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The Macroinvertebrate and Fish Communities of In-Stream Beaver Ponds in Northeastern Utah

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THE MACROINVERTEBRATE AND FISH COMMUNITIES OF IN-STREAM BEAVER PONDS IN NORTHEASTERN UTAH

by

Susan Washko

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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ABSTRACT

The Macroinvertebrate and Fish Communities of In-Stream Beaver Ponds in Northeaster Utah

by

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Department: Watershed Sciences

North American beaver populations have been increasing since 1900, and they are physically changing streams as they recolonize their former range. Beavers construct dams that slow water velocity, resulting in wide, deep lentic habitats that hold deposited fine sediment and organic matter. As habitats change, the communities within streams may respond through shifts in species and functional group assemblage. The objective of this study was to assess differences in macroinvertebrate and trout communities between beaver ponds and lotic stream reaches in tributaries to the Logan River in northeastern Utah. Macroinvertebrates were sampled in beaver ponds and in lotic stream segments, and were found to differ both structurally and functionally. First, taxa richness was lower within beaver ponds, as well as macroinvertebrate density and biomass. In terms of functional feeding groups, beaver ponds contained more detritivores and predators, whereas lotic segments contained more scrapers and filter feeders. Mobility strategies of macroinvertebrate also differed with burrowers and sprawlers dominating beaver ponds, and clingers and swimmers dominating lotic habitats.

Trout were surveyed for size, growth, and diet contents in both lotic reaches and beaver ponds via two electrofishing surveys (one in July and one in September). One-third of recaptured trout were caught in beaver ponds during both surveys, and of fish observed within beaver ponds using a mobile PIT tag antenna, half of the trout were scanned on multiple surveys. These results demonstrate that some trout exhibited habitat fidelity for beaver ponds. Bonneville cutthroat trout caught in lotic reaches were generally larger than those caught in beaver ponds, while brown trout demonstrated the opposite trend. Stomach contents and isotopic signatures of trout caught in lotic and beaver habitats did not differ. Further, the growth of fish recaptured from either habitat and of caged fish within each habitat did not differ. Beavers appear to restructure the macroinvertebrate community when building lentic habitats. However, trout communities appeared to be similar between lotic and beaver ponds, suggesting a weaker effect of beaver at the habitat scale. As the prevalence of beavers increases, both naturally and through stream restoration projects, understanding the communities resulting from beaver engineering will help inform management decisions.

(110 pages)

PUBLIC ABSTRACT

The Macroinvertebrate and Fish Communities of In-Stream Beaver Ponds in Northeaster Utah

Susan Washko

Beavers were virtually extirpated from North America during the fur trade, but populations have since recovered. Dams built by recolonizing beaver alter stream habitat by forming deep, slow ponds within the streams. Such changes to the habitat is likely to have consequences for organisms such as macroinvertebrates and fish. The objective of this study was to identify the differences in the macroinvertebrate and trout community in beaver ponds and lotic (e.g. flowing reaches of a stream) reaches in tributaries to the Logan River in northeastern Utah. The macroinvertebrate community of beaver ponds had fewer species, fewer numbers, and lower biomass of macroinvertebrates compared to lotic reaches. Macroinvertebrates that consume leaf litter and predators that prey on other macroinvertebrates characterized beaver pond macroinvertebrate communities. In contrast, lotic reaches contained macroinvertebrates that consume algae and feed on particles floating through the water column. Macroinvertebrates in lotic reaches were morphologically adapted to cling to rocks in the streamflow, while those in beaver ponds were adapted to living within the fine sediment.

Bonneville cutthroat trout collected from lotic reaches were larger than those collected from beaver ponds, while the opposite was true for brown trout collected from lotic reaches. I also found that short-term and long-term diets of both brown trout and Bonneville cutthroat trout were similar between trout caught in beaver pond and lotic reaches. Finally, I found that growth rates of trout were also similar between the two habitats. In conclusion, the structure and function of macroinvertebrates, which are dependent on small-scale habitat features, were more affected by inclusion of beaver ponds to the stream network. Conversely, trout collected from beaver ponds and lotic regions were similar in growth and diet. Considering that beavers are used as a common restoration tool, further studies on the effects of beaver on stream communities is essential.

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Susan Washko

CONTENTS

CHAPTER

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

History of North American Beavers

North American beavers (*Castor canadensis*) were widespread across the United States before European settlement. Their numbers are estimated to have ranged from 400-600 million individuals, and were found anywhere with flowing water and woody vegetation. Around the year 1700, heavy trapping of beavers began as a result of the escalating fur trade. As beavers became scarce in some areas, trappers simply moved westward to find more. By the year 1900, beavers were virtually gone from US landscapes. After their steep decline, beaver harvesting regulations and reintroduction programs were put into place by many states, and the species naturally rebounded, allowing beavers to reach a population of 6-12 million today. Furthermore, despite continued habitat loss due to wetland conversion and other human land uses, beaver have recolonized much of their former range (Baker & Hill, 2003). The IUCN Red List currently classifies beavers as a species of least concern due to their widespread populations and abundant habitat (Cassola, 2016).

In North America, landowners do not always support the recovery of beaver populations (Müller-Schwarze, 2011). The current public opinion of beavers in North America is largely negative, because they can flood roads and property (Reiter, Brunson & Schmidt, 1999). A study of Wyoming landowners and land managers showed only 39% of landowners with beavers did not attempt to remove them (McKinstry & Anderson, 1998). However, more recently, beaver reintroductions have been proposed as an economical solution to stream restoration, because beaver activity returns species and habitat diversity to the landscape and creates habitat for the life stages of various important fishes such as salmon and trout (Wright, Jones & Flecker, 2002; Bouwes *et al.*, 2016; Law, Mclean & Willby, 2016). Interestingly, in the same Wyoming study discussed above, 11% of landowners with beavers considered the animals to be a tool for riparian management that allowed for higher water tables and more watering opportunities for livestock. Further, 11% of landowners without beaver wanted them on their properties. Both land owners (45%) and land managers (96%) said they would like more information on managing beaver. These results suggest studies on the benefits of North American beavers to stream ecosystems are greatly needed, as well as the dissemination of those results to the public.

Beavers Change the Streamscape

Beavers are considered ecosystem engineers because they introduce considerable heterogeneity to the environment (Pringle *et al.*, 1988; Rolauffs, Hering & Lohse, 2001; Bush & Wissinger, 2016; Law *et al.*, 2016). Their main engineering activities are harvesting wood from the surrounding landscape and building dams in the stream. These blockages slow and trap water, increasing water depth and creating a pool. A wide area of inundation results, known as a beaver pond. Dams control downstream discharge by allowing water to overflow the top of the dam in high flows and trapping it behind the dam during lower flows, like a weir (Gurnell, 1998a). These structures cause a stair-step pattern along the river profile (Gurnell, 1998a), and beaver ponds and wetlands along the sides of montane valleys can create terraces on the slope (Bush & Wissinger, 2016). Beaver habitats are often discussed in the context of patch bodies, meaning they have many substrate or habitat layers that arise from beaver engineering (Johnston & Naiman, 1987). These layers include anaerobic soil, aerobic soil, the pond, and the browsed area surrounding the pond. Patch bodies are important because they create variable habitat types, and affect the transfer of materials and energy across them (Johnston & Naiman, 1987).

Beaver dams obstruct flow, alter water velocity and shear stress, and change the pattern of scour and deposition (Gurnell, 1998a). When water slows behind the beaver dam, the loss of energy causes it to drop its sediment load. The sediment that falls out of the water column is primarily composed of fine particles, which are deposited and accumulate over time behind the dam (Naiman, Johnston & Kelley, 1988). In addition to fine sediment deposition, gravel segments form at the entrance to the pond, adding another habitat type (Bouwes *et al.*, 2016). The quantity of sediment stored in the pond is not related to the dam size, but rather to the surface area of the pond that forms behind it (Butler & Malanson, 1995, 2005; Meentemeyer & Butler, 1999). Dam age is another factor that influences sediment storage. Although older dams contain higher sediment volumes (Butler & Malanson, 1995; Meentemeyer & Butler, 1999), the rate of sediment accumulation is higher in younger dams, and drops off approaching five years of age (Butler & Malanson, 1995; Pollock, Beechie & Jordan, 2007). Sediment storage is long-term, releasing only during flood events that break or breach dams (Butler & Malanson, 2005).

Decreased water velocity in beaver ponds also increases organic matter accumulation behind beaver dams, with older dams storing substantially more organic matter (Butler & Malanson, 1995). Most of this organic matter is allochthonous (i.e. leaves and woody debris) in origin (Hodkinson, 1975b; Benke & Wallace, 2003; Eggert

& Wallace, 2007). However, in some cases, higher nutrient retention in beaver ponds can lead to enhanced autochthonous (i.e. algae) production (Coleman & Dahm, 1990). The availability of this organic matter to the food web is questionable. Some studies have found organic matter enters beaver ponds more quickly than it is broken down, and organic matter decay rates are slower in beaver ponds compared to streams (Hodkinson, 1975a; Naiman, Melillo & Hobbie, 1986). The studies concluded that allochthonous materials (i.e. food resources and nutrient sources) quickly become unavailable because ~56% of the inputs become buried in the sediment before they can be processed by consumers. However, immobilization of nutrients in beaver ponds may be influenced by pond age. For example, Naiman et al. (1986) found no difference in nutrient immobilization between lotic reaches and mature beaver ponds, nor did they find sediment concentrations entering and leaving the pond to be different. These findings may indicate that the burying of organic matter and reduced nutrient supply rate may be temporary. Although the effects of beaver dams on the type (allochthonous & autochthonous) and quantity of organic matter is likely to affect stream food webs, few studies on this topic have been conducted.

The deeper, more stagnant water in beaver ponds has a different temperature regime than shallow, fast flowing streams because water volume, streambed slope, hyporheic exchange, and streambed friction can all influence temperature (Caissie, 2006). However, there is no general consensus on the directional effect of beaver dams on temperature, with findings ranging from increased temperature to no change to decreased temperature, and many studies simply base their conclusions on speculation (Majerova *et al.*, 2015). This diversity in findings is likely related to the landscape position and physical properties of the pond itself. The removal of surrounding forest and riparian vegetation by beaver combined with ponds having larger surface area to volume ratios can expose water in ponds to increased solar radiation (Majerova *et al.*, 2015). As a result, shallow ponds are likely to have higher temperatures, while deeper ponds can have stratified temperatures and increased thermal heterogeneity (Bouwes *et al.*, 2016). Several studies suggest that beaver ponds offer an especially important temperature refuge in western mountain streams because they encompass warmer water spots in extremely cold streams and cool refugia in hot regions, which is beneficial for the growth and survival of cold-water fishes (Collen & Gibson, 2000; Niles, Hartman & Keyser, 2013).

Beaver dams can alter groundwater dynamics by increasing water table height (Bouwes *et al.*, 2016). For example, as the water table rises, the pressure (hydraulic head) increases and pushes the groundwater, resulting in groundwater flowing around the dam and downstream. This effect varies with topography and dam height. The direction of groundwater flow can also depend on the beaver dam's location within the valley's hydraulic gradient; for example, if the dam is parallel to groundwater flow, it likely does not disrupt flow direction, or has minimal influence (Westbrook, Cooper & Baker, 2006). In dryland streams, dams can increase water storage, making an intermittent stream perennial (Gibson & Olden, 2014). Heightened groundwater levels in turn boost floodplain productivity, especially in combination with more organic matter inputs (Rolauffs *et al.*, 2001). Westbrook et al. (2006) found inundation resulting from beaver dams increased interaction time between the riparian soil and the river, enhancing bank infiltration that led to aquifer recharge. Dam removal is associated with decreases in the water table, as well as decreased vegetation diversity and productivity, reduced water quality downstream from nutrient and sediment release, and entrenchment (Butler & Malanson, 2005).

As beavers have resettled North America, they have changed the landscape and aquatic communities by altering stream channels (Naiman *et al.*, 1988), biogeochemistry (Naiman *et al.*, 1994), riparian vegetation and forests (Hood & Bayley, 2009), macroinvertebrate assemblages (Law *et al.*, 2016), and fish populations (Collen & Gibson, 2000). Beaver-altered landscapes are a mosaic of habitats and food sources that support biodiversity (Naiman *et al.*, 1988; Pringle *et al.*, 1988; Hammerson, 1994; Bush & Wissinger, 2016; Law *et al.*, 2016). This ever-growing body of research demonstrates that as beavers recolonize, there is much to learn about how their dams and associated habitat alterations change stream communities.

Macroinvertebrates in Beaver Habitats

Macroinvertebrate taxa employ a variety of life strategies. These strategies are classified into functional feeding groups (FFGs) and mobility groups (MGs). FFGs are determined by the morpho-behavioral mechanisms behind feeding (Wallace & Webster, 1996). The categories are shredders, grazers/scrapers, gatherers/collectors, filter feeders, and predators. Macroinvertebrate FFGs indicate what an organism does and how it obtains its food, consequently implying both habitat characteristics and functions provided by the taxon (Wallace & Webster, 1996). MGs, also known as habit groups, are categories based on locomotion-attachment adaptations, and reflect the way the organism moves in its habitat and its colonization timing (Mackay, 1992; Merritt, Cummins &

Berg, 2008). Five MG categories exist: burrowers, climbers, clingers, swimmers, and sprawlers (Rabení, Doisy & Zweig, 2005).

Understanding changes in macroinvertebrate communities is important because they play a large role in stream ecosystem functioning (Wallace & Webster, 1996; Heino, 2005), and they are an important food resource for fish (Romaniszyn, Hutchens & Bruce, 2007). Shredders are a driver of organic matter decomposition within streams, which can stimulate productivity by freeing nutrients. Further, the act of shredding creates fine particulate organic matter (FPOM) for other organisms to collect and consume, and smaller fragments of organic matter allows further microbial colonization and breakdown (Wallace & Webster, 1996; Hieber & Gessner, 2002). Grazers can mobilize nutrients by scraping, and gatherers can re-suspend organic matter and stimulate bioturbation, which can affect oxygen availability at the sediment surface (Wallace & Webster, 1996; Mermillod-Blondin, 2011).

Beaver-induced changes to stream morphology could alter macroinvertebrate communities, which in turn could alter food webs and ecosystem function. However, studies investigating the effects of North American beaver activities in streams on macroinvertebrates are rare. The magnitude and direction of beaver effects likely depends on the macroinvertebrate population/community variable being investigated as well as the magnitude of beaver disturbance. Several studies have indicated a decrease in macroinvertebrate species richness within beaver ponds compared to streams, although overall stream biodiversity increases because previously absent lentic macroinvertebrate taxa colonize the pond (Bush & Wissinger 2016; Law et al. 2016). It seems to be study site-dependent whether density is higher within beaver ponds or flowing stream habitat

(Rupp, 1955; Huey & Wolfrum, 1956; Gard, 1961; McDowell & Naiman, 1986; Rolauffs *et al.*, 2001; Anderson & Rosemond, 2010; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Biomass (g/m^2) tends to be higher in beaver ponds than streams, although there are fewer studies on this topic (Gard, 1961; McDowell & Naiman, 1986; Rolauffs *et al.*, 2001; Anderson & Rosemond, 2007).

Only seven studies have looked at the effects of beaver-altered streams on macroinvertebrate FFGs. Three of those were conducted on the Eurasian beaver (*Castor fiber*), one is a meta-analysis of largely European data, one was conducted in Argentina where the North American beaver (*Castor canadensis*) is invasive, one in Quebec, Canada, and one in Maryland, USA. The consensus among these studies is beaver ponds have different FFG compositions compared to the non-impounded stream areas (McDowell & Naiman, 1986; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Generally, gatherer and predator densities increase in beaver ponds, while shredders, filterers, and collectors decrease (Table 1). No studies have been conducted on MGs in response to damming by beaver. The paucity of studies on macroinvertebrate groups for western North America suggests this is an important research avenue for the future.

One potential way beaver may be influencing macroinvertebrate communities is through habitat modifications. Habitat plays an important role in determining the proportions of invertebrates from each FFG and MG present (Heino, 2005). Flow, food resources, respiratory and thermal requirements, and biotic interactions all partly determine the structure and function of the macroinvertebrate community (Wallace & Webster, 1996). Habitat also limits food resource availability for macroinvertebrates.

Food is limited by habitat, because habitat conditions determine the quantity, quality, and assemblage of vegetation in the forms of both allochthonous and autochthonous resources (Richardson, 1991; Mackay, 1992). Important habitat characteristics that influence macroinvertebrates change when beavers construct dams. Beaver dams typically increase habitat heterogeneity within the stream by creating a mosaic of habitats with varying water depths, velocities, and substrate. Even the tight bundles of branches in the dam itself create a unique habitat that can support filter-feeding and scraper taxa (Rolauffs *et al.*, 2001).

Stream substrate is considered the most important factor determining macroinvertebrate distribution and abundance (Rabení *et al.*, 2005). Macroinvertebrate substrate requirements can include large rock habitats providing surfaces for grazing and for catching debris, and rocks that provide interstitial spaces. Large pebbles or cobbles can be useful due to their stability, but gravel provides interstitial spaces with better shelter and that trap FPOM, leading to higher macroinvertebrate densities (Mackay, 1992). Fine sediment deposition can lead to an overall decrease in habitat quality displacing macroinvertebrates by coating habitats, filling spaces, and abrading algal growth (Mackay, 1992). In fact, fine sediment is considered a pollutant in some streams and rivers, because it decreases macroinvertebrate abundance and richness and changes the composition of FFGs and MGs. For example, Rabení et al. (2005) determined that in a stream where fine sediment deposition was high, all FFGs decreased in density. For MGs, densities of clingers and sprawlers decreased while densities of burrowers and climbers increased. Further, taxa richness decreased for all FFGs except shredders, and of the MGs, clingers, sprawlers, and swimmers decreased in richness. As discussed above, beaver ponds are characterized by much finer sediment than the adjacent stream channel (Naiman *et al.*, 1988). Therefore, ponds are likely to contain a different macroinvertebrate community because of the effect dams have on substrate. Theoretical work by Bush and Wissinger (2016) describe the assemblage change within beaver-altered habitats as such: the erosional species that live in high-oxygen, turbulently flowing environments with rocky substrate (e.g. mayflies, stoneflies, net-spinning caddisflies, and lotic reach beetles) are replaced with species that live in soft, depositional environments with low oxygen and laminar flow (e.g. dipterans, epibenthic crustaceans, swimming beetles, and sometimes dragonfly or damselfly larvae).

Many macroinvertebrates are dependent on allochthonous resources for their growth (Wallace & Webster, 1996). Detritus trapped in debris dams is often heavily colonized by macroinvertebrates, not only because they are food ‘hotspots,’ but also because the accumulations provide a buffer from disturbances (Entrekin *et al.*, 2009). For example, wood is a reliable habitat resource because it is long lasting and provides a stable surface in flowing water (Entrekin *et al.*, 2009; Schoen, Merten & Wellnitz, 2012). Wood also provides a surface for biofilm growth, which scrapers and grazers can consume. Beaver ponds increase opportunities for algae to take up dissolved nutrients due to the reduction in velocity (Naiman *et al.*, 1988), which could make beaver ponds an important grazing area for macroinvertebrates. This hypothesis is supported by data from Hering et al. (2001), whom found there were more grazers in beaver dams than free-flowing sections, and noted macroinvertebrate biomass was approximately five times higher in the beaver dams. Thus, it is hypothesized that woody material and trapped

TABLE 1.1 Trends in the shift in FFG composition within beaver ponds relative to lotic reaches. Pluses (+) indicate increased importance of the group in beaver ponds, while minuses (–) indicate decreased in importance within beaver ponds, ND means no difference, and NA indicates no data available.

Paper	Gatherer	Shredder	Scraper	Filterer	Predator
Anderson & Rosemond 2007	+	-	-	-	+
Arndt & Domdei 2011	ND	-	-	-	+
Law et al. 2016	+	+	-	-	ND
McDowell & Naiman 1986	+	-	-	ND	+
Margolis et al. 2001	NA	-	NA	-	NA
Pliūraitė & Kesminas 2012	+	-	-	-	+
Hering et al. 2001 (meta-analysis)	+	-	-	+	+

allochthonous inputs are beneficial to macroinvertebrates, and thus beaver ponds may provide important habitat and resources for these organisms.

Trout in Beaver-Altered Habitats

Beavers are important agents in creating dynamic fish habitat potentially benefiting fish diversity. Debris from the damming process can provide attractive cover for trout (Collen & Gibson, 2000). Inundation resulting from beaver damming activity creates deep pools that provide a refuge from heat in the summer and freezing in the winter (Johnson, Rahel & Hubert, 1992; Niles *et al.*, 2013), and act as a stable refuge during variable discharge periods (Dare, Hubert & Gerow, 2002). In fact, beaver ponds can act as reservoirs for fish repopulation after low-water conditions, making beavers important for the persistence of fish communities in streams (Hanson & Campbell, 1963). Beaver dams raise the water table and increase stream permanence, which improves cold-water fish survival during drought conditions (White & Rahel, 2008; Gibson & Olden, 2014). Lastly, habitat heterogeneity can be greater around beaver dams, leading to a higher diversity of fish (Smith & Mather, 2013).

The different habitat types created by beaver dams are beneficial for multiple life stages of salmonids. Inundation connects the stream to the floodplain, which allows fish to access habitats suitable for juvenile life stages (Wheaton *et al.*, 2013). The stream acts as a nursery for young fish while the pool and other deeper areas are more suitable for older fish (Cossette & Rodríguez, 2004; Lokteff, Roper & Wheaton, 2013; Malison *et al.*, 2014). Although small trout can inhabit beaver ponds, typically, several large fish dominate (Johnson *et al.*, 1992). The importance of a gravel bar entering the pond for spawning and juvenile habitat has also been demonstrated, although this may have been noteworthy because of the degraded stream condition. Juvenile steelhead survival increased with beaver dam implementation in a degraded stream, and the juvenile steelhead in the experiment preferred pond areas (Bouwes *et al.*, 2016). In fact, beaver impoundments buffer against drought, resulting in higher production of trout fry in streams with beavers during dry years (White & Rahel, 2008).

The popular belief that beaver dams inhibit trout movement and are detrimental to reproduction and success can be true in low flows, but according to a synthesis by Lokteff et al. (2013), while 43% of studies that say dams block trout movement, 78% of those studies are based on speculation and do not have data providing evidence to the claim. Further, the authors' original data demonstrates trout can indeed pass beaver dams. Most evidence points to beaver complexes as beneficial for trout (Collen & Gibson, 2000; Kemp *et al.*, 2012; Lokteff *et al.*, 2013; Gibson & Olden, 2014; Malison *et al.*, 2014).

Due to the beneficial impacts beavers can have on trout, they have been implemented into fisheries management strategies. Many western states, such as

California, Wyoming, and Colorado are now managing beaver to improve fisheries after noticing trout declines following dam removal or abandonment (Collen & Gibson, 2000). For example, Coho salmon rearing capacity increased with slow-water habitats in Washington, and recruitment success was specifically tied to the quantity of beaver pond habitat. Increasing beaver populations was recommended as a simple yet effective practice to achieve watershed-scale impacts (Pollock *et al.*, 2004). Recommendations like this further incentivize understanding the dynamics between beaver habitats and the pond communities they create. Restoration efforts will likely improve with a more complete understanding of stream communities and how they are affected by beaver activity.

Potential Changes to Trout Foraging

The idea of trout using beaver ponds as a foraging habitat has received little study. Given the growing evidence that beaver ponds alter macroinvertebrate communities (McDowell & Naiman, 1986; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016), and given macroinvertebrates are a major food source for trout (Romaniszyn *et al.*, 2007), beaver-mediated changes in the macroinvertebrate community could have implications for trout feeding and growth. Trout species which do not have specialized feeding, but instead consume macroinvertebrates in proportion to their availability, may be especially affected by beaver-driven changes in the macroinvertebrate community.

There is some evidence, albeit scant, of trout actively foraging within beaver ponds. Rupp (1955) found brook trout in beaver ponds of Maine tended to eat an unexpected quantity of small forage fishes first, followed by highly abundant Odonates. The third highest contributor to diet was terrestrial insects. Differences in the amount of terrestrial input and its contribution to diet are other understudied aspects of fish foraging in beaver ponds. Gard (1961) found trout diets from California’s northern Sierra Nevada range differed based on where fish were caught in the stream. Trout caught in beaver ponds tended have a more diverse diet because their prey encompassed both lentic and lotic insect taxa. Conversely, stream channel-dwelling trout rarely contained macroinvertebrates from the beaver ponds, and their diets were less diverse even though the lotic reach habitats housed a greater diversity of benthic taxa. In another case, Hilderbrand and Kershner (2004) studied Bonneville cutthroat trout and brook trout diets and compared the diets to drift captured in high-gradient stream reaches, low-gradient stream reaches, and beaver ponds of northeastern Utah. They found the average prey caught per fish was almost double in beaver ponds compared to in either stream gradient. Further, the Bonneville cutthroat trout ‘selected’ different prey depending on the habitat. The authors noted a higher consumption of terrestrial insects in stream segments (58.2% of diet in high-gradient, 49.4% of diet in low-gradient) compared to in beaver ponds (10.6%). They also noted a higher consumption of Diptera insects in beaver ponds (87% of diet) compared to in streams (27.2% - 46.6%). While these studies give insight to the foraging dynamics of trout in beaver-altered streams, it is still largely unknown how trout use beaver ponds for foraging and how foraging in beaver ponds versus streams affects trout growth. By integrating what we know about beaver habitats with theories for salmonid foraging, we can hypothesize how trout might utilize beaver ponds as a foraging habitat.

The feeding behavior of stream-dwelling fish is highly dependent on water velocity (Grossman *et al.*, 2002). Trout will monitor habitat conditions such as flow and food availability in the surrounding area and pick a feeding location (Gowan & Fausch, 2002). Fish feeding via a sit-and-wait strategy, such as brown trout (Bachman, 1984), will eat opportunistically in proportion to prey availability (Keeley & Grant, 1997). This being said, these fish are still selective because they can only eat prey within their gape limit (prey that fit in their mouths). As fish grow and reach larger body sizes, they will potentially eat primarily larger food items, choosing an optimal prey size to maximize energetic gain. Evidence suggests trout can evaluate the energy gain from different prey types and then select for the most valuable prey items, likely identifying by prey size or density (Ringler, 1979). Prey abundance is also important to trout feeding because handling time decreases as fish become more experienced with specific prey, thus increasing feeding efficiency.

The habitat heterogeneity and lentic patches created by beaver activity change the foraging habitats available to cold-water fishes (Naiman *et al.*, 1988; Pringle *et al.*, 1988; Hammerson, 1994; Law *et al.*, 2016) and may in turn change their foraging habits and strategies. As explained above, the lentic habitats created by beaver dams have reduced flow velocity and increased water depth (Gurnell, 1998a). The reduction in velocity provides an area where fish can rest instead of fighting the streamflow to stay in one place, thus reducing energy expenditure (Dare *et al.*, 2002). Deeper water can stratify by temperature, creating a thermal refuge in which salmonids may conserve energy otherwise spent on thermoregulation (Johnson *et al.*, 1992; Niles *et al.*, 2013). Temperature has been shown to be important in the growth of young salmonids (Armstrong *et al.*, 2013), and is widely known to be an important limiting factor in salmonid colonization and survival (Wenger *et al.*, 2011). These habitat characteristics are beneficial for salmonids because they will save energy by using beaver-created temperature and flow refuges.

Salmonid foraging efficiency may also improve in older (well-established) beaver pond habitats due to increased light and consequently enhanced prey visibility. The amount of light in beaver ponds is likely higher because beaver removal of vegetation allows more light to reach the channel (Hughes, 2014). Light penetration may depend on the quantity of dissolved organic carbon coloring the water (Kwick & Carter, 1975), which has been shown to increase when the pond is new but decreases with pond age (Vehkaoja *et al.*, 2015). Low light conditions are also possible considering beaver-impounded habitats are more turbid because they store sediment (Popelars, 2008). But, turbidity decreases as ponds age (Stevens et al. 2006), and beaver ponds usually stop accumulating sediment at around five years of establishment (Butler & Malanson, 1995; Pollock *et al.*, 2007). At this point the storage is largely permanent (Butler & Malanson, 2005). Thus, in older, more stable beaver ponds, increased light would likely enhance prey visibility for salmonids, improving their foraging efficiency.

Salmonid foraging efficiency may also increase in beaver ponds because they are likely to contain a higher density and biomass of macroinvertebrates than the adjacent stream (Gard, 1961; McDowell & Naiman, 1986; Anderson & Rosemond, 2007). A recent study by Rosenfeld and Raeburn (2009) provides some evidence for this idea, as they found increased macroinvertebrate drift and fish production in ponds with inlets from constructed side channels. The dominant macroinvertebrate orders present in beaver ponds may also be of high energetic quality, an important characteristic in OFT. While EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) have high caloric values (Table

1) and are more abundant in non-impounded stream reaches (McDowell & Naiman, 1986; Pliūraitė & Kesminas, 2012), there are taxa in beaver ponds that can rival their energy value. Chironomids are considered a dominant taxon in beaver ponds relative to non-impounded stream segments (Huey & Wolfrum, 1956; Gard, 1961; Rolauffs *et al.*, 2001; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Odonates also reach high densities (Rupp, 1955; McDowell & Naiman, 1986; Arndt & Domdei, 2011), and sometimes Ephemeropterans (Arndt & Domdei, 2011). These taxa are of similar caloric value (Table 2), indicating that foraging in beaver ponds can provide ample energy to salmonids, especially if capturing them is easier in lentic habitats. Moreover, considering drift entering at the pond contains lotic taxa, the fish may be able to consume the best of both habitats.

In summary, beaver ponds may be beneficial foraging patches for salmonid fish. They decrease salmonid search time and the energy involved in searching for food in streams. They could also improve trout foraging due to superior light conditions and reduced stream velocity. Together, these structural changes suggest salmonids will spend less time and energy detecting, capturing, and consuming prey. Also, because beaver

TABLE 1.2 Average caloric values for common macroinvertebrate taxa (Cummins & Wuycheck, 1971; Penczak *et al.*, 1999; Cauffope & Heymans, 2004).

Taxa	Avg. Caloric Value (J/g)	Reference
Amphipoda	4429	Cummins & Wuycheck 1971
Annelida	1994	Cauffopé & Heymans 2005
Chironomidae	3304	Cummins & Wuycheck 1971
Coleoptera	2448	Cummins & Wuycheck 1971
Diptera	2377	Cummins & Wuycheck 1971
Ephemeroptera	3715	Cummins & Wuycheck 1971
Odonata	3233	Penczak et al. 1999
Oligochaeta	3740	Cummins & Wuycheck 1971
Plecoptera	3177	Penczak et al. 1999
Trichoptera	3342	Cummins & Wuycheck 1971

ponds can act as thermal refuges, salmonids could reduce metabolic stress. In particular, older, well-established beaver ponds are likely to create favorable foraging conditions. Additionally, food is likely more abundant in beaver ponds and of similar energetic quality to food in non-impounded stream reaches. Increased food availability also could improve the ease of foraging, because salmonids may not need to be as selective about their diet to maximize their growth. When food is not limiting, selectivity is less relevant. Thus, salmonid foraging may be directed to the impounded habitats in beaver-altered streams due to resource abundance and advantageous environmental conditions.

Why Northern Utah?

Many watersheds in Utah have a capacity to hold more beaver dams (Wheaton & Macfarlane, 2014). Beaver reintroduction projects are becoming increasingly popular, providing an opportunity to study how beavers change the landscape from the time they enter. Understanding the role beaver impoundments play in creating habitat heterogeneity and structuring stream food webs is of critical importance because dams could influence stream macroinvertebrate communities as well as trout distribution and behavior. Studying these invertebrate communities will reveal how shifts in assemblage, biomass, and density could translate to different functional roles in stream ecosystems, including the macroinvertebrate community’s role as a critical food resource for salmonid fish. Studying trout diet, growth, and habitat selection in beaver ponds will contribute to the scientific understanding of their basic ecology. Most classic and contemporary steam research has been conducted without beaver influence due to their virtual extirpation. In light of beavers' functional roles as ecological engineers and their high abundance prior to the fur trade, their effects on the landscape were widespread and responsible for structuring many stream communities. Therefore, the scientific community may in reality know little about 'natural' aquatic systems (Naiman *et al.*, 1986).

Climate change is expected to alter precipitation and snowmelt regimes in the intermountain west such that these systems will experience drought more frequently along with shifts in the seasonal patterns of stream hydrology. In addition, western water withdrawals are increasing from rapid urbanization and population growth (Gibson & Olden, 2014). Because beaver engineering activity can result in elevated water tables and intermittent streams becoming more permanent, beavers could be part of a mitigation strategy to combat these anthropogenic stressors. This context makes understanding these systems even more pertinent such that management decisions, by both land managers and landowners, can be made based on factual ecosystem dynamics. Although McKinstry & Anderson's landowner and land manager opinion study is from 1999 (see beginning) and perceptions could have since changed, there is potential for collaboration between humans and beavers. Information needs to be publicly available as part of an initiative to build partnerships between managers, landowners, and scientists. As our understanding of how beavers affect stream ecology improves, beaver management strategies will evolve and become more refined.

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CHAPTER 2

BEAVERS ALTER STREAM MACROINVERTEBRATE COMMUNITIES IN NORTHEASTERN UTAH[1]

SUMMARY

1. Understanding changes in macroinvertebrate communities is important because they play a large role in stream ecosystem functioning, and they are an important food resource for fish. Beaver-induced changes to stream morphology could alter macroinvertebrate communities, which in turn could affect food webs and ecosystem function. However, studies investigating the effects of North American beaver activities on macroinvertebrates are rare.

2. The aim of this study was to quantify differences in the macroinvertebrate community between unaltered segments of streams and within beaver ponds in northeastern Utah, USA. We assessed macroinvertebrate species richness, biomass, density, functional feeding group (FFG) composition, mobility group (MG) composition, and macroinvertebrate habitat characteristics to test the hypothesis that macroinvertebrate communities will differ among habitat types (undammed stream segments and beaver ponds) in beaver-occupied streams.

3. Beaver pond communities significantly differed from lotic reach communities in every aspect examined. Beaver ponds were less diverse with 25% fewer species. Although there was variability among streams, in general beaver ponds contained

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[1] Co-authors: Trisha Atwood and Brett Roper

75% fewer individuals and 90% lower total macroinvertebrate biomass compared to lotic reaches.

4. Regarding FFGs, beaver ponds contained more predators and detritivores, while lotic reaches contained more scrapers and filterers. For MGs, beaver ponds contained proportionally more burrowers and sprawlers, while lotic reaches had more clingers. Swimmers were also more prevalent in lotic reaches, though this is likely due to the abundance of *Baetis* within lotic reaches. A higher proportion of beaver pond taxa were classified as lentic and littoral, while a higher proportion of lotic reach taxa were categorized as lotic and erosional.

5. The creation of ponds by beavers fundamentally altered the macroinvertebrate community in northeastern Utah streams. Such changes to stream macroinvertebrate communities suggests re-colonization of beavers across North America may be altering stream functioning and food webs. Our study highlights the need to further investigate the effects of beaver colonization on stream communities and functions.

INTRODUCTION

Overexploitation of the North American beaver (*Castor canadensis*) from ~1600-1900 brought this species to the brink of extinction. However, declines in the fur trade, stricter trapping regulations, and beaver reintroduction programs have helped this species return to most of its former range (Baker & Hill, 2003). Because beavers are ecosystem engineers with the capacity to alter both physical and chemical characteristics of aquatic ecosystems (Naiman *et al.*, 1986; Smith *et al.*, 1991; Gurnell, 1998a; Correll, Jordan &

Weller, 2000; Wohl, 2013), their expanding populations will undoubtedly influence the aquatic communities residing in the rivers and streams that they colonize.

Research investigating the effects of North American beaver on aquatic ecosystems has largely focused on physiochemical changes to the river/stream system or on fish, with only a few studies investigating their effects on macroinvertebrates. In general, previous research has suggested that beavers are beneficial for stream habitat heterogeneity and fish habitat (Pringle *et al.*, 1988; Rolauffs *et al.*, 2001; Rosell *et al.*, 2005; Bush & Wissinger, 2016; Law *et al.*, 2016), and as a result, agencies are using beavers as a natural solution for stream and riparian restoration (Gibson & Olden, 2014; Pollock *et al.*, 2014; Pilliod *et al.*, 2018). However, studies on Eurasian beaver (*C. fiber*) and on invasive North American beaver in South America have found mixed results for beaver effects on stream macroinvertebrates. Some studies found that beaver ponds increased macroinvertebrate abundance and biomass, while others found they decrease stream macroinvertebrate alpha diversity, diversity of functional feeding groups and altered macroinvertebrate community composition. Surprisingly few studies have been conducted on the effects of North American beaver colonization on stream macroinvertebrate communities in North America, despite this region having undergone extensive beaver recolonization.

The functional integrity of a stream is heavily dependent on its macroinvertebrate community. Macroinvertebrates control detritus processing and nutrient cycling in streams, influence stream primary productivity, and are a major food source for higher trophic level vertebrates like fish (Wallace & Webster, 1996; Heino, 2005). Factors that drive differences in the colonization of different stream macroinvertebrates include many physical and chemical factors such as water velocity, substrate size, nutrient concentrations, and the availability of allochthonous and autochthonous food resources (Heino, 2005). Furthermore, trait characteristics that reflect a species' adaptions to its environment influence its functional role. Thus, the development and presence of beaver dams, which alter physical and chemical characteristics of streams, will likely have consequences for the types and functional characteristics of macroinvertebrates that can colonize streams where beavers are present.

Physical changes to a stream due to the formation of beaver ponds should influence the macroinvertebrate community as it changes the necessary traits for maneuvering through the environment (i.e., mobility group; MGs). As water pools behind a beaver dam, the stream's shape gradually forms a wide pond, characterized by slower, deeper water that might benefit swimming taxa that are excluded from fast-moving lotic reaches (Mackay, 1992). Additionally, the substrate size shifts from gravel or cobble in undammed sections to fine sediments within the beaver ponds (Levine & Meyer, 2014). Sediment grain size is known to be a primary factor that influences macroinvertebrate communities in streams (Mackay, 1992; Rabení *et al.*, 2005; Bo *et al.*, 2007). Size of sediment influences the size of interstitial spaces that macroinvertebrates can occupy. Finer sediments behind beaver ponds may select for macroinvertebrates that can cling to fine particles or burrow in the sediment (Mackay, 1992).

Both physical and chemical changes as a result of beaver ponds can also influence how macroinvertebrates acquire food (i.e., functional feeding groups; FFGs; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Beaver ponds act as important sinks for nutrients (Westbrook *et al.*, 2006; Lazar *et al.*, 2015), which can stimulate *in situ* primary production (Coleman & Dahm, 1990), potentially promoting grazers. However, studies on the effect of Eurasian beaver on macroinvertebrates in European streams found that grazers declined in beaver ponds (Law et al. 2016). This may be because beaver ponds are also large sinks for organic matter, and leaching of dissolved organic carbon can color the water like tea (Kwick & Carter, 1975; Cirmo & Driscoll, 1993; Vehkaoja *et al.*, 2015), inhibiting light penetration and primary production. Conversely, the organic matter entering the pond could be utilized by collector and shredder taxa. However, studies on Eurasian beaver found mixed results for these FFGs, with beaver ponds decreasing shredders in Polish streams and increasing collectors and shredders in Scottish streams. The major consensus from the European literature, as well as one study done on the effects of invasive *C. canadensis* on South American streams, is that predator taxa increase (Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). This increase in predator taxa may be due to enhanced prey availability (Harthun, 1999). Prey drifting into beaver ponds cannot continue to drift further to escape predation because water velocity in the pond is too slow, likely increasing the ability of predatory macroinvertebrates to capture prey (Thorp & Covich, 2001).

The aim of our study was to quantify differences in the macroinvertebrate community between stream lotic reaches and within beaver ponds in northeastern Utah. Understanding the kind of communities resulting from beaver ponds in arid western regions is crucial, because stream communities are important for the biodiversity of these types of ecoregions (Gibson & Olden, 2014), and beaver populations are increasing as a result of natural dispersal and their use in stream restoration projects (Small, Frey &

Gard, 2016). We predict that macroinvertebrate communities will differ between lotic reaches and beaver ponds within beaver-occupied streams in multiple ways. In beaver ponds relative to lotic reaches, we expect **1)** a higher biomass and density of macroinvertebrates (Gard, 1961; McDowell & Naiman, 1986), and **2)** lower species richness through a lack of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa, following the trends seen in previous literature (Gard, 1961; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Further, we expect **3)** more collectors and shredders due to increases in detritus and fine particulate organic matter in beaver ponds, **4)** more predators, and **5)** more swimmers and burrowers due to slow, deep water, and abundant soft sediment in ponds.

METHODS

Study Sites

This study took place in northeastern Utah in three beaver-inhabited streams; Right Hand Fork, Spawn Creek, and Temple Fork (Figure 1). All streams are tributaries to the Logan River and are located within the Wasatch-Cache National Forest. The three streams are in the Semiarid Foothills ecoregion just below the Wasatch Montane Zone ecoregion, between approximately 1,500 and 1,900 meters elevation (Table 1). The Semiarid Foothills are characterized by sagebrush, grama grass, pinyon, juniper, and maple-oak scrub (Woods *et al.*, 2001). All three streams were active beaver habitat at the time of collections. Two habitat types with five replicates of each were sampled within each of the streams (total number of 30 samples; one beaver pond sample was compromised and omitted, leaving 29 samples total): i) lotic reach segments upstream of sampled beaver ponds, and ii) beaver ponds directly behind an in-stream beaver dam. The stream channel habitats were lotic reaches or forced lotic reach geomorphic units (hereafter referred to as lotic reaches) of relatively low gradient (Wheaton *et al.*, 2015). Beaver pond habitats were sampled mid-depth in areas of deposited fine sediment. Ponds chosen within a stream were single ponds (i.e. not part of a multi-pond complex).

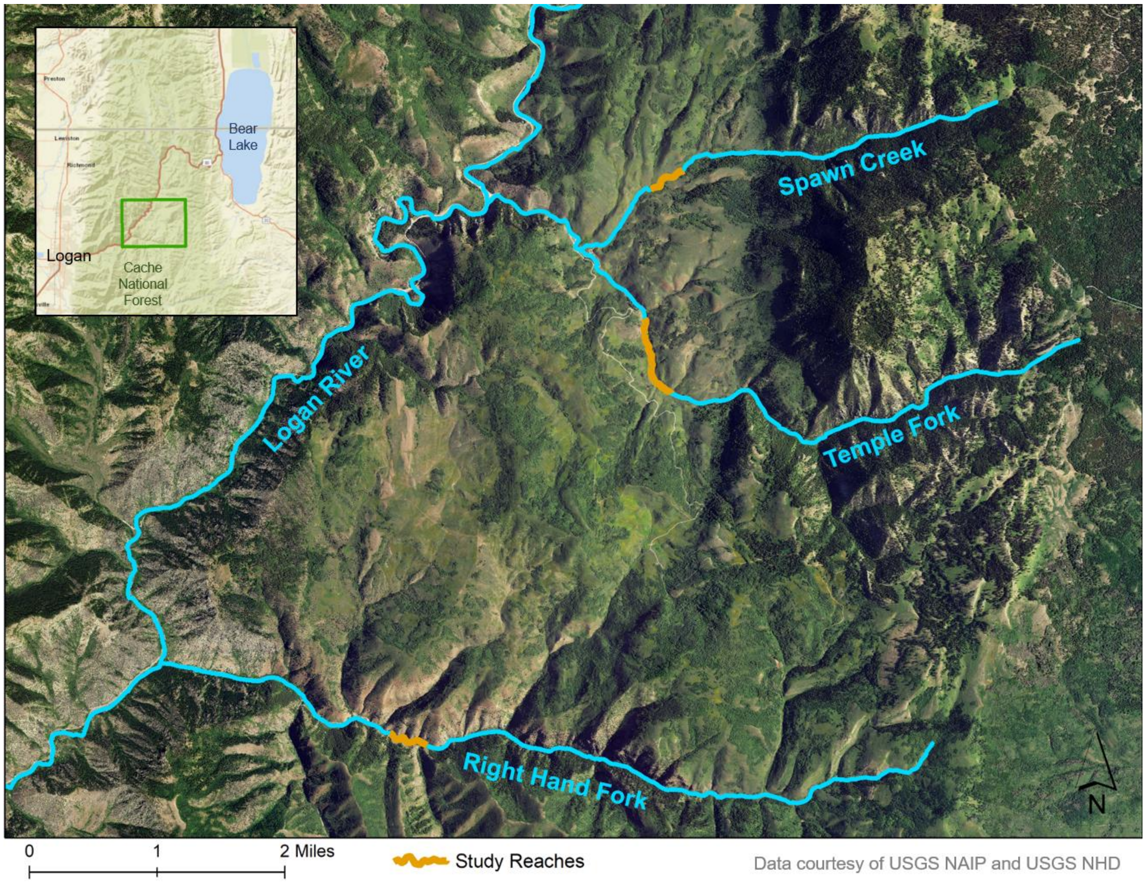

FIGURE 2.1 A map of study reaches within Right Hand Fork, Spawn Creek, and Temple Fork. All streams are tributaries to the Logan River, located in the Cache National Forest in northeastern Utah, USA. Blue lines indicate streams and orange lines indicate study reaches within streams.

TABLE 2.1 Environmental characteristics of streams and habitats sampled for summer 2017 (mean ± standard error).

	Right Hand Fork		**Spawn Creek**		**Temple Fork**	
Variable	*Lotic Reaches*	*Beaver Ponds*	*Lotic Reaches*	*Beaver Ponds*	*Lotic Reaches*	*Beaver Ponds*
Elevation (m)	1710 ± 3	1709 ± 3	1883 ± 5	1883 ± 5	1871 ± 8	1870 ± 8
Temperature (°C)	8.34 ± 0.39	8.66 ± 0.50	6.21 ± 0.26	6.21 ± 0.27	5.33 ± 0.09	5.40 ± 0.08
DO (mg/L)	9.00 ± 0.16	8.83 ± 0.32	9.70 ± 0.08	9.70 ± 0.05	10.04 ± 0.04	9.89 ± 0.02
Flow (m/s)	0.28 ± 0.05	0.11 ± 0.04	0.24 ± 0.04	0.06 ± 0.01	0.34 ± 0.06	0.02 ± 0.01
Grain Size (mm)	34.60 ± 9.14	< 2.00 ± 0	41.72 ± 6.99	< 2.00 ± 0	45.52 ± 8.34	< 2.00 ± 0
Depth (cm)	25.1 ± 1.0	35.2 ± 1.0	20.6 ± 10.0	38.0 ± 3.0	30.2 ± 2.0	39.5 ± 4.0

Environmental Characteristics

Characteristics measured within each habitat of each stream included elevation, water temperature, dissolved oxygen, flow/velocity, and grain size. Elevation was extracted via Google Earth imagery for each sampling location. Water temperature was measured using a Thermochron® iButtons® (Model DS1920, Maxim Integrated, San Jose, CA, USA) from July to September 2017. Flow was measured via a Flo-Mate portable velocity flow meter (Hach Company, Frederick, MD, USA) during September 2017. Dissolved oxygen measurements were taken in September 2017 with miniDOT dissolved oxygen sensors (PME, Inc., Vista, CA, USA). Grain size measurements followed the protocol designed by Wolman (1954), and 100 pebbles were collected at the five beaver ponds and five lotic reaches at each stream in July 2018. Water depth was measured across each habitat type in each stream on a grid system during September 2017.

Macroinvertebrate Sampling Procedure

Macroinvertebrate differences by habitat, either beaver pond or lotic reach, were tested by sampling macroinvertebrates during July 2017 from three beaver-altered streams in Logan Canyon, UT. Macroinvertebrates from lotic reaches were collected using surber samplers (total sample area 0.093 m^2) with a mesh size of 250 μm. Macroinvertebrates from beaver ponds were collected using a sweep net, also a mesh size of 250 μm mesh, by sweeping the net along a one-meter segment of the pond (total sample area 0.305m^2). Macroinvertebrate data was standardized by area sampled to one square meter. Macroinvertebrate collections were fixed in 95% ethanol and taken back to the laboratory where they were identified to genus when possible, otherwise to family. To estimate macroinvertebrate biomass of each genus or family, samples were dried at 60°C to a constant weight and weighed.

We report macroinvertebrate results in both biomass and density as functional dominance can occur as a result of a species being either numerically dominant or as a result of their relatively large body size (Lecerf & Richardson, 2011; Atwood, Hammill & Richardson, 2014). In this study, we aimed to capture any analogous functional community structure, through either a density effect or a biomass effect.

Macroinvertebrates were assigned to a functional feeding group (FFG), mobility group (MG), lotic/lentic habitat, and erosional/depositional habitat categories using Merritt, Cummins, and Berg (2008). Although more than one functional group may have been listed per taxa, only the primary group was utilized in our study.

Statistical Analyses

To determine the effects of beaver dams on macroinvertebrate communities, multiple metrics were compared between beaver ponds and lotic reaches across our three stream systems (Right hand fork, Temple Fork, and Spawn Creek). Metrics included species richness, macroinvertebrate density (# organisms per m^2), macroinvertebrate biomass (dry weight of each taxa type in the sample per m^2), proportions of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa, the proportion of each FFG in the community, the proportion of each MG in the community, the proportions of lentic and lotic insects, and the proportions of insects belonging to a certain habitat characteristic (erosional, depositional, littoral, and hydrophytes). Analyses of variance (ANOVA) were used to compare species richness, density, and biomass between pond and lotic reach habitats. Density and biomass were log-transformed prior to running the ANOVA to meet normality assumptions. To compare proportions of EPT taxa, proportions of FFGs and MGs, proportions of lentic and lotic, and proportion of macroinvertebrates by habitat characteristics between lotic reaches and ponds we used linear models (LMs). All proportional data were arcsine-transformed prior to analyses. In cases where a significant interaction between habitat and stream ID were found, we used Tukey's comparisons for ANOVAs and independent pair-wise comparisons for each stream site for LMs to determine where significant differences between ponds and lotic reaches had occurred. To reduce the occurrence of a Type I error due to multiple comparisons for LMs, we used a Bonferroni correction, which reduced α to a significance level of 0.0167. Environmental characteristic data was also assessed for differences by habitat and stream through ANOVAs.

Community composition in terms of taxa, FFGs and MGs were also compared between beaver ponds and lotic reaches. All three metrics were quantified using both density and biomass. Community compositions were assessed with nonlinear multidimensional scaling (NMDS) ordinations through the ‘vegan’ package (Oksanen *et al.*, 2017) in R. To compare community composition between beaver ponds and lotic reaches, we used permutational multivariate analysis of variance (PERMANOVA) via the ‘adonis’ function within the ‘vegan’ package. Stream was set as a block in the PERMANOVA. To determine which specific groups of macroinvertebrates were driving observed differences between pond and lotic reach communities, we used the similarity percentages test, ‘simper.’ The ‘simper’ function within the ‘vegan’ package uses Bray-Curtis dissimilarities to determine species differences between groups. All statistical analyses were completed using the statistical program R (R Core Team, 2017).

RESULTS

Overall Community Composition: Density

Habitat type had a significant effect on macroinvertebrate density (habitat: $F_{1, 23}$ = 9.040, $p < 0.001$; Figure 2a); however, this trend was not consistent across all streams. There was a significant interaction between stream and habitat (habitat*stream: $F_{2, 23}$ = 9.040, $p = 0.006$), and a post-hoc Tukey’s test demonstrated that Right Hand Fork was the only stream with a significantly higher macroinvertebrate density in lotic reaches compared to beaver ponds ($p < 0.001$) while density was not significantly different between habitat types in Spawn Creek or Temple Fork (all p-values > 0.05).

The proportion of macroinvertebrates based on density classified as lentic, lotic, or both lentic and lotic differed by habitat type (habitat: $F_{1, 23} = 39.730$, $p < 0.001$, Figure 2b). The proportion of taxa in beaver ponds classified as lentic was 741% higher than that of lotic reaches. However, there was a significant interaction between habitat and stream (habitat*stream: $F_{2, 23} = 8.124$, $p = 0.002$) caused by a non-significant difference between ponds and lotic reaches at Right Hand Fork. Meanwhile, the proportion of lotic taxa was ~35% higher in lotic reaches compared to beaver ponds (habitat: $F_{1, 23} = 61.816$, $p < 0.001$), and there was no interaction between habitat and stream (habitat*stream: $F_{2, 23} = 1.127$, $p = 0.341$). Lastly, beaver ponds had 170% more taxa that were classified as both lentic and lotic (habitat: $F_{1, 23} = 23.057$, $p < 0.001$). Lentic-lotic taxa also had a significant interaction between habitat and stream caused by this difference only being observed at Right Hand Fork (habitat*stream: $F_{2, 23} = 10.979$, $p < 0.001$).

Habitat characteristic classifications for macroinvertebrates also differed between beaver ponds and lotic reaches. Taxa classified as inhabiting erosional habitats was ~84% higher in lotic reaches compared to beaver ponds (habitat: $F_{1, 23} = 60.500$, $p < 0.001$), and there was no interaction between habitat and stream (habitat*stream: $F_{2, 23} = 0.734$, $p = 0.491$). Littoral-preferring taxa were 774% higher in proportion within beaver ponds compared to lotic reaches (habitat: $F_{1, 23} = 39.001$, $p < 0.001$). There was a significant interaction between habitat and stream for littoral-preferring taxa (habitat*stream: $F_{2, 23} = 8.082$, $p = 0.002$), which was due to no difference in the proportion of littoral insects between ponds and lotic reaches at Right Hand Fork. Taxa classified as both erosional and depositional were 101% higher in beaver ponds (habitat: $F_{1, 23} = 39.670$, $p < 0.001$), and there was no interaction between habitat and stream (habitat*stream: $F_{2, 23} = 1.751$, p

= 0.196). There was no effect of habitat type on proportions of depositional taxa, hydrophytes-dwelling taxa, margin-preferring taxa, or surface taxa (all p-values > 0.05).

In addition, the taxonomic composition of macroinvertebrates (i.e. taxa present and their densities) also significantly varied between beaver ponds and lotic reaches (habitat: $F_{1, 23} = 9.716$, $p < 0.001$, Figure 2c), and we found a significant interaction between habitat type and stream (habitat*stream: $F_{4, 23} = 6.241$, $p < 0.001$). Differences in community composition were primarily driven by *Baetis*, Ephemerellidae, and Elmidae larvae, which were 99%, 99%, and 97% higher in lotic reaches, respectively, as well as Chironomidae larvae and snails, which were 338% and 77% higher in beaver ponds.

In terms of macroinvertebrate density, the proportion of EPT in beaver ponds was 82% lower than in lotic reaches (habitat: $F_{1, 23} = 28.796$, $p < 0.001$; Figure 2d); this was driven primarily by Ephemeroptera, which was ~91% higher in lotic reaches compared to ponds (habitat: $F_{1, 23} = 22.586$, $p < 0.001$). There were no interactions between habitat type and stream for either total EPT (habitat*stream: $F_{2, 23} = 2.019$, $p = 0.156$) or proportion Ephemeroptera (habitat*stream: $F_{2, 23} = 0.334$, $p = 0.719$). The next group of taxa that contributed to differences in the proportion of EPT was Plecoptera, which was ~53% higher in lotic reaches compared to ponds (habitat: $F_{1, 23} = 9.488$, $p = 0.005$), and there was no interaction between habitat type and stream (habitat*stream: $F_{2, 23} = 2.763$, $p = 0.084$). Proportion Trichoptera was not significantly different between beaver ponds and lotic reaches, but we did find a significant interaction between habitat and stream (habitat*stream: $F_{2, 23} = 8.861$, $p = 0.001$). However, Tukey’s tests showed this interaction was driven by differences among streams for the same habitat type.

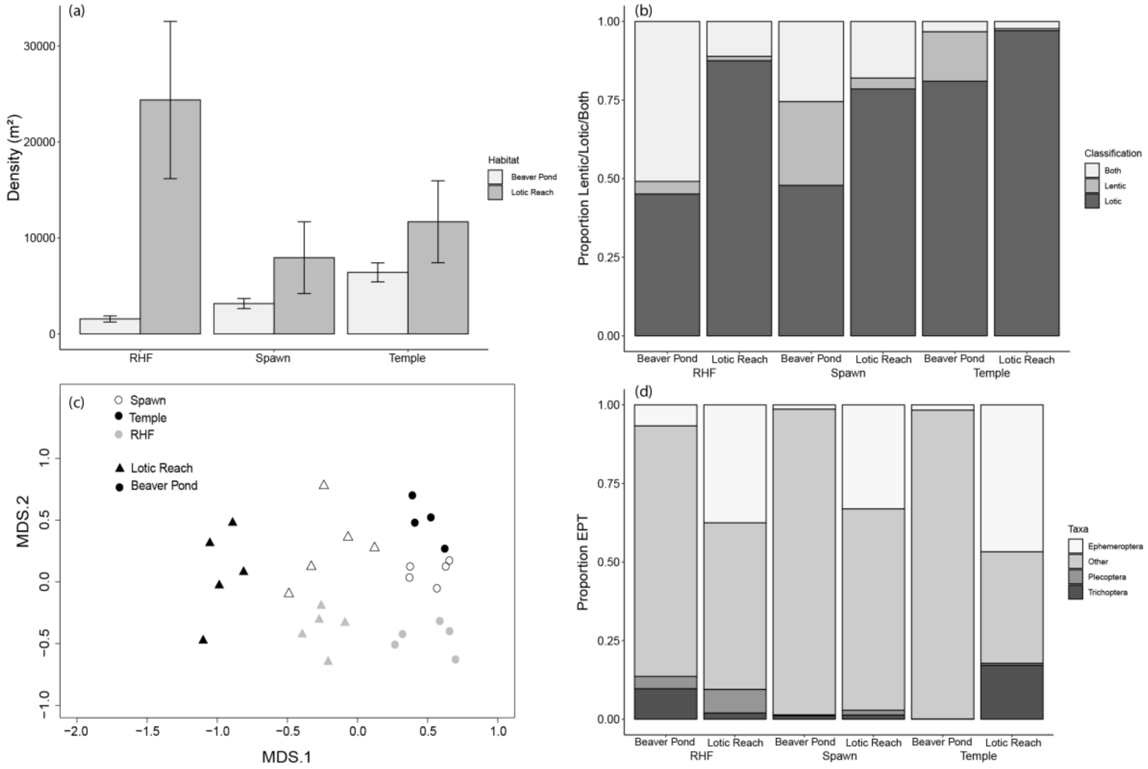

FIGURE 2.2 Differences in community structure measured by density (number of organisms per m^2) for lotic reach and beaver pond habitats: a) total density by habitat type (beaver ponds or lotic reaches) in each stream, b) proportion of lentic, lotic, and lentic-lotic macroinvertebrates in beaver ponds and lotic reaches of each stream, c) nonmetric multidimensional scaling (NMDS) plot illustrating how beaver ponds differ from stream lotic reaches in terms of macroinvertebrate community composition. Each point represents a lotic reach (triangle) or beaver pond (circle) community for each of the three streams studied [Right Hand Fork (RHF) = grey, Temple Fork (Temple) = black, and Spawn Creek (Spawn) = white). The closer together the symbols are in the NMDS plot, the more similar the community composition. d) proportional contribution of Ephemeroptera, Plecoptera, and Trichoptera (EPT) to each stream's community composition by habitat type.

Overall Community Composition: Biomass

Macroinvertebrate biomass was 90% higher in lotic reaches (habitat: $F_{1, 23}$ = 34.872, p < 0.001, Figure 3a), but varied across streams (habitat*stream: $F_{2, 23}$ = 4.804, p = 0.018). Although the average biomass of macroinvertebrates in Spawn Creek was also higher compared to ponds, a post-hoc Tukey's test demonstrated that these two habitats were not statistically different at this site.

The biomass of macroinvertebrates classified as lentic, lotic, or both lentic and lotic differed by habitat. The proportion of taxa in beaver ponds classified as lentic was 1360% higher than that of lotic reaches (habitat: $F_{1, 23} = 19.085$, $p < 0.001$, Figure 3b), and there was no significant interaction between habitat and stream (habitat*stream: $F_{2, 23} = 2.706$, $p = 0.088$). The proportion of lotic taxa was 33% higher in lotic reaches compared to beaver ponds (habitat: $F_{1, 23} = 48.214$, $p < 0.001$). However, the effect of habitat on lotic taxa was not observed between ponds and lotic reaches in Right Hand Fork (habitat*stream: $F_{2, 23} = 6.429$, $p = 0.006$). Lastly, beaver ponds had 213% more taxa that were classified as both lentic and lotic (habitat: $F_{1, 23} = 13.058$, $p = 0.001$), with a significant interaction between habitat and stream that was caused by differences among streams for the same habitat type (ANOVA, $F_{2, 23} = 9.861$, $p < 0.001$).

Proportions of macroinvertebrates by habitat characteristics also differed between beaver ponds and lotic reaches by biomass. The proportion of taxa classified as inhabiting erosional habitats was 87% higher in lotic reaches than for beaver ponds (habitat: $F_{1, 23} = 156.844$, $p < 0.001$), and there was a significant interaction between stream and habitat (habitat*stream: $F_{2, 23} = 3.673$, $p = 0.041$), thought the interaction was not caused by variables of interest. Littoral-preferring taxa were 3062% higher in proportion within beaver ponds compared to lotic reaches (habitat: $F_{1, 23} = 20.470$, $p < 0.001$). Proportions of taxa classified as both erosional and depositional were 307% higher in beaver ponds compared to lotic reaches (habitat: $F_{1, 23} = 45.326$, $p < 0.001$). Categories that were not significantly different between beaver ponds and streams were proportions of taxa associated with depositional, hydrophyte, margin, and surface habitats.

The taxonomic composition in terms of biomass (i.e. taxa present and their biomasses) also significantly varied between beaver ponds and lotic reaches (habitat: $F_{1, 23} = 10.984$, $p < 0.001$, Figure 3c), and differed within each stream (habitat*stream: $F_{4, 23} = 4.923$, $p < 0.001$). Difference in the community composition, according to the ‘simper’ analysis, were driven by a suite of mayfly taxa, *Oligophleobodes* caddisflies (99% higher), Elmidae larvae (97% higher), and *Hesperoperla pacifica* (100% higher) being present in the lotic reaches, whereas *Psychoglypha* (100% higher) and *Lepidostoma* (88% higher) caddisflies and Chironomidae larvae (60% higher) dominated the beaver ponds.

We found a significant effect of habitat on proportion EPT (habitat: $F_{1, 23} = 17.075$, $p < 0.001$, Figure 3d). However, the difference in EPT between beaver ponds and lotic reaches was only observed in Spawn Creek (habitat*stream: $F_{2, 23} = 14.685$, $p < 0.001$). The pattern in Spawn Creek was likely due to a 90% higher proportion of Ephemeroptera in lotic reaches (habitat: $F_{1, 23} = 29.875$, $p < 0.001$), as well as a 72% higher proportion of Plecoptera in lotic reaches (habitat: $F_{1, 23} = 8.140$, $p = 0.009$). There was a significant interaction between habitat and stream for proportion Plecoptera (habitat*stream: $F_{2, 23} = 6.888$, $p = 0.005$), but it was not due to variables of interest. Proportion Trichoptera was not different between beaver ponds and lotic reaches (habitat: $F_{2, 23} = 2.141$, $p = 0.157$).

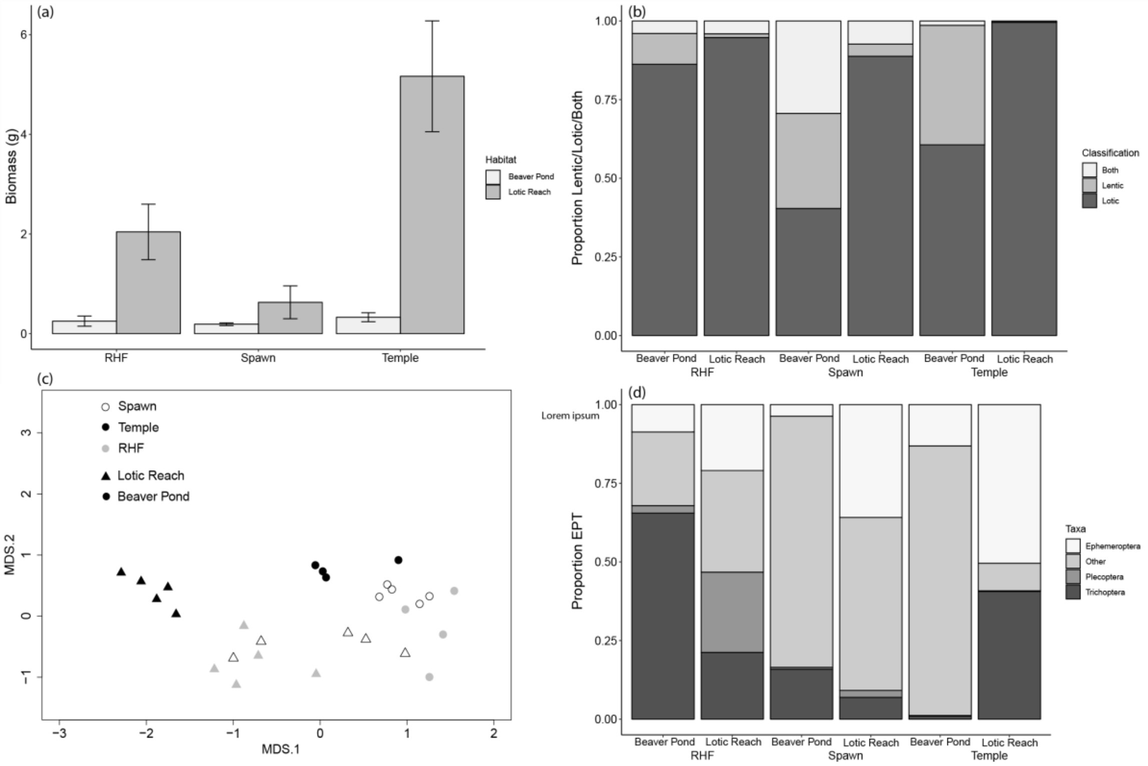

FIGURE 2.3 Differences in community structure measured by biomass (grams of organisms per m^2) for lotic reach habitats and beaver pond habitats: a) total biomass within beaver ponds and lotic reaches in each stream, b) proportion of lentic, lotic, and lentic-lotic macroinvertebrates in beaver ponds and lotic reaches of each stream, c) nonmetric multidimensional scaling (NMDS) plot illustrating how beaver ponds differ from stream lotic reaches in terms of macroinvertebrate community composition. Each point represents a lotic reach (triangle) or beaver pond (circle) community for each of the three streams studied [Right Hand Fork (RHF) = grey, Temple Fork (Temple) = black, and Spawn Creek (Spawn) = white). The closer together the symbols are in the NMDS plot, the more similar the community composition. d) proportional contribution of Ephemeroptera, Plecoptera, and Trichoptera to each stream's community composition by habitat type.

Richness

Overall, beaver ponds were less taxa-rich compared to lotic reaches, with 25% fewer genera than lotic reaches (habitat: $F_{1, 23} = 16.621$, $p < 0.001$). There was not a significant interaction between habitat and stream for richness (habitat*stream: $F_{2, 23} = 0.066$, $p = 0.526$).

Functional Feeding Groups: Density

The composition of FFGs (i.e. the FFGs present and their densities) was significantly different between beaver ponds and lotic reaches (habitat: $F_{1, 23} = 5.217$, $p = 0.003$, Figure 4a). According to 'simper,' these differences were driven by gatherers and scrapers in lotic reaches. However, we only found differences in predator taxa using proportions. The proportion of engulfers in beaver ponds was 76% higher than in lotic reaches (habitat: $F_{1, 23} = 11.775$, $p = 0.002$), and there was a significant interaction between stream and habitat (habitat: $F_{2, 23} = 7.80$, $p = 0.003$), though the interaction could not be attributed to variables of interest. The proportion of piercers was 63% higher in beaver ponds than in lotic reaches (habitat: $F_{1, 23} = 5.657$, $p = 0.026$), and there was not a significant interaction between habitat and stream (habitat*stream: $F_{2, 23} = 3.141$, $p = 0.062$).

Functional Feeding Groups: Biomass

The composition of FFGs based on biomass (i.e. the FFGs present and their biomasses) were significantly different between beaver ponds and lotic reaches (habitat: $F_{1, 23} = 12.488$, $p < 0.001$, Figure 4b). Based on 'simper' outputs, we attributed this difference to scrapers and gatherers. When we compared scraper proportions using LM, we found they were higher in lotic reaches compared to beaver ponds (habitat: $F_{1, 23} = 96.205$, $p < 0.001$) with the exception of Spawn Creek where no significant difference between habitat was observed (habitat*stream: $F_{2, 23} = 32.381$, $p < 0.001$). The proportion of gatherers was 20% higher in beaver ponds (habitat: $F_{1, 23} = 4.919$, $p = 0.037$), although this trend was only exhibited in Temple Fork, leading to a significant interaction between stream and habitat (habitat*stream: $F_{2, 23} = 26.033$, $p < 0.001$). In addition to differences in scraper and gatherer proportions, as suggested by the simper analysis, ANOVA analyses also found a significant effect of habitat on the proportions of filter, shredder and piercer biomass. Beaver ponds exhibited proportions of filterer biomass that were ~94% higher in lotic reaches (habitat: $F_{1, 23} = 5.364$, $p = 0.030$). Conversely, beaver ponds had 354% higher proportion of piercers by biomass than lotic reaches (habitat: $F_{1, 23} = 8.752$, $p = 0.007$). Lastly, beaver ponds exhibited proportions of shredder biomass more than 247% higher than in lotic reaches (habitat: $F_{1, 23} = 15.635$, $p < 0.001$), although the effect of habitat on shredder biomass was only significant for Right Hand Fork (habitat*stream, $F_{2, 23} = 6.037$, $p = 0.008$).

Mobility Groups: Density

The composition of MGs (i.e. the MGs present and their densities) was different between beaver ponds and lotic reaches (habitat: $F_{1, 23} = 11.669$, $p < 0.001$, Figure 4c). ‘Simper’ outputs determined that this was due to clingers, burrowers, and swimmers. When comparing proportion of different MG using LM, on average, the proportion of burrowers was 174% higher in beaver ponds (habitat: $F_{1, 23} = 66.769$, $p < 0.001$). However, the proportion of burrowers was not different between habitats at Right Hand Fork (habitat*stream: $F_{2, 23} = 9.156$, $p = 0.001$). Similarly, on average clingers were ~65% higher in lotic reaches (ANOVA, $F_{1, 23} = 16.021$, $p < 0.001$), but again a difference between habitats was not observed at Right Hand Fork (habitat: $F_{2, 23} = 6.688$, $p = 0.005$). Finally, the proportion of swimming taxa was higher in lotic reaches compared to ponds (habitat: $F_{1, 23} = 11.279$, $p = 0.003$).

Mobility Groups: Biomass

Similar to our density results, we found that the composition of MGs using biomass (i.e. the MGs present and their biomasses) was also significantly affected by habitat type (habitat: $F_{1, 23} = 18.423$, $p < 0.001$, Figure 4d). According to 'simper' outputs, clingers and swimmers drove this pattern; however, there was some disagreement between simper results and ANOVAs.

Clingers were more prominent in lotic reaches, with proportions more than 95% higher than those of beaver ponds (habitat: $F_{1, 23} = 453.355$, $p < 0.001$). Although there was a significant interaction between stream and habitat (habitat*stream: $F_{2, 23} = 17.564$, $p < 0.001$), the cause could not be attributed to variables of interest. In addition to clingers, ANOVA results showed that the biomass of sprawlers and burrowers were significantly affected by habitat, at least in some stream systems. Beaver ponds were proportionally higher in sprawlers by 502% (habitat: $F_{1, 23} = 28.932$, $p < 0.001$) with a significant interaction between stream and habitat (habitat*stream: $F_{2, 23} = 8.526$, $p = 0.002$) that could not be attributed to variables of interest. Beaver ponds were proportionally higher in burrowers (habitat: $F_{1, 23} = 45.243$, $p < 0.001$), but this trend only occurred in Temple Fork (habitat*stream: $F_{2, 23} = 17.564$, $p < 0.001$). The proportions of climbers, swimmers, and skaters were not different by habitat (all p-values > 0.05).

Environmental Characteristics

Multiple environmental characteristics (Table 1) differed between beaver ponds and lotic reaches. The average grain size was 95.1% smaller in beaver ponds (habitat: $F_{1, 24} = 66.421$, $p < 0.001$), and the difference is likely underestimated because all grains smaller than the smallest gravelometer section were classified into the general category of

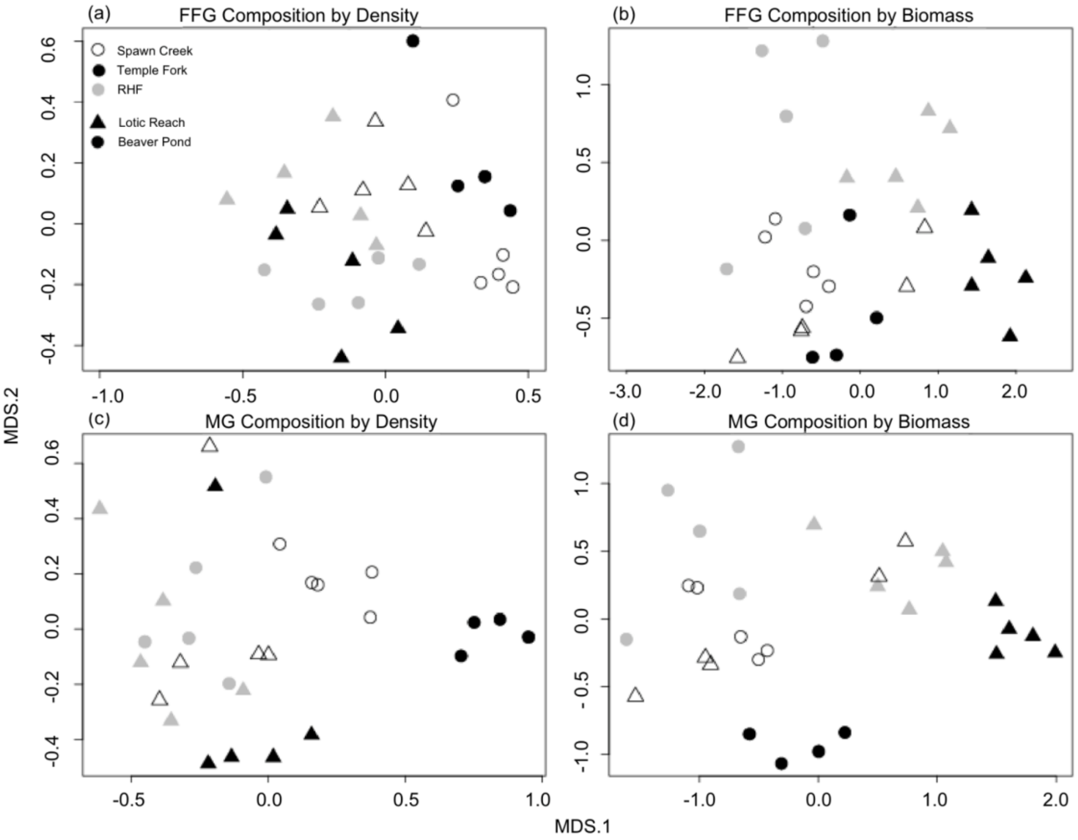

FIGURE 2.4 Differences in Functional Feeding Groups (FFGs) and Mobility Groups (MGs) of macroinvertebrates between beaver ponds and lotic reaches. Composition differences are measured by comparing functional groups present and their respective biomasses or densities per m^2: a) FFG composition by density, b) FFG composition by biomass, c) MG composition by density, and d) MG composition by biomass. Symbols closer together represent more functionally similar communities. Each point represents a lotic reach (triangle) or beaver pond (circle) community for each of the three streams studied [Right Hand Fork (RHF) = grey, Temple Fork (Temple) = black, and Spawn Creek (Spawn) = white).

< 2 mm. The average water velocity was 78.3% lower in beaver ponds (habitat: $F_{1, 54}$ = 67.119, $p < 0.001$), and the average beaver pond depth was 37.8% deeper than the average lotic reach depth (habitat: $F_{1, 67}$ = 8.526, $p < 0.001$). Characteristics that were only different between streams included temperature (stream: $F_{1, 48}$ = 230.833, $p < 0.001$), dissolved oxygen (stream: $F_{1, 18}$ = 25.812, $p < 0.001$), and elevation (stream: $F_{1, 24}$ = 616.285, $p < 0.001$). Temple Fork was approximately 2°C colder than Spawn Creek and

Right Hand Fork. Right Hand Fork was over 150 meters lower in elevation than the other two streams, and approximately 0.5mg/L lower in dissolved oxygen. We found no significant interactions between habitat and stream for any of our environmental characteristics (all p-values s > 0.05).

DISCUSSION

Our results demonstrate the macroinvertebrate community of beaver ponds is significantly different from that of lotic reaches. We observed beaver ponds to have lower species richness, biomass, and density of macroinvertebrates compared to lotic reaches. Our study also demonstrated the community composition, dominant functional feeding groups, and dominant mobility groups differed between beaver ponds and lotic reaches. However, the trends varied with expression in terms of macroinvertebrate biomass or density, and varied among streams. Overall, our results suggest that beavers, and their effects on habitat through the building of dams, are likely to restructure macroinvertebrate communities.

We observed mixed results for the effects of beaver ponds on both density and biomass. In terms of density, only Right Hand Fork demonstrated a statistical significant difference between beaver ponds and lotic reaches. However, the overall trend for all three streams was a higher average density in lotic reaches compared to beaver ponds. Past studies on the effects of beavers on the density of macroinvertebrates have also observed mixed results, with some studies reporting an increase in ponds and others a decrease (Rupp, 1955; Huey & Wolfrum, 1956; Gard, 1961; McDowell & Naiman, 1986; Rolauffs *et al.*, 2001; Anderson & Rosemond, 2010; Arndt & Domdei, 2011; Pliūraitė &

Kesminas, 2012; Law *et al.*, 2016). In terms of macroinvertebrate biomass, we found that all three streams had an average higher biomass in lotic reaches compared to beaver ponds, although this was not statistically significant in Spawn Creek. These results differ from past studies which found that beaver ponds generally had higher biomass of macroinvertebrates compared to lotic reaches (Gard, 1961; McDowell & Naiman, 1986; Anderson & Rosemond, 2010), or show no difference in biomass (Rolauffs *et al.*, 2001). In our stream systems, fine sediments in beaver ponds may preclude the colonization of most stream invertebrates, as interstitial spaces are less available (Bo *et al.*, 2007). We found that on average sediment size was 17-23 times larger in lotic reaches than in ponds. The significantly smaller sediment size in ponds may select for smaller individuals that inherently weigh less, reducing overall biomass in beaver ponds. Additionally, the diversity of gravel sizes in ponds is low, which may constrain the number of niches available to colonizing macroinvertebrates. This idea is further supported by the fact that we observed 25% fewer genera/families of macroinvertebrates in beaver ponds compared to streams. Considering macroinvertebrates are a major food source for fish, lower densities and biomass of macroinvertebrates in ponds may mean that these pond habitats are poorer foraging ground for fish, at least in northeastern Utah. To date, however, few studies have looked at whether fish are using pond habitats for foraging.

Beaver ponds differed from lotic reaches for several FFGs, although which FFG contributed to the differences varied for biomass and density. First, beaver ponds contain more predators (piercers and engulfers) compared to lotic reaches. The higher biomass (piercers) and density (piercers and engulfers) of predators in beaver ponds compare to lotic reaches coincide with past studies from all beaver-occupied continents (McDowell

& Naiman, 1986; Harthun, 1999; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Although the mechanism behind a dominance of predators in beaver ponds is unknown, it is speculated the physical environment of ponds may be beneficial to predators. Specifically, slower water velocity and finer sediments with little interstitial space may help predators capture prey that drift into the pond from upstream sections or fall into the pond from the riparian zone. Second, shredders were also more prominent in beaver ponds in terms of density, but not biomass. The large amount of organic matter such as terrestrial leaves that become trapped behind beaver ponds may help support high densities of detritivorous macroinvertebrates (Hodkinson, 1975a; Butler & Malanson, 1995). Higher densities of shredders in ponds may suggest that these habitats are hotspots for allochthonous nutrient cycling. Third, beaver dams contained less biomass of scrapers, which primarily feed on periphyton. While the fine sediments of beaver ponds can support periphyton (Coleman & Dahm, 1990), fine grains are likely to be too small for scraping taxa to manipulate. Fourth, beaver dams also contained less biomass of filter-feeding taxa than beaver ponds. These results differ from those of McDowell and Naiman (1986), which found no effect of beavers on filter feeders. We hypothesize higher density and biomass of filterers in lotic reaches in our study may stem from faster water velocity that increases suspended food particles (Wallace, Webster & Meyer, 1995). Lotic reaches in our study had 2.5-17 times faster water velocities than ponds. FFG and resource acquisition are traits found to be highly associated with ecosystem functioning. Differences between lotic reaches and beaver ponds in the dominance of FFGs found in our study suggests these two habitats may function differently, especially in terms of nutrient cycling.

Beaver ponds also differed from lotic reaches for several MGs. Beaver ponds contained higher densities and biomass of burrowers, which are known to inhabit fine sediment (Rabení *et al.*, 2005). Sprawlers were also more prevalent in beaver ponds by biomass. Sprawlers are associated with fine sediment and litter (Johnson, Breneman & Richards, 2003; Gillies, Hose & Turak, 2009), and may move and forage well in small spaces (Richards *et al.*, 1997), making sprawlers well-adapted for inhabiting the fine sediments and organic matter within beaver ponds. Conversely, lotic reaches contained higher densities and biomass of clingers. Clingers are adapted to withstand flowing water in erosional areas, and heavily rely on interstitial spaces for refuge (Johnson *et al.*, 2003; Rabení *et al.*, 2005). The low quantity of gravel substrate for both clinging and hiding within beaver ponds in our study system make clinging taxa ill-equipped to tolerate ponded conditions. Differences in MGs likely indicate differences in structural resource types within ponds (Heino, 2005), which can demonstrate habitat heterogeneity for the streams that contain beaver ponds (Pringle *et al.*, 1988; Rolauffs *et al.*, 2001; Bush & Wissinger, 2016; Law *et al.*, 2016).

Surprisingly, swimmer density was higher in lotic reaches than in beaver ponds. This pattern was likely driven by the dominance of *Baetis* in lotic reaches. *Baetis* on average accounted for 97.6% and 94.5% of swimmers in lotic reaches by density and biomass, respectively with the remainder of the swimmers in lotic reaches represented by only three other taxa. Contrarily, there were at least eight types of swimming taxa in beaver ponds (small Dytiscidae larvae were only identified to family, therefore likely underestimated), and *Baetis* accounted for only 37.5% of beaver pond swimmers by density, and 46.2% of swimmers by biomass. Although a beaver pond may be more conducive to swimming taxa due to the low water velocity and increased depth, *Baetis* may simply be well adapted to swimming through more turbulent conditions, allowing them to be abundant in lotic reaches.

Beaver pond taxa were different in their habitat classifications from lotic reach taxa using both biomass and density. Organisms in beaver ponds were decidedly lentic, while the lotic reach taxa were lotic. Similarly, a higher proportion of beaver pond taxa were considered littoral compared to lotic reach taxa, while the lotic reach organisms were considered erosional. This is not surprising due to the differences in habitat structure. However, beaver ponds did not include some of the more common taxa associated with completely lentic habitats (e.g., lakes and ponds). Very few Hemipterans were found in beaver ponds, and Odonates were completely absent. Beaver ponds were also devoid of other wetland taxa such as *Callibaetis*, Megalopterans, and Isopods. This was despite the fact that potential source wetlands are common in the Cache National Forest. This lack of other lentic macroinvertebrates could be due to the high gradient of the mountain streams, keeping the flow in beaver ponds just high enough to exclude specific lentic organisms. This may also explain why so many beaver pond taxa were also classified as both lentic and lotic.

Overall, we found that beaver ponds significantly influenced macroinvertebrate biomass, community composition and functional traits. Such changes to the community composition suggest that beaver ponds may function differently than non-ponded segments, and that streams containing beaver may function differently than those without. In future studies, links to other ecosystem functions should be considered. Although ponds contained lower species richness compared to lotic reaches, the overall stream or reach richness is likely increased by adding ponds to overall habitat considering they contained Dytiscid beetles, *Siphlonurus* mayflies, *Psychoglypha* caddisflies, and other taxa not recorded in lotic reaches. Beaver ponds provide substantial lentic habitat, adding lentic taxa to the suite of organisms present within the streamscape. Understanding the effects of beavers on macroinvertebrates is important for predicting changes in stream communities and ecosystem functions as a result of the rewilding of beavers in North America. Results from our study suggests the macroinvertebrate communities can change as a result of beaver pond construction, and such changes may have consequences for fish and ecosystem functioning.

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CHAPTER 3

A COMPARISON OF LOTIC AND BEAVER POND-DWELLING TROUT IN NORTHEASTERN UTAH

ABSTRACT

Beavers are increasingly implemented as agents in stream restoration, though little work has shown how fish utilize beaver habitats. While beaver ponds provide many types of refugia to fish, foraging habits, habitat preference, and growth within beaver ponds remains unclear. Trout were expected to contain diets more indicative of lotic foraging due to a lower density and biomass of macroinvertebrates in beaver ponds. We also hypothesized lower velocity habitat would result in higher growth for trout that use beaver ponds, and due to this we suspected trout would demonstrate a preference for beaver ponds over lotic reaches. Through a variety of stream surveys and experiments in the Logan River watershed, we determined there were no differences in growth or diet between trout caught in beaver ponds and trout caught in lotic sections. Brown trout were significantly larger in beaver ponds, while Bonneville cutthroat trout were significantly larger in lotic areas. Some trout did exhibit signs of site fidelity to beaver ponds, though lotic reaches contained more trout per volume of habitat. In this largely pristine system with a long history of beaver use, trout may be highly adapted to beaver-created habitats such that they can utilize both beaver ponds and lotic stream sections.

INTRODUCTION

As of 2018, 164 species of North American freshwater fishes have been listed as vulnerable, endangered, or critically endangered by the International Union for Conservation of Nature (IUCN 2018). Although many, often compounding factors are to blame for declines in North American freshwater fishes, habitat degradation is one of the most prolific threats (Harig and Fausch 2002; Arthington et al. 2016; Penaluna et al. 2016; Lynch et al. 2017). In order to improve freshwater habitats, large- and small-scale stream/river restoration projects are used to enhance bank stabilization, alter water flow, enhance fish passage, reconnect floodplains, improve water quality, and improve instream habitat with the hopes that such efforts will help recover declining fish populations (Roni et al. 2002; Mueller et al. 2014; Palmer et al. 2014; Kail et al. 2015). However, such restoration projects are costly (Moore and Rutherfurd 2017), with the USA spending an estimated $1 billion a year on restoration efforts (Bernhardt et al. 2005). In order to reduce restoration costs and reinstate streams/rivers to more natural states, beavers have demonstrated to be a potential low-cost natural solution to stream restoration in North America (Pollock et al. 2004; Wheaton et al. 2013; Bouwes et al. 2016).

Previous work aimed at understanding how beaver modifications to streams affect salmonids have observed several positive effects. First, deposited gravel on the upstream ends of beaver pond complexes can create spawning habitat (Johnson et al. 1992; Bylak et al. 2014; Malison et al. 2014; Bouwes et al. 2016), especially in streams undergoing restoration (Bouwes et al. 2016). Second, native species of salmonids that co-evolved with beaver are able to pass through beaver dams or use flooded channels to move between lower and upper stream reaches. Thus, dams are not a detrimental barrier to native migrating salmonid populations (Lokteff et al. 2013; Bylak et al. 2014; Malison et al. 2014; Bouwes et al. 2016). Third, beaver dams may act as a natural barrier between native and invasive fish species, though the effects are context-dependent. For example, in side channels of the Provo River, UT, beaver dams separated nonnative brown trout (*Salmo trutta*) from native fish species (Billman et al. 2013). Although brown trout are capable of passing dams, another study conducted in northeastern Utah showed that they did so infrequently when compared to native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) and introduced brook trout (*Salvelinus fontinalis*) (Lokteff et al. 2013). Fourth, fish can use beaver ponds that develop behind beaver dams as thermal (Johnson et al. 1992; Niles et al. 2013) or drought refuges (Hanson and Campbell 1963; Dare et al. 2002). Although it is clear that beaver ponds provide some benefits to fish, it is not known whether the composition and structure of the fish community is similar between beaver ponds and adjacent lotic sections. There is some evidence that certain size classes of fish are selectively inhabiting beaver ponds (Johnson et al. 1992; Pollock et al. 2004; Bylak et al. 2014 Malison et al. 2014; Bouwes et al. 2016), though no generalizable patterns have emerged.

Few studies have considered whether trout are using beaver ponds as foraging habitat. Studies conducted on stream macroinvertebrates, a major food source for trout, demonstrated the total biomass, total density, and composition of the macroinvertebrate communities markedly differ between beaver ponds and lotic reaches (McDowell & Naiman, 1986; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016; Washko et al. 2018 *in review*). In some cases, studies reported higher biomass and densities of macroinvertebrates inside beaver ponds compared to lotic segments (Gard 1961; McDowell and Naiman 1986; Anderson and Rosemond 2010) while other studies have found the contrary (Arndt and Domdei 2011; Pliūraitė and Kesminas 2012). Studies have shown that fish collected from lotic reaches and those collected from inside beaver ponds differed in their stomach contents (Rupp 1955; Gard 1961; Hilderbrand and Kershner 2004), suggesting beaver-mediated changes to the macroinvertebrate community may have consequences on fish growth. In addition to alterations in the availability of specific diet items, temperature regimes within ponds could alter metabolic maintenance costs, and potentially providing a resting place for trout from high water velocities, thereby decreasing energetic demands. To date, however, no study has assessed whether such changes to diet and metabolism affect growth or body condition of fish utilizing beaver ponds.

Here, we used a combination of field observations and experimentation to test patterns of habitat use, diets, and growth of Bonneville cutthroat trout (*Oncorhynchus clarkii utah;* hereafter BCT) and brown trout (*Salmo trutta*) within beaver-altered habitats. First, we observationally surveyed trout size distributions in beaver ponds and estimated their habitat preference (beaver ponds versus lotic reaches) through mark-recapture surveys. Further, we examined if trout actively used beaver ponds as foraging habitat by examining whether trout caught in beaver ponds had diet compositions consistent with beaver pond macroinvertebrate communities. We hypothesized **1)** trout in beaver ponds will be larger than those captured in lotic reaches, **2)** individual fish will repeatedly be found within beaver ponds, indicating a preference for beaver pond habitat, and **3)** the gut contents of trout captured in beaver ponds will reflect pond-dwelling organisms, while trout caught in lotic reaches would have gut contents that reflect lotic-dwelling organisms and terrestrial organisms. Lastly, we experimentally tested trout growth within beaver ponds and within lotic reaches using a combination of experimental and observational approaches. Because we expected energy quality of food to be similar between beaver ponds and lotic reaches (see Chapter 1: Table 2), and we expected reduced energy expenditure for trout due to lower water velocities and favorable thermal regimes in beaver ponds (Naiman et al. 1988; Johnson et al. 1992; Gurnell 1998; Niles et al. 2013), our prediction was **4)** trout specific growth rates will be higher in beaver ponds than in lotic reaches of streams.

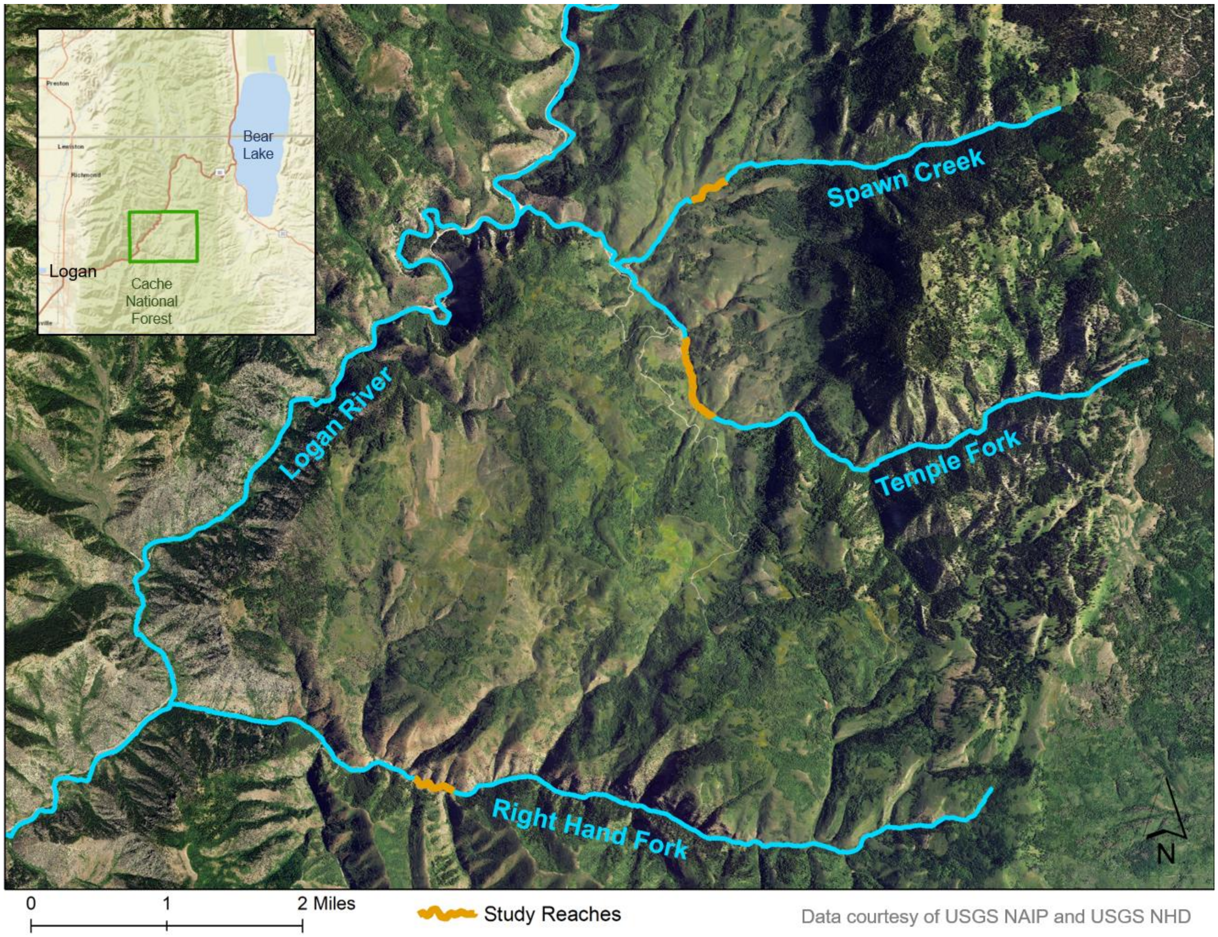
METHODS

Study Site

This study occurred in the Cache National Forest in northeastern Utah. Our study focused on three beaver-altered tributaries to the Logan River (Figure 1): Spawn Creek, Temple Fork, and Right Hand Fork. All three streams are located in the Semiarid Foothills ecoregion between approximately 5,000 and 8,000 feet elevation. Spawn Creek and Temple Fork house both BCT and nonnative brown trout. However, the sites utilized in my study at Temple Fork were mostly above a natural barrier that excluded brown trout. Thus, my data at Temple Fork only included BCT. Right Hand Fork underwent a nonnative trout removal project in 2013, and BCT was the only fish species present in that tributary the time of this study.

Focal Species

BCT is an endemic subspecies of cutthroat trout from the Bonneville Basin (Utah, Idaho, Nevada). Populations declined as a result of competition and hybridization with nonnative salmonids, habitat loss, and overharvesting (Behnke 1992; Duncan and Lockwood 2001; Fausch 2008). While previous studies have indicated BCT may forage in beaver ponds (Hilderbrand and Kershner 2004) and older individuals can benefit from



Data courtesy of USGS NAIP and USGS NHD

FIGURE 3.1. Reaches studied (orange) on each of the three tributaries to the Logan River in the Cache National Forest.

the deep pools and wood cover provided by beaver ponds (White and Rahel 2008), there is little information on how beaver ponds change BCT communities (i.e. age and size structure within each habitat) through the addition of in-stream pond habitats. In the Logan River watershed, BCT are almost exclusively insectivores, and commonly eat drifting Ephemeropterans and terrestrial prey. They are nonselective feeders, eating prey in proportion to their availability in the environment from drift and from the water surface (McHugh et al. 2008).

Brown trout (*Salmo trutta*) are native to coastal and inland Europe, North Africa, and western Asia. They were introduced to North America and due to their ability to tolerate a broad range of environmental conditions, have effectively colonized many streams and rivers in Utah and elsewhere in North America (Klemetsen et al. 2003; Budy and Gaeta 2018). Brown trout prey upon and outcompete native trout (e.g., BCT) in the western United States, and can cause loss of diversity through hybridization (Dowling and Childs 1992; McHugh et al. 2008; Muhlfeld et al. 2009). Brown trout are known to be dominant over native trout in occupying habitat within North American streams (Fausch and White 1981; Kruse et al. 2000; Hitt et al. 2017), and are opportunistic, epibenthic feeders (Klemetsen et al. 2003; McHugh et al. 2008). In the Logan River watershed, brown trout consume prey in proportion to their availability, especially Trichoptera, and occasionally prey upon smaller fish such as sculpin (McHugh et al. 2008).

Trout Habitat Use Assessment

Fish presence in ponds was tracked to better understand how fish utilize beaver ponds. Trout were collected through single-pass electrofishing in July and in September

2017. Collected fish were anesthetized, and the species, weight, total length, and passive integrated transponder (PIT) tag ID were recorded (both recaptures and newly inserted tags), along with the habitat of capture (beaver pond or lotic). During August 2017, Right Hand Fork was surveyed using a PIT tag reader (Biomark® HPR Plus and mobile antenna). The antenna was probed through the beaver ponds every other day to detect the PIT tag signal for fish residing in the beaver ponds (Lokteff et al. 2013). Fish use of beaver ponds was assessed by the number of times a fish was recorded residing in a beaver pond. This method was only used in Right Hand Fork, where the fish density was high enough to obtain sufficient data.

Habitat use was also assessed using the number and biomass of fish per volume of stream habitat (beaver pond or lotic). Lotic reach and beaver pond surface areas were calculated in ImageJ using drone-captured aerial imagery of each sampling location. Surface areas were multiplied by average depth, which was collected in the field during September 2017, to estimate the total volume of beaver ponds and of lotic reaches for each sampled stream reach (m^3).

Foraging Assessment: Diet Contents

The extent to which brown trout and BCT are foraging in beaver ponds was assessed by comparing stomach contents with available macroinvertebrate prey. Data from July 2017 macroinvertebrate surveys from lotic reaches and beaver ponds (Washko et al. in review) were utilized to compare diet samples to available prey. Fish diet collections coincided with macroinvertebrate sampling, reducing temporal effects that may mask foraging locations. Fish were collected through single-pass electrofishing in

July and in September 2017. Collected fish were anesthetized, and stomach contents were collected from trout from each habitat type (pond or lotic) in each stream using non-lethal gastric lavage. At Right Hand Fork and upper Temple Fork, only BCT diets were collected due to the absence of brown trout, but brown trout diets were collected at Spawn Creek. Stomach contents were fixed with 95% ethanol and transported to the lab to be identified to the lowest taxonomic level possible using a dissection microscope. In total, 40 diet samples were assessed (5 pond BCT x 3 streams + 5 lotic BCT x 3 streams + 5 pond brown x 1 stream + 5 lotic brown x 1 stream).

Stomach content composition of trout caught within habitat was compared using nonlinear multidimensional scaling (NMDS) ordinations through the ‘vegan’ package (Oksanen et al. 2017). To test for differences between beaver pond trout and lotic reach trout stomach contents, we used permutational multivariate analysis of variance (PERMANOVA) with the ‘adonis’ function within the ‘vegan’ package. Stream was set as a block in the PERMANOVA. To determine which specific groups of macroinvertebrates were driving observed differences between pond and lotic reach trout stomach contents, we used the similarity percentages test, ‘simper.’ The ‘simper’ function within the ‘vegan’ package uses Bray-Curtis dissimilarities to determine species differences between groups. All statistical analyses were completed using the statistical program R (R Core Team 2017).

Diet item origin was assessed through the proportion of each diet classified as lentic, lotic, or terrestrial macroinvertebrates to elucidate differences in trout foraging by habitat. To compare diets between habitats we used linear models (LM). All diet proportions were arcsine-transformed to meet normality assumptions.

An electivity index was used to compare fish diets with available prey. We used the R package “selectapref” (Richardson 2017) to model diets of pond-dwelling trout and lotic-dwelling trout through Chesson’s α (Chesson 1978) (function ‘manlysalpha’), chosen for its reduced sensitivity to rarely available taxa compared to other indices (Lechowicz 1982). Chesson’s α compares the mass of diet items consumed to the available mass of those diet items in the environment, assigning an index. The index output for diet item was compared between beaver pond trout diets and lotic trout diets.

Foraging Assessment: Isotopes

To further understand how trout diet and trophic position might differ between lotic and beaver pond trout over a longer time period, we analyzed $\delta^{13}C$ and $\delta^{15}N$ stable isotopic signatures of potential diet items. Specifically, we analyzed stream macroinvertebrates, riparian terrestrial insects, and trout adipose fins. Our aim was to test if trout from different habitats were consuming different quantities of terrestrial or aquatic invertebrates. Aquatic macroinvertebrates were collected from each stream with surber samplers, and the most readily available taxa were rinsed in deionized water and frozen. The same was done for terrestrial insects, which were caught in riparian vegetation using aluminum pie pans set out for three hours at midday (Right Hand Fork terrestrial invertebrate samples were damaged, therefore only aquatic invertebrates were tested for that stream). Pans were filled with deionized water, plus one drop of dish soap to break surface tension to better trap insects. Trout adipose fins were collected from fish caught for the stomach content analysis.

Aquatic and terrestrial insects and fish fins were dried for 48 hours at 60°C, and then finely crushed and homogenized. Samples were packed in 4x6 mm tins and processed on a Costech Elemental Analyzer (Costech Analytical Technologies, Inc., Valencia, CA, USA) in the Newell Lab at Utah State University.

Isotopic analyses were conducted using the ‘siar’ mixing model (Parnell and Jackson 2013) in R for each stream’s fish and prey items. For aquatic insects, a trophic discrimination factors of 0.1 ± 2.2‰ for $\delta^{13}C$ and 2.6 ± 2.0‰ for $\delta^{15}N$ were used (Brauns et al. 2018). For terrestrial insects, the widely accepted values of 0.4 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 1.0‰ for $\delta^{15}N$ were utilized due to a lack of more specific discrimination factor. Trout fin isotopic values were plotted, and ellipses were created for trout of each habitat type. Ellipse overlap was calculated within the ‘siar’ package to estimate foraging differences. Differences in isotopic signature were tested by comparing average $\delta^{15}N$ and average $\delta^{13}C$ values through ANOVAs.

Trout Growth by Habitat: Fish Size and Body Condition

Again, for each fish caught, the species, weight, total length, and PIT tag ID were recorded, along with the habitat (beaver pond or lotic). The adipose fins of tagged fish were clipped for recognition during later sampling events, and fin clips were saved for isotopic analysis. Fish were released back to the stream following a recovery period.

Associations between fish body characteristics and habitat were investigated using a linear mixed effects model. All analyses were conducted in the R-Cran statistical software (R Core Team 2017) with the statistical packages ‘nlme’ (Pinheiro et al. 2018). Model selection was hypothesis-driven, taking into account the fixed effects of habitat and stream and the random effect of month. Three models were run, one each for trout total length, weight, and body condition. Body condition was calculated using Fulton's K (Pope and Kruse 2007):

$$K = \left(\frac{Length}{Weight^3}\right) * 100$$

In cases where a significant interaction between habitat and stream were found, we used independent pair-wise comparisons to determine where significant differences between ponds and lotic reaches had occurred for each stream site. To reduce the occurrence of a Type I error due to multiple comparisons for LMs, we used a Bonferroni correction, which reduced α to a significance level of 0.0167.

Trout Growth by Habitat: Caging Experiment

During July 2017, juvenile BCT and brown trout were caught via single pass electrofishing, weighed, measured for total length, and assigned to a cage in one of two habitat treatments: lotic or beaver pond. Fish remained in the stream in which they were caught. One fish of two years old or younger (approximately 50-150 mm in length) resided in each cage to avoid density dependent effects of intraspecific competition. There were two fish per lotic reach and two fish per beaver pond, totaling 20 fish per stream (2 individuals x 2 habitats x 5 sites), and overall 60 fish (20 fish per stream x 3 streams).

Fish cages were cylinders of black 9mm^2 plastic mesh, designed to allow small drifting macroinvertebrates to enter the cage, and were approximately 50cm long with a 15cm side diameter. Cages were attached to rebar in the stream, and were cleaned of debris by hand every other day or as needed. After 40 days, trout were removed from cages, re-weighed and re-measured. Trout growth by habitat and species was assessed via ANOVAS in R. The growth metric used was specific growth rate (μ), where W_1 is the final weight, W_0 is the initial weight, and t is the number of days of growth (Fausch 1984):

$$\mu = \frac{\ln W_1 - \ln W_0}{t}$$

Environmental characteristics were measured for the cage locations. We placed a Thermochron® iButton® temperature logger (Model DS1920, Maxim Integrated, San Jose, CA, USA) within each cage. Velocity was measured at each cage mid-way through the experiment using a Flo-Mate portable velocity flow meter (Hach Company, Frederick, MD, USA). After caging, miniDOT dissolved oxygen sensors (PME, Inc., Vista, CA, USA) were deployed to test for differences in oxygen content between lotic reaches and beaver ponds. Environmental characteristic data was assessed for differences by habitat and stream through ANOVAs.

RESULTS

Fish Composition by Stream

Fish species composition varied between sampled reaches. Spawn Creek contained approximately 36% Bonneville cutthroat and 67% brown trout, whereas Temple Fork had a natural barrier which reduced brown trout, resulting in 95% Bonneville cutthroat. Right Hand Fork underwent a nonnative trout removal project in 2013 to create a cutthroat sanctuary, thus contained 100% Bonneville cutthroat trout.

Generally, we observed fewer fish per volume of stream in beaver ponds relative to lotic reaches by both density and biomass. Overall, Spawn Creek contained 0.17 trout per m^3 of beaver pond, but 0.88 trout per m^3 of lotic reach. Similarly, Temple Fork contained 0.04 fish per m^3 of beaver pond, but 0.05 trout per m^3 of lotic reach. Right Hand Fork's density of fish was the highest, with 0.72 trout per m^3 of beaver pond, and 0.84 trout per m^3 of lotic reach. Translated to biomass per volume of stream, the pattern remained the same. Within Spawn Creek beaver ponds contained ~32.06 g of trout per m^3, and 106.92 g of trout per m^3 of lotic reach. Temple Fork contained 6.97g of trout per m^3 of beaver pond and 11.74g of trout per m^3 of lotic reach. Lastly, Right Hand Fork contained 44.2 0g of trout per m^3 of beaver pond and 60.42 g of trout per m^3 of lotic reach.

Trout of all sizes and weights were found in both beaver ponds and lotic reaches (Figure 2). Specific ponds were not recorded for each individual trout, rendering pond-by-pond size assemblages impossible. However, as a personal note, when recording the number of fish visually observed in a beaver pond and when electrofishing, the fish from one specific habitat at a time were not uniform in size.

Habitat Use

Recapture rates indicated some fish (all BCT) were repeatedly observed within beaver ponds. Only 6.6% of all fish caught during the second electrofishing survey were recaptures from the first electrofishing survey (n=63). Of these trout, 31.7% were caught in lotic reaches during both sampling events (n=20), and 33.3% were caught in beaver ponds during both sampling events (n=21). The remaining 34.9% were caught in either a beaver pond or a lotic reach during the first survey, and the opposite habitat during the second survey.

When sweeping beaver ponds at Right Hand Fork with a mobile PIT tag antenna, approximately 51% of the trout scanned were observed during multiple sweep surveys. Each trout was always observed to be in the same pond as the previous encounter. Scanning active fish in the stream is difficult because many fish simply swim out of reach of the antenna, so visual counts were conducted prior to sweeping. These counts indicated ponds could be inhabited by 0-25 trout on a given late summer day. Recording the use of ponds by trout, and repeated use of specific ponds by individuals, demonstrated certain fish may exhibit habitat fidelity.

Trout Diets

Diet compositions of trout caught in lotic reaches and trout caught in beaver ponds, measured as the diet items present and the total mass of each of those item types, were not different within BCT (habitat: $F_{1,24} = 0.8329$, $p = 0.615$, Figure 3a) or within brown trout (habitat: $F_{1,8} = 0.106$, $p = 0.537$, Figure 3b). There were no interactions between habitat and stream for BCT (habitat*stream: $F_{4,32} = 3.143$, $p = 0.27$), and brown trout were only found in one stream.

The proportion of lentic, lotic, and terrestrial food sources was also not different by habitat, and there were no interactions between habitat and stream (all p's > 0.05; Figure 4). Overall, trout diets were 11% lentic, 33% lotic, and 22% terrestrial, and the remaining 34% of diet items could not be identified or were classified as both lentic and lotic.

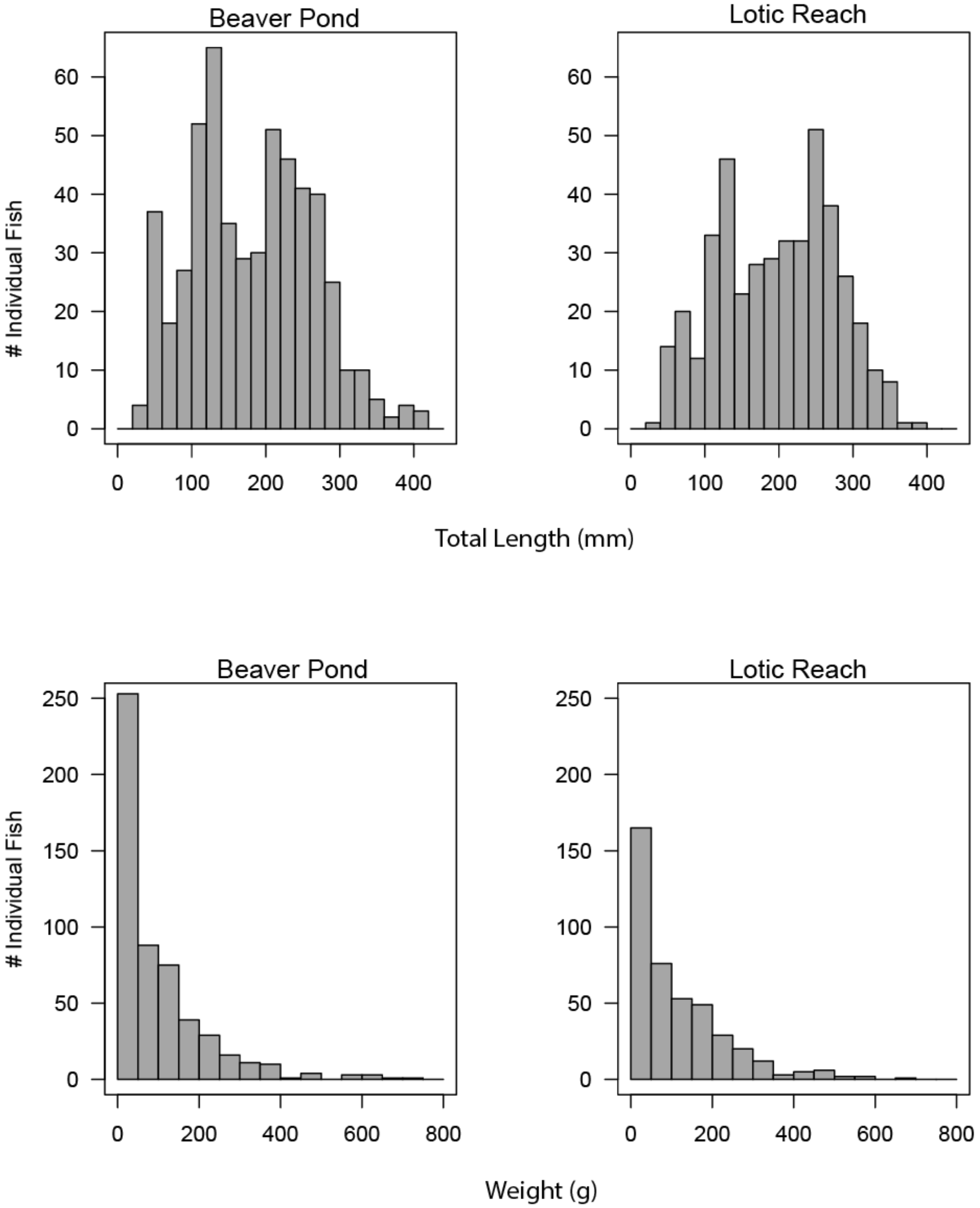


FIGURE 3.2. Size structure (weight and total length) of trout collected from beaver ponds and lotic habitats, pooled over the three streams (Temple Fork, Sawn Creek, and Right Hand Fork).

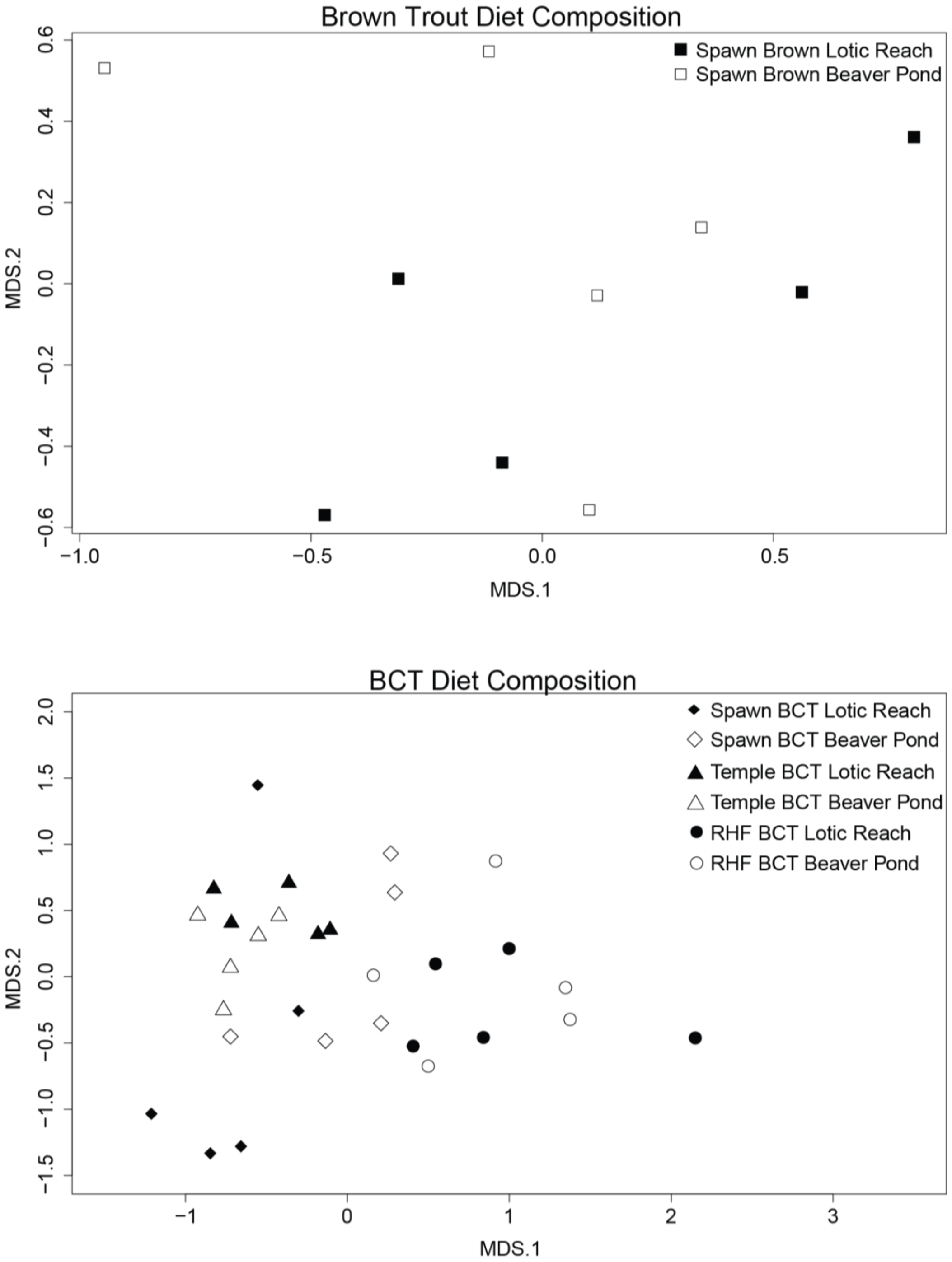


FIGURE 3.3. Diet composition of fish collected from beaver ponds and lotic regions in Spawn Creek, Temple Fork, and Right Hand Fork (RHF). The closer one point is to another, the more similar the diet sample. BCT= Bonneville cutthroat trout, Brown = brown trout

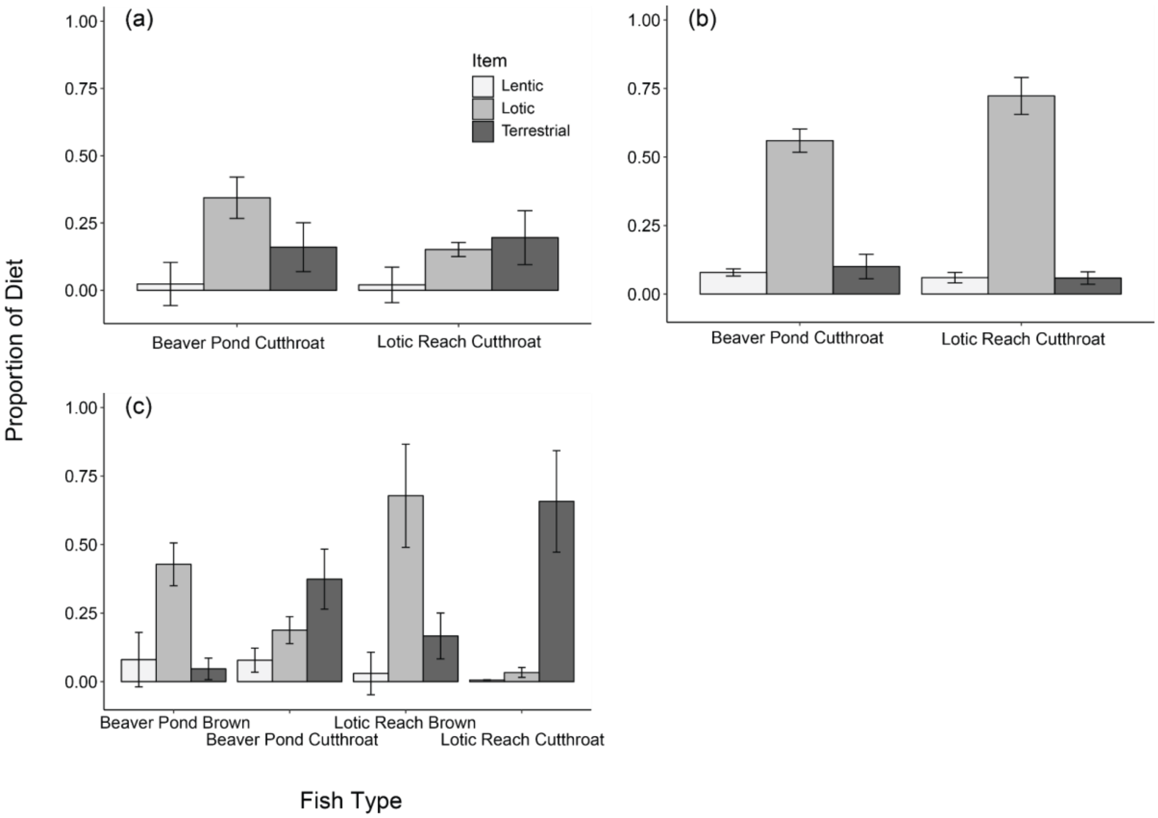


FIGURE 3.4. Proportions of lentic, lotic, and terrestrial macroinvertebrate within the diets for each trout collected from beaver ponds and lotic habitats in a) Right Hand Fork, b) Temple Fork, and c) Spawn Creek. PC = Beaver Pond Cutthroat, RC = Lotic Cutthroat, PB = Beaver Pond Brown, and RB = Lotic Brown.

Electivity models suggested the aquatic portion of diets did not differ by habitat (Figure 5). Lotic-caught trout and beaver pond-caught trout selected the same prey according to the Chesson's α electivity index. Many taxa that were not often consumed are benthic invertebrates that rarely drift, such as Glossostomatidae, Elmidae, Siphlonuridae, Uenoidae, Chironomidae, and Empididae (Rader 1997), or are usually found at the bottom of the water column when drifting, such as Trombidiformes and Chironomidae (Fenoglio et al. 2004). Invertebrate consumption did not always match

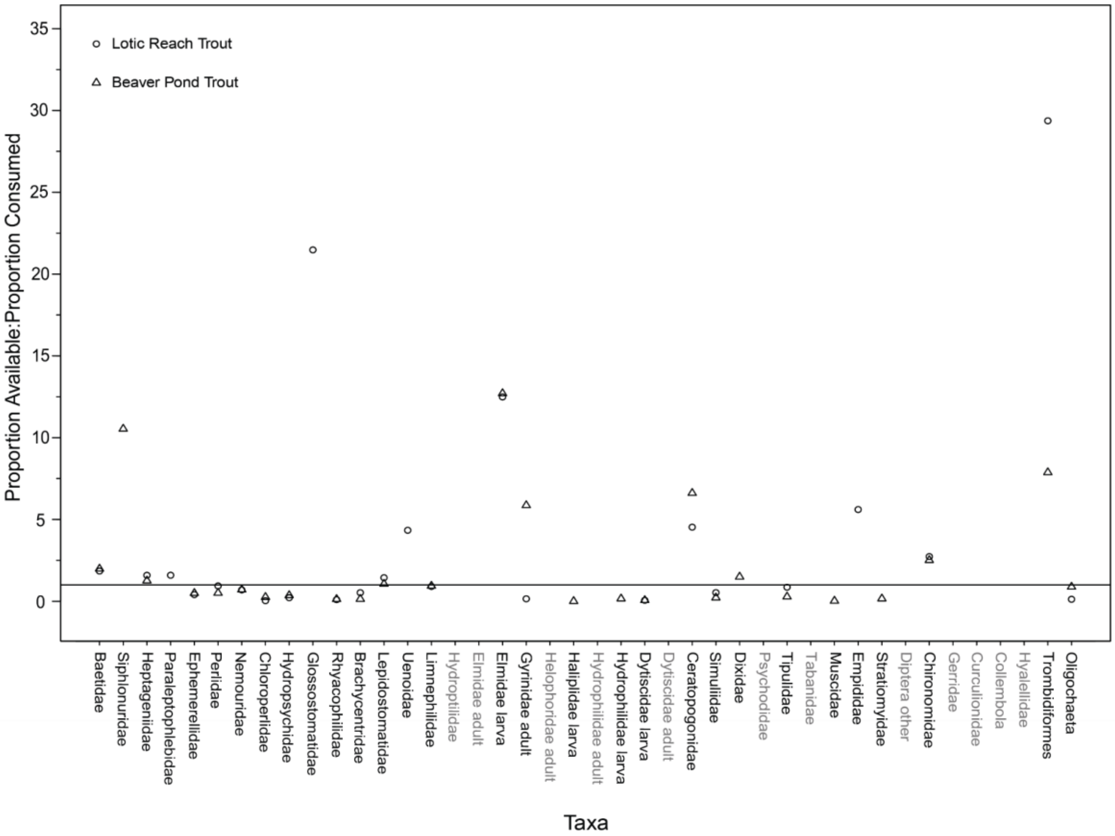


FIGURE 3.5. Prey as a ratio of availability to consumption by trout. Points on the line represent taxa eaten by trout in proportion to their availability in the environment. Points above the line were taxa more available than consumed, and points below the were taxa consumed more than they were available. Taxa in grey text were available in the environment, but not consumed by any trout.

habitat origin. For example, Gyrinidae beetles were only found in beaver ponds, though were only eaten by lotic-caught fish. Further, many of the taxa that were available but not eaten were Coleoptera only found within beaver ponds.

Isotopes

The carbon and nitrogen isotopic signatures of trout caught in ponds did not differ from trout caught in lotic reaches, except for BCT in Spawn Creek (Figure 6). Ellipses of average isotope values were oriented around the $\delta^{13}C$ and $\delta^{15}N$ signatures of trout from different habitats, and ellipse overlap was calculated. Beaver pond-caught and lotic-caught BCT ellipses in Spawn Creek were almost completely separated, with an overlap area of $6.072e^{-18}$. The $\delta^{15}N$ signature of BCT in Spawn Creek was 9.4% lower in pond fish (habitat: $F_{1,15} = 7.042$, $p = 0.018$), and the $\delta^{13}C$ signature was 6.8% higher in pond fish (habitat: $F_{1,15} = 6.923$, $p = 0.019$). Lotic-caught and beaver pond-caught brown trout in Spawn Creek had an overlap area of 0.8875, which was 33.1% of the beaver pond brown trout ellipse total area and 33.8% of the lotic brown trout ellipse total area. Brown trout signatures were not different by habitat for $\delta^{13}C$ (habitat: $F_{1,22} = 0.177$, $p = 0.678$) or $\delta^{15}N$ (habitat: $F_{1,22} = 2.989$, $p = 0.098$). Temple Fork trout (all BCT) had an overlap area of 1.455, which was 46.7% of the beaver pond trout ellipse, and 64.5% of the lotic trout ellipse. BCT signatures were not different by habitat for $\delta^{13}C$ (habitat: $F_{1,22} = 0.360$, $p = 0.554$) or $\delta^{15}N$ (habitat: $F_{1,22} = 0.609$, $p = 0.443$) in Temple Fork. Lastly, Right Hand Fork trout (all BCT) had an overlap area of 1.099, which was 53.2% of the beaver pond trout ellipse, and 35.1% of the lotic trout ellipse. BCT signatures were not different by habitat for $\delta^{13}C$ (habitat: $F_{1,22} = 0.003$, $p = 0.954$) or $\delta^{15}N$ (habitat: $F_{1,22} = 0.011$, $p = 0.919$) in Right Hand Fork.

Terrestrial diet items seemed to contribute more to trout isotopic signature than aquatic invertebrates (Figure 7). Terrestrial insects were not available for Right Hand Fork, thus aquatic organisms were the only prey modeled. The mean $\delta^{15}N$ values for terrestrial invertebrates were not statistically different between streams (ANOVA, $F_{1,22} = 0.042$, $p = 0.840$), and neither were the mean $\delta^{13}C$ values (ANOVA, $F_{1,22} = 0.017$, $p = 0.896$).

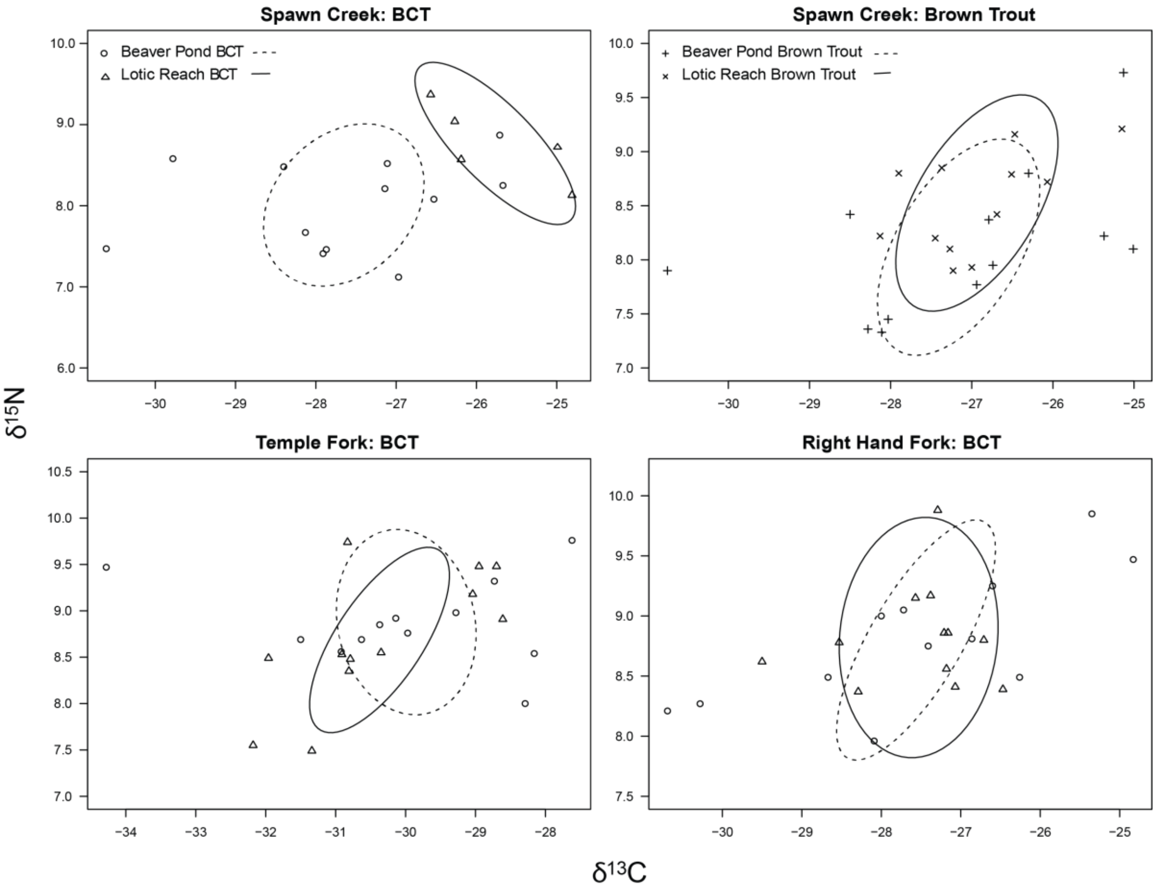


FIGURE 3.6. Carbon and nitrogen isotopic signatures of Brown trout, Bonneville cutthroat trout BCT) collected from beaver ponds and lotic habitats in three streams (Spawn Creek, Temple Fork, and Right Hand Fork) in northeastern Utah.

The mean δ^{15}N values for aquatic insects were not statistically different between streams (ANOVA, $F_{2,48} = 0.307$, $p = 0.737$), while the mean δ^{13}C values were significantly different by stream (ANOVA, $F_{2,48} = 3.679$, $p = 0.033$). A Tukey’s HSD revealed the difference to exist only between Spawn Creek and Temple Fork; Right Hand Fork’s aquatic prey values were not different from those at Spawn Creek or Temple Fork.

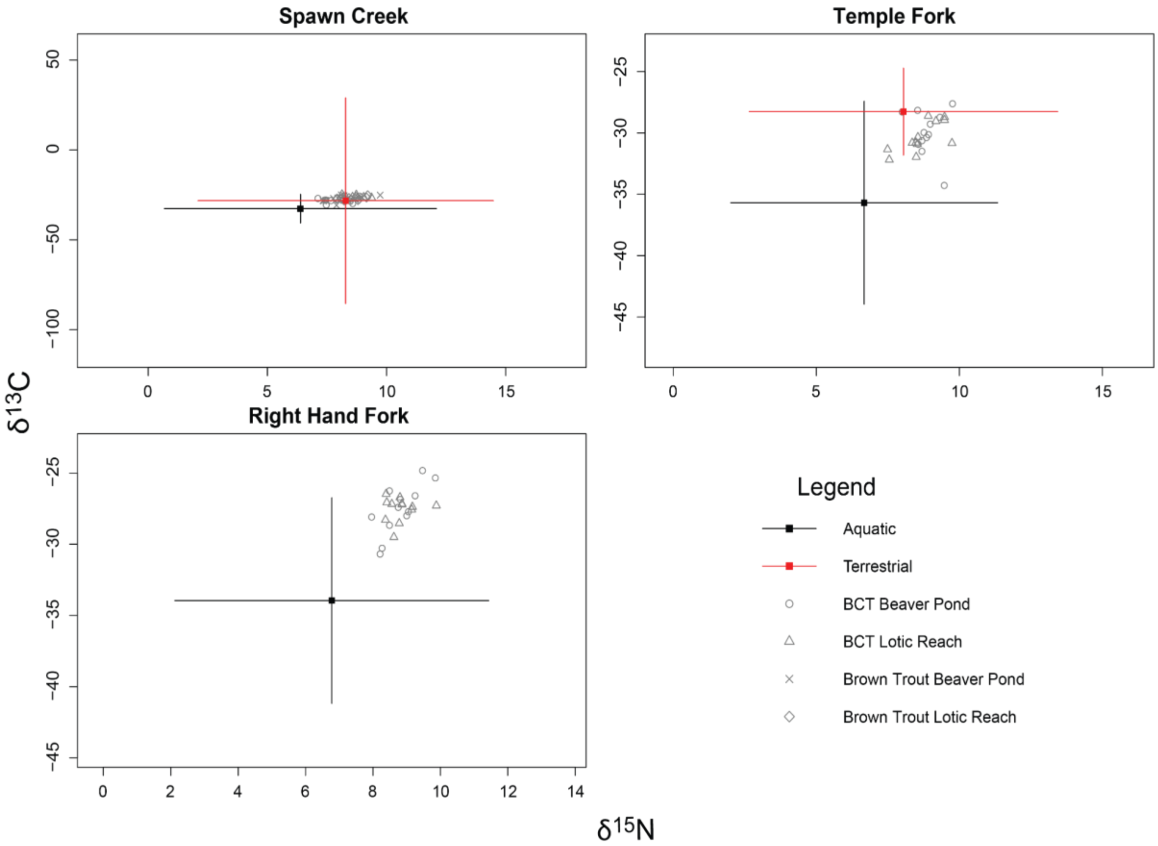


FIGURE 3.7. Carbon and nitrogen isotopic signatures of terrestrial invertebrates, aquatic invertebrates, Bonneville cutthroat trout (BCT) and Brown trout collected from Spawn Creek, Temple Fork, and Right Hand Fork.

Trout Growth

The mixed effects model output demonstrated a difference in fish size by habitat. Brown trout caught in beaver ponds were 28% longer than brown trout caught in lotic reaches (habitat: $F_{1,143} = 12.247$, $p < 0.001$; Figure 8). Brown trout length was also significant by stream (stream: $F_{2,143} = 5.860$, $p = 0.017$), but there was no interaction between habitat and stream (habitat*stream: $F_{2,143} = 0.133$, $p = 0.716$). Brown trout weight for fish caught in beaver ponds was 65% heavier relative to fish caught in lotic reaches (habitat: $F_{1,143} = 9.569$, $p = 0.002$; Figure 8). Weight was also significant by stream (stream: $F_{2,143} = 5.893$, $p = 0.016$), and there was no significant interaction between habitat and stream (habitat*stream: $F_{2,143} = 0.486$, $p = 0.486$). Body condition (Fulton's K) of brown trout was not different by habitat (habitat: $F_{1,143} = 2.336$, $p = 0.129$; Figure 8), or by stream (stream: $F_{2,143} = 0.110$, $p = 0.740$), and there was no interaction between habitat and stream (habitat*stream: $F_{2,143} = 0.155$, $p = 0.694$).

BCT total length was 14% longer for fish caught in in lotic reaches than caught in beaver ponds (habitat: $F_{1,802} = 32.981$, $p < 0.001$). Length was also significant by stream (stream: $F_{2,802} = 55.765$, $p < 0.001$; Figure 8), and there was an interaction between stream and habitat (habitat*stream: $F_{2,802} = 9.864$, $p < 0.001$). The interaction was attributed to a non-significant difference in fish length by habitat at Spawn Creek. BCT weight was 30% lower for fish caught in beaver ponds relative to fish caught in lotic reaches (habitat: $F_{1,802} = 33.303$, $p < 0.001$; Figure 8). Weight was also significant by stream (stream: $F_{2,802} = 147.548$, $p < 0.001$), and there was an interaction between stream and habitat (habitat*stream: $F_{2,802} = 11.226$, $p < 0.001$). The interaction was caused by this pattern only existing for Temple Fork; weights at Spawn Creek and Right Hand Fork were the same for lotic BCT and beaver pond BCT. Body condition of BCT was not different by habitat (habitat: $F_{1,802} = 2.083$, $p = 0.149$; Figure 8), or by stream (stream: $F_{2,802} = 0.050$, $p = 0.952$), and there was no interaction between habitat and stream (habitat*stream: $F_{2,802} = 0.161$, $p = 0.851$).

The growth rates of trout caught in beaver ponds and in lotic reaches were not different. For recaptured fish (all BCT), the specific growth rate did not differ by habitat (habitat: $F_{1,34} = 1.520$, $p = 0.226$). There were no differences by stream (stream: $F_{2,34} = 1.063$, $p = 0.357$), and there was no interaction between habitat and stream (habitat*stream: $F_{1,34} = 0.381$, $p = 0.541$). The specific growth rate of trout in cages was also not different by habitat (Figure 9). Specific growth was the same for beaver ponds and lotic reaches at Spawn Creek (habitat: $F_{1,7} = 3.706$, $p = 0.096$), Temple Fork (habitat: $F_{1,11} = 0.425$, $p = 0.528$), and Right Hand Fork (habitat: $F_{1,15} = 0.045$, $p = 0.835$). Temperature was not different between lotic cages and beaver pond cages (habitat: $F_{1,48} = 0.00$, $p = 0.987$), and neither was dissolved oxygen (habitat: $F_{1,18} = 0.677$, $p = 0.421$). The average water velocity was 78.3% lower at beaver pond cages than at lotic cages (habitat: $F_{1, 54} = 67.119$, $p < 0.001$). Characteristics differing between streams were temperature (stream: $F_{2, 48} = 230.833$, $p < 0.001$) and dissolved oxygen (stream: $F_{2,18} = 25.812$, $p < 0.001$). Temple Fork was approximately 2°C colder than both Spawn Creek and Right Hand Fork, and Right Hand Fork was approximately 0.5mg/L lower in dissolved oxygen.

DISCUSSION

We collected BCT and Brown trout of all size classes within both beaver ponds and lotic habitats. However, there was little indication that trout were exclusively using beaver ponds as foraging habitat. Diet results showed that trout collected from beaver ponds did not significantly differ in stomach contents or carbon and nitrogen isotopic signatures. Diets of trout collected from beaver ponds and lotic habitats contained few lentic taxa, suggesting that trout are not foraging in the benthic habitats of beaver ponds. In conjunction with our diet results, we found that fish collected from beaver ponds and lotic habitats did not differ in specific growth rates or body condition.

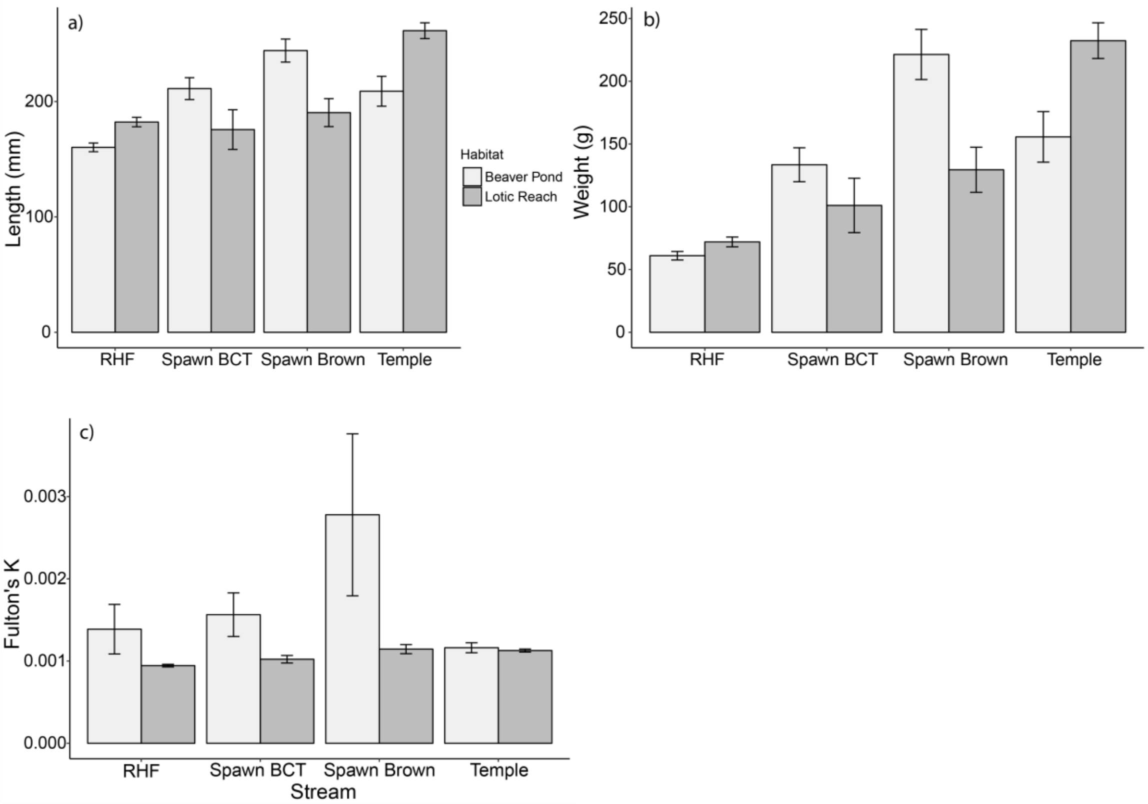


FIGURE 3.8. Differences in size and growth of Brown trout (Brown) and Bonneville cutthroat trout (BCT) trout collected from beaver ponds and lotic reaches in Spawn Creek (Spawn), Temple Fork (Temple), and Right Hand Fork (RHF). a) Trout total length, b) weight, and c) body condition measured as Fulton’s K.

Habitat Use and Community Structure

Both the mark recapture and non-invasive pit tag scanning provided some evidence of habitat fidelity, with approximately half of the recaptured fish reoccurring in the same pond over multiple sampling days. Although our methods prevented the identification of habitat preferences by trout, a recent study found that 68% of the steelhead trout occurring in beaver ponds showed affinity for that habitat, while fewer fish preferentially occupied runs (Wathen et al. 2018). Fish may occupy different habitats

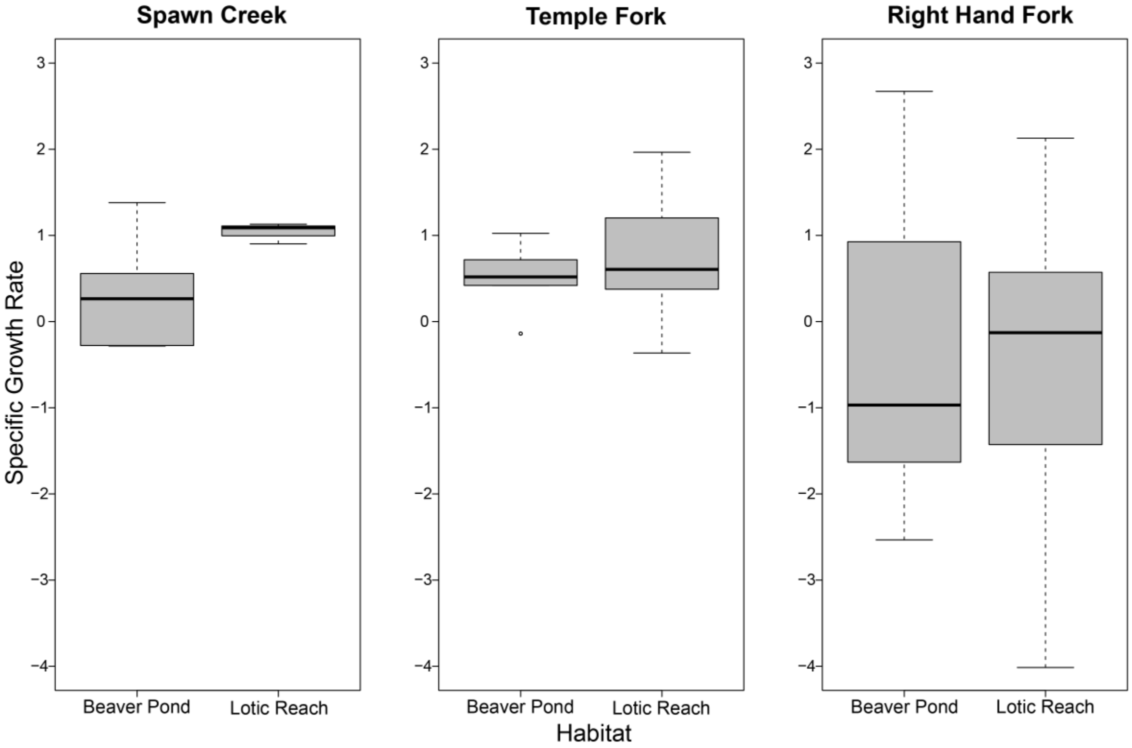


FIGURE 3.9. Specific growth rate of caged juvenile trout collected from beaver ponds and lotic habitats in Spawn Creek (brown trout only), Temple Fork (Brown trout only), and Right Hand Fork (Bonneville cutthroat trout only).

to avoid intra- or inter-specific competition. For example, Rosenfeld and Boss (2001) found young-of-year cutthroat trout seek out small pool habitats, while larger cutthroat trout use larger pools as resting habitat (2001). However, in beaver ponds in our study system we found trout of all size classes, suggesting that beaver ponds are not acting as a niche refuge for specific size classes.

Our study focused on how trout caught in beaver ponds and lotic habitats differed over summer months and during the day. Trout, however, may use different habitats depending on the time of day and season (Bonneau and Scarnecchia 1998; Hilderbrand and Kershner 2000; Wathen et al. 2018). Several studies have suggested that beaver ponds are an important overwintering habitat for fish. Deep beaver ponds do not ice completely through, leaving space underneath the ice layer for fish to survive the winter (Collen and Gibson 2000). In the spring beaver ponds may provide a flow refuge, protecting fish from large spring runoffs (Kemp et al. 2012). Finally, during fall months, beaver ponds may collect allochthonous leaf litter (Hodkinson 1975; Naiman and Melillo 1984; Butler and Malanson 1995), which could stimulate higher invertebrate biomass (Cummins et al. 1989; Hieber and Gessner 2002) providing a large food base for fish. To understand fish use of beaver pond habitats, further studies should investigate habitat use and preference over different diel and seasonal periods.

Trout Diets

Other research on Spawn Creek, Right Hand Fork, and Temple Fork has shown the macroinvertebrate community differs between beaver pond and lotic habitats (Washko et al. in review/Chapter 2). Although some fish showed a preference for pond habitats, we observed no difference in the stomach contents or prey selectivity by fish collected from ponds versus those collected in lotic reaches, regardless of the trout species examined. In addition, there was no significant difference between pond-caught and lotic-caught fish $\delta^{13}C$ or $\delta^{15}N$ isotopic signatures. Collectively, these results suggest fish collected from the two habitats were utilizing similar food resources over the summer months, and their trophic position was similar.

Our results suggest beaver ponds are not utilized as primary foraging habitat. Lentic taxa, which represented the highest proportion of macroinvertebrates in beaver ponds, only comprised 11% of fish diets by mass. One reason why fish may not be utilizing beaver ponds as foraging habitat is beaver ponds had 75% fewer macroinvertebrates m^2 compared to lotic reaches, and beaver pond macroinvertebrate biomass was on average 90% lower than that of lotic reaches (Washko et al. in review). Further, the proportion of burrowing taxa was also 174% higher in beaver ponds than in lotic reaches, meaning much of the prey within beaver ponds may be inaccessible to trout (Washko et al. in review). However, studies conducted in other regions reported higher biomass and/or density of macroinvertebrates in beaver ponds (Gard 1961; McDowell and Naiman 1986; Anderson and Rosemond 2010). If prey availability is the primary driver behind whether trout use the ponds as foraging habitat, then beaver ponds in other regions may serve as more important foraging grounds than what was observed in our study, where food may not be limiting (Budy et al. 2007).

Fish are mobile individuals, and diet items can be linked to a diversity of habitats utilized by a fish. As a result, fish that primarily reside in ponds may travel to lotic zones where the density of drifting macroinvertebrates. Migration between habitats may explain why fish caught in ponds and fish caught in lotic habitats did not differ in diets or stable isotopic signature. Furthermore, trout inhabiting ponds could make use of the drift entering beaver ponds from the lotic regions above. If fish occupying ponds are primarily consuming organisms that drift into the pond from the lotic regions above, this may explain why we observed no difference between diets or isotopic signatures of pond-caught and lotic-caught trout, despite some evidence that certain fish may prefer pond habitat. (differences in Spawn Creek BCT isotopic signatures may be due to under-sampling lotic BCT (n=5)). For example, in another tributary to the Logan River, BCT in beaver ponds were observed to consume prey in proportion to what was available in the drift coming into the beaver ponds. Further, the drift entering beaver ponds (18.9 organisms/m^3) was not substantially different in density than the drift in high and low-gradient lotic sections (26.5 and 17.2 organisms/m^3, respectively; Hilderbrand & Kershner, 2004).

Trout Growth

We observed no difference in body condition or specific growth rates between recaptured fish in ponds and lotic reaches. This could be due to short duration between sampling events, the first being in July and the second in September. Our caging study also showed no difference in specific growth rates for young trout. However, negative growth rates expressed by several fish suggest a caging effect. Cages may have resulted in high stress and reduced growth as a result of a limited ability to seek shelter, the stress of isolation (trout were alone in each cage), and possible barring of food. We predicted trout in beaver ponds would have higher specific growth rates due to lower water velocities, and possibly favorable thermal regimes (Naiman et al. 1988; Johnson et al. 1992; Gurnell 1998; Niles et al. 2013). While the water velocity was 78.3% lower in beaver ponds, the average temperature was not significantly different from in lotic reaches. Since the average temperature in lotic reaches and beaver ponds is the same, though may be more variable within beaver ponds than we measured (Majerova et al. 2015), trout may be tolerating a higher velocity habitat as a tradeoff for better foraging. Fish in higher velocity habitats but encountering more prey may have similar growth to fish in lower velocity beaver ponds consuming less prey. As a result, the ‘optimal’ habitat may be mixed use of beaver ponds and lotic reaches. Previous work in the Logan River watershed found most trout inhabited lower-velocity areas at night and higher-velocity areas during the day, postulating that they were feeding during the daylight hours

(Hilderbrand and Kershner 2000). These results indicate beaver ponds may provide important resting places for trout when conditions are too dark to forage.

The size of trout in each habitat type varied by species. Brown trout captured within beaver ponds were larger by both length and weight relative to Brown trout caught within lotic reaches. In Europe, larger brown trout inhabited beaver ponds while smaller brown trout resided in lotic reaches (Bylak et al. 2014). BCT caught in lotic reaches were longer than BCT caught in beaver ponds, but only for Temple Fork and Right Hand Fork, where brown trout were largely absent. Larger BCT in lotic reaches was surprising considering cutthroat trout prefer deeper water with age (Bisson et al. 1988), and low-velocity habitats are energetically necessary for all life stages of cutthroat trout (Rosenfeld and Boss 2001). Brown trout are thought to be largely epibenthic feeders, whereas BCT feed mainly on drifting prey (McHugh et al. 2008). Therefore, the feeding strategy of brown trout may allow them to reach larger sizes in ponds.

Conclusion

Our study showed that fish captured in beaver ponds and lotic reaches of Logan River tributaries showed similar diets and growth rates. Overall, this suggests that at the broad habitat scale the construction of beaver ponds may have little effect on the structure of trout communities utilizing lentic and lotic habitats. However, our study design contained several limitations with our ability to discern habitat preference by fish and to directly link community difference in fish to beaver ponds. To better understand the effects of beaver dams on fish habitat use, streams without beaver activity should be compared to highly dammed systems (such as the sites discussed here). Beaver ponds are highly variable in shape, size, and content, which makes defining their limits difficult.

Studying fish habitat use on a microhabitat scale, within and outside of beaver-impounded areas, may provide insight to water velocities, temperatures, and prey encountered by fish. There may be uninvestigated tradeoffs trout face in this system that govern beaver pond use in conjunction with possible refugia and foraging, such as predation risk between habitats (Kruzic et al. 2001). As restoration efforts using beaver become more popular, our study suggests trout adaptations to beaver-created habitats may allow them to use both lotic and beaver pond habitats to their advantage.

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CHAPTER 4

CONCLUSION

Beavers are expected to continue recolonizing North America, and understanding how their stream engineering can affect aquatic communities will inform stream management and restoration efforts, including beaver introductions. The aim of this thesis was to determine how aquatic macroinvertebrate and fish communities are using habitats created by beavers.

Chapter 1 provided background to my thesis. I first described the history of the North American beaver and how beavers change streams physically. Next, I predicted how changes to stream structure might affect macroinvertebrate communities based on freshwater invertebrate life history traits. Lastly, I predicted how beaver effects on the physiochemical and biological characteristics of streams might affect fish, specifically trout. My hypotheses concerning the effects of beaver on macroinvertebrates and trout were then tested in Chapters 2 and 3.

In Chapter 2, I assessed how the macroinvertebrate communities of beaver ponds and lotic reaches differ, which demonstrated how beaver-driven alterations in habitat can result in changes to community structure. The density and biomass of dominant mobility groups and functional feeding groups differed between lotic reaches and beaver ponds. My results in northeastern Utah beaver ponds agree with studies conducted on the Eurasian beaver (*Castor fiber*) in Europe, which found that beaver ponds had more predators and gatherers, and fewer scrapers and filterers. Macroinvertebrate richness was also lower in beaver ponds, as was overall macroinvertebrate biomass and density. Overall, my results suggest that in northeastern Utah, beaver activity alters the structure and functional traits of the macroinvertebrate community. However, my results differed from previous work conducted in other regions of North America. These previous studies found higher densities of macroinvertebrates within beaver ponds (Huey & Wolfrum, 1956; McDowell & Naiman, 1986). Variation in beaver pond macroinvertebrate density and biomass suggests there may be regional differences in the way beavers influence macroinvertebrate communities. These macroinvertebrate differences likely have profound impacts on ecosystem functioning and on fish foraging.

Having identified beaver-driven changes in habitat structure and the macroinvertebrate community, linking these changes to ecosystem function would be a fruitful topic for future research. While assumptions can be made about ecosystem function based on the aquatic invertebrate communities present in these systems, detritus availability and breakdown data, as well as primary production data would help determine whether beaver-mediated changes to biotic communities affect ecosystem functioning of streams. Further, sampling the macroinvertebrate taxa of sub-habitats within lotic reaches and beaver ponds may increase the resolution of changes to the macroinvertebrate community. The possibility of different feeding groups on woody structures (such as the dam itself), at the upstream entrance, within the water column, and at different pond depths may demonstrate gradients of functional traits, and expose more taxa specific to certain microhabitats created by beaver dams. Taxa specializing in lentic habitats may be indicative of functional attributes largely absent within lotic reaches, contributing to differences in ecosystem function between habitats.

In Chapter 3, I compared the foraging, growth, and size of trout caught within beaver ponds to trout caught within lotic reaches. I also measured how often individual trout were found occupying the same habitat type. Some trout in this system were seen within beaver ponds on multiple occasions, and always within the same beaver pond as previously captured. Repeated use suggested some site and habitat fidelity, though the sample size was limited. Trout were scanned with a mobile antenna instead of passively, which led to difficulty in obtaining data as the fish were disturbed by movement of the antenna through the water, and proximity of the fish to the antenna needed to be within 30cm. Under-sampling of trout within beaver ponds may mean trout scanned were not representative of the entire population, and trout that are more mobile could have been missed. In addition, the use of a mobile antenna prevented the detection of fish that may have moved between the two habitats.

Stomach content and stable isotope analyses revealed that trout caught in beaver ponds and trout caught in lotic reaches had similar diets. Trout in both habitats consumed mostly terrestrial invertebrates and lotic macroinvertebrates, with lentic macroinvertebrates constituting only a small proportion of the diet. Further, I demonstrated that trout from both habitats had the same growth rate and body condition. However, the size and size structure of trout caught varied by habitat. While all sizes of trout were found in both habitats, I observed differences in the average lengths and weights of trout collected in beaver ponds compared to those collected in lotic habitats. Brown trout were larger within beaver ponds, while Bonneville cutthroat trout were generally larger within lotic habitats. These results suggest trout size structure differences between beaver ponds and lotic reaches are driven by physical or metabolic aspects of beaver ponds rather than by consumption of lentic prey.

A main limitation of the trout study was my inability to directly assess habitat preference. Future studies should aim to install PIT tag antenna cables at the upstream entrances to ponds to record how many fish and which individuals (therefore species, size, etc.) are utilizing beaver ponds, and for how long and at what time of day. While assumptions about habitat use can be made based on foraging and growth data, trout movement data is needed to determine site fidelity and habitat preference. Lastly, a comparison of streams with and without beaver activity would better demonstrate overall effects on fish, as fish are likely moving in and out of beaver ponds. The mosaic of habitat heterogeneity in beaver-altered systems may affect fish in ways that cannot be measured by studying both lotic and beaver pond habitats within the same stream.

A limitation for understanding trout diets was the omission of macroinvertebrate drift samples in favor of benthic macroinvertebrate samples. Trout are suspected to forage largely on drifting macroinvertebrates (McHugh *et al.*, 2008). To improve our understanding of how beaver activity affects fish foraging, future efforts should include measuring the quantity and assemblage of macroinvertebrate drift within beaver ponds and lotic reaches, as well as quantifying the terrestrial invertebrate input to each habitat. These factors may reveal how trout in this system are feeding, especially given Brown trout are largely epibenthic foragers and Bonneville cutthroat trout feed primarily on drift (McHugh *et al.*, 2008).

Beavers are known as ecosystem engineers, physically re-shaping streams into novel habitats. In the case of northeastern Utah streams, beaver modifications of the stream channel affected two levels of the in-stream community: macroinvertebrates (primary and secondary consumers) and trout (top predators). My study suggests that beaver-mediated changes to the streams can have large influences on the structure and composition of the macroinvertebrate community. Conversely, at the habitat scale trout appeared less affected by beaver-mediated changes. Studies like mine should be conducted in other locations to continue building on the scientific understanding of the changes in community structure and function following beaver reintroduction.

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