DO DIDYMOSPHENIA GEMINATA BLOOMS AFFECT FISHES IN THE

KOOTENAI RIVER BASIN?

by

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ABSTRACT

Do *Didymosphenia geminata* Blooms Affect Fishes in the

Kootenai River Basin?

by

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Stream habitat changes that affect primary consumers often indirectly impact

secondary consumers such as fishes. Blooms of the benthic algae *Didymosphenia*

geminata (Didymo) represent one such habitat change known to affect stream

macroinvertebrates. However, the potential indirect trophic impacts on fish consumers

via modifications to their diet are poorly understood. The overall goal of this project was

to determine if Didymo blooms in streams of the Kootenai River basin of British

Columbia and Montana affect the condition and growth of fishes, and to see whether

trophic mechanisms were responsible for any observed changes. We therefore quantified

the diet, condition, and growth rate of trout, charr, and sculpin in a paired, Didymo vs.

reference study, during the summer of 2018 and across a gradient of Didymo abundance

in 2019. In the 2018 study, trout diets were 81% similar despite obvious differences in

the composition of macroinvertebrate assemblages between the Didymo and reference

streams. Trout abundance was higher in the stream with Didymo, but the amount of

invertebrates in the drift was higher in the stream without Didymo. Growth rate and energy demand by individual trout was similar between the two streams. In the 2019 study, across a gradient of coverage, Didymo abundance was correlated only with the percent of aquatic invertebrates in trout diets and did not affect diets of charr or sculpin. Variation in fish condition was low across study streams. Thus, Didymo blooms may impact trout diets to a small extent, but we found no evidence this impact translates to changes in condition or growth. The relationship of fish abundance to Didymo blooms bears further study, but we found no obvious trophic mechanisms that would explain any differences. We suggest future studies prioritize research on potential impacts during winter months and on species with limited mobility that may be most greatly impacted by Didymo.

(60 pages)

PUBLIC ABSTRACT

Do *Didymosphenia geminata* Blooms Affect Fishes in the

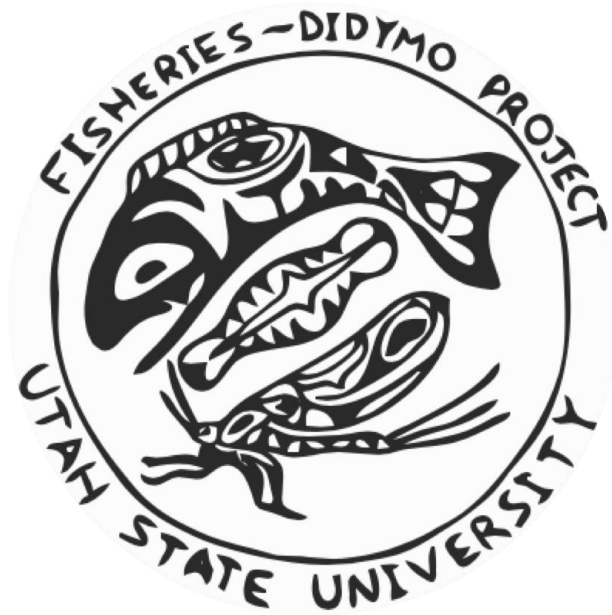Kootenai River Basin?

Niall G. Clancy

Didymosphenia geminata (Didymo) is a nuisance algae that can cover entire streambeds under certain environmental conditions. Numerous studies have shown that it changes the composition of stream invertebrates. Fishes in many headwaters are known to feed almost exclusively on invertebrates. Thus, there is concern changes to the amount or type of invertebrates caused by Didymo blooms will impact fishes such as trout, charr, and sculpin. In the Kootenai River basin of Montana and British Columbia, we examined stream invertebrates and fish diets, condition, and growth across 25 streams during the summers of 2018 and 2019. The severity of Didymo blooms in these streams ranged from 0 – 80% coverage of the entire streambed. In 2018, we observed significant shifts in the types of stream invertebrates available to trout in Didymo-affected streams. However, trout diets and growth rate were not affected. In 2019, trout, charr, and sculpin diets in streams with severe Didymo blooms were similar to streams with little to no Didymo. Condition of all three types of fish were unaffected. We therefore conclude that summer Didymo blooms have no obvious impacts on the diet, condition, or growth of these fishes. We suggest further studies document potential impacts during winter months and on sensitive invertebrates such as freshwater mussels.

DEDICATION

This manuscript is dedicated to my parents, Tara Gallagher and Chris Clancy.

It is truly an honor to be your son.

FRONTISPIECE

Project logo

ACKNOWLEDGMENTS

Lastly, thanks to my family and friends for the incredible support they've shown me over the past two years. A special "tip o' the hat" to the three stooges (Marshall Wolf, Austin Bartos, and Nick Barrett), Emily Leonard, Christina Morrisett, Leighton King, Farooq Abdulwahab, and Jennie Weathered.

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INTRODUCTION

Fish growth and production in coldwater systems is highly dependent on both allochthonous and autochthonous sources of energy (Horton 1961; Huryn 1996; Bellmore et al. 2013). In the interior Columbia River basin, a long history of logging, mineral extraction, and river impoundment has altered in-stream habitats and riparian areas (Hand et al. 2018), resulting in a lack of structure and nutrients that alters the availability of food resources to aquatic organisms (Meredith et al. 2014; Minshall et al. 2014). Habitat change can alter stream macroinvertebrate assemblages and impact consumers of both larval and adult life-stages of aquatic insects (Power et al. 1996; Nakano et al. 1999; Baxter et al. 2005; Malison and Baxter 2010). Such changes within the interior Columbia River basin have indeed led to shifts in fish assemblage structure (Frissell 1993). Understanding how specific habitat change alters the flow of in-stream energy sources to fish consumers can thus be of great importance to conservation and management efforts (Cross et al. 2011, 2013; Bellmore et al. 2012; Scholl et al. 2019).

Instream habitat components that alter primary and secondary production such as woody debris and stream substrates are major topics of research, but ephemeral habitat components such as macrophytes and algaes are less often considered in restoration and management. In recent years, increasing reports of severe blooms of the diatomaceous algae *Didymosphenia geminata* (hereafter, Didymo) have led to significant concern about its causes and consequences for freshwater organisms (Bickel and Close 2008; Gillis and Chalifour 2010; James et al. 2010; Anderson et al. 2014; James and Chipps 2016; Jellyman and Harding 2016). Overgrowths (colloquially, blooms) of this North American-native are characterized by production of a long polysaccharide stalk from

individual diatoms which can lead to large areas of the substrate becoming covered. However, the precise causes of Didymo blooms remain a current topic of investigation (Taylor and Bothwell 2014).

At high Didymo bloom coverage, stream invertebrate assemblages originally dominated by Ephemeroptera, Plecoptera, and Trichoptera (EPT taxa), typically shift towards dominance by Chironomidae, Oligochaeta, Nematoda, or Cladocera, taxa generally associated with reduced habitat quality in trout streams (Kilroy et al. 2009; Gillis and Chalifour 2010; James et al. 2010; Byle 2014; Larned and Kilroy 2014; Jellyman and Harding 2016). There has been widespread concern about the consequences of blooms for trout (Gillis and Chalifour 2010; James et al. 2010; Jellyman and Harding 2016) because EPT taxa are often a primary food source for salmonid species (Behnke 2010). However, to date, it is unclear if Didymo blooms have any significant negative or positive impacts on trout species. Jellyman and Harding (2016) found that blooms in several New Zealand rivers were correlated with lower trout abundances, dietary percent EPT, and stomach fullness. In contrast, production of Atlantic Salmon (*Salmo salar*) in Icelandic and Norwegian rivers has remained high despite the presence of severe Didymo blooms (Jonsson et al. 2008; Lindstrøm and Skulberg 2008), and spawner abundance and escapement of Pacific salmon and steelhead (*Oncorhynchus spp.*) in Vancouver Island streams either increased or did not change in relation to blooms (Bothwell et al. 2008). In four South Dakota streams the condition and feeding of large Brown Trout (*Salmo trutta*) was not correlated with Didymo blooms, while body condition in juveniles was higher (James and Chipps 2010). However, the study was also affected by drought, making causal inference difficult. As such, no individual study has successfully examined the

mechanistic links between Didymo blooms, macroinvertebrates, and fishes necessary to make causal inference. Further, no studies have addressed the potential effects of blooms on inland native trout populations or on nongame species such as members of the family Cottidae.

To better understand the trophic consequences of Didymo blooms, we assessed the relationship between blooms, fish diet, condition, and growth over two summers in a Columbia River subbasin, the mountainous Kootenai (Kootenay in Canada) basin of British Columbia, Idaho, and Montana (Fig. 1), much of which falls within the globally-rare, inland temperate rainforest biome (Dellasala et al. 2011). We employed a multi-faceted research approach in which we examined potential Didymo bloom impacts on fish: 1) temporally - in a reference-impact study of two streams during one summer, and 2) spatially – in a survey of fishes across Kootenai basin streams representing a gradient of bloom severity.

STUDY AREA

To determine the potential effects of Didymo blooms on fishes, we combined a high frequency sampling approach with a high spatial resolution approach. Twice-monthly through the summer of 2018, we sampled two streams located in the Cabinet Mountains of northwestern Montana, Bear Creek and nearby Ramsey Creek (Fig. 1). Both creeks have similar physical characteristics (Table 1), but Bear Creek contains obvious Didymo blooms while Ramsey Creek does not. The two streams thus offer an opportunity to examine potential effects of blooms on biotic communities in a paired, reference-impact framework.

During both the summer of 2018 and 2019, we examined 131 locations on 103 individual streams for presence of Didymo blooms in the Kootenai River basin (Appendix 1). In 2019, we surveyed fishes in 28 of those streams (Fig. 1) representing large differences in bloom coverage: 0 – 80% (Table 2).

METHODS

Didymo vs. Control Stream Study - 2018

We selected a three-hundred meter long reach for study in both Bear and Ramsey Creeks. The fish assemblages of both were predominantly composed of Columbia River Redband Trout (*O. mykiss gairdneri*) and Bull Trout (*Salvelninus confluentus*). Ramsey Creek also contained a small number of Columbia Slimy Sculpin (*Uranidea cognata* syn. *Cottus cognatus*). We measured five habitat variables to ensure Bear and Ramsey Creeks were suitable for comparison: mean substrate size (*sensu* Wolman 1954), channel width, mesohabitat composition (percent cascade, riffle, & pool), water temperature (30-minute recording interval, Onset HOBO© data loggers), and water chemistry (Lachat 8500 Direct Flow analyzer). Every two weeks, we systematically estimated percent-of-substrate covered by blooming Didymo using a five-gallon bucket with a clear bottom, making five evenly-spaced estimates along lateral transects, each twenty paces apart from reach-top to bottom. We then combined, twice-monthly estimates to form monthly Didymo bloom coverage estimates.

Food-web structure was determined by macroinvertebrate and fish sampling concurrent with Didymo coverage estimation. In conjunction with Didymo bloom measurements, we collected drifting macroinvertebrates by placing two separate 10 x 18 in. drift nets in the stream for 30 minutes and pooling the combined samples in 70% ethanol. Samples were always taken between the hours of 10:00 a.m. and 5:00 p.m. The day following each Didymo and macroinvertebrate sampling event, we collected fishes through single-pass backpack electroshocking (LR-24 Backpack Shocker Smith-Root©, Vancouver, WA). We completed multiple passes during the final sampling event

(September) to maximize summer-long recapture. Each fish was anesthetized with clove oil, weighed, measured, and marked by clipping a small section of the caudal fin. We gastrically lavaged individuals larger than 100 mm to collect diets and, if captured during June or July, implanted a uniquely-coded, 12 mm passive integrated transponder (PIT) tag (Model HDX12, Biomark©, Boise, ID). Gut evacuation was assumed to be minimal due to cold temperatures and processing generally less than an hour after capture. Using the average percent growth between individuals measured in June and July, we back-calculated June weights for individuals tagged in July. This represented 57% of Redband Trout in Bear Creek and 68% in Ramsey Creek. For PIT-tagged Redband and Bull Trout captured in September, we also compared summer growth to the total number of times that fish had been captured to test for handling effects.

We identified and measured drift and diet macroinvertebrates to family and used published length-to-mass conversions to estimate biomass (Benke et al. 1999; Sabo et al. 2002; Baumgärtner and Rothhaupt 2003; Gruner 2007; Miyasaka et al. 2008) and caloric content (Montana Fish, Wildlife & Parks, unpublished data). Conversions are provided in Appendix 2.

Because a shift to a macroinvertebrate assemblage of smaller and more abundant individuals may favor juvenile fishes (James and Chipps 2016), we identified large and small size-classes of Redband and Bull Trout using length-frequency histograms (Appendix 3). We then calculated size-specific abundances using Lincoln-Petersen mark-recapture estimation in which the final sampling date was the recapture event and all previous sampling events a single marking event (Lincoln 1930). We determined this approach to be a reasonable because movement of PIT-tagged fishes between the abutting

upper and lower halves of Bear Creek was negligible and thus assumed the closed

population assumption of Lincoln-Petersen estimation was satisfied (Appendix 4).

We compared taxon-specific proportions of drifting macroinvertebrates in Bear

and Ramsey Creeks by calculating the monthly percent similarity (Schoener 1970):

(1)

$$Percent\ Similarity = 100 - 0.5\left(\sum_{i=1}^{n} |B_i - R_i|\right)$$

where B_i is the percent of invertebrates of taxa i in Bear Creek and R_i is the percent of

invertebrates of taxa i in Ramsey Creek. Using the same equation, we compared trout

diets to the availability of invertebrates in the drift as a measure of selection. Then, we

also compared trout diets between the two streams using percent energetic content for

each diet taxa. To evaluate how likely observed differences between groups were (drift

vs. drift, diet vs. drift, and diet vs. diet), we used Pearson's chi-squared tests. We further

report monthly and summer-long gut fullness and relative number and energetic content

of invertebrates in the drift between the two streams.

By pairing individual caloric demand with trout diet composition, we created

energy-flow food webs. We used a novel modification of the Benke-Wallace trophic-

basis of production method that accounts for thermal preferences to calculate energetic

demand (Benke and Wallace 1980) and validated results with fish bioenergetics models

(Deslauriers et al. 2017). Bioenergetics inputs were stream temperatures for the entire

summer, start and end weights, and output was summer-long energetic consumption. We

used species-specific bioenergetics models for Redband (Rainbow) Trout (Railsback and

Rose 2004) and Bull Trout (Mesa et al. 2013) and substituted a model for Prickly Sculpin

(*Cottopsis asper* syn. *Cottus asper*) for Slimy Sculpin (Moss 2001).

The Benke-Wallace method was originally developed for use with benthic macroinvertebrates and does not account for differential allocation of energy by organism size and water temperature, factors known to strongly influence fish growth (Brown et al. 2004). Thus we used two different numbers for proportion of total assimilated energy allocated to growth (net production efficiency or NPE) in large vs. small fishes as suggested by Bellmore et al. (2013). We then modified this proportion by observed stream temperatures as compared to species' thermal optimums such that a fish's consumption in kilocalories was calculated

(2)

$$Consumption = \sum_{i=1}^{n} \frac{(DietProportion_i \times Growth \times EnergyDensity)}{(TempFactor \times TissueAllocation \times (Digestible_i - 0.2Digestible_i))}$$

where *DietProportion_i* is the average proportion by kilocalories of food type *i* in the diet; *Growth* is the summer growth (Jun.-Sept.) in grams of the average fish; *EnergyDensity* is the energy density (kcal/gram) of the fish; *TissueAllocation* is the theoretical maximum proportion of assimilated energy allocated to fish tissue growth (net production efficiency) which was set as 0.22 for large size-class trout and 0.5 for small size-class trout and Slimy Sculpin; *Digestible_i* is the estimated digestible proportion of food type *i*; and*TempFactor* is the temperature correction factor calculated according to the equation

(3)

$$TempFactor = e^{-((0.2 \times (StreamTemp - OptimTemp))^4)}$$

where *StreamTemp* is the average stream temperature for the measurement interval over which growth was recorded and *OptimTemp* is the thermal optimum for the given species of fish. This equation is an approximation of a fish's thermal optimum curve that asymptotes at an energy-allocation-to-tissue value of zero (Appendix 5). We derived thermal optimum values from previous field and laboratory studies: 13.1°C for Redband Trout (Bear et al. 2007), 12.0°C for Bull Trout (Dunham et al. 2004), and 12.1°C for Slimy Sculpin (Wehrly et al. 2004).

We used estimated digestible proportions ($Digestible_i$) for each food type from Hanson et al. (1997) and subtracted a value of $0.2Digestible_i$ to account for specific dynamic action (Hanson et al. 1997). Thus $Digestible_i – 0.2Digestible_i$ is the assimilation efficiency of food type i.

To derive total estimated consumption by each species, we multiplied estimated summer Benke-Wallace consumption values by calculated fish abundances in each stream. Then, we multiplied the proportion of energy of each prey item in the average diet of each fish species by the reach-level consumption estimates. Thus, we obtained estimates of total energy flow from all prey to fish predators and compared results for Bear and Ramsey Creeks (Appendix 6).

Multi-Stream Didymo Survey - 2019

In a representative 30.5 meter (100 ft.) reach of each selected stream, we estimated Didymo coverage using the same method as in 2018. We also recorded, six other habitat variables: wetted-width (n=5), canopy density (n=5 using a densitometer [Strickler 1959]), dominant vegetation type, substrate type (Cummins 1962), Rosgen channel type (Rosgen 1994), number of large woody debris items (*sensu* Kershner et al.

2004), and stream temperature. From reach top-to-bottom, we measured wetted width and canopy density, while we qualitatively assessed vegetation, substrate, and channel type. We estimated mean August temperatures by adding the time-specific difference of each stream's temperature to a reference temperature logger (Bear Creek for streams flowing into the Kootenai River below the Fisher River confluence, Outlet Creek for those above the Fisher confluence, and Trail Creek for Fisher River tributaries).

In the same reach, we collected fishes through two-pass (one upstream, one downstream) backpack electroshocking. We anesthetized, weighed and measured all fishes and then released leuciscids and catostomids. Using an in-field assessment in which we gastrically-lavaged fish, we assessed the diets of salmonids and cottids by spreading the diet contents in a 30 x 15 cm white pan and recording the number of individuals of each invertebrate taxa. We identified insects to order except for Simuliidae and Chironomidae which we identified to family. Other invertebrates we identified to Class or Phylum, and vertebrates to the lowest practical taxonomic level (usually species).

We generated two response metrics of fish condition (Fulton's K [Heincke 1908; Ricker 1975] and residual analysis of observed vs. predicted weights [Fechhelm et al. 1995]) and four metrics of diet composition (%Diptera, %EPT, %Aquatics, and gut fullness [# Diet Items/Fish Length]) for each fish. Using weighted, univariate logistic (%Diptera, %EPT, %Aquatics) and linear regressions (gut fullness and fish condition) in which fish sample size was the relative weight of each stream in the regression, we analyzed each response metric compared to Didymo and the other six habitat variables. We removed four streams (Kokanee, Coffee, Mobbs & Solo Joe Creeks) from regressions

due to low sample size or substantially different substrate type. We grouped fish by genus

due to otherwise small sample size if compared only within species (charr *Salvelinus* and

sculpin *Uranidea*) or significant hybridization in the basin (trout *Oncorhynchus*), which

made some field ID's difficult. For each comparison of a habitat variable to a diet metric,

we calculated an R^2 (or Nagelkerke's pseudo-R^2 for logistic regression [Nagelkerke

1991]) and p-value, and considered variables with an R^2 greater than 0.2 and a p-value

less than 0.2 to be a non-spurious correlation.

Further, we used Random Forest regression to rank the relative explanatory power

of each habitat variable for each diet metric. Random Forest regression is an increasingly

popular machine learning technique that generates a large number of regression trees on

random subsets of a dataset, allowing the unanalyzed portion of the dataset to determine

accuracy of each tree's combination of explanatory variables (Cutler et al. 2007).

RESULTS

Didymo vs. Reference Stream Study - 2018

Differences in all four habitat variables were small between Bear (Didymo) and Ramsey Creeks (No Didymo), giving us confidence the two were suitable for comparison (Table 1). Didymo bloom severity in Bear Creek increased from 10.9% coverage in June to 22.6% coverage in August before falling to 18.9% in September (Fig. 2). The June to August Didymo growth was significant (p<0.01) but the decline from August to September was not (p = 0.21).

Percent composition of drifting invertebrates between the two streams generally became less similar as Didymo coverage increased (June-September: 84.2%, 63.1%, 68.5% and 66.6% similar; Fig. 2, Appendix 7). Percent EPT in the drift was initially 12.1% higher in Ramsey Creek but by September was 20.3% higher in Bear Creek. However, Ephemeroptera larvae were proportionally more abundant in Ramsey Creek during all months (June-September: 10.5%, 0.7%, 11.8%, and 8.5% higher; Fig. 3). Percent of larval and pupal Diptera in Bear Creek was 17.8% higher than Ramsey Creek in June, 32.1% higher in July, 30.6% higher in August, and 12.0% lower in September. Both total drifting invertebrates and total energy of drifting invertebrates similarly diverged later in the summer with the streams having similar numbers in June, Ramsey Creek having higher numbers in July and August, and Bear Creek having higher numbers in September. Summer-long amount of total energy of drifting invertebrates was 2.2 times higher in Ramsey Creek.

Reach abundance estimates for Redband and Bull Trout were higher in Bear Creek (Table 2). Slimy Sculpin (n=20) were only in Ramsey Creek. Relative growth of

Redband Trout varied by size-class. Summer relative growth of small trout (<105 mm) was estimated to be 0.0292 g/g/d in Bear Creek but only 0.0033 g/g/d in Ramsey Creek, but this difference was likely driven by a very small sample size of small Redband Trout during June (3 in Bear Creek and 1 in Ramsey Creek). Relative growth of large size-class Redband Trout (>105 mm) was similar between the two streams: 0.0027±0.0004 g/g/d in Bear Creek and 0.0029±0.0007 g/g/d in Ramsey Creek (mean ± standard error; Table 3). Growth for similar size class trout was likewise similar between the two streams (Appendix 8). We observed no negative impact of even frequent capture on growth of PIT-tagged fish (Appendix 9).

Redband Trout diets were 40.7% similar to the drift in Bear Creek (χ^2 test: p < 0.01) and 40.1% similar to the drift in Ramsey Creek (χ^2 test: p < 0.01). By energetic content, Redband diets were 81.2% similar between Bear and Ramsey Creeks for the whole summer (χ^2 test: p = 0.84): 55.6% similar in June, 77.5% similar in July, 99.7% similar in August, and 75.0% similar in September (Appendix 7). Gut fullness was not significantly different between the two streams in any month. Diets of small individual Redband Trout in Bear Creek had more EPT (78.6%±8.4) than large individuals (46.4%±3.0), while gut fullness and %Diptera were similar.

Benke-Wallace consumption estimates for large, individual Redbands were 39% higher in Bear Creek while small size-class estimates were similar between the two streams (Table 2). Reach-level energetic demand by all Redband Trout was estimated at 17,500 kcal in Bear Creek and 6,111 kcal in Ramsey Creek (Table 2). Consumption estimates using the Benke-Wallace method were similar to those estimated using species-specific bioenergetics models (Table 2).

The primary sources of energy (>5% of demand) for Redband Trout in Bear Creek were Ephemeroptera (38.0% of energy intake), Hymenoptera (15.1%), Trichoptera (14.4%), Plecoptera (9.5%) and Diptera (7.6%); (Fig. 4). Primary energy sources for Ramsey Creek Redbands were Ephemeroptera (45.8%), Hymenoptera (15.7%), Diptera (9.8%), Trichoptera (9.0%), and Plecoptera (6.3%); (Fig. 4). Primary sources of energy for Bull Trout in Bear Creek were Ephemeroptera (48.0%), Trichoptera (13.1%), Nematoda (7.2%), Plecoptera (6.3%), and Hymenoptera (5.1%); (Fig. 4). We collected only 4 Bull Trout 3 Slimy Sculpin diets in Ramsey Creek, and we did not consider this sufficient to draw conclusions as to average diet compositions.

Multi-Stream Didymo Survey - 2019

Between-site variation in Fulton's K was too low to assess possible explanatory variables (coefficients of variation [CV] $\leq$ 0.1; Appendix 10). Between-site variation in fish relative condition, calculated as a fish's observed weight compared to its predicted weight, was similarly low for trout and sculpin (CV of 0.12 and 0.04, respectively) and moderately low for charr (CV = 0.28). Despite slightly more variation in charr relative condition between sites, there was no relationship between condition and Didymo coverage (R^2 = 0.03, p = 0.46).

For all diet metrics across all three fish taxa, percent Didymo cover was only correlated with percent of aquatic invertebrates in *Oncorhynchus* diets (Fig. 5). Canopy cover, LWD, riparian vegetation type, and stream temperature were also correlated with percent aquatic invertebrates in *Oncorhynchus* diets, with LWD having the highest pseudo-R^2 (Appendix 10). In fact, few fish diet metrics were correlated with any habitat variable (Appendix 11). However, percent of aquatic invertebrates in trout diets was

positively associated with pine vegetation types (Fig. 6).

Ranking of variables by random forest regression similarly indicated habitat variables had little explanatory power for diet metrics (Appendix 12). Didymo was the top predictor only of percent dietary midges of trout.

DISCUSSION

During the summers of 2018 and 2019, we examined the response of trout, charr, and sculpin to Didymo blooms over space and time. While Didymo appeared to impact the macroinvertebrate assemblage of Bear Creek, the macroinvertebrate food sources and subsequent growth rates of trout did not appear to be affected. Across a gradient of Didymo bloom coverages in 2019, Didymo was weakly correlated with percent of aquatic invertebrates in trout diets but we observed little variation in condition of trout, charr, & sculpin.

As Didymo bloom coverage in Bear Creek increased to its maximum in August 2018, the proportion of the invertebrate drift made up by larval Diptera (primarily Simuliidae and Chironomidae) diverged between the two streams, remaining relatively high in Bear Creek while decreasing in Ramsey Creek. Numerous other studies have similarly found high proportions of Diptera, especially Chironomid larvae, where Didymo is in bloom (Marshall 2007; Kilroy et al. 2009; Gillis and Chalifour 2010; Anderson et al. 2014; Ladrera et al. 2015; Sanmiguel et al. 2016). Yet despite their relative abundance in Bear Creek, Diptera comprised a disproportionately small percent of Redband Trout diets in both streams, indicating strong negative selection. Ephemeroptera, Hymenoptera and Nematoda were strongly selected for by Redband Trout in both streams. Overall, Redband Trout diets were highly similar between the Didymo and reference streams in 2018 (81.2% similar) despite differences in availability of certain prey taxa. In fact, diets were most similar in August (99.7% similar), when Didymo coverage was at its peak. Correspondingly, major energy sources and growth rates of trout did not differ greatly between Bear and Ramsey Creeks. It is however

possible that Didymo coverage in Bear Creek was not severe enough to cause the

proportional shifts in macroinvertebrate composition such that trout would have been

impacted by food limitation. While a no-Didymo comparison was not available for Bull

Trout since so few were captured in Ramsey Creek, Bull Trout in Bear Creek also did not

utilize larval Diptera as a major energy source, which may be consequential only at very

high Didymo coverage. Further, sexually mature Bull Trout in these systems were likely

allocating energy to pre-spawn gamete production, which may have affected overall

growth.

Stream resident trout are considered generalist invertivores (Behnke 1992), but

strong selection by Redband Trout in both Bear and Ramsey Creeks in 2018 for the same

taxa indicates this subspecies may show strong preferences for mayflies

(Ephemeroptera). However, given interior (non-steelhead) Redband Trout occupy only

42% of their historic range across the West and only 2% of historic range in Montana

(Muhlfeld et al. 2015), it is important to carefully evaluate land management actions such

as timber harvest or road construction that may impact sensitive mayfly species.

In our 2019 survey of 28 streams with varying levels of coverage, Didymo bloom

severity was not correlated with most measures of fish diet and was only a weak predictor

of aquatic invertebrates in trout diets. In conjunction with the 81.2% similarity of diets

between Bear and Ramsey Creeks in 2018, this suggests Didymo may alter the

composition of trout dietary macroinvertebrates to a small extent, but that shift does not

alter condition or growth rates of trout. This disconnect may indicate trout in Kootenai

River headwaters are not food limited during summer months, or that much greater diet

perturbations are necessary to affect trout growth. Alternatively, the lack of variability in

fish condition across streams may suggest fishes in these populations conform to the

theory of ideal-free distribution (Fretwell 1969; Sutherland et al. 1988) such that fish

condition between streams is relatively homogenous but abundances vary based on where

forage is most available. As such, distribution of fish condition in Kootenai basin

headwaters may be relatively stable - i.e. exist in a state of equilibrium (*sensu* Nash

1951).

Although not the impetus of our study, we observed interesting differences in

percent of aquatic invertebrates in trout diets in streams with differing riparian vegetation

(Fig. 6). Allan et al. (2003) found riparian communities dominated by alder in Alaska

coastal temperate rainforests, provided more terrestrial invertebrates to juvenile salmon

(*Oncorhynchus kisutch*) than did those dominated by a mix of hemlock and spruce (*Picea*

spp.). Similarly, we observed higher proportions of riparian invertebrates in trout diets in

alder-dominated streams than in pine-dominated streams (largely lodgepole pine *Pinus*

contorta). In contrast to the finding of Allan et al. (2003), trout in our inland temperate

rainforest streams with riparian communities dominated by cedar and hemlock, had

similar aquatic-terrestrial ratios to alder-dominated streams (Fig. 6).

Our study examined the impacts of Didymo blooms only into early Fall during

both years, a time when terrestrial invertebrate inputs, and trout reliance upon them, are

high (Nakano and Murakami 2001). It is possible terrestrial inputs act as a buffer to shifts

in aquatic invertebrate composition caused by blooms and some negative or positive

consequence of Didymo can only be observed by studying fishes across seasons. In fact,

some studies have reported severe Didymo blooms during winter months (e.g. Kolmakov

et al. 2008), and we observed severe blooms in the Lardeau River during April of 2018

when snowpack was still high. Trout growth in headwater streams is higher in summer

months but foraging (Thurow 1997) and growth (Al-Chokhachy et al. 2019) still occur

over winter. We therefore suggest potential impacts of Didymo on fishes be examined

during winter. Further, due to the multitude of studies indicating impacts to

macroinvertebrate assemblages, the relationship of Didymo to imperiled invertebrates,

especially sedentary taxa that may not be able to avoid Didymo blooms such as

freshwater mussels, bears further study.

Benke-Wallace Consumption Estimates

Consumption estimates using the modified Benke-Wallace method were similar

to those generated using traditional bioenergetics models. Discrepancies between Bull

Trout estimates are likely due to the fact we used a thermal optimum value of 12.0°C

(Dunham et al. 2004) that was likely more appropriate for resident Kootenai basin Bull

Trout than the 16.0°C optimum (Mesa et al. 2013) used by Fish Bioenergetics 4.0

(Deslauriers et al. 2017). Because bioenergetics models require significant laboratory-

generated parameterization for individual species, resultant models can be biased by the

particular fishes used for parameterization (Chipps and Wahl 2008). Thermal growth

optimums may also be higher when laboratory fishes are fed unlimited amounts of food

than when food is limited (Brett et al. 1969). As such, bioenergetics models are not

universally appropriate for all populations of species for which models have been

developed and models are not available for all species. The relative similarities between

consumption estimates generated by Fish Bioenergetics 4.0 and the modified Benke-

Wallace equation we present here demonstrates the potential utility of the Benke-Wallace

equation. While further refinement of the Benke-Wallace equation, especially of the size-

specific tissue allocation, will certainly make estimates more accurate, the approach may provide biologists with the means to generate consumption estimates when bioenergetics models are not available or otherwise appropriate.

Implications for Management

Authors of previous studies have suggested nutrient amendments (James et al. 2015; Coyle 2016) and dam releases (Cullis et al. 2015) as viable means to manage nuisance Didymo blooms. Indeed, both methods show promise for reduction of blooms at local scales. The impetus for this bloom reduction may be independent of concern for fishes, including aesthetics, fouling of infrastructure, or to prevent hypoxia. However, we did not observe any major impacts of Didymo blooms on the diet, condition, or growth of trout in Kootenai basin headwaters. This overall result is similar to those for Brown Trout in a South Dakota stream (James and Chipps 2016). Therefore, it is not clear efforts to control Didymo blooms in headwater streams will benefit fish.

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TABLES AND FIGURES

Table 1. Bear and Ramsey Creek habitat measurement - 2018.

2018 Habitat Measurements		
	Bear Ck. (Didymo)	Ramsey Ck. (No Didymo)
Temp. (°C) ±SD	9.79 ± 2.32	9.79 ± 2.40
Mesohabitat		
Cascade	76%	83%
Riffle	16%	10%
Pool	8%	7%
Substrate Size	26.7 cm	23.2 cm
Wetted Width	7.24 m	7.17 m
Nutrients (µg/L) ±SD		
SRP	1.995 ±0.368	1.530 ±0.409
Bromide	below detection	below detection
Fluoride	below detection	below detection
Nitrate	74.5	25
Phosphate	below detection	below detection
Sulfate	1235	930

Table 2. List of streams surveyed in 2019.

					Streams Surveyed in 2019				
Stream	Subbasin (State/Prov.)	% Didymo Coverage	% Overstory Cover	Wetted Width (m)	Dominant Vegetation	Rosgen Channel Type	Large Woody Debris #	Aug. Stream Temp. (°C)	Fish Spp. Observed
		DIDYMO	COV	WW	VEG	CHAN	LWD	TEMP	
Blacktail Cr.	Yaak R. (MT)	1.7	82.6	3.4	Pine	B	12	10.1	RB
Boulder Cr.	Koocanusa (MT)	33.3	80.2	4.7	Cedar	A	6	12.5	WCT
Bear Cr.	Kootenai R. (MT)	30.6	88.7	8.3	Cedar	B	19	11.9	BULL, RB
Big Cherry Cr.	Kootenai R. (MT)	29.0	74.5	5.9	Cedar	A	75	12.5	BULL, RB, RBxCT, WCT, SLCOT
Burnt Cr.	Yaak R. (MT)	31.6	64.5	7.3	Cedar	A	12	14.4	EB, LN DC, MWF, RB, SLCOT
Coffee Cr.	Kootenay L. (BC)	2.0		14.3	Cedar	A		12.9	BULL, WCT
Davis Cr.	Kootenay L. (BC)	20.5	60.6	9.8	Cedar	A	5	11.8	BULL, MWF, RB, SLCOT
E. Fork Pipe Cr.	Kootenai R. (MT)	24.6	83.7	3.2	Alder	B	12	10.9	EB, RB, RBxCT, SL COT
E. Fork Yaak R.	Yaak R. (MT)	52.6	31.5	7.6	Pine	B	4	11.4	RB
Granite Cr.	Kootenai R. (MT)	21.3	68.1	10.3	Cedar	B	7	11.6	BULL, EB, RB, SLCOT
Hope Cr.	Lardeau R. (BC)	16.6	67.3	4.8	Cedar	A	16	12.7	BULL, MWF, RB
Kokanee Cr.	Kootenay L. (BC)	0.0	32.0	15.9	Alder	A		13.9	RB
Lake Cr.	Kootenai R. (MT)	27.0	6.3	19.0	Alder	B	0		RB, TCOT
Leigh Cr.	Kootenai R. (MT)	3.2	88.0	4.6	Cedar	A	20	9.9	EB, RBxCT
Lizard Cr.	Elk R. (BC)	15.4	26.0	6.8	Pine	B	5	11.5	EB, RBxCT
Lockhart Cr.	Kootenay L. (BC)	40.6	80.4	5.0	Cedar	A		11.5	BULL, LNDC, MWF, RB
Mobbs Cr.	Lardeau R. (BC)	48.3	28.1	3.2	Alder	Side Channel	8	10.6	BULL, RB, SLCOT
Lost Ledge Cr.	Kootenay L. (BC)	5.7	69.2	4.9	Cedar	A	9	12.8	RB
N. Fork 17 Mile Cr.	Yaak R. (MT)	17.7	66.0	3.8	Cedar	A	15	11.9	EB, RB, SLCOT, WCT
Outlet Cr.	White R. (BC)	80.5	64.0	6.3	Pine	B	8	18.2	RB
Parmenter Cr.	Kootenai R. (MT)	0.9	83.2	7.7	Cedar	B	40	10.7	EB, RB, SLCOT
Pinkham Cr.	Koocanusa (MT)	39.4	53.4	4.5	Alder	A		11.3	EB, RB
Solo Joe Cr.	Yaak R. (MT)	0.0	81.1	2.8	Pine	A	21	11.7	RB
Trail Cr.	Fisher R. (MT)	13.0	63.7	4.9	Pine	B	10	13.9	EB, TCOT, WCT
W. Fisher Cr.	Fisher R. (MT)	1.3	26.9	5.6	Pine	B	2	11.1	BULL, TCOT, WCT
Wolf Cr.	Fisher R. (MT)	0.0	32.0	9.8	Alder	B	3	20.2	LNDC, LSSU, MWF, RSSH, TCOT, WCT
Woodbury Cr.	Kootenay L. (BC)	0.2	37.9	10.1	Cedar	B		8.6	BULL, WCT
Weasel Cr.	Wigwam R. (MT)	52.5	58.0	3.5	Pine	B	5	15.3	RBxCT

<u>Species Codes:</u> Brook Trout (EB), Bull Trout (BULL), Longnose Dace (LNDC), Largescale Sucker (LSSU), Mountain Whitefish (MWF), Rainbow Trout (RB), Rainbow-Cutthroat Hybrid (RBxCT), Redside Shiner (RSSH), Slimy Sculpin (SLCOT), Torrent Sculpin (TCOT), and Westslope Cutthroat Trout (WCT)

Table 3. Population (reach) abundance, growth, and consumption estimates for each fish species and size class in Bear and Ramsey Creeks. Bioenergetics consumption estimates are shown for comparison to Benke-Wallace estimates though population-level estimates used the Benke-Wallace method.

	Stream	Pop Abundance	Individual Growth	Indiv Summer Consumption	Pop Consumption
Redband Trout			(g/g/d)	(kcal)	(kcal)
Small	Bear	132	0.0292	20.9	2755.8
	Ramsey	91	0.0033	18.8	1712.5
Large	Bear	196	0.0027	75.3	14724.5
	Ramsey	81	0.0029	54.2	4398.1
Bull Trout					
Small	Bear	60	0.0136	21.3	1277.0
	Ramsey	2	NA	NA	NA
Large	Bear	45	0.0011	23.9	1080.5
	Ramsey	3	NA	NA	NA
Slimy Sculpin					
	Ramsey	20	0.0030	8.8	176.8
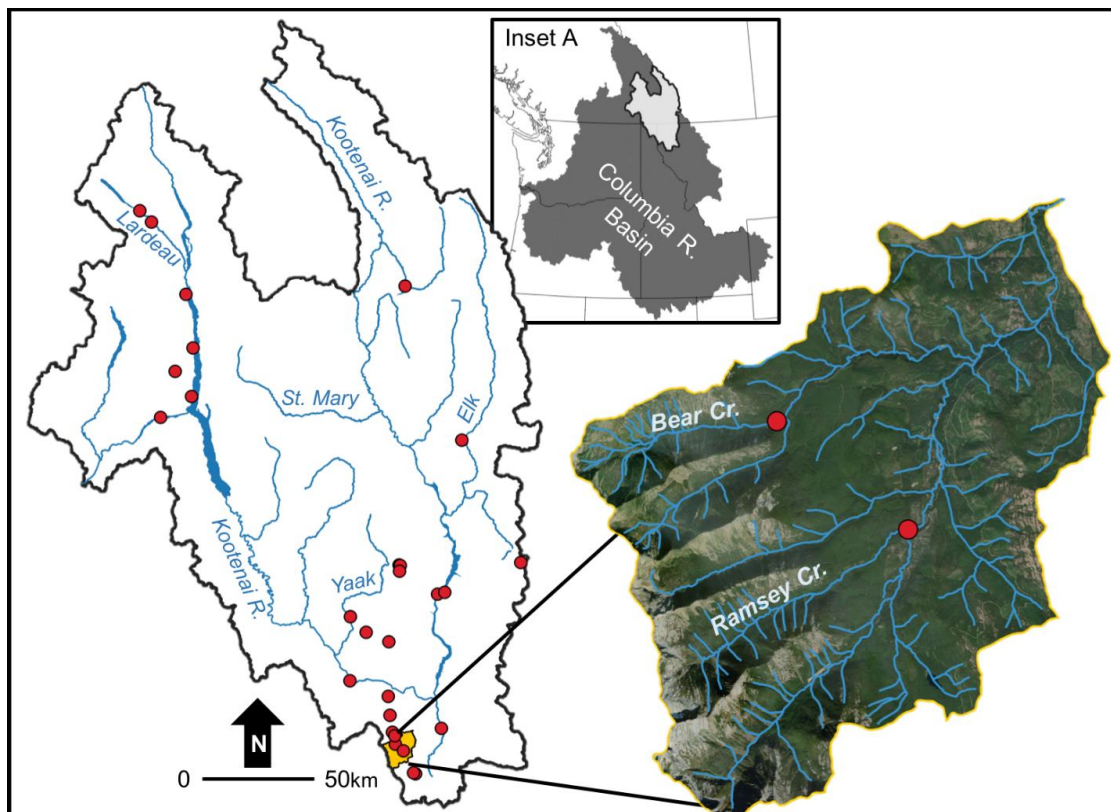
Fig. 1. Location of study streams (red dots) within the Kootenai River basin (left) and the upper Libby Creek subbasin (right). Inset A shows the location of the Kootenai basin within the larger Columbia River watershed.
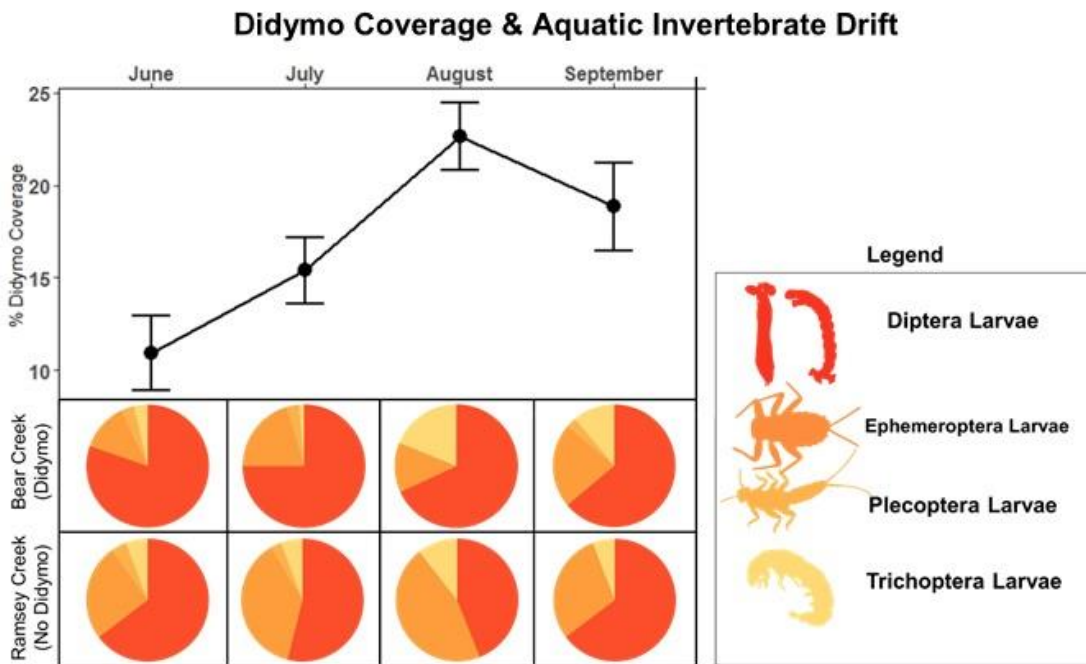
Fig. 2. Monthly, percent of stream substrate covered by Didymo in Bear Creek, 2018 (top). Pie charts show proportions of major aquatic invertebrate taxa in the drift in Bear and Ramsey Creeks.
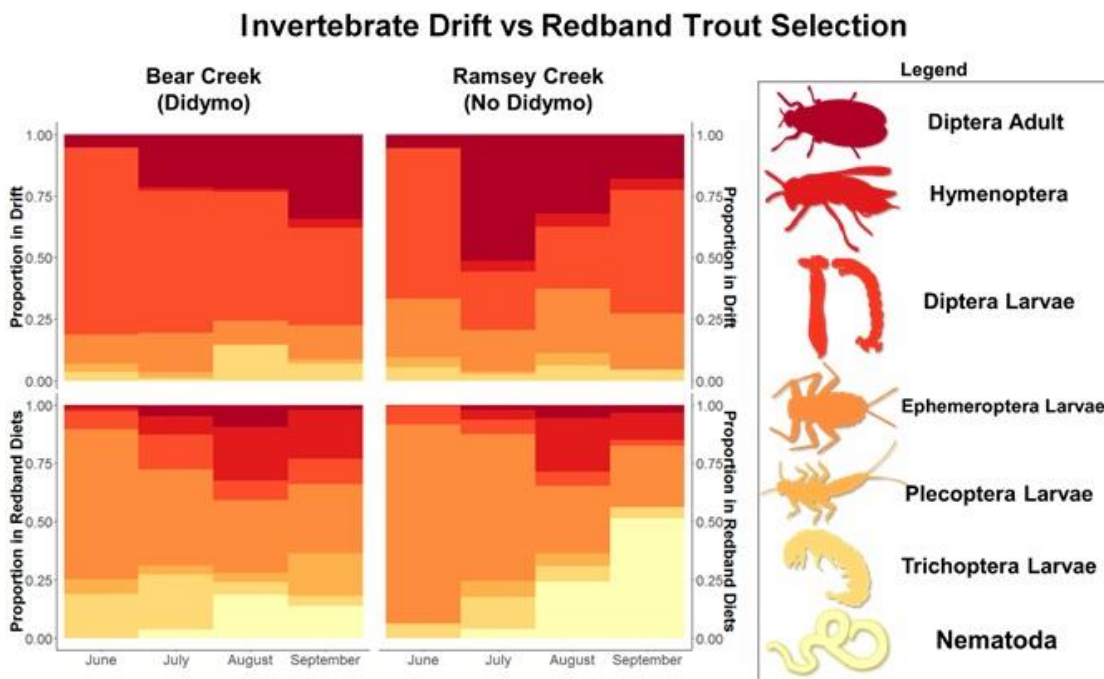
Fig. 3. Invertebrate taxa in Bear and Ramsey Creek drift (top) and proportion in Redband Trout diets (bottom) by month.
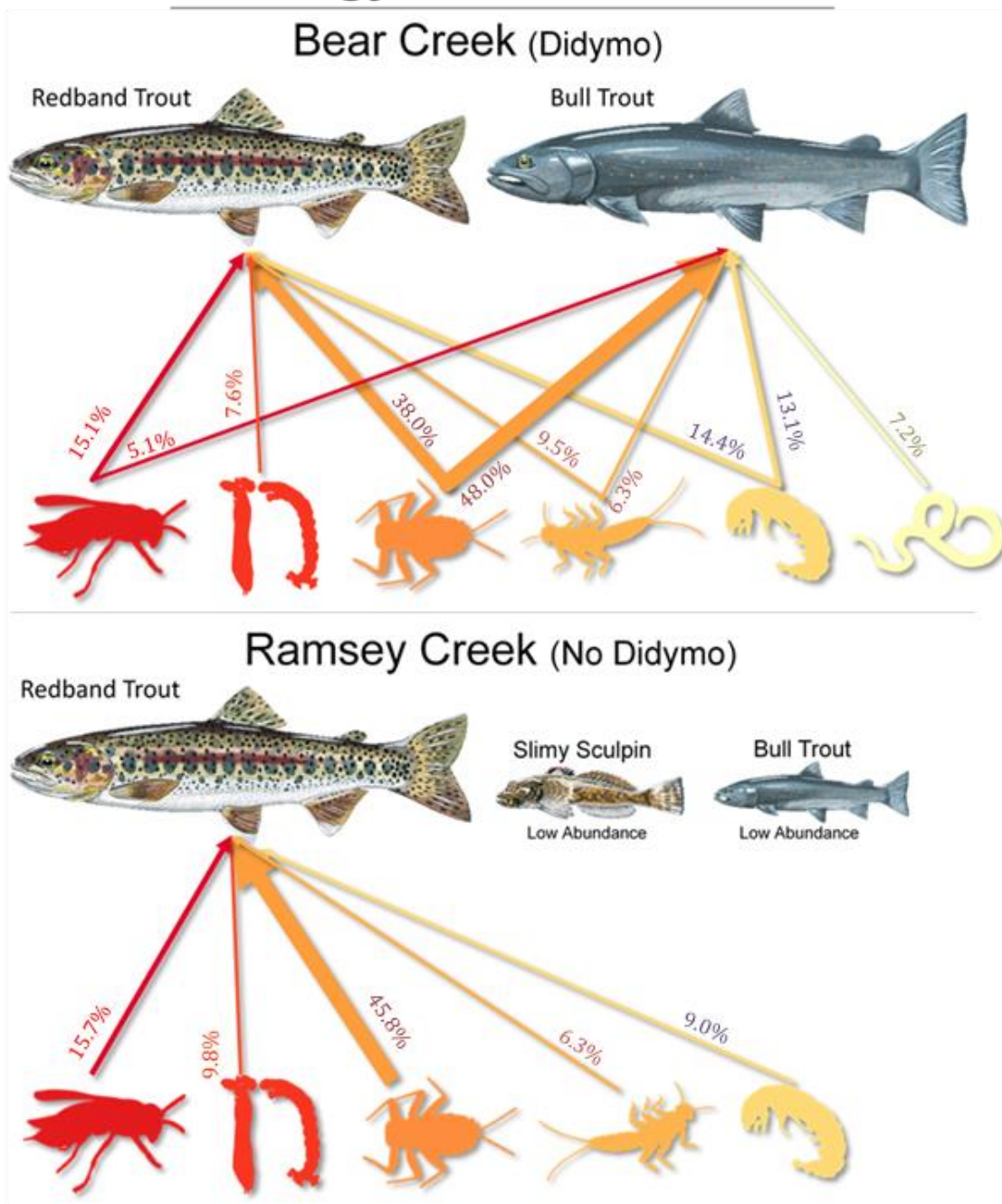
Fig. 4. Energy-flow food web for fishes in Bear and Ramsey Creeks. Line thickness represents proportion of total energy demand by the given fish species met by each invertebrate taxa. Only taxa representing at least 5% of energy demand are shown.

Fish Diet vs. Didymo Coverage
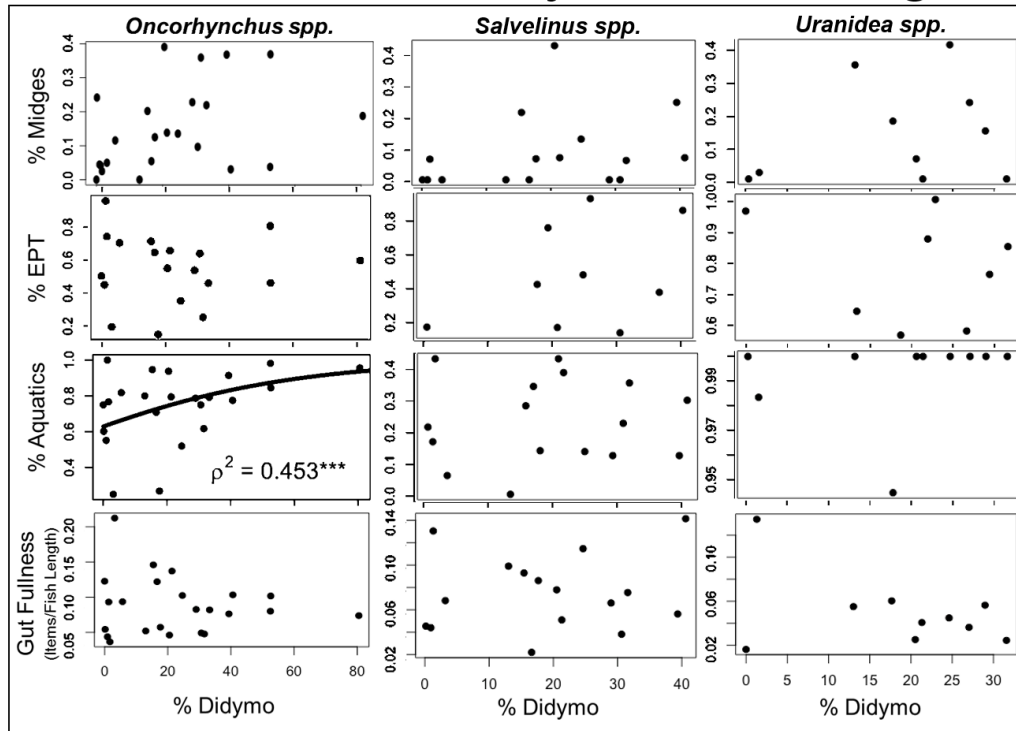
Fig. 5. Correlations of Didymo coverage to each fish taxa's diet and condition response metrics from 2019. Each dot represents the average value for fish in a single stream. ρ^2 is Nagelkerke's pseudo-R^2 value. *** indicates a p-value ≤ 0.05.

Fig. 6. Violin plot of percent aquatic invertebrates in trout diets showing the spread across different riparian vegetation types.

APPENDICES

Appendix 1. All 131 unique stream locations examined for presence of Didymo blooms in the Kootenai basin. Streams which we quantitatively assessed coverage are listed as 'Y'. We visually estimated covered for streams listed as 'N'.

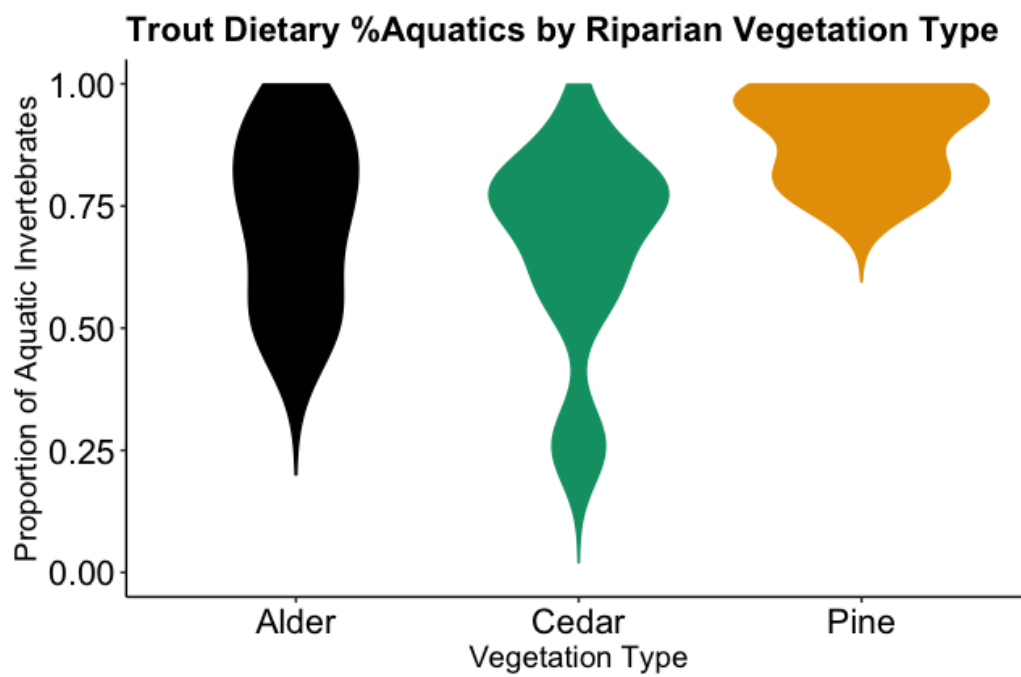|						All Locations Examined for Didymo Blooms
Date	Stream Name	State/ Province	Latitude	Longitude	% Didymo	Measured (Y) or Estimated (N)
2019-Aug	Alexander Creek	MT	48.39266	-115.32864	0%	N
2019-Aug	Barron Creek	MT	48.51344	-115.30235	0%	N
2018-Jun	Bear Creek	MT	48.17997	-115.573182	10.9%	Y
2018-Aug	Bear Creek	MT	48.16893	-115.587733	22.6%	Y
2019-Aug	Bear Creek	MT	48.16886	-115.58853	30.6%	Y
2018-Aug	Big Cherry Creek	MT	48.32744	-115.529159	0	N
2018-Aug	Big Cherry Creek	MT	48.35288	-115.525966	0	N
2019-Aug	Big Cherry Creek	MT	48.26734	-115.53004	0%	N
2019-Aug	Big Creek	MT	48.82052	-115.35209	0%	N
2019-Aug	Big Foot Creek	MT	48.58376	-115.70378	0%	N
2019-Jun	Big Sand Creek	BC	49.37202	-115.240065	0%	N
2019-Aug	Blacktail Creek	MT	48.95124	-115.54154	5-10%	N
2019-Aug	Boulder Creek	MT	48.82052	-115.29097	33.3%	Y
2018-Aug	Bramlet Creek	MT	48.03754	-115.49219	0%	N
2019-Aug	Bristow Creek	MT	48.54427	-115.29245	0%	N
2019-Aug	Bunker Hill Creek	MT	48.8969	-115.64668	0%	N
2019-Aug	Burnt Creek	MT	48.72936	-115.87002	31.6%	Y
2018-Jun	Cable Creek	MT	48.16965	-115.585025	0%	N
2019-Aug	Callahan Creek	MT	48.45636	-115.89153	0%	N
2019-Jun	Canyon Creek	MT	48.43051	-115.283832	0%	N
2019-Aug	Cascade Creek	BC	50.39822	-117.09391	<5%	N
2018-Aug	Cedar Creek	MT	48.40931	-115.665338	0	N
2018-Aug	Cedar Creek	MT	48.43052	-115.628991	<5%	N
2019-Aug	Cedar Creek	MT	48.4096	-115.66522	<5%	N
2019-Aug	Cedar Creek (Kootenay L.)	BC	49.74661	-116.91241	0%	N
2019-Aug	Coffee Creek	BC	49.69663	-116.91781	2%	Y
2019-Aug	Cooper Creek	BC	50.19901	-116.96092	<5%	N
2019-Jun	Cripple Horse Creek	MT	48.47742	-115.25535	0%	N
2019-Aug	Davis Creek	BC	50.14236	-116.9552	20.5%	Y
2019-Aug	Deep Creek	MT	48.26923	-115.53397	0%	N
2019-Aug	Deer Creek	ID	48.81707	-116.11524	0%	N
2019-Aug	Duhamel Creek	BC	49.57474	-117.22723	0%	N
2019-Aug	Duncan River	BC	50.19634	-116.95234	0%	N
2019-Jun	Dunn Creek	MT	48.3851	-115.313085	0%	N
2019-Aug	East Fork Pipe Creek	MT	48.61675	-115.61885	24.6%	Y
2019-Aug	East Fork Yaak River	MT	48.94885	-115.53378	52.6%	Y
2018-Aug	Elliot Creek	MT	48.23637	-115.46749	0%	N
2018-Aug	Fisher River	MT	48.06978	-115.374032	5%	N
2019-Jun	Five Mile Creek	MT	48.53573	-115.210572	0%	N
2019-Aug	Flattail Creek	MT	48.63315	-115.70071	0%	N
2018-Aug	Flower Creek	MT	48.38299	-115.56261	0	N
2018-Aug	Flower Creek	MT	48.34452	-115.606768	0	N
2018-Aug	Flower Creek	MT	48.39004	-115.560911	0%	N
2018-Aug	Granite Creek	MT	48.30597	-115.543096	0	N
2019-Aug	Granite Creek	MT	48.30613	-115.54307	<5%	N
2019-Aug	Granite Creek	MT	48.29544	-115.62011	21.3%	Y
2019-Aug	Hammill Creek	BC	50.20204	-116.94646	5-10%	N
2019-Aug	Hellroaring Creek	MT	48.78759	-115.91856	0%	N
2019-Aug	Hope Creek	BC	50.45751	-117.19081	16.6%	Y
2018-Aug	Horse Creek	MT	48.30163	-115.598662	0	N
2019-Aug	Horse Creek	MT	48.30166	-115.59863	0%	N
2019-Aug	Hudson Creek	MT	48.91834	-115.52186	0%	N
2019-Aug	Jackson Creek	MT	48.46479	-115.31589	0%	N
2019-Aug	Kaslo River	BC	49.9085	-116.90636	0%	N
2019-Aug	Kokanee Creek	BC	49.60506	-117.12635	0%	Y
2018-Aug	Lake Creek (Fisher R.)	MT	48.03812	-115.482052	0	N
2018-Aug	Lake Creek (Fisher R.)	MT	48.03766	-115.490971	0	N
2018-Aug	Lake Creek (Fisher R.)	MT	48.03915	-115.471111	0%	N
2019- Aug	Lake Creek (Kootenai R.)	MT	48.44915	-115.879329	27%	Y
2019-Aug	Leigh Creek	MT	48.22127	-115.60603	3.2%	Y
2018-Aug	Libby Creek	MT	48.31436	-115.537251	0	N
2018-Aug	Libby Creek	MT	48.22552	-115.477984	0	N

Appendix 1 (cont.)

2018-Aug	Libby Creek	MT	48.22456	-115.477006	0	N
2018-Aug	Libby Creek	MT	48.31436	-115.504728	0%	N
2019-Jun	Little Sand Creek	BC	49.37789	-115.29201	5-10%	N
2019-Sep	Lizard Creek	BC	49.48972	-115.104813	15.4%	Y
2019-Aug	Lockhart Creek	BC	49.5084	-116.785994	40.6%	Y
2019-Aug	Lost Ledge Creek	BC	49.90834	-116.90733	5.68%	Y
2019-Aug	McKillop Creek	MT	48.148	-115.27532	0%	N
2019-Aug	Meadow Creek	ID	48.81943	-116.1462	0%	N
2019-Aug	Meadow Creek (Lardeau R.)	BC	50.22831	-116.98587	0%	N
2019-Aug	Meadow Creek (Yaak R.)	MT	48.78425	-115.92321	20-30%	N
2019-Aug	Mobbs Creek (side-channel)	BC	50.50673	-117.27104	48.3%	Y
2019-Aug	Moyie River	ID	48.82036	-116.1462	30%	N
2019-Aug	North Fork 17 Mile Creek	MT	48.66022	-115.7675	17.7%	Y
2019-Aug	North Fork Parsnip Creek	MT	48.67594	-115.34289	0%	N
2019-Aug	North Fork Yaak River (Yaak R.)	MT	48.95893	-115.61128	0%	N
2019-Sep	Outlet Creek	BC	50.16812	-115.464053	80.5%	Y
2018-Aug	Parmenter Creek	MT	48.39906	-115.57565	0	N
2018-Aug	Parmenter Creek	MT	48.37799	-115.628871	0	N
2018-Aug	Parmenter Creek	MT	48.39272	-115.579392	0%	N
2019-Aug	Parmenter Creek	MT	48.37814	-115.62908	0.9%	Y
2019-Jun	Pinkham Creek	MT	48.82799	-115.24295	39.4%	Y
2019-Aug	Pinkham Creek	MT	48.82799	-115.24295	39.4%	Y
2019-Aug	Pipe Creek	MT	48.4278	-115.59636	<5%	N
2019-Aug	Pipe Creek	MT	48.61675	-115.61885	0%	N
2019-Aug	Placer Creek	ID	48.82678	-116.13982	0%	N
2019-Aug	Pleasant Valley Fisher River	MT	48.04044	-115.29337	5-10%	N
2019-Aug	Poplar Creek	BC	50.41548	-117.12218	5-10%	N
2018-Aug	Prospect Creek	MT	48.31877	-115.575627	0%	N
2019-Aug	Quartz Creek	MT	48.60519	-115.6947	20-30%	N
2018-Jun	Ramsey Creek	MT	48.13918	-115.536531	0%	Y
2019-Aug	Rapid Creek	BC	50.43936	-117.15664	<5%	N
2019-Aug	Raven Creek	MT	48.04519	-115.28715	0%	N
2019-Aug	Red Top Creek	MT	48.76113	-115.91794	0%	N
2019-Aug	Redfish Creek	BC	49.65643	-117.04791	0%	N
2019-Aug	Ross Creek	BC	49.65643	-116.93315	0%	N
2018-Aug	Shaughnessy Creek	MT	48.30308	-115.594735	0%	N
2019-Jun	Sheep Creek	MT	48.62266	-115.258591	0%	N
2019-Aug	Sitkum Creek	BC	49.59986	-117.17427	0%	N
2019-Aug	Skin Creek	ID	48.77154	-116.12033	0%	N
2019-Aug	Snell Creek	MT	48.19548	-115.27532	0%	N
2019-Aug	Snowshoe Creek	MT	48.2138	-115.59783	0%	N
2019-Aug	Solo Joe Creek	MT	48.92425	-115.53963	0%	Y
2018-Aug	South Fork Flower Creek	MT	48.34277	-115.602578	0%	N
2019-Aug	South Fork Miller Creek	MT	48.03825	-115.4603	<5%	N
2019-Aug	Spread Creek	MT	48.82335	-115.85119	5-10%	N
2019-Jun	Staples Creek	BC	49.917	-115.648183	0%	N
2019-Aug	Sullivan Creek	MT	48.87102	-115.25779	0%	N
2019-Jun	Sutton Creek	MT	48.76062	-115.280701	0%	N
2018-Aug	Swamp Creek	MT	48.17664	-115.448145	0%	N
2019-Jun	Ten Mile Creek	MT	48.595	-115.206589	0%	N
2019-Aug	Tenderfoot Creek	BC	50.48269	-117.21991	<5%	N
2018-Aug	Trail Creek	MT	48.03856	-115.460284	0	N
2019-Aug	Trail Creek	MT	48.03825	-115.4603	13%	Y
2019-Aug	Unnamed Tributary	MT	48.24024	-115.56314	0%	N
2019-Aug	Unnamed Tributary (Quartz Cr.)	MT	48.57516	-115.69742	0%	N
2019-Aug	Upper Big Cherry Creek	MT	48.20577	-115.59134	29%	Y
2019-Aug	Vinal Creek	MT	48.86076	-115.64443	0%	N
2019-Jun	Warland Creek	MT	48.50581	-115.211244	0%	N
2019-Sep	Weasel Creek	MT	48.94904	-114.734004	52.5%	Y
2018-Aug	West Fisher Creek	MT	48.05131	-115.428994	<5%	N
2018-Aug	West Fisher Creek	MT	48.04227	-115.472995	0	N
2018-Aug	West Fisher Creek	MT	48.05628	-115.40039	<5%	N
2019-Aug	West Fisher Creek	MT	48.04253	-115.47351	1.3%	Y
2019-Aug	West Fork Creek	MT	48.42768	-115.60329	0%	N
2019-Aug	West Fork Yaak River	MT	48.934	-115.67286	0%	N
2019-Aug	Wolf Creek	MT	48.23393	-115.28529	0%	Y
2019-Aug	Woodbury Creek	BC	49.80625	-117.028353	0.16%	Y
2019-Aug	Yaak River	MT	48.78713	-115.91965	20-30%	N
2019-Aug	Young Creek	MT	48.87102	-115.21744	0%	N

Appendix 2. Redband Trout length-frequency histograms for Bear and Ramsey Creeks. The black bar represents the cutoff for 'small' vs. 'large' fish.


Bear Creek Redband Trout Length-Frequency

Ramsey Creek Redband Trout Length-Frequency
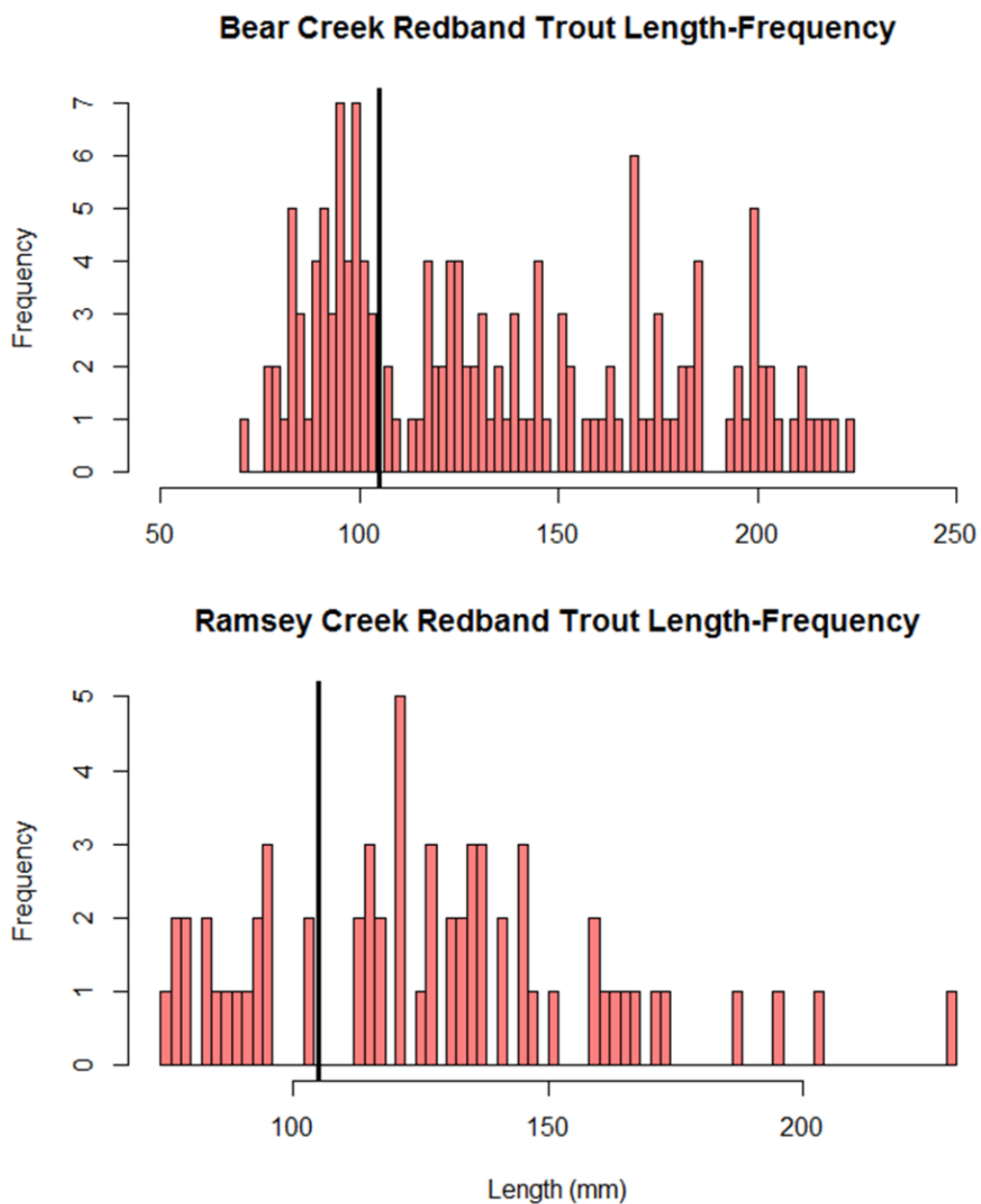
Appendix 3. Biomass and energy conversions for fish prey items. Length (in millimeters)-to-mass (grams$_{DryMass}$) conversions follow the equation: *Mass = a*Length^b*

		Prey Mass & Energy Conversions			
		Length to Mass Coefficients			
Taxa	Stage			Source	kilocalories per gram dry mass	Proportion Indigestible
		b	a			
Insecta	Larvae	2.788	0.0064	Benke et al. 1999	5.115310533	0.1
Diptera	Larvae	2.692	0.0025	Benke et al. 1999	4.549379925	0.1
Athericidae	Larvae	2.586	0.004	Benke et al. 1999	4.278861568	0.1
Blepharicidae	Larvae	3.292	0.0067	Benke et al. 1999	4.278861568	0.1
Ceratopogonidae	Larvae	2.469	0.0025	Benke et al. 1999	4.742017466	0.1
Chironomidae	Larvae	2.617	0.0018	Benke et al. 1999	5.427629828	0.1
Simuliidae	Larvae	3.011	0.002	Benke et al. 1999	4.290047555	0.1
Tipulidae	Larvae	2.681	0.0029	Benke et al. 1999	4.278861568	0.1
Hemiptera	Larvae	2.734	0.0108	Benke et al. 1999	5.457649904	0.1
Corixidae	Larvae	2.904	0.0031	Benke et al. 1999	4.826227629	0.1
Gerridae	Larvae	2.596	0.015	Benke et al. 1999	5.457649904	0.1
Veliidae	Larvae	2.719	0.0126	Benke et al. 1999	5.457649904	0.1
Plecoptera	Larvae	2.754	0.0094	Benke et al. 1999	4.826227629	0.1
Capniidae	Larvae	2.562	0.0049	Benke et al. 1999	4.826227629	0.1
Chloroperlidae	Larvae	2.724	0.0065	Benke et al. 1999	4.826227629	0.1
Nemouridae	Larvae	2.762	0.0056	Benke et al. 1999	5.457649904	0.1
Perlidae	Larvae	2.879	0.0099	Benke et al. 1999	4.826227629	0.1
Perlodidae	Larvae	2.742	0.0196	Benke et al. 1999	4.826227629	0.1
Pteronarcyidae	Larvae	2.573	0.0324	Benke et al. 1999	4.826227629	0.1
Odonata	Larvae	2.792	0.0078	Benke et al. 1999	4.826227629	0.1
Ephemeroptera	Larvae	2.832	0.0071	Benke et al. 1999	5.472659943	0.1
Ameletidae	Larvae	2.588	0.0077	Benke et al. 2000	5.472659943	0.1
Baetidae	Larvae	2.875	0.0053	Benke et al. 1999	5.472659943	0.1
Baetiscidae	Larvae	2.905	0.0116	Benke et al. 1999	5.472659943	0.1
Caenidae	Larvae	2.772	0.0054	Benke et al. 1999	5.472659943	0.1
Ephemerellidae	Larvae	2.676	0.0103	Benke et al. 1999	5.472659943	0.1
Heptageniidae	Larvae	2.754	0.0108	Benke et al. 1999	5.589738241	0.1
Siphlonuridae	Larvae	3.446	0.0027	Benke et al. 1999	5.472659943	0.1
Trichoptera	Larvae	2.839	0.0056	Benke et al. 1999	5.002345411	0.1
Brachycentridae	Larvae	2.818	0.0083	Benke et al. 1999	5.002345411	0.1
Glossosomatidae	Larvae	2.958	0.0082	Benke et al. 1999	5.002345411	0.1
Hydropsychidae	Larvae	2.926	0.0046	Benke et al. 1999	5.389604398	0.1
Lepidostomatidae	Larvae	2.649	0.0079	Benke et al. 1999	5.002345411	0.1
Leptoceridae	Larvae	3.212	0.0034	Benke et al. 1999	5.002345411	0.1
Limnephilidae	Larvae	2.933	0.004	Benke et al. 1999	4.615086424	0.1
Polycentropodidae	Larvae	2.705	0.0047	Benke et al. 1999	5.002345411	0.1
Psychomyiidae	Larvae	2.873	0.0039	Benke et al. 1999	5.002345411	0.1
Rhyacophilidae	Larvae	2.48	0.0099	Benke et al. 1999	5.002345411	0.1
Coleoptera	Larvae	2.91	0.0077	Benke et al. 1999	5.559718164	0.1
Elmidae	Larvae	2.879	0.0074	Benke et al. 1999	4.826227629	0.1
Amphipoda	Larvae	3.015	0.0058	Benke et al. 1999	4.004678203	0.1
Decapoda	Larvae	3.626	0.0147	Benke et al. 1999	3.946639388	0.1
Hydrachnidia	Larvae	1.66	0.1327	Baumgartner & Rothhaupt 2003	4.828228967	0.1
Oligochaeta	--	1.888	0.008	Miyasaka et al. 2008	4.663456122	0.1
Nematoda	--	1	0.00983607	Clancy, *unpublished data*	4.716154015	0.1
Ephemeroptera	Adult	2.49	0.014	Sabo et al. 2002	5.457649904	0.1
Lepidoptera	Adult	2.69	0.012	Sabo et al. 2002	5.457649904	0.1
Plecoptera	Adult	1.69	0.26	Sabo et al. 2002	5.457649904	0.1
Hemiptera	Adult	3.33	0.005	Sabo et al. 2003	5.457649904	0.1
Trichoptera	Adult	2.9	0.01	Sabo et al. 2002	5.457649904	0.1
Coleoptera	Adult	2.64	0.04	Sabo et al. 2002	5.559718164	0.1
Hymenoptera	Adult	1.56	0.56	Sabo et al. 2002	4.632097801	0.1
Orthoptera	Adult	2.55	0.03	Sabo et al. 2002	5.08039761	0.1
Araneae	Adult	2.74	0.05	Sabo et al. 2002	4.828228967	0.1
Diptera	Adult	2.26	0.04	Sabo et al. 2002	5.786870076	0.1
Culicidae	Adult	2.038	0.032	Sabo et al. 2002	5.786870076	0.1
Formicidae	Adult	2.666	0.027	Sabo et al. 2002	4.552044264	0.1
Perlidae	Adult	2.819	0.008	Sabo et al. 2002	5.457649904	0.1
Staphylinidae	Adult	4.026	0.001	Sabo et al. 2002	5.559718164	0.1
Vespidae	Adult	3.723	0.001	Sabo et al. 2002	4.632097801	0.1
Lepidoptera	Adult	2.318	0.0179	Gruner 2003	5.45765	0.1
Collembola	Adult	2.809	0.0056	Gruner 2003	5.457649904	0.1
Insecta	Adult	2.583	0.07460526	Calculated Average	5.361210409	0.1
Actinopterygii	--	2.935	0.00000307	Clancy, *unpublished data*	5.089403633	0.033

Appendix 4. Movement of trout between the abutting lower and upper halves of Bear Creek, MT.

Fish Movement Between Bear Creek Sections		
	Percent of Tagged Fish	
Month	Recaptured in Adjacent Section	Recaptured in Same Section
July	3.4%	96.6%
August	22.4%	77.6%
September	8.3%	91.7%

Appendix 5. Example thermal adjustment curve for the modified Benke-Wallace method for a fish with a 13.1°C thermal optimum.

$$TempFactor = e^{-((0.2*(StreamTemp - 13.1))^{4})}$$
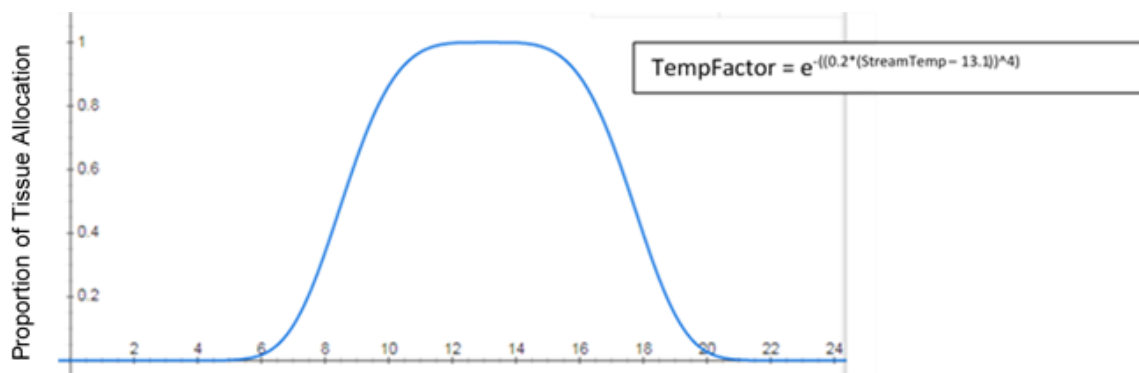
Appendix 6. Average percent-of-energy derived from different prey sources by Redband Trout in Bear and Ramsey Creeks during the summer of 2018.

| 2018 Redband Trout Energy Sources		
	% Total Energy Demand	
Prey Source	Bear Cr.	Ramsey Cr.
Actinopterygii	0.2	0.0
Arachnida	0.8	0.1
Coleoptera	4.8	3.7
Collembola	<0.1	<0.1
Diptera Adult	3.0	3.0
Diptera Larvae	4.6	6.8
Ephemeroptera Adult	5.3	2.0
Ephemeroptera Larvae	32.7	43.8
Hemiptera Adult	0.6	0.1
Hymenoptera	15.1	15.7
Lepidoptera	2.1	1.2
Nematoda	2.5	7.6
Oligochaeta	1.7	0.6
Plecoptera Adult	2.4	0.6
Plecoptera Larvae	7.1	5.7
Trichoptera Adult	0.4	0.2
Trichoptera Larvae	14.0	8.8
Other Insecta Adult	2.7	0.2

Appendix 7. Pearson's Chi-squared test results comparing macroinvertebrate drift between Bear and Ramsey Creeks, Redband Trout diets to drift in each stream, and diets between the streams. χ^2 is the chi-squared test statistic and df is degrees of freedom.

Results of Pearson's Chi-squared tests			
Bear Cr. Drift vs. Ramsey Cr. Drift			
	χ^2	df	p-value
June	5.9	3	0.11
July	6.4	3	0.09
August	22.5	3	5.2×10^{-5}
September	3.2	3	0.37
Full Summer	5.0	3	0.17
Bear Cr. Redband Diets vs. Bear Cr. Drift			
	χ^2	df	p-value
Full Summer	79.1	19	2.7×10^{-9}
Ramsey Cr. Drift vs. Ramsey Cr. Redband Diets			
	χ^2	df	p-value
Full Summer	82.9	16	4.9×10^{-11}
Bear Cr. Redband Diets vs. Ramsey Cr. Diets			
	χ^2	df	p-value
June	53.4	12	3.5×10^{-7}
July	16.9	15	0.32
August	18.2	15	0.25
September	26.5	13	0.01
Full Summer	12.2	18	0.84

Appendix 8. Redband Trout length (at first capture) compared to its summer long growth. Bear Creek (Didymo) is in red and Ramsey Creek (No Didymo) is in blue.
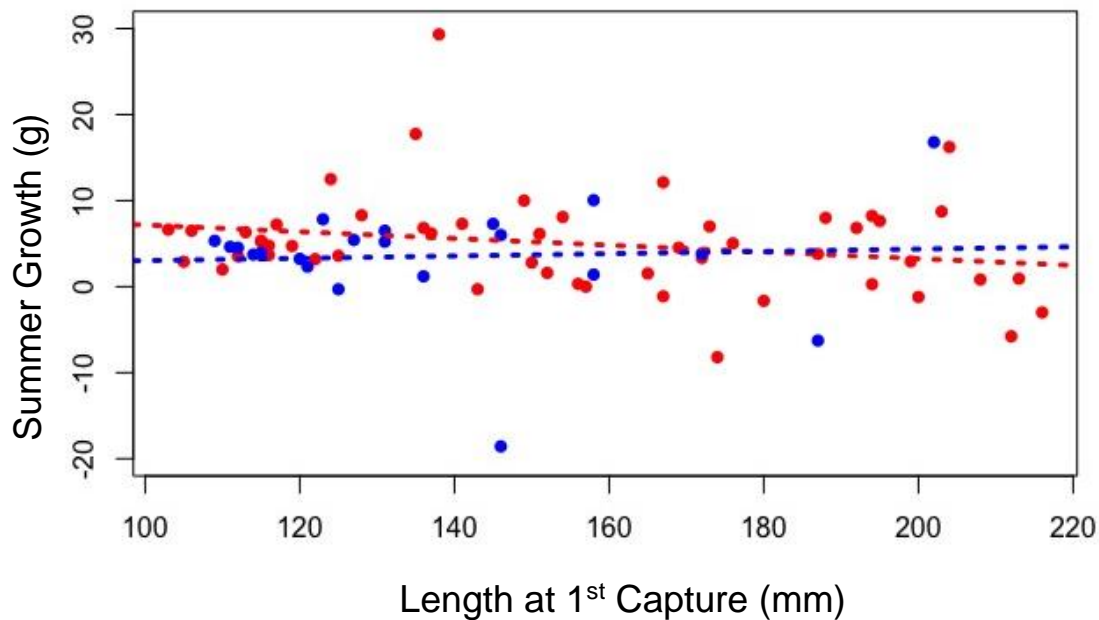
Appendix 9. Relationship of handling pressure and growth of trout during summer 2018 in Bear Creek.
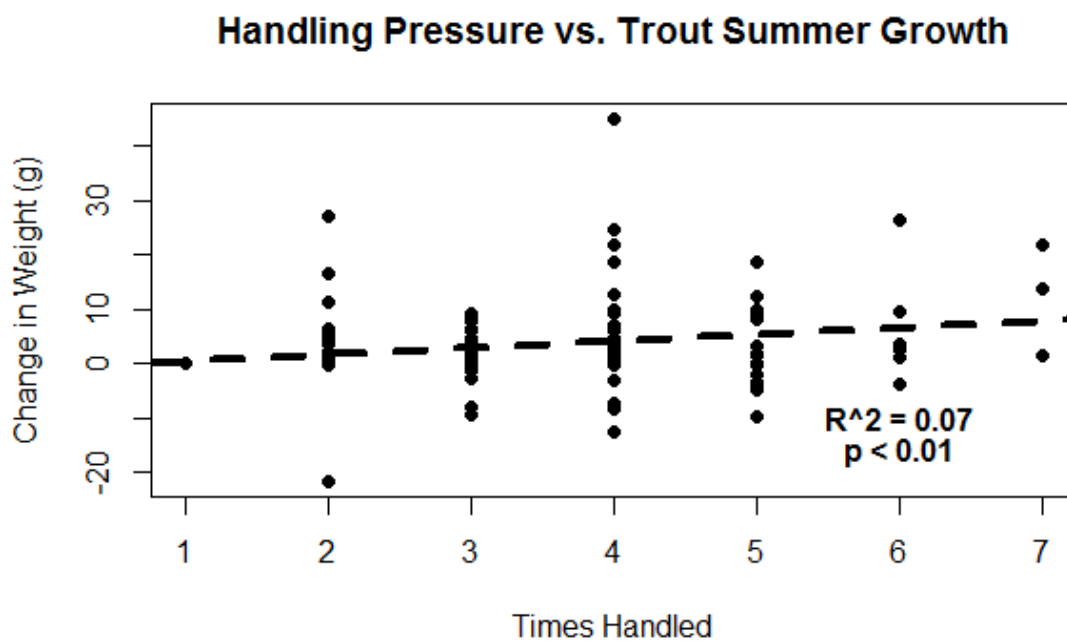
Appendix 10. Statistics of spread for trout, charr, and sculpin condition (K) and gut fullness across the 24 streams included in analyses of 2019 data.

Dispersion Statistics for Condition & Gut Fullness			
		Mean	Coefficient of Variation
Trout	K	0.943	0.0612
	Fullness	0.0878	0.471
Charr	K	0.901	0.0764
	Fullness	0.0756	0.447
Sculpin	K	1.08	0.112
	Fullness	0.0494	0.677

Appendix 11. Univariate linear regression results for the five continuous and two categorical habitat variables on trout, charr, and sculpin diet metrics. Categorical variables were assessed with an anova and post-hoc Tukey test. COV is canopy cover, WW is wetted width, LWD is large woody debris, TEMP is average August stream temperature, VEG is riparian vegetation type, and CHAN is Rosgen channel type.

Habitat Predictors of Fish Diet							
	R^2 or pseduo-$R^2_{\text{Nagelkerke's}}$					Variable Difference?	
	DIDYMO	COV	WW	LWD	TEMP	VEG	CHAN
Oncorhynchus spp.							
% Midges	0.15	0.26***	0.08	0.53	0.00	No	No
% EPT	0.00	0.00	0.03	0.51	0.05	No	No
% Aquatics	0.45***	0.46***	0.00	0.53**	0.44***	Yes$_{\text{Pine-Cedar}}$***	No
Fullness	-0.01	0.00	0.01	0.27	0.02	No	No
Salvelinus spp.							
% Midges	-0.02	0.04	0.01	0.38*	0.0	No	No
% EPT	0.00	-0.01	0.28**	0.33	0.03	No	No
% Aquatics	0.00	0.05	0.32*	0.36	0.02	No	No
Fullness	0.02	0.02	0.10	0.15	0.00	No	No
Uranidea spp.							
% Midges	0.22	0.00	0.03	0.00	0.02	No	No
% EPT	0.13	0.02	0.00	0.00	0.00	No	No
% Aquatics	-0.01	0.12	0.44	0.00	0.06	No	Yes*
Fullness	-0.04	0.00	0.03	0.00	-0.02	No	No

* indicates $p \leq 0.2$, ** indicates $p \leq 0.1$, *** indicates $p \leq 0.05$

Appendix 12. Variables importance plots for each diet metric for trout, charr, and sculpin in 2019. %IncMSE is the percent increase in mean square error, a measure how much each variable increases accuracy of random forests. A partial dependence plot is inset in the %Midges plot for trout (top-left).

Random Forest Importance Plots for Continuous Variables