Benthic resource availability and variability in the diet of *Baetis* in Rapid Creek, S.D.

By

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Abstract

Benthic resources for macroinvertebrates take a variety of forms including biofilm, coarse benthic organic matter and fine benthic organic matter. These food subsidies are a critical component of the trophic relationships present in a stream habitat and are subject to alteration by biotic and abiotic processes. Understanding how benthic resource availability changes in response to environmental variables in Rapid Creek, SD is important for predicting future impacts on individual species and landscape level food-web interactions.

We assessed the variability of benthic resources for benthic macroinvertebrates in Rapid Creek, South Dakota from April 2014 – April 2015. Through gut content analysis, we examined relationships in the diet of *Baetidae Baetis* and compared this to the resource present in its immediate vicinity.

We found that biofilm organic matter and chl-*a* concentrations were suppressed by high flows that occur during our sampling regime, but showed resiliency to additional bankfull flows later in the summer. Estimates of coarse benthic organic matter indicate constant transport out of the sampling reach with the highest seston values occurring during elevated discharge events. A significant increase in embeddedness occurred following the early summer bankfull discharge events, which altered the ability of riffle habitats to retain CBOM and FBOM.

Additionally, since 2002, Rapid Creek has had the nuisance diatom, *Didymosphenia geminata*. Our biofilm characterization suggests that *D.geminata* mats offered the best microhabitat for diatoms in Rapid Creek during high flow events. We observed higher diatom consumption by *Baetis* with increasing *D. geminata* presence, but *Baetis* exhibited diet preference against the consumption *D. geminata* cells at locations with the most pronounced *D. geminata* mat development. The alteration in the availability of benthic resources in Rapid Creek was driven by discharge and can have direct effects on the stability of Rapid Creek's food web and possibly limit production at higher trophic levels.

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Introduction

Fluvial ecosystems are a critical component of our freshwater resources and manipulation can directly impact the integrity and structure of these habitats. Modification of a river's discharge can cause the losses of crucial ecosystem services, the decimation of profound biologic diversity and the possible disruption of its ecologic integrity. (Postel 1996). Most civilizations have been established around rivers that are altered to provide water for domestic, industrial and agricultural use (Malmqvist and Rundle 2002). The use of running water for the advancement of society's well-being has come at the expense of the ecological integrity of these fragile systems. The increased reliance on rivers as a source of water for many uses including agriculture, drinking, and energy production has heightened the need to conserve and protect these resources.

Hydrogeomorphology describes the 3-dimensional geologic structures and constructs that influence the unique local character of a watershed and river. These geologic structures shape the physical template and, in turn, the ecological processes that occur within the fluvial landscape (Poole 2010). This concept is grounded in the work of William Morris Davis, who initially described the process by which current landforms represent their interaction with the underlying geologic structures. Using this work, Leopold et al. (1964) determined that, although the physical template of the watershed was important, attention must also be paid to the basic laws of thermodynamics. The longitudinal profile of a river represented a balance between the uniform distribution of energy along the river and the tendency to find the lowest possible entropy within the stream channel.

The systematic downstream change that Leopold and Davis presented was re-interpreted by the River Continuum Concept (RCC) to include the longitudinal variation that these landscape level processes had on the structure of aquatic communities. The RCC characterizes rivers and streams as a continuum of physical conditions that control and facilitate the ecological processes from headwaters to large floodplains (Vannote et al 1980). The RCC suggests that there will be gradual adjustment to the biological processes as the hydrologic and geomorphic processes change downstream.

Opponents of the RCC cite that it fails to account for the fact that localized variability brought on by disturbance or anthropogenic activity will alter the community composition or ecologic integrity of the riverine ecosystem. These effects operate at smaller scales than the RCC proposes and cannot be organized in space and time by this construct (Montgomery 1999). Local variation, be it natural or induced, determines the level of biological diversity and the total ecological integrity of the catchment (Poff 1997).

The importance of variability in abiotic and biotic conditions in structuring biologic communities and driving ecologic processes has been a long-standing area of research (Poff and Ward 1989). With all of these processes interwoven, some researchers view discharge as a master variable due to its strong correlation to critical ecosystem structuring processes. Water temperature, chemistry, stream channel morphology, habitat diversity and species composition are all dependent on the wide range of conditions that discharge can affect in any given drainage (Poff 1997). For instance, discharge distributes and exports organic matter that is critical to sustaining biologic communities. The community composition and species abundance present at any given time or location is a direct reflection of the recent history of flows within that habitat. Natural flow regime not only accounts for the role of total variability, but also indicates that disturbance plays a critical function in maintaining ecologic integrity. Bankfull flows, or a flood event with a 1.5 – 2 year return interval, will perform essential habitat-forming physical processes and provide the variation in the physical template that influences population and processes at the community level. The spatial and temporal variation of channel-modifying events will create unique habitat patches (Formna and Gordon 1978, Pringle et al. 1988) which define the physical template of the biologic processes and patterns specific to that reach of river.

The natural spatial and temporal variability of the flow regime promotes and sustains a locally diverse composition of benthic macro and microorganisms by structuring the habitat and trophic interactions. Discharge as a selective pressure, controls the adaptive strategies and life history traits for a species' success within a given system (Minshall 1988, Power et al. 1988, Poff 1992). Similarly, the control structure of predation of those species can be both primary producer-driven (Hart and Robinson 1990) and, at other times, dictated by the herbivory of periphyton in the system (Lamberti and Resh 1983, Steinman et al. 1987, Power et al. 1988). This interplay of biotic and abiotic variables has been shown to control the accrual of benthic stream periphyton (Hynes 1970, Dodds and Biggs 2002, Biggs et al. 2005). Any disruption or change to the natural flow regime will have direct impacts on ecological processes within a fluvial ecosystem.

The Serial Discontinuity Concept (SDC) states that the placement of a dam within the river corridor will create a discontinuity in longitudinal flow of water and resources in the system and that these ecologic consequences of flow modification can be viewed explicitly (Ward and Stafford 1983). This discontinuity once established will result in alterations that extend upstream and downstream from the dam and have discrete, quantifiable impacts on the total river ecosystem (Ward and Stafford 1983). Variability in discharge can directly modify the habitat and resources within the system. The abiotic and biotic processes respond to spatial and temporal fluctuations in discharge which can influence the relative success of species by impacting their abundance, distribution, and trophic interactions (Poff and Allen 1995, Standford et al. 1996). Benthic macroinvertebrate community composition is regulated by the availability of basal food resources which can be disrupted by flow modification (Wellard-Kelly et al. 2013).

Additionally, excessive modification of flow regime can leave a drainage more susceptible to non-native species invasion (Moyle and Light 1996). The degree of alteration and individual character of the drainage will influence the intensity of colonization associated with the non-native species. Rapid Creek in Pennington County, SD, since 2002 has contained mats of the nuisance diatom, *Didymosphenia geminata* (Larson 2010). This mat development can cover a majority of the substrate and has been shown to have differential impacts on the stream's ecological processes (Kilroy 2004, Spaulding and Elwell 2007).

We investigated the role that flow-mediated resource alteration and *D.geminata* mat development have on the availability of benthic resources over the course of one year. Through gut content analysis we examined whether the alteration of benthic resources had a significant influence on the diet selection of *Baeti*s, a mayfly, in Rapid Creek. Resource availability directly influences the structure and stability of the benthic macroinvertebrate community present within a system (Vannote et al. 1980). Alteration of these resources can lead to changes in abundance and composition of the macroinvertebrate community, impacting the critical role they play in the function of the ecosystem as a whole (Hall et al. 2000).

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Introduction

Discharge has been strongly linked to biotic and abiotic processes and can directly affect the relative success of species by impacting their trophic interactions (Poff and Allen 1995, Stanford et al. 1996). Flow regime represents a complex intermingling of ecological process that can act on multiple scales and has direct and indirect effects on habitat characteristics, species dispersal and the acquisition and availability of resources. The spatial and temporal variability of the discharge promotes and sustains ecosystem integrity, but excessive modification can cause alterations to the availability of resources and community composition (Poff and Allen 1995).

Benthic resource availability influences the structure and stability of the benthic macroinvertebrate community present within a system (Vannote et al. 1980) and a reduction of the subsidies residence time or total quantity of benthic resources can lead to changes in abundance and composition of the macroinvertebrate community (Hall et al. 2000). When flow modification alters basal food resources, discharge plays a large role in structuring benthic macroinvertebrate communities (Wellard-Kelly et al. 2013). Understanding how benthic resource availability changes in response to environmental variables is central to creating a clear picture of how future alteration can be expected to impact the individual species and influence landscape level interactions (Power 1995).

Excessive modification of flow regime can leave a drainage more susceptible to non-native species invasion (Moyle and Light 1996), or increase native species that have invasive tendencies. Recently, researchers worldwide recorded the increased prevalence of the diatom, *Didymosphenia geminata (Dg)* in riverine ecosystems (Kilroy 2004, Spaulding and Elwell 2007). *D. geminata* cells secrete stalk material that can form mats that can cover a majority of the substrate in the river and alters species abundances and composition of the biofilm and benthic macroinvertebrate (BMI) communities (Spaulding and Elwell 2007).

Numerous studies have suggested that *D. geminata* could have significant ecological impacts on native species and local biodiversity (Campbell 2005, Kilroy et al. 2006, Spaulding and Elwell 2007). *D. geminata* mats increase the abundance of smaller sized taxa, such as Chironomidae, and decrease the abundance of larger taxa, including Ephemeroptera, Plecoptera and Tricoptera (Gillis and Chalifour 2010, Kilroy et al. 2009). The observed shifts in macroinvertebrate assemblages may be explained by a change in benthic food resources associated with *D. geminata* mat development (Larned et al. 2007). The stalk matrix provides additional refuge and increased substrate complexity for periphyton growth (Kilroy et al. 2006, Spaulding and Elwell 2007), but changes the physical structure of the substrate surface. BMI taxa that are able to utilize this change in physical habitat, such as Chironomidae, increase in total abundance (Gillis and Chalifour 2010, Kilroy et al. 2009). Additionally, stalk material may not be palatable or may have lower nutritional value (Holderman and Hardy 2004) and its total growth and coverage of a stream substrate may reduce total food quantity and quality (Larned et al. 2007, Spaulding and Elwell 2007, Blanco and Ector 2009). Tadpoles of *Rana boylii*, a biofilm grazer in Sierra Nevada streams, experienced a reduced growth rates at sites impacted by *D. geminata* mat development compared to non-impacted sites, suggesting that mat material significantly altered the availability of high-quality benthic resources (Furey et al. 2012).

Since 2002, Rapid Creek has supported *D. geminata* with seasonal development of mat material (James 2010). Research on Rapid Creek has shown that mat development has altered the benthic macroinvertebrate community composition and abundance (Larson and Carriero 2008, James 2010), but additional research is needed to elucidate the direct effects of mat development on the availability of benthic resources and the diet of BMI in Rapid Creek. Our research investigated the spatial and temporal heterogeneity of benthic food resources in Rapid Creek from April 2014 to April 2015 and the diet of a grazer, *Baetis*. Benthic resources control BMI composition and function (Polis 1991), and an alteration of these resources can influence food web relationships and the flow of energy within the ecosystem (Taveares-Cromar and Williams 1996).

Methods

Rapid Creek is the largest watershed in the Black Hill National Forest, occupying a 1,062 km^2 drainage basin with its headwaters draining the north-eastern slopes of the Black Hills. Rapid Creek is a regulated waterway, broken into multiple sections by dams ranging from 36 m to 70 m in height. We focused on the 36 river kilometers below Pactola Dam. Rapid Creek has a yearly average discharge of 1.49 $m^3\ s^{-1}$ (USGS 1964-2013) at Pactola Dam. After gaining tributary inputs, discharge increases to 1.97 $m^3\ s^{-1}$ (USGS 1964 – 2013) before entering Canyon Lake in Rapid City, SD.

To begin the site selection process, we divided Rapid Creek into 4 sampling reaches demarcated by the major tributaries: Deer Creek, Prairie Creek and Victoria Creek. Using ArcGIS Desktop Version 10.2.2 (Esri), we randomly selected one point within each section and identified the riffle closest to the point that provided best access and safety for sampling. Due to planned stream restoration work and localized high *D. geminata* growth, an additional sampling location was added below Pactola Dam, for a total of five sampling sites (Fig. 1). The sampling sites selected were named beginning with the site at the lowest downstream riffle as RC1 and naming the sites sequentially as we moved upstream finishing with RC5 located below Pactola Dam. We randomly placed five transects along the length of the riffle at each site by rolling a 12-sided dice twice. Our first die roll provided the distance (m) from the downstream end of the riffle for the first transect and the second roll justified the distance (m) between each of the 5 transects. When the riffle did not have sufficient length to place five transects, we sampled the next suitable upstream riffle with the same spacing scheme. After five transects were placed at each sampling site, we recorded GPS coordinates for each transect and these locations constant through the duration of the research.

Local terrestrial habitat, physical terrain and stream morphology at each sampling location creates unique riffle structures. RC1 is approximately 1000 meters upstream of Canyon Lake and has the greatest amount of deciduous forest canopy in the riparian zone. This location, with a relatively flat stream bottom and low bank morphology, has the greatest potential for the floodplain interaction. Both RC2 and RC4 are flanked by steep banks and the stream bed morphology of each shows the likelihood of two active streams channels under higher flows. RC3, located near Hisega, is constrained by riprap from roadway bridges with little to no canopy cover. RC5, located in the spillway below Pactola Dam, has almost no canopy cover and exhibits broad, flat riffle reaches and limited lateral expansion.

We examined the physical habitat characteristics and stream morphology of our sites during each sampling event. This data collection consisted of measuring depth, canopy cover and substrate biofilm composition. We measured and recorded wetted width (WW) with a TruPulse Laser Range Finder and divided each transect into ten equal sampling points and recorded depth at each point (Depth). To assess stream bed composition, we randomly selected a rock at each sampling point on the transect and recorded sediment size using a modified Wolmann pebble count to estimate the distribution of sediment size classes (SC) (Bevenger and King 1995). We also recorded an embeddedness estimate for each randomly selected rock. During this process, we estimated percent coverage of *D. geminata* mat development as a percentage of available area (%Dg) for each rock selected during the pebble count. When *D. geminata* was present in a transect, a 25 cm^2 section of cobble containing *D. geminata* was sampled to calculate *D.geminata* ash-free dry mass (AFDM). To estimate canopy cover (CC), we used a spherical densitometer (Lazorchak et al. 2000) and recorded values for each transect at stream center and each bank. Using the standard point flow measurement method (Platts et al. 1983, Ott ADC Current Meter), we estimated the discharge upstream and downstream of each sampling reach.

For benthic macroinvertebrate collection (BMI), identification, and gut content analysis, we collected BMI samples at each transect using a 500µm Hess sampler (Moulton et al. 2002). We preserved the BMI samples with Kahle's Solution (Stehr 1987) and stored them for safe transport to the laboratory. From the BMI samples collected, we selected *Baetis* for gut content analysis. *Baetis* is a common mayfly and a generalist grazer species. Additionally, during our sampling regime, *Baetis* was predominate grazer species present in all samples. We dissected and removed the fore guts of *Baetis* from three transects at each sampling location during our April 2014, August 2014, October 2014, and April 2015 sampling events. Dissection was completed under a stereo microscope and the foreguts collected were filtered onto gridded filters (Pall Corporation) and slide mounted for fractional area analysis (Benke and Wallace 1980, Rosi-Marshall and Wallace 2002, Wellard et al. 2013). Using 100x magnification and the Cellsens – Count & Measure software package (Olympus Europa SE & -CO. KG.), we quantified total benthic resources consumed into five classifications; diatoms (Dia), *D. gemianta* cell (Dg), algal (Alg), terrestrial plant material (Plt), and amorphous detritus (Det). We assigned a number of 1-12 to the transect intersections in the middle column of the gridded cell. Using a 12-sided die, we randomly selected a transect intersection in this area and characterized particle types and recorded the surface area of the first 100 particles within the viewing area. We used the same selection procedure if an additional sampling area was necessary to obtain the threshold particle count. With particle type, particle surface area, total filter surface area and number of individual guts collected per sample, we were able to estimate the surface area of each particle type (SA) per individual mayfly. Additionally, we calculated the surface area of each particle type as a proportion of total surface area of all particles counted (SA %) to better understand the relative diet selection of *Baetis* for each gut sample characterized.

To estimate the quantity of benthic resources present in Rapid Creek, we sampled biofilm, coarse benthic organic matter (CBOM) and fine benthic organic matter (FBOM) at each transect. To sample biofilm, we selected a rock adjacent to the location of the Hess Sampler at each transect and scrubbed the rock with a small brush to create a biofilm slurry. The slurry was rinsed into a volumetric container, the total volume of slurry was recorded and a 250 ml subsample was collected for analysis. We outlined each rock to estimate planar surface area. We filtered a subsample of the biofilm slurry onto a 45-mm glass fiber filter for ash-free dry mass analysis (AFDM). We oven-dried the biofilm at 60°C, weighed them and then placed them in a muffle furnace for 4 hours at 500°C. The filters were re-weighted and the difference was used to calculate the organic matter (OM) estimates of this benthic resource (Steinmann et al. 1996). A biofilm subsample was filtered onto a 25-mm glass-fiber filter for analysis of chlorophyll a concentrations (chl-*a*) using the acid method (Nusch et al. 1980). To complete the characterization of benthic resources in Rapid Creek, we collected CBOM, FBOM and seston from each transect (Mulholland et al. 2000) and filtered these samples for AFDM.

Finally, we preserved an additional 25 ml subsample of biofilm with 2% Glutaraldehyde. From this biofilm subsample, we diluted a 1-3 ml sample and filtered that for fractional area analysis (Benke and Wallace 1980, Rosi-Marshall and Wallace 2002, Wellard-Kelly et al. 2013). The analysis for biofilm fractional area employed the same procedure as the BMI gut content analysis.

We simulated variable discharge conditions in Rapid Creek by creating 3D models of each riffle using the River Analysis System modeling software (HEC-RAS, Hydrologic Engineering Center, U.S. Corps 2014) and the HEC-GeoRAS extension in ArcGIS (ESRI Redlands, CA). We modeled each riffle under two different flow conditions: the average mean daily discharge (Qavg) since the previous sampling event and the maximum mean daily discharge (Qmax) since the previous sampling event. With these two model inputs, we simulated average channel velocity at each transect and recorded two flow metrics, v(Qavg) and v(Qmax). These two variables help us describe the variability of discharge between sampling events, as viewed through duration (Qavg) and magnitude (Qmax), observed in Rapid Creek during the sampling regime.

Data Analysis

To identify points in time or locations where possible significant habitat alteration influenced benthic resource availability in Rapid Creek, we performed one-way analysis of variance (ANOVA) with post-hoc Tukey Honestly Significant Differences (TSD) ($p < 0.05$) on the physical habitat data average by sampling site and date. Additionally, we conducted ANOVA with TSD of the benthic resource data, biofilm characterization and gut content characterizations averaged by site and collection date to further identify the effect that habitat alteration had on benthic resources availability and *Baetis* diet selection.

Multiple Linear Regression – Stepwise ($p < 0.05$) was conducted to identify which habitat variables (v(Qmax), v(Qavg), Depth, WW, CC, Emb, SC, Dg, %Dg) explain the variability present in the benthic resource data (biofilm OM, chl-a, CBOM, FBOM, Dg OM), the biofilm characterization and the gut content characterization averaged by site and collection date. Square-root transformations were applied to the physical habitat as needed to meet the assumptions of normality necessary for this test. All data was statistically analyzed using Minitab v. 17 (State College, PA USA) and Microsoft Excel (Redmond, WA USA).

Results:

Due to the 330 cm of snowfall in the winter of 2013/14 and with May through September of 2014 receiving excess of 12.29 cm of rain, discharge in Rapid Creek routinely exceeded daily recorded averages during the entirety of our sampling. Rapid Creek was at or above bankfull discharge (3.96 m^3 s^{-1}) for 89 days with the maximum discharge of 8.21 $m^3 \bullet s^{-1}$ recorded on May 12, 2014 (Fig. 2). Discharge during our sampling regime was above 50% exceedance for a majority of the summer and was above or near bankfull discharge for this section of Rapid Creek as well. Local morphology at each sampling site created variability in the physical habitat characteristics that we measured (Table 1).

Due to high flows in Rapid Creek, continuous export of CBOM and FBOM occurred through our sampling reach. We found that CBOM estimates averaged for all sites peaked in April 2014 (1.27 g/m^2), and these values steadily decreased throughout the course of the sampling regime (Fig. 3). In addition, average seston estimates for all sites peaked during July 2014 (2.3 mg L^{-1}) before falling off to a minimum in October 2014 (0.82 mg L^{-1}) (Fig. 3).

Average depth of Rapid Creek varied by sampling date and discharge. Average depths at all sites during the June 2014 (0.48 m) and July 2014 (0.42 m) sampling events were almost twofold greater than the lowest average depths recorded in October 2014 (0.22 m) (Fig. 4). Average biofilm organic matter decreased during the July 2014 (0.0004 g m^{-2}) sampling events before increasing (Fig. 5) to a maximum average in October 2014 (0.22 g m^{-2}). Chl-*a* concentrations grouped by collection date displayed a similar pattern (Fig. 5) with minimum average chl-*a* concentrations recorded in the April, June, and July (0.49 µg/L, 0.72 µg/L, 0.60 µg L^{-1} respectively) sampling events in 2014. In the next sampling event, average chl-a concentration for Rapid Creek increased by greater than 170% in August 2014 (1.95 µg L^{-1}) (Fig. 5). Our regression of benthic resource organic matter estimates and the habitat variables by site shows the frequent reoccurrence of depth as an explanatory variable with respect to the biofilm organic matter estimates at RC1, RC3, RC4 and RC5 (R^2 – 48.95, 53.12, 33.35 and 32.02 respectively).

Our data shows a distinct shift of FBOM accrual in Rapid Creek with a marked change in percent embeddedness estimates recorded during this time. FBOM estimates for Rapid Creek peaked in June 2014 (3.23 g/m^2) with the lowest FBOM average observed in October 2014 (1.42 g m^{-2}). This change results in a 56% reduction in the FBOM estimates over the span of 3 months (Fig. 5). Percent embeddedness estimates exhibited two clear groups (Fig. 4) over the course of the sampling regime. The lowest recorded average percent embeddedness occurred in July 2014 (14.8%), with the highest values recorded in October 2014 (28.6 %). We see that FBOM organic matter estimates drop off explicitly when the embeddedness estimates increase over the year-long sampling regime.

Diatom and detritus particles make up roughly one-half of the benthic resources available for macroinvertebrate consumption. This relative abundance is reflected in the seasonal diet of *Baetis* (Fig 6). We found that highest *D. geminata* surface area % in the biofilm occurred at RC5 (21%) and this average declined downstream (Fig. 7). Consumption of diatoms by *Baetis* followed a similar pattern, with diatom surface area % constituting a larger proportion of total diet at RC5 (46.8%) than at RC1 (24.9%) (Fig. 7).

Diatom surface area % in the biofilm at RC3 and RC4 were positively related to the Dg organic matter estimates (R^2 - 23.8, 34.71). We found that consumption of the diatoms and detritus by *Baetis* at RC5 exhibits expected values from a generalist grazer, but that D. geminata has a marked reduction in consumption in comparison to the amount present in the biofilm at this site (Fig. 8). In August 2014, the surface area % of diatoms present in the gut content of *Baetis* was positively related to % Dg (R^2 – 24. 49%). Interestingly, the consumption of detritus by *Baetis* exhibits a positive correlation to the total amount of *D. geminata* present during the April 2014 and April 2015 sampling events.

Discussion

The retention and processing of organic matter (OM) is integral to the biotic processes in a stream ecosystem (Cummings 1974, Brookshire and Dwire 2003), but the longitudinal flow of OM can be disrupted due to the placement of dams (Ward and Standford 1983). The export of OM in most watersheds is a continuous process that has been shown to peak during high flows (Fisher and Likens 1973, Wallace 1995). A recent experimental flood study on a comparative watershed found that seston and suspended organic matter reached maximums in the first hour of an 8 hour experimental flood and decreased by an order of magnitude in the following hour (Robinson et al 2004). Alteration of the residence time of CBOM has the potential to impact food web dynamics and ecosystem metabolism (Tank et al. 2010). Our data displays a constant export of CBOM out of all sampling sites throughout the study. This would suggest that bankfull flow diminished retention and processing time of CBOM which directly affects the availability of a critical benthic resource. Furthermore, the duration of bankfull flows in

Rapid Creek during the summer far outstripped those used in the cited experimental study and the average discharge based on record for Rapid Creek. Our results suggest sustained alteration of CBOM's availability for macroinvertebrate consumption in Rapid Creek during this time.

Detritus is a critical component of primary and secondary production (Hall et al 2000), but the modification of a stream's physical habitat can led to direct and indirect effects on the availability of this benthic food resources for the BMI (Poff 1997). Riffle habitat alteration can occur because bankfull flows have the power to suspend and transport higher grain size substrate. Bankfull flows, when sustained or repeated, will cause excessive sorting of riffle habitats by removing all substrate particles of or below a certain size class (Wolman and Miller 1960). This can lead to substrate solidification with the rapid deposition of fine sediment following the repeated flood events reducing the available area for retention of benthic resources and habitat for BMI (Jain 1990). The loss of interstitial space can reduce particle retention time and negatively impact primary productivity (O'Conner et. al 2012). In Rapid Creek, which has limited lateral resource inputs from tributaries or leaf litter fall, detritus represents a vital component of the benthic subsidies available to BMI. Manipulation of the physical habitats alters its ability to retain this resource, which can impact the availability. Our results follow these previous findings, indicating that flow-mediated habitat alteration was directly reducing the availability of FBOM over the course of the sampling regime.

Depth, as a physical habitat parameter associated with flow, can have deleterious effect, such as the increased scouring of the substrate and increased nutrient uptake lengths (Biggs, Goring and Nikora, 1998). Previous research to understand the role of discharge and periphyton biomass accrual found that scour events reduced chl-a concentrations (Holms et al. 1998). The frequency and intensity of flood events can directly affect the abundance of biofilm species in the stream (Meffee and Minckley 1987). Our data supports this finding and highlights the effect of repeated scour events in reducing biofilm organic matter estimates to near trace levels.

Excessive modification of flow, high or low, can create community bottlenecks that present dynamic forces that stress the biofilm species composition (Poff and Ward 1998). Additionally, grazers have been documented to maintain biofilm communities in early successional stages under increased flow conditions (Poff and Ward 1995). Discharge as control mechanism on biofilm community composition will favor species with faster life cycles and adaptive advantages for colonization (Fisher 1983). The accumulation of biomass by the biofilm following the high flows in the early summer indicates that resiliency of the biofilm to the persistent scouring conditions. Small biofilm organisms that can be opportunistic and will exhibit increased growth rates once more favorable conditions are available (Sigee 2005). We observed the trend of an initial suppression and subsequent rebound of biofilm organic matter estimates and chl-a concentrations in Rapid Creek.

D. geminata mat material can act as a sieve which entrains macroinvertebrates, algal material and detritus from the water column (Gretz 2008). *D.geminata* mat material may also increase the available surface area for epilithic organisms (Rosemer et al. 1984), thus creating a microhabitat within the mat for other substrate dwelling species (Kilroy et al 2006, Spaulding and Elwell 2007). Aboal and others (2012) suggest that mat production offers the competitive advantage of shading competition and moving the diatom away from the cobble surface where uptake lower nutrient concentrations exist. In Rapid Creek, both diatom surface area in the biofilm and *D. geminata* mat coverage by site increased moving upstream. This suggests, that under the conditions present during this study, *D. geminata* mat material offered the best habitat for native diatoms. Additionally, *Baetis* consumed more diatoms at the sampling sites with a greater *D. geminata* mat development, which suggests that *D. geminata* mat material facilitated growth of diatoms and increased the availability and consumption of this food resource. *Baetis*, a mobile swimmer, consumed more detritus, a lower quality food resource, over other resources when not inhibited by high flows in Rapid Creek. Grazers tend to increase their foraging area once the stress of high flow conditions are removed (Poff and Ward, 1992). The increased availability of FBOM and reduced habitat disturbance directly translates to detritus occupying a greater proportion of the diet of *Baetis* in Rapid Creek during these sampling periods. *Baetis* exhibits generalist grazer forging behavior at a majority of sites, but preliminary assessment of diet preference appears to indicate some avoidance of *D. geminata* cells at RC5, the site with the highest *D. geminata* OM and percent coverage estimates recorded in Rapid Creek during our sampling regime.

Conclusion

The heightened discharge in Rapid Creek during the late spring and early summer of 2014 was the dominant force driving benthic resource availability. We observed localized influence of *D. geminata* on the quality and quantity of food for *Baetis* in Rapid Creek, but these effects were diminished by the initial reduction of *D. geminata* mat development under bankfull flows. The biofilm did display resiliency to an additional bankfull discharge event later in the growing season, which is important as this indicates that the base of the food web was not completely decimated. The natural variation of discharge is known to help maintain ecosystem stability, but repeated disturbance can alter benthic resource availability and may drive the trophic interactions in an unwanted direction. If Rapid Creek is to be managed for total ecosystem health and integrity, consideration in the future should be made for the effect discharge will have on the availability of benthic resources.

We captured a stream ecosystem experiencing dynamic change, and this research may serve as an excellent reference point for investigations of benthic resource availability and impact of *D. geminata* on trophic relationships during average flow conditions. CBOM, FBOM and biofilm are the core components of Rapid Creek's energy balance and higher trophic levels could be impacted by the alteration of these resources. Documenting fluctuations in these resources offers a clearer understanding of how change in discharge can impact the availability of benthic resources for individual species and the implications this could have at the landscape level.

Thesis Conclusion

The conclusions presented about benthic resource variability and trophic interactions in the presence of *D. geminata* in Rapid Creek may prove valuable to future research, but very few projects cannot be improved for the next researcher. Review of the research provides opportunities to understand how experimental design and field research methods can be honed to produce more salient findings. Collecting average velocity measurements at each transect and more *D. geminata* mat material samples at each riffle would be two suggested additions for future work. HEC-RAS modeling software responds poorly to minute changes in stream geometry, and field recorded measurements of stream velocity would bolster the analysis. During our sampling regime, we had numerous zero values in the *D. geminata* organic matter estimates, which was likely a result of flow scouring the substrate. Additional *D. geminata* sampling of mat material at each transect in future studies will add more statistical power to the organic matter and total mat coverage estimates.

The conditions under which this research was conducted proved highly unusual in that Rapid Creek experienced substantially above-average flows in the spring and summer of 2014. Through casual conversation with state and local officials, we found that, any time that flows exceed 2.83 $m^3 s^{-1}$ in Rapid Creek, conditions are considered unsafe, and sampling in the stream is highly discouraged. Because our data was collected routinely near this level of discharge, the data represents a system in a state of flux. The logical extension of this work is to perform the same analysis during a year of average flow conditions. Carrying out this research would allow us to build a greater understanding of the pool of benthic resources available and to add a magnitude to the change in availability in benthic resources between bankfull and average flow conditions.

Constructing food webs is exhaustive work, but mapping of these relationships is critical for understanding community structure and function. *D. geminata* research is in its infancy and large questions remain to be addressed in relation to the effect that mat development has with respect to trophic structure and dynamics. Our work has given us insight into the availability of benthic resources in these systems, but additional research is necessary to build a food web and begin to examine the flow of energy in locations impacted by *D. geminata*.

Tables

Table 1. Range and average for physical habitat metrics recorded during field sampling.

	Depth (m)	Wetted Width (m)	Embeddedness (%)	Size Class (cm)	Canopy Cover (%)
RC1	**0.01 - .8 (0.31)**	**9 - 15 (12.5)**	**0 - 90 (20.7)**	**0 - 200 (96.3)**	**0.0 - 86.8 (29.2)**
RC2	**0.01 - 1.5 (0.32)**	**13 - 19 (16.6)**	**0 -100 (33.5)**	**0 - 200 (105.0)**	**0.0 - 5.8 (1.8)**
RC3	**0.02 - .8 (0.35)**	**8 - 19 (11)**	**0 - 90 (24.3)**	**0 - 300 (111.2)**	**0.0 - 16.2 (4.4)**
RC4	**0.01 - .66 (0.28)**	**6 - 20 (13.9)**	**0 - 90 (11.3)**	**0 - 200 (52.2)**	**0.0 - 75.0 (12.9)**
RC5	**0.02 - .0.8 (0.37)**	**8 - 15 (11.1)**	**0 - 90 (14.1)**	**0 - 300 (80.9)**	**0.0 - 30.9 (8.67)**
Apr-14	**0.04 - .55 (0.26)**	**8 - 19 (13.0)**	**0 - 100 (16.6)**	**0 - 300 (80.6)**	**0 .0 - 16.2 (5.4)**
Jun-14	**0.01 - 1.50 (0.42)**	**9 -23 (13.6)**	**0 -100 (16.5)**	**0 - 300 (79.1)**	**0.0 - 86.8 (14.7)**
Jul-14	**0.01 - 1.50 (0.48)**	**10 -19 (13.8)**	**0 -90 (14.9)**	**0 -300 (88.9)**	**0.0 - 76.74 (16.7)**
Aug-14	**0.01 - 1.50 (0.37)**	**8 - 18 (12.6)**	**0 -100 (26.1)**	**0 -300 (88.6)**	**0.0 - 88.2 (24.3)**
Oct-14	**0.01 - .54 (0.18)**	**6 - 18 (11.6)**	**0 - 100 (28.7)**	**0 -300 (92.9)**	**0.0 - 27.9 (7.1)**
Apr-15	**0.01 - .7 (0.29)**	**10 -18 (13.4)**	**0 -90 (21.9)**	**0 -300 (93.1)**	**0.0 - 29.4 (5.1)**

Figures

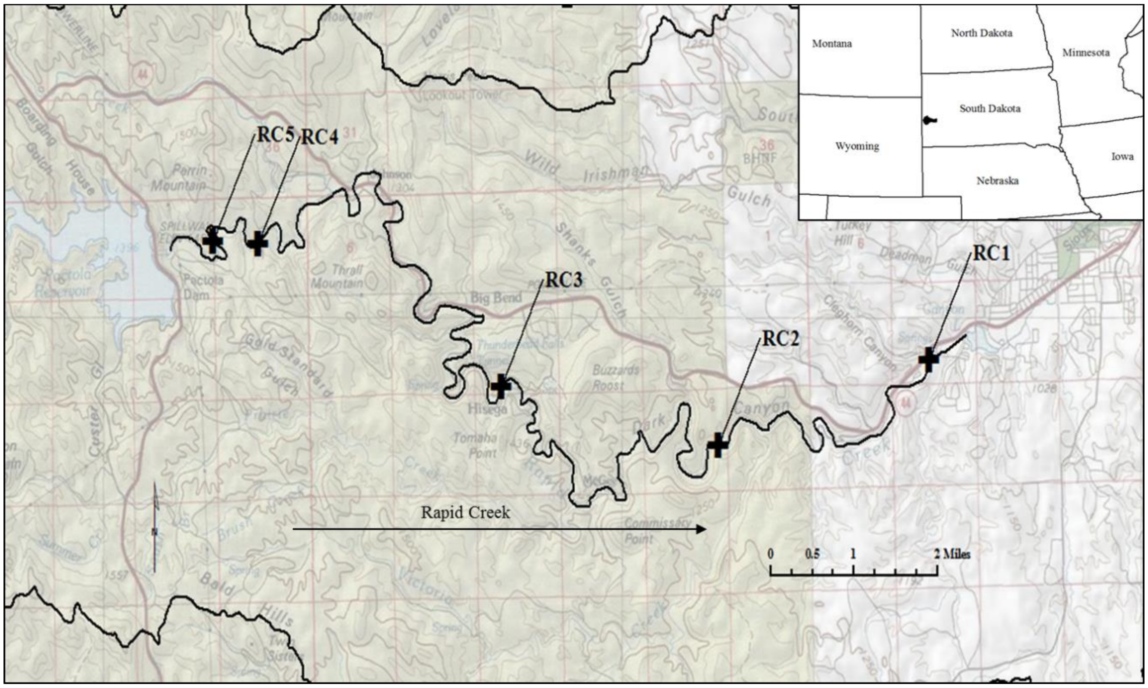

Figure 1: Highlights the location of Rapid Creek and the placement of the sampling sites. The sampling location RC5 is located below Pactola Dam and sites continue sequentially downstream to RC1, above Canyon Lake's inlet. The darker shaded portion of the map represents Black Hills Forest Service Land. Samples were collected at each location from April 2014 – April 2015.

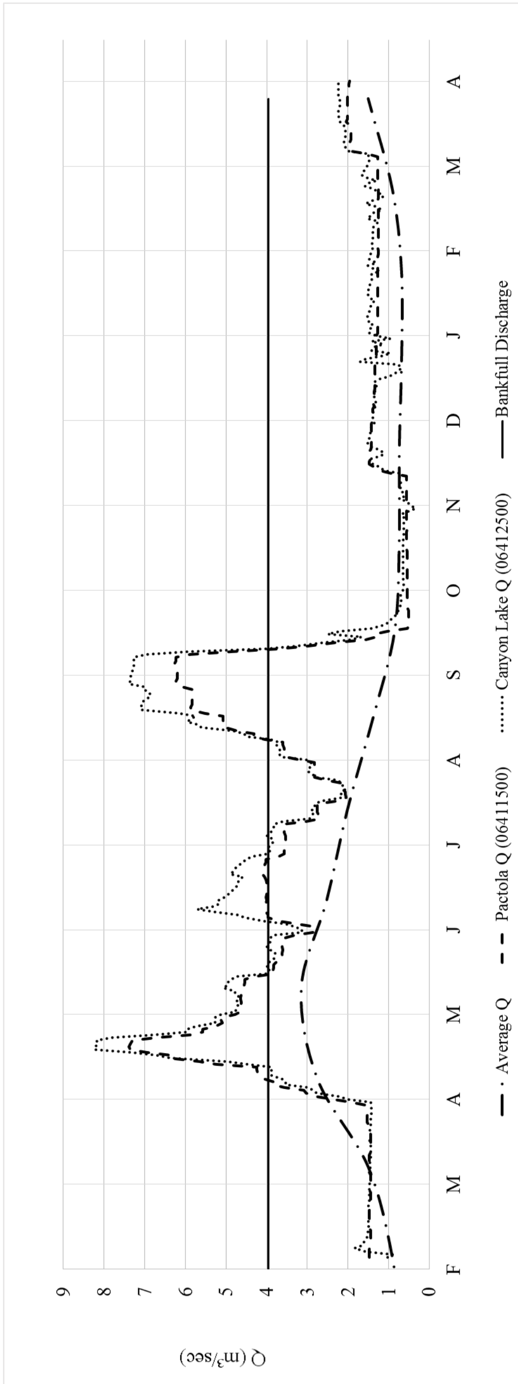

Figure 2: Daily average discharge for gaging stations below Pactola Dam (USGS, 06410500) and above Canyon Lake (USGS, 06412500) from Feb 2014 – April 2015 with the Rapid Creek's average daily discharge for the length of the recorded at the Canyon Lake station. The solid line indicates the calculated bankfull flood frequency discharge from the Canyon Lake gage data from 1994-2014.

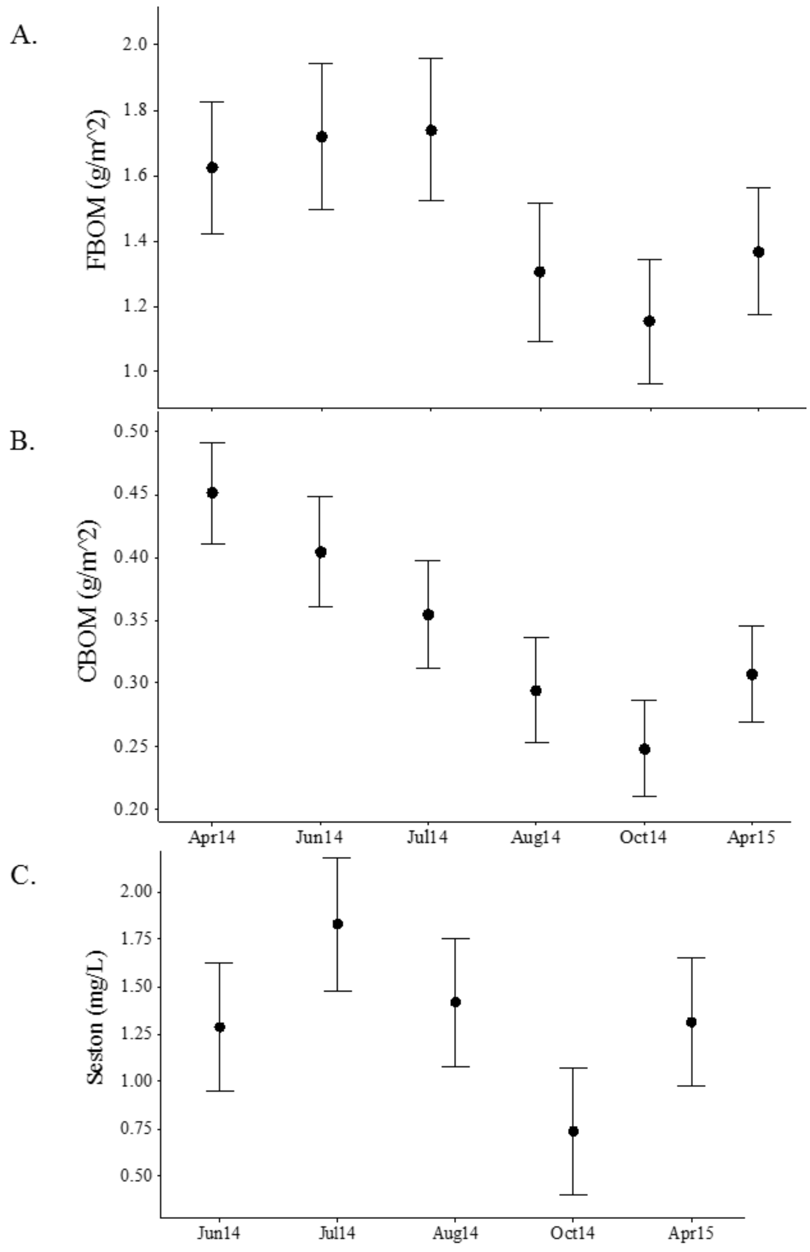

Figure 3. Interval plots of (A) FBOM (g/m^2) estimates and (B) CBOM (g/m^2) and (C) seston (mg/L) in Rapid Creek. The black dots represent the average recorded surface area % for this particle and bars are 95% CIs for that data point.

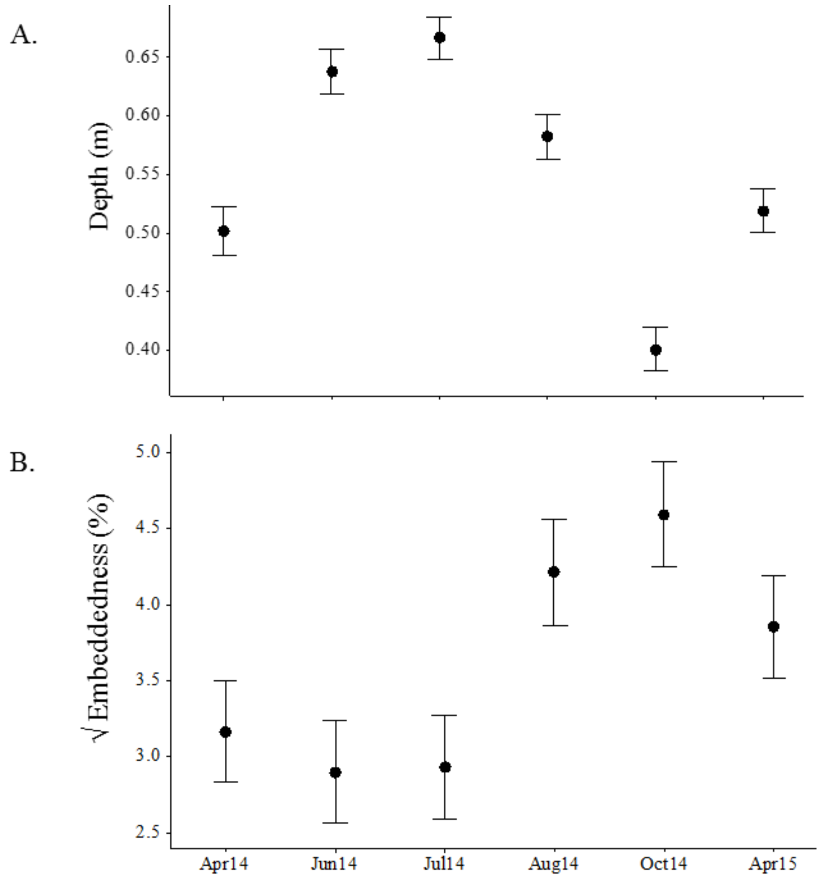

Figure 4: Interval plot for physical habitat parameters, (A) Depth and (B) % Embeddedness, for Rapid Creek based on sampling date. The black dots represent the average recorded value for this variable and bars are 95% Cis for that data point. Embeddedness data √-transformed to obtain equal variance.

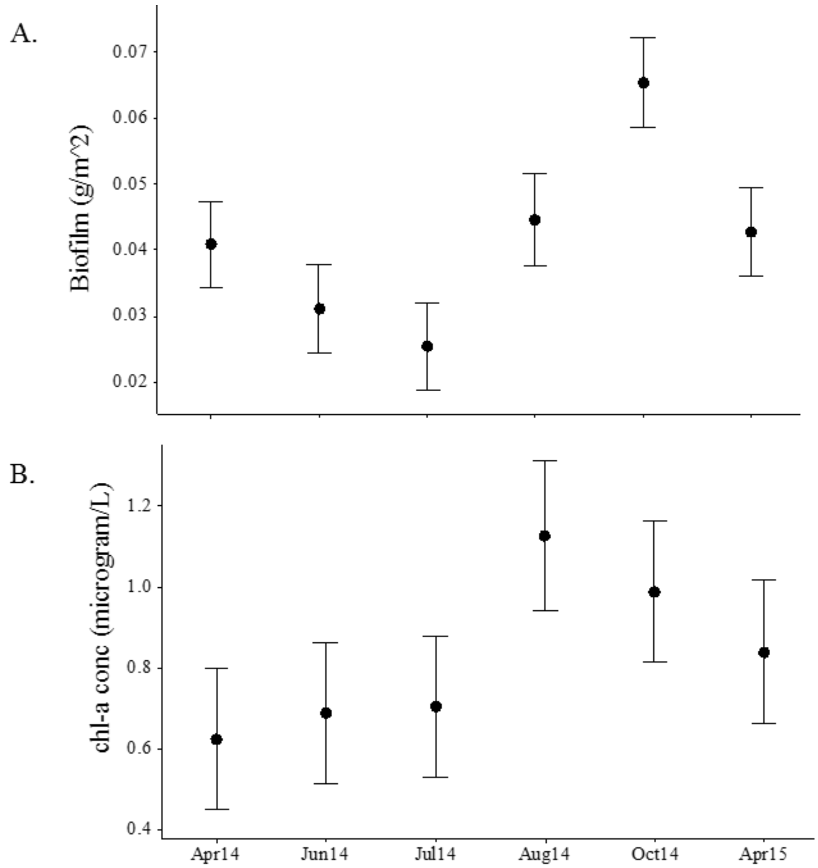

Figure 5: Interval plots of the (A) biofilm organic matter estimate (g/m^2) and (B) chl-*a* concentrations (µg/L). The black dots represent the average recorded value for this resource and bars are 95% Cis for that data point.

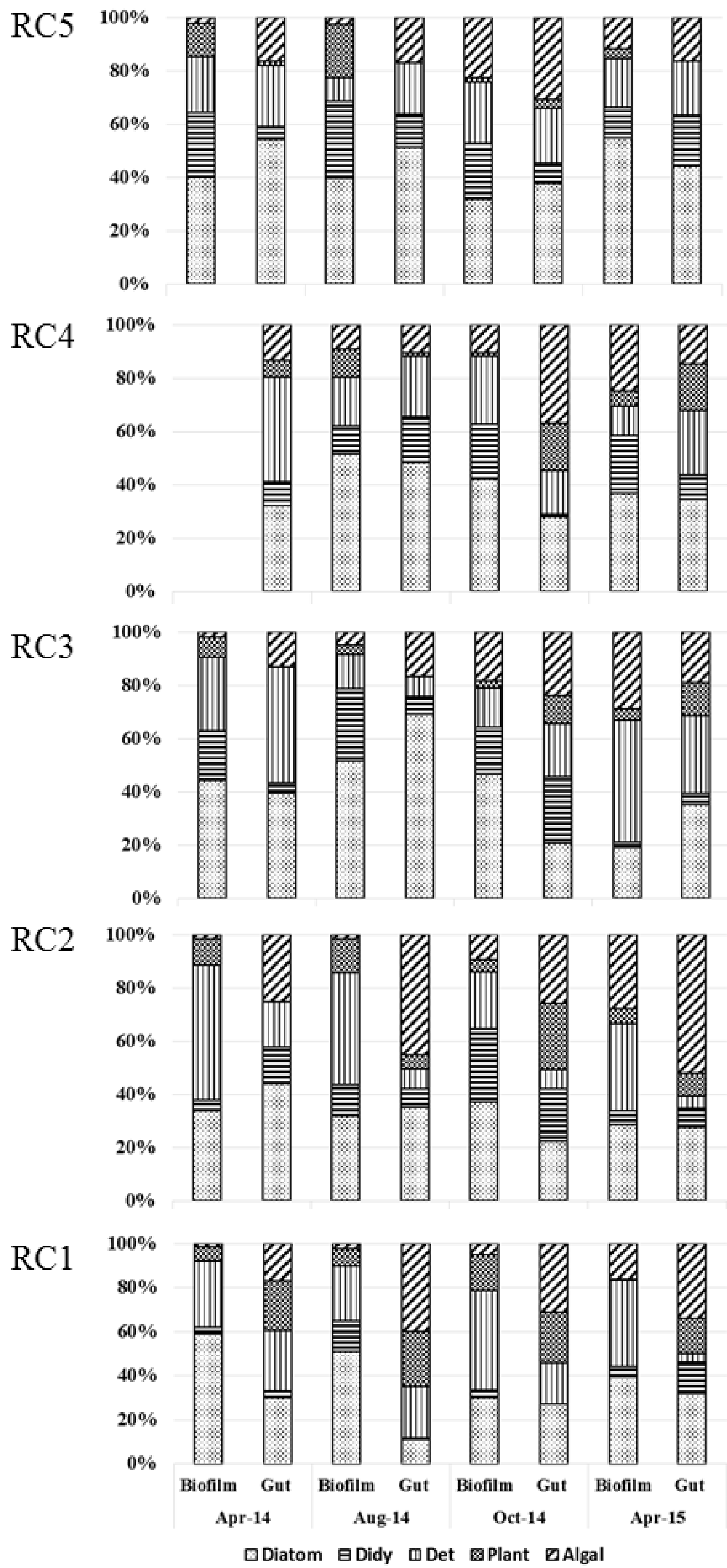

Figure 6: Comparison of biofilm surface area % and gut content surface % for all sites by season.

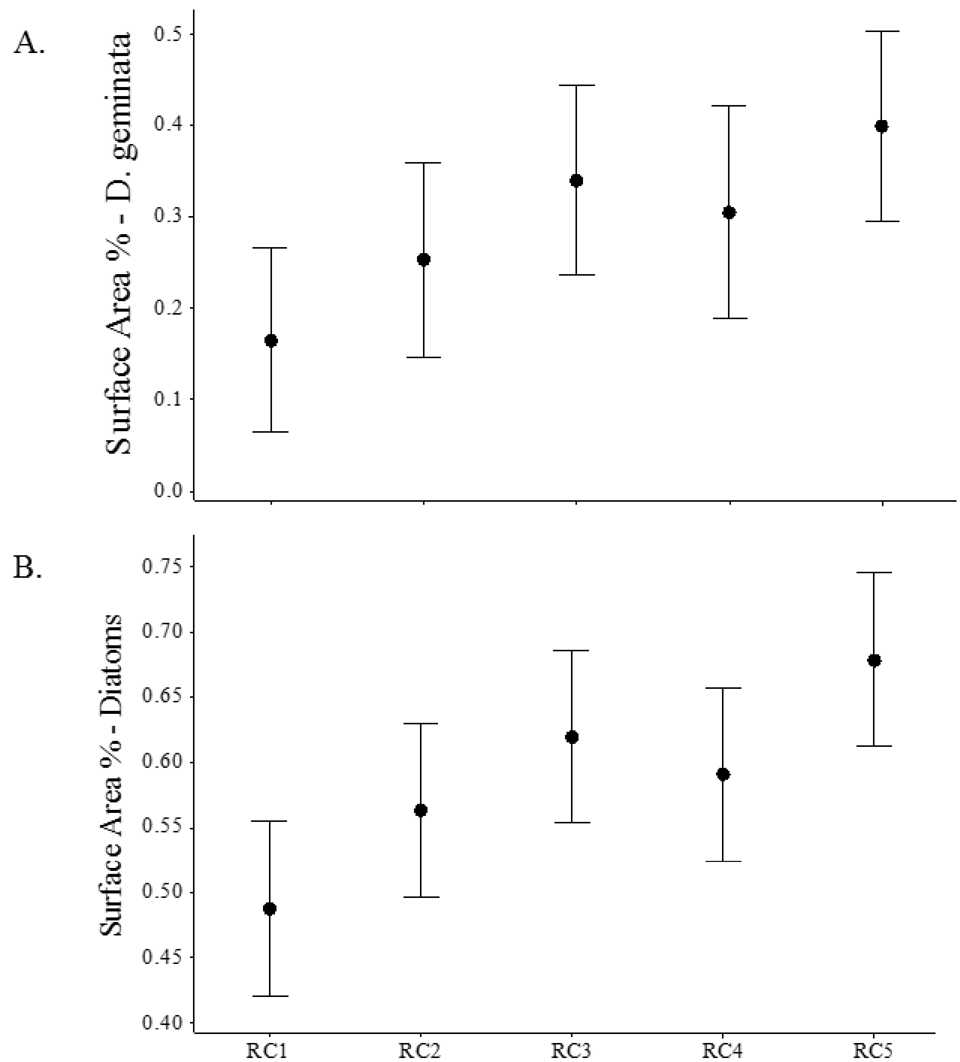

Figure 7. Interval plots of the (A) surface area % of *D. geminata* in the biofilm characterization compared to the (B) surface area % of diatoms in the gut content of *Baetis*. The black dots represent the average recorded surface area % for this particle and bars are 95% CIs for that data point. All data √-transformed to obtain equal variance.

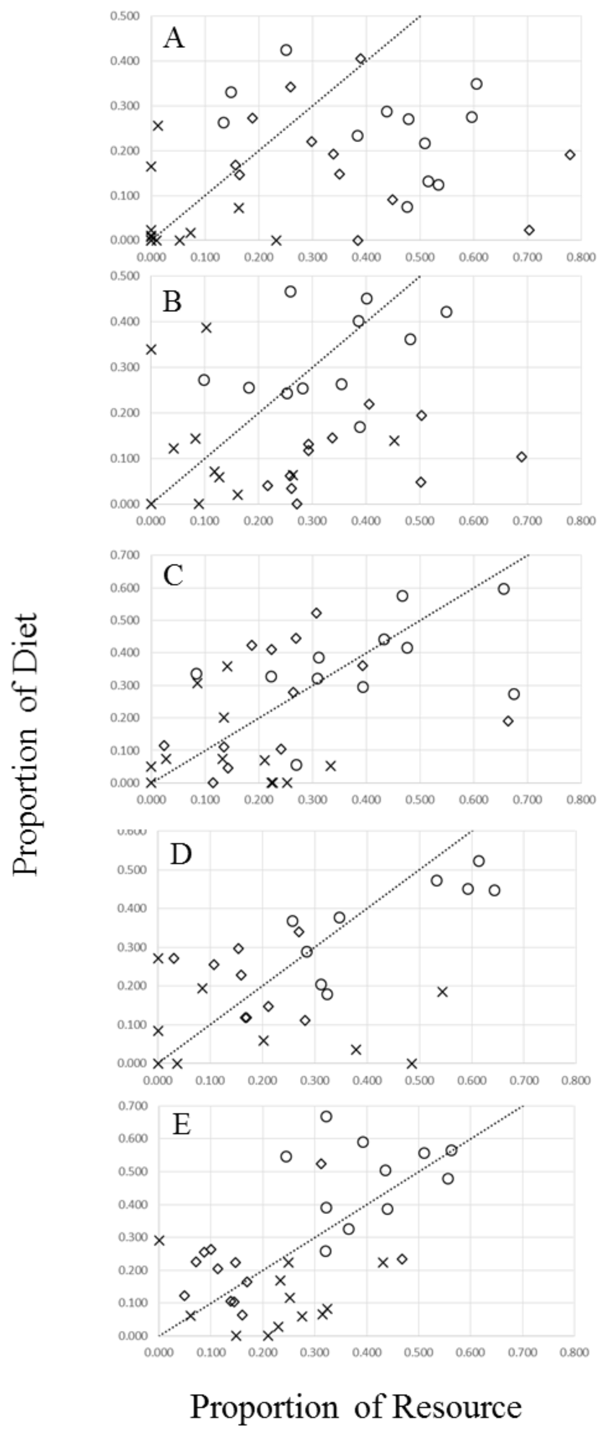

Figure 8. Pair-wise comparison of biofilm resource characterization and gut content analysis of *Baetis* for RC1 (A), RC2 (B), RC3 (C), RC4 (D) and RC5 (E). The open circles denotes diatoms, the diamonds signify detritus particles and the crosses symbolize D. geminata cells, with the dash line indicating a 1:1 relationship.

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Vita

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