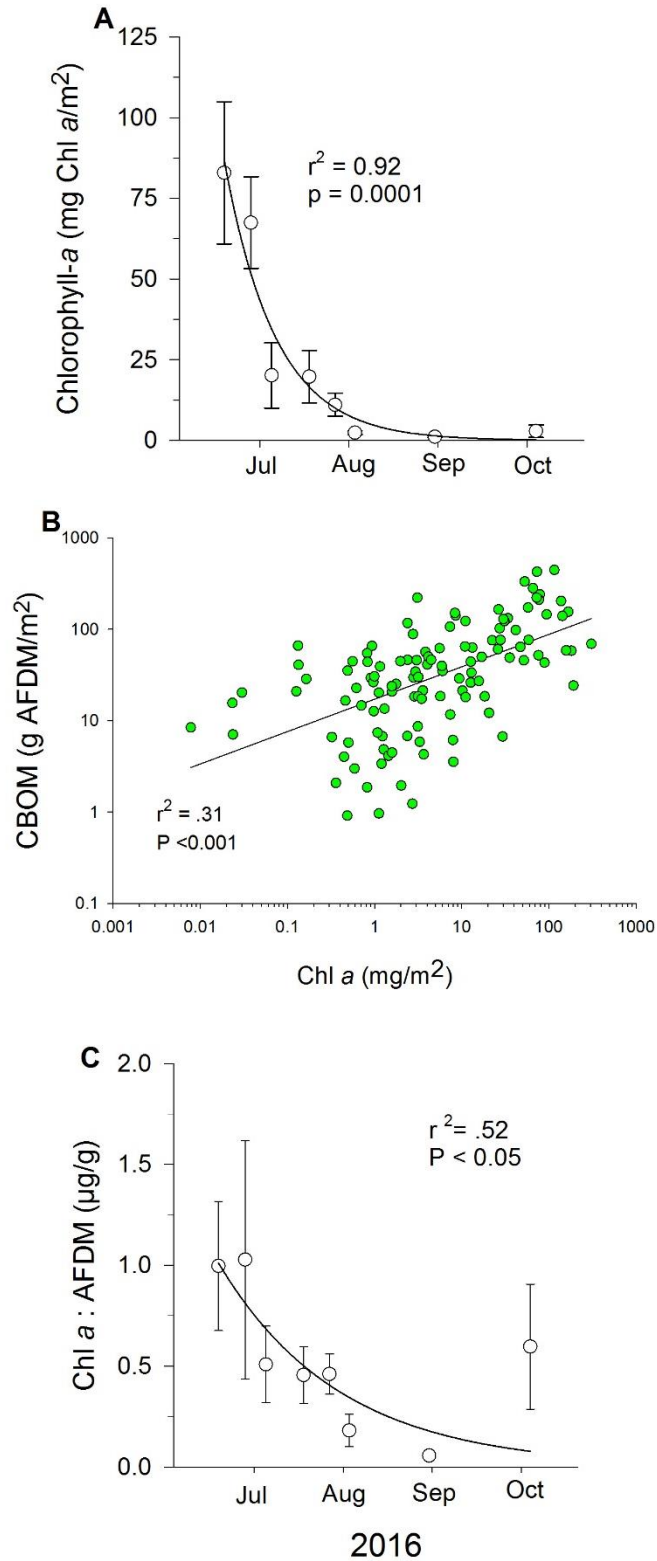


Figure 7. Growing season pattern of (A) Chl *a* standing crop, (B) relationship of Chl *a* to CBOM in log-log space and (C) temporal trend of the Chl *a*:AFDM ratio. Data are means \pm SE, except (B), where relationship was derived from individual observations.

Suspended organic matter and Chl a drift density — Drift density of SOM varied over the course of the study period by over two orders of magnitude (Figure 8A), following a pattern coherent with BOM standing crops, but lagged in time. As CBOM declined with seasonal transition to mid-summer base flows (Figure 4A), abrupt increases in SOM were noted for two consecutive samplings (III & IV, Figure 8A). During sampling IV, SOM transport peaked at 1.07 ± 0.03 g AFDM/m³. For the remainder of the growing season, SOM density declined, and drifting algal OM reached a seasonal minimum of 0.04 ± 0.01 g/m³ by September. Similar to BOM abundance and Chl *a* crop, SOM transport abundance rebounded slightly by the end of the study period, but mean drift density (0.10 ± 0.02 g AFDM/m³) increased to levels only slightly greater than seasonal minimum values observed one month prior. Over the first four samplings, % OM content for SOM was initially high (> 75 %, Figure 8B) and relatively invariant (CV = 6 %). After reaching maximum levels of 84.2 ± 1.2 % in mid-July, % OM content of drift algae exhibited a sharp decline, falling to seasonal minimum of 38.5 ± 14.1 %. In general, the % OM content for drift algae increased over the last half of the study period (Figure 8B). The % OM content of drifting algae was significantly greater than % OM for attached benthic algae (*t*-test, *p* < 0.001) for all samplings. Multiple linear regression analysis indicated SOM drift density was positively related to discharge (coefficient = 1.596), which accounted for 56.1 % of the variation in observed SOM drift density. Regression analysis also indicated that when square-root transformed, time was significantly and negatively related to SOM drift density (coefficient = -0.186) and adding this factor into the model accounted for an additional 40 % of model residual variation (Table 3). Together, these variables account for 92.3 % of variation in SOM drift density.

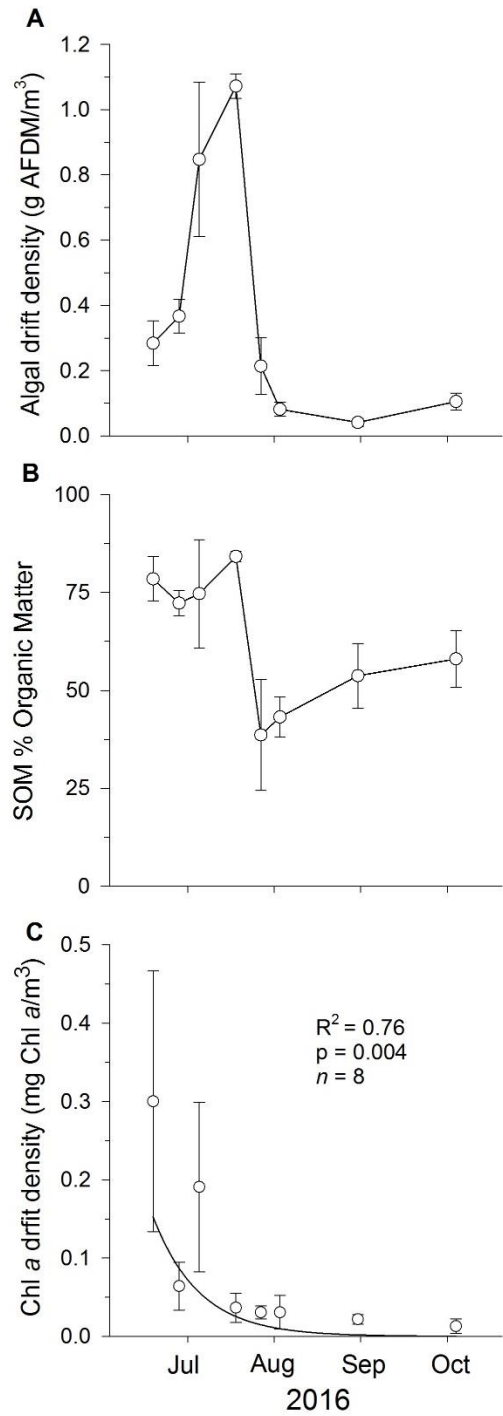


Figure 8. Temporal patterns in algal drift for (A) SOM drift density (B) percent organic matter content of SOM and (C) concentration of Chl *a* drift in mg Chl *a*/m³. Data are means \pm SE.

Chl *a* drift density (Figure 8C) exhibited patterns during the early growing season dissimilar to those observed for SOM drift density. Drift density of Chl *a* in the study reach was highest during the early growing season, as standing crops of benthic Chl *a* were abundant (Figure 7A), while drift density for OM (i.e., SOM) was generally low (Figure 8A). Unlike SOM drift density, however, which rose and fell over the study period, Chl *a* drift density (Figure 8C) declined continuously and exponentially ($r^2 = 0.76$, $p = 0.004$). While drift density for Chl *a* tended to increase with benthic Chl *a* standing crops (Figures 7A, 8C), the two variables were not significantly related ($r = 0.71$, $p = 0.07$, data not shown). Multiple regression analyses indicated that when negative-reciprocal transformed Chl *a* drift was negatively related to time (coefficient = -12.601) and cubed-transformed discharge (coefficient = -13.611). Time as a factor explained the vast majority (93.0 %) of the variation in Chl *a* drift, with the inclusion of discharge improving the prediction of Chl *a* drift by only 1 %. The inclusion of square-transformed temperature only improved the model fit by 0.6 % and this factor was left out of the final model (Table 3).

Discussion

Snowmelt pulse and spates — Compared to years with heavy snowpack (e.g., 2011) when roughly linear and gradual decreases in runoff occur during the recessional limb until mid-July, 2016 streamflow patterns in the UCFR study reach were indicative of less-than-average snowpack, with discharge declining abruptly in the period of time after peak runoff (Figure 2B).

The development of benthic algal standing crops of *C. glomerata* co-occurs with spring runoff, i.e., measureable and elevated BOM and Chl *a* occurred during the recessional limb (Figures 4, 7). Biomass clearly accrues during this window of high flow and cold temperatures, despite shear force generated by increased stream power during annual snowmelt pulse. The

ability of *C. glomerata* to withstand stream power associated with spring runoff may represent an adaptation by this alga to the typical disturbance regime of Rocky Mountain streams. Others have shown the coupling of seasonal *C. glomerata* blooms to the character of the annual hydrograph (Power et al. 2015).

Substantial declines in flow and the associated lack of disturbance correspond to approximate base flow conditions in the UCFR study reach by the beginning of July. Patterns of streamflow during my study prior to mid-July flooding met Biggs' (1995) criteria for lack of significant hydrological disturbance, since the hydrograph for the entire month of June did not include any increases in discharge that were greater than three times the mean flow for the prior seven-day period. Overall, however, base flow discharge in the UCFR during 2016 was more variable than noted by Valett et al. (2017) for the preceding summer. Rapid and relatively brief increases in discharge (i.e., spates) were observed within the study reach (Figure 2B) on at least one occasion. The steeply ascending hydrograph of 10 – 11 July, 2016 suggests that the rain event and resultant increases in discharge in the UCFR was localized to upper segments of the drainage basin, including the agricultural land draining to Flint Creek, the major tributary delineating the upstream boundary of the study reach. Flint Creek appeared to have received ample precipitation as evidenced by an increase in discharge from 0.66 to 5.81 m³/s overnight (USGS gauge no. 12331500, data not shown). The principal downstream tributary (Rock Creek, USGS gauge no. 12334510, data not shown) did not display the drastically increased flow as seen in Flint Creek over the same period. These hydrograph characteristics suggest that the Flint Creek system was associated with the abrupt increase in UCFR discharge. The effect of the mid-July spate on streamflow in Flint Creek was pronounced and prolonged; return to base flow in Flint Creek required more than a month, compared to the one week required for flows in the

UCFR to return to pre-storm values. Flooding of Flint Creek likely resulted in inundation of parts of its heavily agrarian floodplain as well. Hydrograph characteristics suggest that the Flint Creek system acted as a large inundated source that drained slowly for the next 30 days. Agrarian bottomlands like those surrounding the Flint Creek corridor can be important source areas for organic and inorganic inputs to larger stream ecosystems, even with moderate increases in flow (Golladay 1997).

Dissolved Oxygen, Temperature and Conductance — During the study period, all daytime observations of DO concentrations indicated supersaturated conditions. Oxygenic photosynthesis occurring in robust benthic algal standing crops found during June are probably associated with high oxygen saturation during this period. Saturation did not decline significantly, however, following the reduction of benthic autotrophic production in the study reach. This may be due in part to mixing by the water column and atmosphere in this high-gradient segment of stream and associated replenishment of DO, along with delivery of oxygen from phytobenthic communities in productive upstream reaches of the UCFR. Dodds (1991) noted that oxygen bubbles in portions of mats can be removed by flow, and hypothesized that overall oxygen concentrations found in mats could be the result of transport of this dissolved chemical species from algae upstream. Flourishing algal standing crops in upstream reaches of the UCFR may supply oxygen to downstream reaches.

All temperature measurements made during the period of initial period of biomass accrual (samplings I-II) are within the optimal range for *C. glomerata* growth (13 – 17 °C) reported by Wong et al. (1978) (as cited in Dodds 1991). However, temperatures were suboptimal by the beginning of July, and remained unfavorable for new biomass growth through the end of August, until stream temperatures cooled in autumn. A bi-modal peak in biomass

often described for *C. glomerata* over the growing season (i.e., early spring peaks & autumnal regrowth) is attributed to temperature change (Muller 1983, Whitton 1970, Wong et al. 1978, as cited in Dodds 1991). While bimodal biomass abundance was not strongly evident in this study, slight regrowth observed in autumn (Figure 4A) may be attributed to temperature declining to the optimal window where new *C. glomerata* growth is more likely to occur (Table 2).

Specific conductance (Table 2) was typical of summertime conditions in the study reach. Greater values observed during the end of August throughout the study reach may have been related to unusual inputs of fine sediment and other material associated with spates and bank failures. Biggs (1995) noted that stream conductivity should be greater in drainages containing nutrient-rich, sedimentary alkaline rocks and supporting agricultural land use. Western MT is rich in sedimentary rock deposits, and much of the UCFR is sourced from watersheds that lie within calcareous rock. Alkaline lithology may contribute to high concentrations of divalent cations that promote stream water hardness and alkalinity. In addition, agricultural land use is prevalent along the study reach and the tributaries that feed into it (Ingman 1992a, as cited in Dodds et al. 1997).

Dissolved Inorganic Nitrogen — Routine monitoring of the UCFR (H.M. Valett, unpublished data) suggest that at base flow, $\text{NO}_3\text{-N}$ is often low or undetectable, while $\text{NH}_4\text{-N}$ is more abundant with background concentrations typically less than 20 $\mu\text{g/L}$. Over the 2016 summer growing season, the predominant form of DIN in the study reach was $\text{NH}_4\text{-N}$ and concentrations varied independently of $\text{NO}_3\text{-N}$, which was robustly low during daytime sampling hours. In the UCFR, declines in $\text{NO}_3\text{-N}$ have been linked to periods of high algal biomass accrual, and increased availability of this reactive form of N outside of the growing season is common (Valett et al. 2017, Tri-State Water Quality Council 2009). Low $\text{NO}_3\text{-N}$ concentrations

may result from nutrient demand by autotrophic algal mats. Standing crops of benthic algae in the study reach did not co-vary with $\text{NO}_3\text{-N}$, as concentrations were low and varied little while standing crop ranged by orders of magnitude (Figures 3A, 4A). Main-stem DIN increased by approximately an order of magnitude above background levels during July. While the source of enhanced $\text{NH}_4\text{-N}$ is unknown, it may have been imported from upstream reaches.

Ammonification (mineralization) of organic N in stream water during algal community senescence and decomposition may serve as an in-stream source of $\text{NH}_4\text{-N}$.

It is more likely, however, that temporal spikes in $\text{NH}_4\text{-N}$ levels in the main stem UCFR were driven by episodes of intense precipitation during July. Spate-induced increases in flow magnitude in lower Flint Creek may have caused pulses of $\text{NH}_4\text{-N}$, generating concentrations that are uncharacteristic of the UCFR base flow period (Figure 3A). Agricultural land use in the lower portion of the Flint Creek valley may promote elevated DIN during times of high flows (Peipoch and Valett, in review). During flooding of riparian forests along the Rio Grande, NM., Valett et al. (2005) attributed spikes in $\text{NH}_4\text{-N}$ observed during initial stages of forest inundation to mobilization and desorption of $\text{NH}_4\text{-N}$ from floodplain forest detrital accumulations. Mechanisms evoked by Valett et al. (2005) may help to partly explain observed spikes of $\text{NH}_4\text{-N}$ in the UCFR. Spate-induced high flows and resultant partial inundation of Flint Creek bottomlands may have liberated $\text{NH}_4\text{-N}$ in great enough quantities to explain observed DIN dynamics during the study period.

SRP — Watersheds in western MT are rich in edaphic sources of P (Pardee 1917, Priscu 1986) and it is reasonable to believe P-rich lithology contributes to high background SRP levels throughout the UCFR. Notable declines in SRP coincided with periods of biomass accrual between samplings I & II. Uptake of P by autotrophic mats of benthic *C. glomerata* during

accrual phases was observed in the Eel River, CA, where workers attributed sharp decreases in dissolved P concentrations to nutrient demand by growing algal mats. Thus, biological processes in the UCFR such as primary production and algal growth may affect concentrations of SRP similarly. However, SRP was neither correlated to standing crops of BOM nor Chl *a*, measures of biomass abundance used in this study. Others have observed a lack of statistically significant relationships between ambient water column SRP concentrations and *C. glomerata* biomass in MT streams (Dodds 1991). In the period following peak biomass and low water column SRP concentrations, SRP immediately rebounded and generally continued to increase until autumn sampling. The abrupt shift to increasing SRP concentrations (Figure 3B) co-occurred with declining benthic algal standing crops (Figure 4A). A lack of P uptake later in the growing season, suggested by sharply increasing SRP concentrations with time, may reflect a return to background levels. Also, the increase in P over time may reflect release of cellular P sequestered by benthic algae. Lohman and Priscu (1992) noted increasing cellular P concentrations in UCFR *C. glomerata* throughout the growing season as ambient SRP declined, suggesting ample storage capacity for P. Decaying algae in upstream reaches of the UCFR may produce a supply of P that becomes available to downstream reaches. Paalme et al. (2002) found 40 – 65 % of P content is released in decomposing mats of *C. glomerata*. This could be an especially important source of nutrients when higher flows return to inundate expanses of stream channel covered in stranded *C. glomerata*. Wide, perched gravel bars at study site 3 are routinely covered by algal debris during base flows.

CBOM abundance and character — In ‘Reach C’ of the UCFR, CBOM is autochthonous and was maximal during the hydrograph recessional limb of 2016, and abundance declined over the course of the summer to generate FBOM and drifting algal OM. Biomass of attached *C.*

glomerata in the study reach varied 400-fold, a range probably typical for this reach of UCFR during summertime, and in agreement with levels observed during the 2015 growing season (Valett et al. 2017) and during previous years (Suplee et al. 2012). Summertime levels of benthic algal standing crops in the UCFR are comparable to literature reported values for *C. glomerata* in well-lit cobble-bottom stream ecosystems (Dodds et al. 1997). Freeman (1986) reported a *C. glomerata* bloom with standing crops of similar magnitude in a New Zealand stream. Blinn et al. (1995) found levels of *C. glomerata* attached to cobbles in the Colorado River, AZ to be comparable to those observed in my study. Standing crops of *C. glomerata* have been shown to be an important in Sycamore Creek, a semi-arid desert stream noted for autochthonous production. Autochthonous BOM in Sycamore Creek has been shown to be an integral component of that stream's food web (e.g., Fisher and Gray 1983) and OM budget (Jones et al. 1997). Over the course of seasonal succession, Fisher et al. (1982) showed the greatest streambed biomass in Sycamore Creek was associated with *C. glomerata* at levels similar to those observed in the UCFR.

In my study, benthic algal standing crops were in excess of nuisance level biomass abundance (greater than 50 g/m², Wharfe et al. 1984, Biggs and Price 1987, Benenati et al. 1998) in 36 % of observations. These data support the notion of persistent nuisance algae blooms in this reach of UCFR. Suplee et al. (2012) noted that during the period 1998 – 2004, mean summer biomass was frequently double the literature-defined nuisance biomass threshold. In my study, only for a brief span of several weeks during peak biomass did benthic algal standing crops reach levels comparable to historical nuisance levels described by Suplee et al. (2012).

Results from a multiple regression analysis suggest the total amount of BOM on the streambed (TOM, Figure 5A) was best predicted by benthic Chl *a* abundance (Table 3). These

findings suggest that the major process shaping the character of the TOM pool is autochthonous primary production. Acuña et al. (2004) found Chl *a* explained a substantial proportion of variation in gross primary productivity, and thus, autochthonous BOM in a Mediterranean headwater stream. Including Chl *a* drift in the model helped to explain some residual variation and suggests a dynamic coupling of suspended and benthic OM in the UCFR. Others have observed strong associations between various forms of BOM and OM material transport (Minshall et al. 2000, Power et al. 2015).

Chlorophyll a standing crops, Chl a:AFDM ratio — Time was best predictor of Chl *a* standing crop (Table 3). As the season progressed into the base flow period, the mass of Chl *a* on the streambed was declining exponentially (Figure 7A). A lack of Chl *a* accrual, evidenced by the downward trend in abundance over the course of the season, suggests little significant in situ regrowth of autotrophs and gradual depletion of the BOM pool without regeneration or recovery. The relationship between Chl *a* standing crops and time (Figure 7A) observed in this study suggests that there is a predictable relationship between OM material with respect to the length of the summer growing season. Given the dynamics of *C. glomerata* observed during the 2016 summer growing season, it would be interesting to test whether this exponential-decay model holds for historical seasonal biomass data, or for future temporal studies of the seasonal progression of benthic algal standing crops in the UCFR. The stepwise regression model also indicated ammonium concentrations were related to Chl *a*. This relationship may reflect algal senescence. Other studies have observed the liberation of ammonium as *C. glomerata* decomposes (Peckol and Rivers 1995). Interestingly, benthic Chl *a* was better predicted by the % OM content of CBOM than by standing crops of algae as AFDM. However, benthic TOM also accounted for a proportion of the variation in Chl *a*. Since FBOM is one of the principal

components of the TOM pool in this study, this relationship suggests that the manifestation of primary production as Chl *a* contributes to both the coarse and fine size fraction of OM pools.

In this study, biomass levels deemed excessive and adopted by the state of MT to designate nuisance growth in the Clark Fork river (100 mg/m² Chl *a* (Welch et al 1988, Dodds et al. 1997, Suplee et al. 2012) were exceeded in several ($n = 4$) individual observations from the period prior to the onset of decline in benthic Chl *a* crops. Low values for Chl *a* abundance observed in this study represent ca. 25 % of the literature derived nuisance level, findings which suggest an acceptable seasonal average biomass condition for this reach of river. The levels of benthic Chl *a* abundance were much lower and below the average observed for the 2015 summer growing season in the same reach (Valett et al. 2017). Biggs (2000) noted nuisance Chl *a* abundance occurring at times of base flow in a New Zealand stream. In my study, peak biomass as Chl *a* did not occur during base flow. This observation is consistent with those made in other MT streams where peak biomass of *C. glomerata* occurs immediately after spring runoff (Dodds 1991). Benthic autotrophic production was apparently already declining within the study reach by the end of June, as suggested by declining Chl *a* (Figure 7A), just as base flows were only beginning to set in (Figure 2A).

The positive and significant relationship between CBOM and Chl *a* (Figure 7B) suggests increases in BOM are related to Chl *a* abundance. Other studies have found a significant positive relationship between Chl *a* and BOM (e.g., Ameziane et al. 2002) in river ecosystems. Data presented in my study provides corroborates the notion of a putative autochthonous origin of streambed OM material.

No significant relationships were observed between Chl *a* and mean dissolved nutrient concentrations. The lack of significance between dissolved nutrients and Chl *a* is perhaps not

surprising, as relationships between these variables are typically poor for lotic ecosystems (e.g., Dodds 1991). Dodds et al. (1997) found that when seasonal mean values for DIN and SRP were combined, they explained a very low proportion (ca. 16 %) of variance in mean monthly Chl *a* for 205 streams throughout North America and New Zealand. However, among these streams, relationships between DIN, SRP, and Chl *a* became slightly more robust when regressions were run on Clark Fork River data only. Lastly, despite Chételat et al. (1999) assertion that nutrients have more pronounced effect on biomass during periods of low-flow, the observations made in this study do not support the notion of enhanced influence of nutrients on primary productivity during times of base flow. This could be due to observed variability in streamflow that disrupted low-flow conditions, an observation that is partially supported by Biggs' (2000) assertion that flow regime is more important than nutrients in determining the potential for algal proliferations. Variability in flow observed during 2016, may have, therefore, exerted some influence on nuisance proliferations of *C. glomerata* in the study reach, and rendered the low-flow nutrient effect negligible.

The Chl *a*:AFDM ratio can be used to estimate the percentage of BOM present as Chl *a* (Valett et al. 1994). At the initiation of the study period, as biomass accrued, the Chl *a*:AFDM ($\mu\text{g/g}$) approached one, reflecting a substantial contribution from Chl *a* to the BOM pool. Studies on Sycamore Creek (Valett et al. 1994) found that values for this ratio increased significantly during benthic autotroph recovery following flooding. Contrarily, decreasing values for this ratio were observed over successional time during my study. It is difficult to pinpoint the factors driving the decline in this ratio. It is plausible that summertime conditions in the UCFR became unfavorable to the viability and production of Chl *a* soon after peak biomass occurred. High insolation of the benthic environment during periods of low-flow could have promoted

photoinhibition of benthic autotrophic primary production (Hill 1996) resulting in cessation of Chl *a* production by *C. glomerata* mats. By September, the ratio fell to the seasonal minimum. Only as benthic autotrophic production recovered slightly towards the end of the growing season did the ratio increase to a value of similar magnitude to those observed during the early season.

Nevertheless, the magnitude of the Chl *a*:AFDM ratios reported during this study of the UCFR are quite high, an order of magnitude greater than for peak values reported by Valett et al. (1994) for algae in Sycamore Creek. In fact, Chl *a*:AFDM values observed in this study are in the same range as cultured algae (Schagerl and Müller 2006). Findings in my study suggest that during periods characteristic of early bloom development, benthic algal standing crops of *C. glomerata* are robustly healthy, and that OM dynamics in this segment of the UCFR ecosystem are intimately linked to autochthonous production.

The % OM content for attached benthic *C. glomerata* mats was initially low (Figure 5A), illustrating the capacity for mats to trap inorganic material. Other studies have shown the efficiency of fine sediment trapping by *C. glomerata*. Yamada and Nakamura (2002) demonstrated the amount of fine sediment trapped by algal-periphyton mats was positively related to biomass as AFDM. Patterns observed in this study partly support those of Yamada and Nakamura (2002), as the greatest values (as high as 30 %) of % OM content in CBOM occurred late in the season when benthic algal standing crops were minimal (Figures 4A, 5A). Elevated % OM content observed for CBOM (Figure 5A) and TOM (Figure 6B) in the latter portion of the study period may be due to the reduction of biomass and the associated reduction in the fine sediment filtering capacity of algal filaments. Low abundance of BOM standing crops and increases in stream water velocity in the benthic environment of the shallower, mid-summer channel at times of base flow may have contributed to this increase in % OM content. While

discharge was highest at the beginning of the season, the combination of high biomass and considerable water depth during early season may have precluded the effect of shear in winnowing away and removal of fines trapped in *C. glomerata*. Flinders and Hart (2009) found significant increases in % OM of attached benthic *C. glomerata* subjected to higher flow velocities, even as biomass as AFDM and Chl *a* declined. In their study, initial values for % OM content in *C. glomerata* were in the same range as found in my study and increased to values similar to those observed in the UCFR study reach at the end of the study period.

FBOM abundance and character — Despite the gradual and linear increase in FBOM standing crops during the study period, time was a relatively poor predictor of FBOM abundance and was not included in the multiple regression model. Inclusion of other variables (SRP and DO %) explained some amount of additional variation. In both cases, however, these factors were negatively related to FBOM and were likely acting as response variables and not predictors of FBOM. The negative relationship between SRP and FBOM could stem from the role of fine OM deposited on the streambed and the internal recycling of this dissolved nutrient within the benthic environment of the UCFR. Others have observed internal recycling of P in benthic environments as a function of algal sedimentation (Andersen et al. 2000). Depth and FBOM were positively related, probably owing to effect of fine OM settling at greater depths in some portions of the study reach. Fine OM can be an important energetic and biogeochemical component in stream ecosystems (Minshall et al. 2000). The contribution of algal-derived detritus as fine OM to riverine food webs is often high (Fisher and Gray 1983). Indeed, the River Continuum Concept (Vannote et al. 1980) posits that fine particulate OM is the principal source of C for food webs of large rivers. In this study, fine OM is of autochthonous origin, and is likely a more labile C source compared to contributions from allochthonous sources (Thorp and Delong 1994).

Initially, FBOM increased in abundance as discharge declined, and reached its seasonal maximum following the initial decline in CBOM observed early in the study period (Figure 4A). FBOM declined with declining CBOM, but represented a larger proportional abundance of the TOM pool in a nearly linearly increasing manner (Figure 4B). Data from this study supports the notion that breakdown of *C. glomerata* contributes directly to the fine size fraction of the TOM pool. Others have noted a similar progression of shifts in the composition of BOM standing crops over seasonal time scales. In Sycamore Creek, where the dominant primary producer is also *C. glomerata*, fine OM derived from algae makes up the bulk of fine organic particles, and 60-90 % of the total OM pool in late-successional stages (Fisher and Gray 1983). Despite gradual accumulation of FBOM in the UCFR, CBOM remained the dominant form of streambed organic material throughout the growing season. Nevertheless, findings in this study do suggest a direct contribution from *C. glomerata* to the compilation of FBOM with time. This behavior reinforces the notion that BOM dynamics in the UCFR are governed by endogenous process and underscore the importance of an autochthonous origin.

DOC — To constrain the source of this biologically active C, Finlay et al. (2011) employed a two-source isotopic mixing model and found that 87 % of DOC in the Eel River, CA was sourced from *C. glomerata*, with a smaller contribution from terrestrial plants in the drainage. In my study, CBOM and DOC were positively related, suggesting that DOC dynamics are likely being driven by CBOM throughout the seasonal progression of *C. glomerata* bloom and eventual senescence.

Generally, DOC concentrations were stable throughout most of the study period (Figure 3D), but an evident increase was observed late in the growing season. Others studies have observed release of DOC by primary producers in response to decomposition processes

(Byerrum and Benson 1975, Pregnall 1983, as cited in Peckol and Rivers 1995). Though I did not account for DOM sourcing in this study, findings by Finlay et al. (2011) and others suggests the potential importance of in situ autotrophic production in the UCFR as a primary determinant of stream water DOC concentrations. At the same time, changing DOC concentrations may reflect external influences. Valett et al. (2017) illustrated higher DOC concentrations in Flint Creek than in the main stem UCFR during the 2015 summer growing season. If Flint Creek and its floodplain were acting as sources for DOC, then the spate-induced increase in discharge during mid-July would have generated concomitant increases in UCFR stream water DOC concentrations. Valett et al. (2005) found inundation of river floodplains generated spikes in surface water DOC concentrations. In my study, however, no obvious flow-related increase in DOC concentrations were observed. Stream water DOC concentrations showed substantial increases only during autumn sampling following declines in CBOM and Chl *a* standing crops.

Algal drift and SOM Transport — Temporal patterns of SOM drift density appeared strongly linked to the progression of the growing season, and perhaps to a somewhat lesser extent, patterns of streamflow. Multiple linear regression models run on algal drift metrics indicate time and discharge explained a large proportion of variation algal drift abundance.

The decline in Chl *a* drift density with time suggests that over the course of the growing season Chl *a* drift was supply-limited. As standing crops of benthic Chl *a* deteriorate with time, there is simply far less of this material available for transport within the system. Perhaps because of this, variable flows later in the summer growing season (Figure 2B) may have only a moderate influence on the quantity of Chl *a* in transport. Conversely, BOM was plentiful enough throughout the growing season to be readily dislodged and transported by stream flow both early and late in the growing season.

Values for SOM drift observed in my study during base flows (0.05 – 0.2 g/m³, Figure 8A) were comparable to levels reported for OM drift in a Japanese stream, where workers reported drifting abundances of macroscopic plant material including filamentous algae during July base flows of 0.021 g/m³. The magnitude of algal transport observed during base flow in my study was similar to that reported by Valett et al. (2017) for the same period of time (late July) during the preceding summer, even though benthic algal standing crops available for transport during my study were considerably lower than those observed by Valett et al. (2017), suggesting drifting algal OM may be imported from upstream reaches. Alternatively, this discrepancy may relate to the influences of receding floodwaters in the period after the spate that resuspended and entrained previously detached *C. glomerata* stranded in low velocity areas of stream channel margins or the bottoms of pools.

Despite the plausible role of discharge governing drifting algal dynamics as indicated by stepwise regression, metrics describing algal transport were not statistically related to reach-scale mean discharge (data not shown). The lack of a correlation in part reflects the lack of transport during the first sampling round, when discharge was at its maximum. During this period, standing crops of *C. glomerata* were fresh and healthy, as indicated by high values for the Chl *a*:AFDM ratio. As such, *C. glomerata* was probably attached firmly to streambed substrate via holdfasts, and apparent sloughing and export of algae derived from within the reach was minimal. During this early phase of bloom development, *C. glomerata* is likely to be resistant to endogenic sloughing and subsequent transport.

In my study, a combination of endogenic sloughing and elevated discharge likely contributed to increased algal drift densities. Algal filaments undergoing endogenous physiological stressors, as evidenced by the declining benthic Chl *a* standing crops, could have

detached and became entrained in flow, as evidenced by the increase in algal drift density early in the season prior to any exogenous disturbance. Whereas, in terms of the effect of physical disturbance (i.e., spate) on drift density, post-spate flows were probably partially responsible for enhanced drift density. Measured UCFR drifting algae attained peak levels in the days following the spate, as mean discharge nearly doubled due to storm flow. However, it is clear that algal drift was not solely a function of increased discharge. Valett et al. (2017) noted greater drift density within 'Reach C' when compared to various upstream and downstream sampling locations along the UCFR, even at times of steady summertime low-flow. This lends support to the idea that 'Reach C' is acting as a source of autochthonous BOM, and that conditions within the study reach can promote endogenic sloughing without agents of disturbance.

Most work dealing with OM drift in streams concerns allochthonous material and studies quantifying drifting algal material are typically used to evaluate the effects of hydroelectric facilities and associated discharge fluctuations on aquatic primary producers (Blinn et al. 1995). For example, in the reservoir-fed River Spöl (Europe) Jakob et al. (2003) found flooding increased suspended Chl *a* from a low of less than 5 mg/m³ to greater than 40 mg/m³, whereas the effect on SOM concentrations (as g AFDM/m³) for the same event was less pronounced. In my study, the effect of elevated flow was more pronounced for SOM as AFDM than for Chl *a*, opposite to the response observed by Jakob et al. (2003).

During years without abrupt changes in base flow discharge (e.g., 2015) UCFR algae may accrue during early summer and then undergo synchronized sloughing and export (Valett et al. 2017). Other studies have documented similar synchronized sloughing by *C. glomerata*. Endogenic sloughing, as Higgins et al. (1998) note, probably occurs at some critical level of attached algal biomass, when autotrophic metabolism in filaments of *C. glomerata* is

compromised by the conditions in the surrounding mat environment. Thus, mechanisms that regulate SOM transport in the UCFR are, on average, likely governed by the endogenous features (e.g., growth, physiological status) and exogenous forces like flow and disturbances associated with it.

Conclusion

Standing crops of *C. glomerata* biomass, in its various forms, may exert significant influence on benthic ecosystem structure and function in the UCFR. On an average year, this alga comprises nearly all of the OM found on the streambed over the summer growing season. In my study, *C. glomerata*, as attached algae, was the dominant form of BOM throughout spring and summer, and was especially abundant early in the growing season. Coarse algae remained dominant while its abundance varied 400-fold, likely in response to both endogenous and exogenous factors.

During the 2016 growing season, benthic algal standing crops of *C. glomerata* in the UCFR were similar to values reported in the literature for growing season algal biomass on a global basis (Dodds et al. 1997). Data from this study indicate that, at times of peak attached algal biomass, nuisance criteria for benthic algae were exceeded. Despite initial observations made in the study reach illustrating algal proliferation, overall conditions that favor *C. glomerata* biomass accrual appeared to be transient, evidenced by declines in standing crops of biomass by mid-summer.

In the UCFR, during the short summer growing season window, a combination of factors drive intense biological activity, illustrated by characteristic bloom development of autotrophic algal biomass concomitant with spring runoff. It is likely average peak flows do not possess the magnitude of flow force needed to scour benthic surfaces and effectively reset *C. glomerata*

assemblages. As climate-induced changes to aquatic ecosystems are expected to occur in MT (Pedersen et al. 2010), many of the well-lit, nutrient-enriched stream ecosystems suffering from seasonal algal blooms may experience more extensive *C. glomerata* dominance of benthic environments.

From the results of this study, it is evident the seasonal progression of the *C. glomerata* bloom can be variable, and as a result, so are its impacts on aquatic ecosystem structure and function. However, with an understanding of various combinations of endogenous and exogenous factors, the overall nature and character of the UCFR *C. glomerata* bloom should be somewhat predictable. Even though stream ecosystems are inherently stochastic, predictive power in forecasting characteristics of BOM during summer in an ecosystem like the UCFR is perhaps even more approachable than for other stream ecosystems, given the relatively low inter-annual variability in many UCFR exogenous factors (i.e., flow timing and duration, irradiance regime, water temperatures, nutrient conditions). In my 2016 study, however, variability in flow appeared to be a factor influencing standing crops of autochthonous BOM to some degree as well.

In terms of OM origins and their implications to food webs, Chl *a*:AFDM ratios of BOM clearly suggest an autochthonous source, underscoring the notion that aquatic-terrestrial linkages are not as important in overall OM dynamics in the UCFR than has been shown in other stream ecosystems (Vannote et al. 1980). Land use in the region has caused river-channel entrenchment and significantly constrained the main-stem UCFR channel. As a result, there is relatively little influence on OM dynamics from channel-floodplain interactions, and likely a very small proportion of energy is driven by interactions with the surrounding landscape.

Drifting algae and algal-derived detritus in this ecosystem may represent an unknown contribution of energy to downstream communities, as has been shown by ecologists working on *C. glomerata* in the Colorado River, AZ (Shannon et al. 1996). The translation of attached, benthic algal standing crops to drifting OM is linked to endogenous (i.e., growth and physiological status) and exogenous (flow) factors, with implications for secondary production and the success of game fisheries. Synchronized endogenic sloughing and transport of drifting algae can be a highly punctuated event, one that may drastically alter in-stream physicochemical and biogeochemical attributes. Drifting *C. glomerata* algae is often abundant, texturally coarse, and has a high surface area to volume ratio. As such, greater transport of drifting algae may have a disproportionate effect on the surrounding stream environment. Further work is needed to couple the sequence of mat formation and drift production to riverine benthic conditions and food web character, as well as to explore the fates of this material throughout the Clark Fork ecosystem.

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