

# Ecological role of *Limnephilus abbreviatus* in detritus dynamics

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## Abstract

Caddisflies are the dominant detritivores in ponds and wetlands in many high elevation freshwaters. By processing detritus, caddisflies mobilize nutrients and energy that are not used by primary consumers which can play an important role in secondary production and nutrient cycling. Thus, caddisflies are significant for these oligotrophic ecosystems because they are often oligotrophic and therefore limited by nutrients. Previous studies have shown detritus processing by caddisflies stimulates algal growth. Historical data shows that certain species of caddisflies are shifting their range to higher elevations due to increasing temperatures. Past experiments at the Rocky Mountain Biological Laboratory have quantified caddisfly diet, detritus breakdown rates, and influences on algal growth, and other measures for several species of caddisfly in this guild. However, data is missing for several species of caddisflies, including those recently expanding their range upslope. I used a microcosms experiment with *Limnephilus abbreviatus*, *Limnephilus externus*, and *Anabolia bimaculata* caddisflies to measure their contribution to detritus breakdown and algal dynamics. Compared to *L. externus*, I predicted that *L. abbreviatus* would have a lower detrital breakdown rate and *Anabolia bimaculata* would have a higher detrital breakdown rate; and patterns in chlorophyll-a concentration would match these detritus trends. Our results support both predictions for *L. abbreviatus* however while we found that and that *A. bimaculata* had a slightly lower detrital breakdown rate than *L. externus*, their contribution to chlorophyll-a growth was greater. Moving forward, we will be able to use this data to create models that simulate real world conditions to anticipate how caddisflies range shifts affect ecosystem functions.

## Keywords

ecosystem function, *Trichoptera*, nutrient cycling, algal growth

## Introduction

Most plant nutrients and energy enter terrestrial and aquatic food webs as detritus, or dead organic matter, and these nutrients are crucial for high secondary production (Oertli, 1993). Detritus plays a critical role in ecosystems because it can support a greater diversity of species and greater biomass of predators than autotrophs can do alone (Hairston and Hairston, 1993). In addition, detritus can alter nutrient and energy flow efficiency across trophic levels and it can affect community dynamics (Moore et al., 2004). Detritivores make nutrients and energy available to secondary consumers by consuming detritus (Giller et al., 2004) and can mobilize nutrients that fertilize autotrophs. Thus, detritivores have broad importance in ecosystems.

In the northern hemisphere, caddisflies (Trichoptera) are the biomass-dominant animals that process coarse detritus (Wissinger et al., 1999). Since caddisflies are detritivores, they link the brown food web (food web based on detritus) to the green food web (food web based on primary production) and play an important role in the function of the ecosystem (Zou, Thébault, Lacroix, and Barot, 2016). In addition, caddisflies are important for the green food web in these ecosystems because they are also the biomass-dominant prey resource for predators such as salamanders and fish (Wissinger et al., 1999). I studied a guild of caddisflies that live in oligotrophic ponds and wetlands surrounding the Rocky Mountain Biological Laboratory (RMBL). These ecosystems are low in nutrients, so other organisms rely on caddisflies to mobilize detritus-sourced nutrients into the food web (Klemmer, Wissinger, Greig, and Ostrofsky, 2012). Detrital breakdown and excretion by caddisflies can increase nitrogen and phosphorus concentrations in these ecosystems (Balik, Taylor, Washko, and Wissinger, 2018) which increases algal growth (Klemmer et al., 2012). Thus there are multiple pathways by which caddisflies connect the 'brown' and 'green' food webs.

Historical data from the Rocky Mountain Biological Laboratory gives evidence that caddisflies are shifting their ranges upslope to higher elevations in response to increasing temperatures (S. A. Wissinger, Brown, and Jannot, 2003). This can lead to new combinations of species and different abundances of species which can affect overall rates of ecosystem processes in these ecosystems (Semmartin, et al., 2004). Additionally, the habitats that this guild of caddisflies live in (shallow lakes, ponds, and wetlands) are under threat from climate change due to changes in snowmelt, precipitation, and evaporation (Tuytens et al., 2014). These high altitude ecosystems are climate change indicators for similar ecosystems at high latitudes (Wissinger et al. 2016). Therefore, it is important to understand caddisflies and their role in these ecosystems. Furthermore, it has been shown that there is high interspecific variation in the excretion rates of ten species of caddisflies with high variation for nitrogen excretion and intermediate variation for phosphorus excretion (Balik, Taylor, Washko, and Wissinger, 2018). Since ponds at subalpine elevations are co-limited by nitrogen and phosphorous (Elser et al., 2009), caddisfly excretion plays an important role in providing nutrients in these ecosystems. Due to the importance and variation in caddisfly excretion, shifts in caddisfly ranges can have large effects on ecosystem processes.

Previous studies at the Rocky Mountain Biological Station have found detrital breakdown rates, caddisfly biomass, diet, excretion rates, and the effect on algal biomass for seven species of caddisflies that live in the kettle ponds, marshes, and wetlands in the surrounding area (Krejsa

and Wissinger, 2011, unpublished). However, this historical dataset is missing data on several species of caddisflies including *Limnephilus abbreviatus* and *Anabolia bimaculata*. I will also use *Limnephilus externus* because previous studies have shown that it is the dominant detritus processor compared to other species of caddisfly (Klemmer et al., 2012). Therefore, we used *L. externus* as a baseline species to compare other species against. We also used it to control for inter-annual variation.

The purpose of my study was to collect data on the species of caddisflies that are missing from the historical database so that we can understand species-specific rates and how they affect larger ecosystem functions. I will do this by measuring detritus breakdown rates and the effect on chlorophyll-a concentration for each treatment. Also, by comparing algal biomass in the presence and absence of caddisflies, I will see how caddisflies affect primary productivity. This can be scaled up in the future experiments to determine the effect on phytoplankton and herbivores. I will compare these results to the historical data for other caddisfly species that live in the area. This will allow us to create models based on these parameters that predict how these species interact and affect overall ecosystem function while accounting for new combinations of species. These models will help us predict how different species interact along the permanence and elevational gradient in the East River Valley. Also, these models will allow us to scale up future experiments to create more natural conditions. I predicted higher detritus breakdown rate in microcosms with caddisflies than the control treatment with no caddisflies. I also predicted that algal growth and chlorophyll-a concentration will be higher in the presence of caddisflies than in their absence. More specifically and compared to *L. externus*, I predicted that *L. abbreviatus* would have a lower detrital breakdown rate and *A. bimaculata* would have a higher detrital breakdown rate. These predictions also hold for chlorophyll-a concentration.

## Methods

### Experimental Design

I conducted my study in the town of Gothic, Colorado at the Rocky Mountain Biological Laboratory inside a temporary field laboratory (WeatherPORT) outside the Willey Laboratory. In the weatherport, I used microcosms and set up five treatments with five replicates each for a total of 25 microcosms (following Krejsa and Wissinger, 2011, unpublished).

| Treatment             | Control (sedge) | <i>L. externus</i> | <i>L. picturatus</i> | <i>L. abbreviatus</i> | <i>A. bimaculata</i> |
|-----------------------|-----------------|--------------------|----------------------|-----------------------|----------------------|
| Microcosm replication | <i>n</i> = 5    | <i>n</i> = 5       | <i>n</i> = 5         | <i>n</i> = 5          | <i>n</i> = 5         |

I collected caddisflies with a 0.3m diameter D-frame (1-mm mesh) net from fish hook pond (Fig. 1) in the riparian zone along the East River (lat 38.974289, long -106.997360), from kingfisher pond (Fig. 1) in the riparian zone along the East River (lat 38.975151, long -106.999599), and a Beaver Pond (Fig 3.) along the 401 Trail (38.976933, -106.991355). I also collected senesced sedge (*Carex aquatilis*) detritus from marsh 2 (lat 38.944322, long -106.974721) near the kettle ponds adjacent to the RMBL to provide detrital resources. Each 0.25 m<sup>2</sup> (51x36x13cm) microcosm had 25 grams (g) of sedge and 24 caddisflies. I aimed to use third

instar individuals, although some second and fourth instars were also included. The control treatment only had sedge which allowed us to quantify background rates of detritus breakdown not attributed to caddisfly activity. The density of caddisflies in the microcosms (100 m<sup>-2</sup>) corresponded to the peak detritus breakdown rates observed in a *L. externus* density manipulation experiment (Krejsa and Wissinger, 2011, unpublished). *L. externus* acted as the control species of caddisfly because previous studies have investigated its detrital dynamics, ecological functions, and range (S. A. Wissinger et al., 2003). The treatments were randomized inside the WeatherPORT to prevent bias from sunlight exposure, temperature, and other weather conditions (Krejsa and Wissinger, 2011, unpublished).

### *Microcosm setup*

I filled twenty-five microcosms with 9 L of pond water, 25g of air-dried sedge, and the corresponding species of caddisflies for each treatment. I air dried the sedge for 96 hours and then weighed and divided the sedge for each microcosm. The sedge was incubated in the microcosms for five days to encourage microbial colonization before introducing the caddisflies (Klemmer et al., 2012). I also placed a small, circular mesh cage in each microcosm that was small enough to keep out caddisflies but still allowed the flow of water. I placed six periphyton tiles (area = 6.25 cm<sup>2</sup> for each) inside the mesh cages, and a further six tiles in the adjacent corner without a screen (Krejsa and Wissinger, 2011, unpublished). This enclosure procedure allowed me to quantify how caddisfly grazing affected chlorophyll-a concentration and algal growth. Furthermore, I collected an algal solution from a marsh (M2) near the kettle ponds and washed 100 mL of the solution in each microcosm to encourage algal growth and simulate natural pond conditions. (Krejsa and Wissinger, 2011, unpublished).

### *Analysis of Detritus Breakdown and Caddisfly biomass*

At the end of the experiment, I separated the remaining detritus into coarse particulate organic matter (>1mm) and fine particulate organic matter (<1mm) using a 1mm mesh screen. I dried the coarse detritus at 60°C for 24 hours and then weighed it. I compared the mean coarse detritus mass for each treatment with a one-way analysis of variance (ANOVA). Additionally, I collected ten extra caddisflies of each species to estimate initial caddisfly biomass. I measured their dry mass (AFDM) by drying (60°C for 24 hours) and weighing individuals of each species (Wissinger et al., 2018).

### *Chlorophyll-a Analysis*

I placed twelve periphyton tiles in each microcosm to estimate algal responses to detritus processing. Approximately every ten days, I collected two unprotected and two protected tiles to measure chlorophyll-a concentration. I placed each pair of tiles in a small plastic bag or a small container and froze the tiles. Also, I added twenty milliliters of buffered ethanol (90%) to each bag of tiles to lyse the algal cells and release photosynthetic pigments (Krejsa and Wissinger, 2011, unpublished). I lysed the bags for six hours and then analyzed a 3 mL aliquot of the ethanol extract for chlorophyll-a concentration with a Turner Designs Trilogy Laboratory Fluorometer (model #7200; Sunnyvale, CA 94085). I then treated the aliquot with 1 mL of 0.1 N

hydrochloric acid, and then reanalyzed it to account for phaeophytin (Krejsa and Wissinger, 2011, unpublished).

### *Statistical Analysis*

For each of my response variables, I performed a one-way ANOVA (Analysis of Variance) Test and Tukey's Honest Significant Difference (HSD) Test to determine significance between treatments. Before performing an ANOVA Test and Tukey's HSD, I standardized CPOM consumption and FPOM production to per caddisfly biomass per day rates.

To test for date effects, caddisfly treatment effects, and grazing effects on the periphyton tiles, I used a three-way ANOVA. On days 10, 20, and 30 of my experiment, I analyzed and measured new periphyton tiles and water samples, so I did not use repeated measures. I also used a two-way ANOVA test to analyze the effects of caddisfly treatments and grazing on final chlorophyll-a concentration on ungrazed tiles (Krejsa and Wissinger, 2011, unpublished).

## **Results**

### *Detrital Breakdown*

There were significant differences in coarse particulate organic matter consumed (CPOM) per day among the treatments ( $F_{2,12} = 89.33$ ,  $p = 6.21e-08$ ). Tukey's HSD analysis showed that *L. externus* and *A. bimaculata* (group A) were not significantly different from each other, but consumed detritus at a greater rate than *L. abbreviatus*, *L. picturatus*, and the control treatment (group B). Also, *L. abbreviatus*, *L. picturatus*, and the control treatment were not significantly different from each other for CPOM consumed per day. *L. externus* and *A. bimaculata* were significantly different than *L. abbreviatus*, *L. picturatus*, and the control treatment (Fig. 4). For FPOM generated per day, Tukey's HSD showed that *L. externus* and *A. bimaculata* (group A) were not significantly different, *L. abbreviatus* and *L. picturatus* were not significantly different (group B and C), and *L. abbreviatus* was not significantly different than the control treatment (group D) ( $F_{2,12} = 54.26$ ,  $p = 9.75e-07$ ). However *L. externus* and *A. bimaculata* were significantly different than all other groups and *L. picturatus* was significantly different than the control treatment (Fig 5.) When taking into account caddisfly biomass, there were significant differences in CPOM consumed per day per gram of caddisfly among all species ( $F_{2,12} = 37.43$ ,  $p = 6.95e-06$ ). Tukey's HSD (Honest Significant Difference) revealed that there were significant differences between *L. externus* (group A), *A. bimaculata* (group B), and *L. abbreviatus* (group C) for both CPOM (Fig. 6). There were also significant differences in FPOM generated per day per gram of caddisfly that mirrored patterns in CPOM breakdown (Fig. 7) ( $F_{2,12} = 48.59$ ,  $p = 1.76e-06$ ). We could not calculate detrital breakdown with caddisfly biomass for *L. picturatus* because it pupated before the end of the experiment, so we could not record final biomass.

### *Chlorophyll-a Analysis*

Average chlorophyll-a concentration ( $\text{mg}/\text{m}^2$ ) for ungrazed tiles increased from the initial reading to the final reading in each treatment except for *L. abbreviatus* which decreased slightly

(Fig. 8). In addition with ungrazed tiles, each treatment experienced a slight decrease in average chlorophyll-a concentration from the initial reading to the second reading, but all treatments also had increased concentrations from the second reading to the final reading. When comparing between species, *A. bimaculata* facilitated significantly higher concentrations than all other treatments. Also, *L. externus* had a significantly lower effect on chlorophyll-a concentration than *A. bimaculata*, but it had a significantly higher effect than *L. abbreviatus* and the control treatment. While *L. abbreviatus* had similar concentrations to the control treatment with no caddisflies.

For grazed tiles, average chlorophyll-a concentration increased from the initial reading to the final reading for all treatments (Fig. 9). However, *A. bimaculata* and the control treatment had increased average concentrations at each time interval, but *L. externus* and *L. abbreviatus* experienced small decreases between the first and second reading. Similar to the ungrazed tiles, average chlorophyll-a concentration for the *A. bimaculata* treatment was significantly higher than all other treatments. Additionally, *L. abbreviatus* and *L. externus* had similar average concentrations to the control treatment. When comparing average chlorophyll-a concentrations between ungrazed and grazed tiles, ungrazed tiles had significantly higher concentrations for each treatment.

## Discussion

### Detrital Breakdown

Caddisflies play a critical role in ecosystems because they live in oligotrophic ponds which are co-limited by nitrogen and phosphorous (Elser et al., 2009). Caddisflies mobilize nutrients from the brown food web back into the green food web by consuming coarse particulate organic matter and generating fine particulate organic matter (Zou, Thébault, Lacroix, and Barot, 2016).

Therefore, it is significant that we found that *L. externus* and *A. bimaculata* clearly increased detrital breakdown rates of coarse particulate organic matter. While, *L. abbreviatus* and *L. picturatus* did not significantly increase detritus breakdown compared to the control treatment with no caddisflies. In the control treatment, detritus breakdown can be attributed to microbial processing. These results suggest that *L. externus* and *A. bimaculata* are important for the ecosystem because of their high detrital breakdown rates compared to the control treatment. On the other hand, microbial processing provides a similar level of detrital breakdown to *L. abbreviatus* and *L. picturatus* which suggests these species either consume alternative resources (e.g., FPOM) or were less active foragers. In addition, caddisflies help the ecosystem because they generate fine particulate organic matter which serves as food for caddisflies and other organisms such as filter-feeders (Wissinger et al., 2018). Thus, it is significant that we found that *L. externus* and *A. bimaculata* enhanced FPOM generation compared to the other caddisfly treatments and the control. While, *L. picturatus* increased FPOM generation to a lesser amount and *L. abbreviatus* did not have a significant effect compared to the control. Similar to CPOM consumption, this tells us that *L. externus* and *A. bimaculata* are particularly important for these ecosystems.

Different species of caddisflies vary in body mass and their stage of development during the experiment, therefore it was important to adjust each species' detrital breakdown rate to take into account their final biomass. When rates were corrected for body mass, we found that *L.*

*externus* had a higher rate of CPOM consumption and FPOM generation than *A. bimaculata*. It is also important to look at CPOM consumption and FPOM generation for each species compared to not only the control treatment, but also *L. externus*. This is because *L. externus* is the dominant detritus processor in this guild of caddisflies (Klemmer et al., 2012). Taking this into account, our results show that *A. bimaculata* consumes slightly less detritus, but *L. abbreviatus* consumes significantly less detritus on per biomass basis.

The results suggest that if *A. bimaculata* were to replace *L. externus* in a pond, then there would not be a significant loss in detrital breakdown and therefore ecosystem function. However, if *L. abbreviatus* or *L. picturatus* replaced *L. externus*, then there would be a significant loss in detrital breakdown which could affect overall ecosystem function. In addition, if *L. externus* or *A. bimaculata* were to vacate a pond, then there would be significant loss in detrital breakdown.

### *Algal Growth*

By measuring chlorophyll-a concentration, we could see how the presence of caddisflies affects algal growth and therefore primary productivity in the ecosystem. The data suggests that algal growth is stimulated when caddisflies are not allowed to graze on algae. Therefore, the presence of caddisflies has a positive effect on algal growth. This could be the result of caddisfly excretion which has been shown to contain nitrogen and phosphorous (Balik, Taylor, Washko, and Wissinger, 2018), but both ungrazed and grazed tiles were exposed to caddisfly excretion. Therefore, it is possible that the difference can be attributed to caddisflies grazing on the algae as another source of food in addition to the detritus. In addition, the data shows that *A. bimaculata* had a significantly higher effect on chlorophyll-a concentrations than the other treatments which indicates that it is important for primary production in these ecosystems.

We can apply the same idea to the chlorophyll-a results which reveal similar conclusions. If *A. bimaculata* were to replace *L. externus* in terms of their effect on algal growth, there would be an increase in primary productivity in the ecosystem. On the other hand, if *L. abbreviatus* or if *L. externus* left a pond, then there would be a significant loss in algal growth which could have harmful impacts on the ecosystem.

## **Conclusions**

Data on detrital breakdown, diet, and excretion for the species tested in this experiment and those tested previously will ultimately be used to parameterize a model to anticipate the ecosystem consequences of species range shifts along the local elevational and permanence gradients. This model will also allow us to predict what would happen if a species of caddisfly shifts its range to replace another species of caddisfly or create a new composition of species in a pond. If *A. bimaculata* were to replace *L. externus* in terms of their effect on algal growth, there would be an increase in primary productivity in the ecosystem. On the other hand, if *L. abbreviatus* or if *L. externus* left a pond, then there would be a significant loss in algal growth which could have harmful impacts on the ecosystem.

In the future, it would be interesting to see similar studies in microcosms with this guild of caddisflies that uses treatments with combinations of species that coexist. This would be important to study because as species are shifting their ranges, not only are species replacing other species, but these shifts could also result in new combinations of species. This study

would help us understand how certain species interact with each other and how species interactions alter detrital breakdown rates, diets, and algal fertilization.

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## Tables and Figures

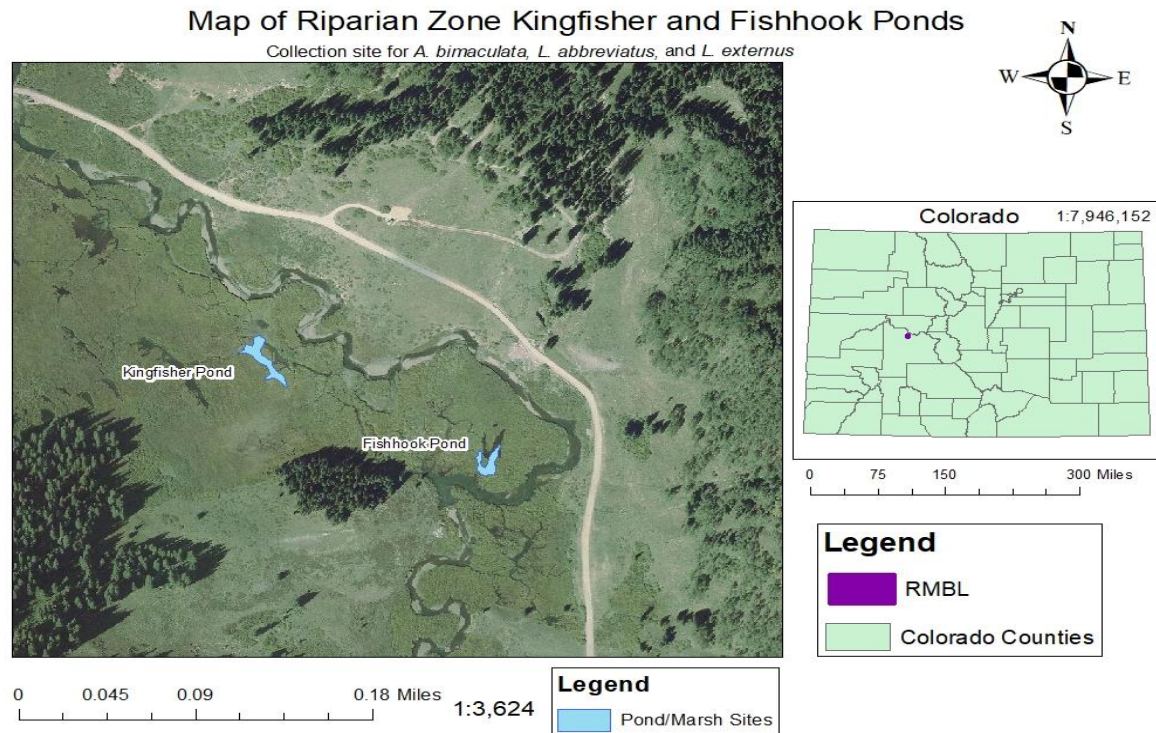


Figure 1: Map of Riparian Zone Kingfisher and Fish Hook Ponds

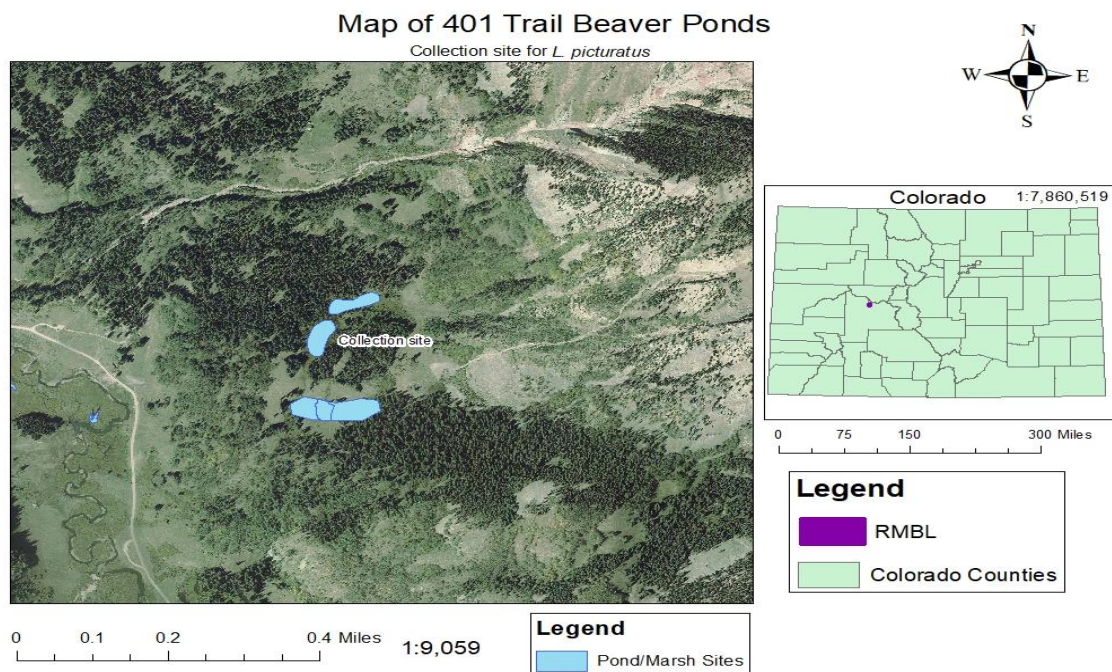


Figure 2: Map of 401 Trail Beaver Ponds

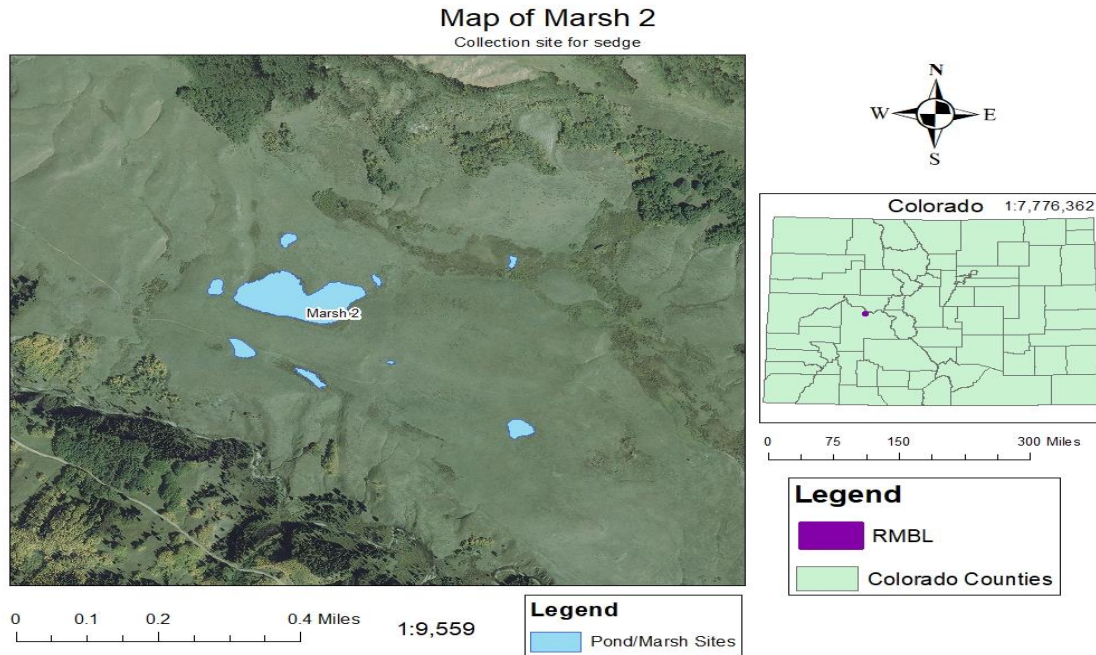


Figure 3: Map of Marsh 2

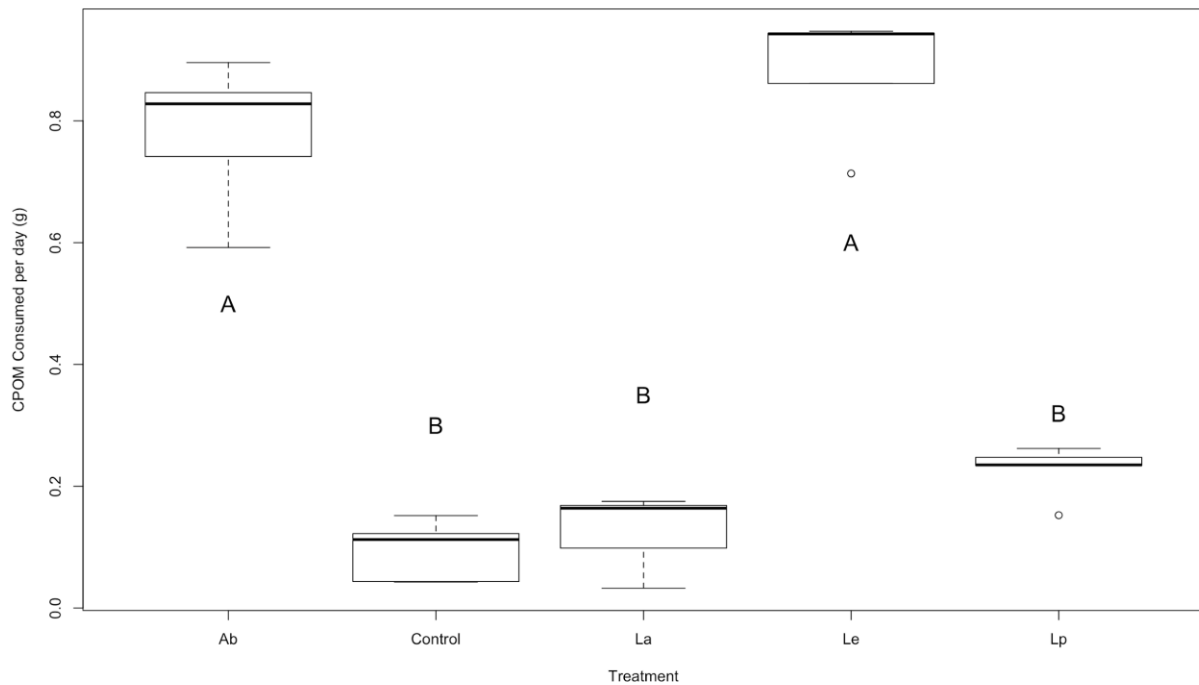


Figure 4: Coarse particulate organic matter (CPOM) consumed per day (g). Ab = *Anabolia bimaculata*; La = *Limnephilus abbreviatus*; Le = *Limnephilus externus*; and Lp = *Limnephilus picturatus*. The letter next to each boxplot indicate significant differences according to Tukey's HSD Test.

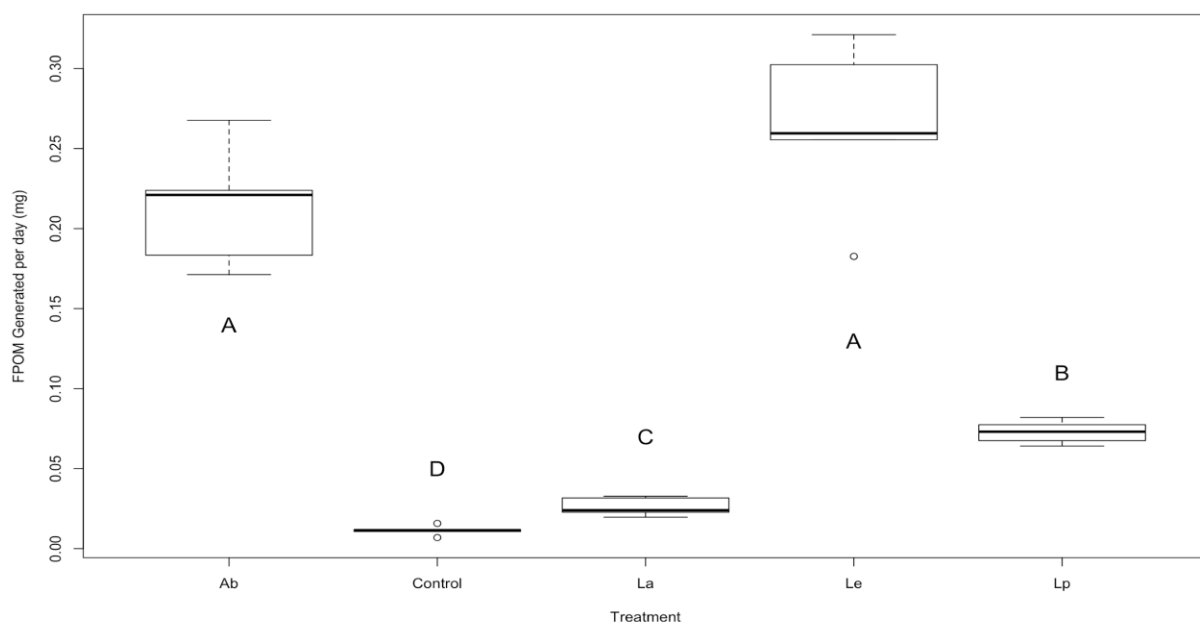


Figure 5: Fine particulate organic matter (FPOM) consumed per day (g). Ab = *Anabolia bimaculata*; La = *Limnephilus abbreviatus*; Le = *Limnephilus externus*; and Lp = *Limnephilus picturatus*. The letter next to each boxplot indicate significant differences according to Tukey's HSD Test.

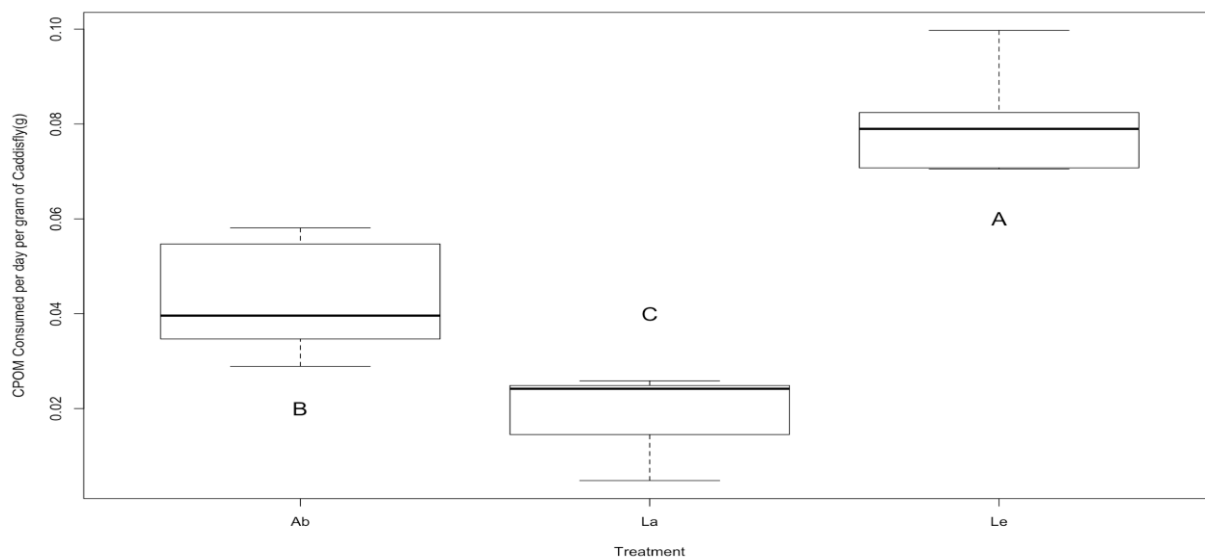


Figure 6: Coarse particulate organic matter (CPOM) consumed per day per gram of Caddisfly (g). Ab = *Anabolia bimaculata*; La = *Limnephilus abbreviatus*; and Le = *Limnephilus externus*. The letter next to each boxplot indicate significant differences according to Tukey's HSD Test.

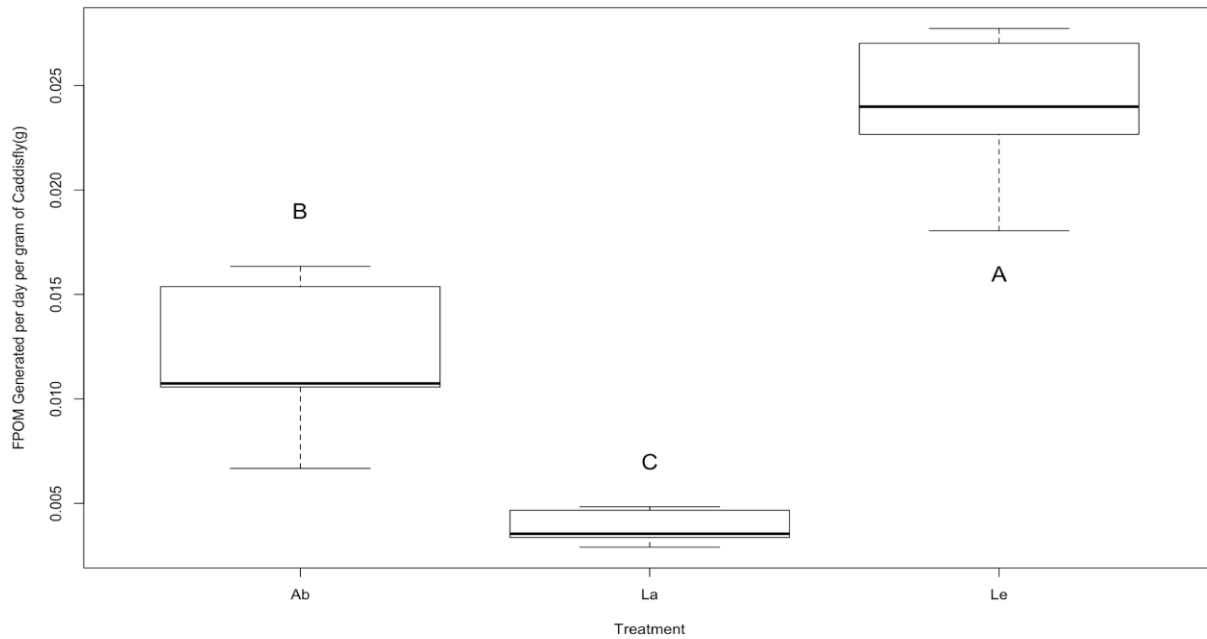


Figure 7: Fine particulate organic matter (FPOM) consumed per day per gram of Caddisfly (g). Ab = *Anabolia bimaculata*; La = *Limnephilus abbreviatus*; and Le = *Limnephilus externus*. The letter next to each boxplot indicate significant differences according to Tukey's HSD Test.

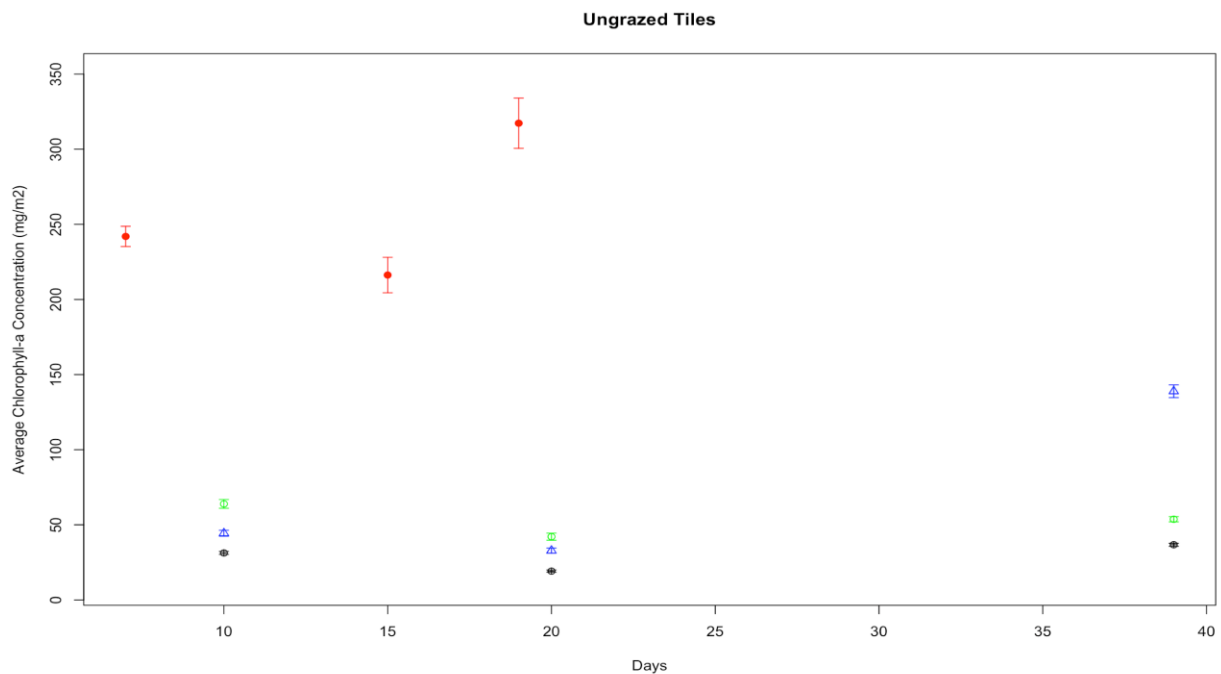


Figure 8: Average Chlorophyll-a Concentration (mg/m<sup>2</sup>) per day for Ungrazed Tiles. Red = *Anabolia bimaculata*; Blue = *Limnephilus externus*; Green = *Limnephilus abbreviatus*; and Black = Control treatment.

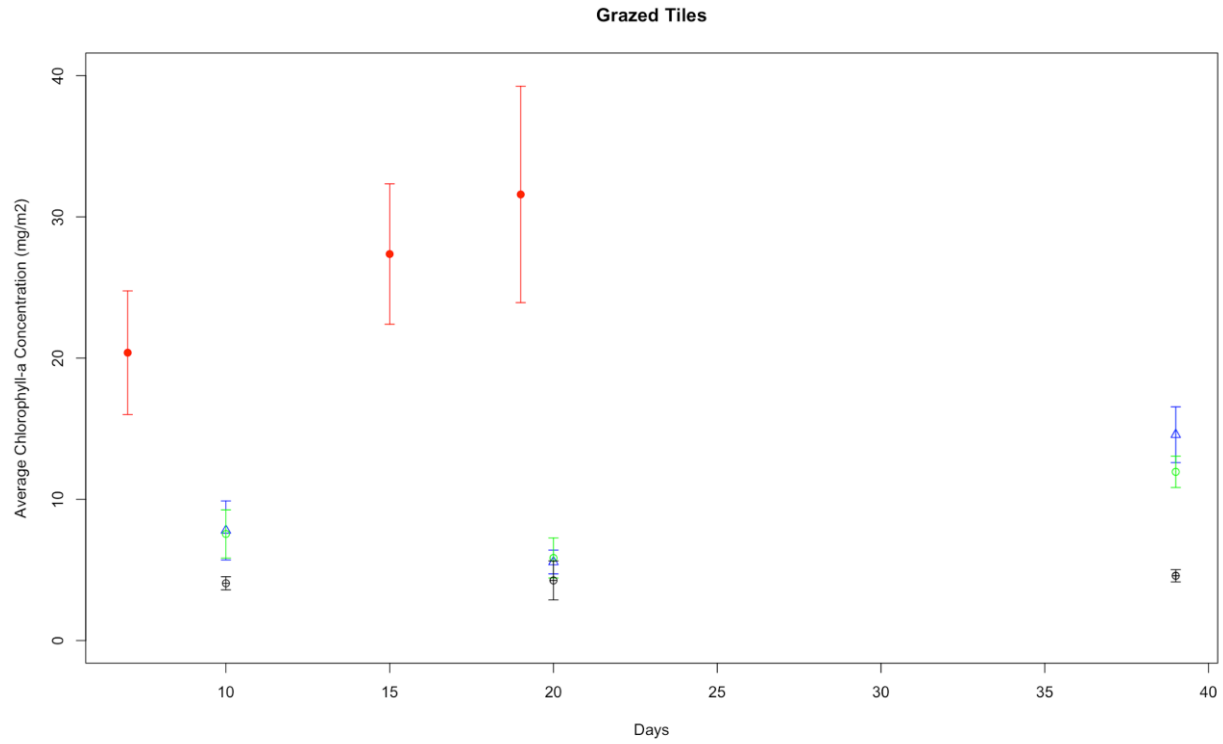


Figure 9: Average Chlorophyll-a Concentration ( $\text{mg/m}^2$ ) per day for Grazed Tiles. Red = *Anabolia bimaculata*; Blue = *Limnephilus externus*; Green = *Limnephilus abbreviatus*; and Black = Control treatment.

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