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THE INFLUENCE OF AN ECOSYSTEM ENGINEER ON NUTRIENT SUBSIDIES AND FISH INVASIONS IN SOUTHWESTERN MONTANA

By

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The influence of an ecosystem engineer on nutrient subsidies and fish invasions in southwestern Montana

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Streams and associated riparian zones are among the world's most highly valued yet threatened ecosystems. Interest in using the ecosystem engineering behavior of beaver to meet watershed conservation goals is becoming more pervasive, owing to substantive work documenting the physical effects of beaver impoundments on freshwater ecosystems. However, it is unclear how beaver modify ecological processes linking abiotic factors to changes in the surrounding biotic community. I investigated how beaver impoundments influence local food web processes, as well as impact native fish species threatened by nonnative invasions.

I showed that beaver impoundments enhanced aquatic resource availability to terrestrial consumers. Beaver impounded watersheds had increased densities of emerging aquatic macroinvertebrates and higher levels of aquatic carbon in terrestrial consumer tissues, resulting in higher terrestrial consumer abundances.

Beaver impoundments also had measurable effects on invasion dynamics between nonnative brook charr and native cutthroat trout populations. Brook charr are native to the eastern U.S., and are a key factor in native cutthroat declines in western watersheds. Streams with beaver had potential negative impacts for cutthroat, with higher brook charr densities, and increased spatial overlap between these species. In contrast, young-of-the-year cutthroat in invaded streams maintained high growth rates with beaver present, but showed growth reductions without beaver. Thus beaver conveyed both negative and positive impacts to cutthroat trout.

At the population level, I found that cutthroat in the non-beaver invaded watershed exhibited low survival rates, negative population growth, and a short median time to extinction. With beaver present in invaded streams, cutthroat exhibited 40 % higher survival rates relative to the non-beaver control. This led to cutthroat population growth rates 5 – 20 % higher than in non-beaver streams, with longer median times to extinction. Therefore, beaver impoundments had positive implications for cutthroat persistence in brook charr invaded streams.

My research links the habitat altering effects of beaver to changing ecological processes that influence community and population structure of other elements of the system, with implications for persistence of native species. Understanding the ecosystem effects of a highly interactive species like beaver is crucial to predicting repercussions of using beaver in a restoration context.

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CHAPTER 1

INTRODUCTION AND OVERVIEW

Freshwater streams are dynamic ecosystems, influenced by a multitude of abiotic and biotic factors working synergistically to define watershed habitat characteristics (Moore 2006). A rich body of theory, developed over the past 40 years (e.g. Junk et al. 1989; Stanford et al. 2005; Stanford & Ward 1993; Vannote et al. 1980), has advanced our understanding of how physical and biological processes can control the characteristics of aquatic systems, resulting in a complex mosaic of heterogeneous habitat patches within stream watersheds. Biota that directly or indirectly regulate resource availability to other organisms through the modification, maintenance, or creation of habitats, are termed ecosystem engineers (Jones et al. 1997). When beaver (*Castor* spp.) impound water through damming and feeding behaviors, they are often considered the quintessential ecosystem engineer. Beaver drive an extensive watershed disturbance regime (McKinstry & Anderson 2002) through the creation of lentic habitat, triggering fundamental changes in channel geomorphology, hydrology and nutrient cycling (Naiman et al. 1988; Naiman & Melillo 1984; Naiman et al. 1986). Thus, beaver naturally perform many of the functions that we attempt to engineer during restoration of degraded stream ecosystems.

Severe overexploitation of global beaver populations until the early 20th century likely simplified many freshwater ecosystems, engendering large changes in ecological processes and stream habitat characteristics. Following cessation of harvest, beaver are again becoming abundant across their former ranges in Eurasia and North America (Rosell et al. 2005). Population increases of a species capable of significantly altering and reconnecting natural ecosystem processes is of considerable scientific and management interest (Rosell et al. 2005), spurring on reintroduction programs throughout Europe (Jones et al. 2009), and leading to the incorporation of beaver into some aquatic restoration plans in North America (Pollock et al. 1995).

An intriguing facet of ecosystem engineers is their potential to link many levels of biological organization within an ecosystem: they can influence individuals at the physiological and behavioral levels, which has repercussions for populations and communities, and culminates with changes at the landscape scale (Wright & Jones 2006). Research of beaver engineering has typically concentrated on shifts in system geomorphology and hydrology (Naiman et al. 1986), sediment characteristics (Rosell et al. 2005), and nutrient cycling (Johnston & Naiman 1990). These changes in physical processes have been associated with altered riparian successional dynamics, increased invertebrate biotic productivity, and positive effects on diversity of several animal species (Collen & Gibson 2001; Naiman 1994; Naiman et al. 1988; Naiman et al. 1986; Schlosser 1995). However, less is known about how beaver influence population or community structuring processes that produce these patterns. Some research suggests that beaver ponds augment breeding habitat availability for amphibian species, thereby increasing occurrence (Popescu & Gibbs 2009; Stevens et al. 2007), and supporting richer amphibian assemblages on the landscape than without beaver ponds (Cunningham et al. 2007). It is however, unclear how beaver regulate fundamental community processes of predation, competition, or resource cycling between habitats. Ecosystem engineers that influence key community interactions on the landscape will be important in structuring communities. It is therefore essential that we consider these processes through the lens of species assemblages (Crain & Bertness 2006).

Establishing the effects of beaver on other components of the stream community allows us to assess the utility of beaver as potential restoration agents. Conservation of freshwater ecosystems requires a sound understanding of the biophysical linkages between geomorphic form, flow regime, and watershed ecology (Montgomery et al. 2003). Watershed restoration practices seek to reconnect physical and biotic linkages across habitats, in order to sustain intact and functioning food webs, and to promote the persistence of native species in the face of invasive species (Jackson et al. 1995; Montgomery et al. 2003).

Management efforts using beaver should be based on a sound scientific understanding of the ecological mechanisms operating within the system. Beaver are naturally a ubiquitous element of most Holarctic freshwater ecosystems and as such identifying their role in ecological processes that may influence conservation of these ecosystems is highly desirable. I therefore set out to elucidate the impacts of beaver activity on aspects of freshwater ecosystems of immediate conservation concern. I specifically examined two pressing issues. In Chapter 2, I examined the influence of beaver on stream invertebrate composition, emergence, and nutrient subsidization of terrestrial systems. In Chapters 3 and 4, I mechanistically examined how beaver affect the habitat, stream distribution, and individual and population impacts to native fish species in the face of exotic invasions.

The basic components of food webs—nutrients, detritus, and organisms—naturally span spatial boundaries (Polis et al. 1997). It is well established that allochthonous inputs of terrestrial organic matter act to subsidize stream systems (e.g. England & Rosemond 2004), with major impacts on freshwater biotic productivity and biodiversity (Naiman et al. 1986; 1988; France 1997; Collen and Gibson 2001). Stream aquatic nutrients have also been shown to seasonally subsidize terrestrial food webs (Baxter et al. 2005; Nakano & Murakami 2001). Ecologists recognize the importance of energy and nutrient transfers across system boundaries (Polis et al. 1997), which can lead to an increased diversity and abundance of consumers in receiving systems (e.g. Baxter et al. 2004; Power 2001; Stapp & Polis 2003). Using stable isotopes of carbon and nitrogen, studies have demonstrated that terrestrial habitats with a relatively poor resource base can support higher densities of terrestrial consumers in the presence of stream and marine subsidy than would otherwise be possible (e.g. Darimont & Reimchen 2002; Hilderbrand et al. 1999; Roth 2003; Stapp & Polis 2003). In Chapter 2, I describe the mechanisms by which beaver impoundments change nutrient dynamics and terrestrial community structures through enlargement of aquatic resource sheds. Specifically, I found that beaver ponds produced substantially higher emergence densities of aquatic macroinvertebrates relative to non-beaver stream sites, and that these served as link organisms, enlarging the spatial extent of aquatic resources by dispersing more aquatic nutrients, farther into the terrestrial food web.

In addition to shaping terrestrial communities, beaver impoundments may alter aquatic communities. For the second part of my dissertation, I examined the role that beaver play in fish invasion ecology. The effects of beaver impoundments on fish assemblages can be highly variable among and within regions, with results affected by beaver pond age, position in the watershed, the original (pre-beaver) conditions and fish species present (Collen & Gibson 2001; Snodgrass & Meffe 1998). Hence, patterns and mechanisms associated with how beaver influence fish community structure, abundance and distribution are unclear. Formation of pool habitat may increase water temperatures, prey availability to fish, and juvenile rearing habitat for many species, with important effects on diversity, growth rates, and relative abundance of species such as Atlantic salmon (*Salmo salar*), brook charr (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and minnows (*Phoxinus phoxinus*) (Hagglund & Sjoberg 1999; Scruton et al. 1998). In addition, beaver have been shown to provide critical winter habitat for sensitive stream fishes including cutthroat trout (*Oncorhynchus clarkii*) and bull trout (*Salvelinus confluentus)* (Jakober et al. 2000). However, these positive changes in stream habitat structure for native fish species may also benefit exotic species, fuelling fears that beaver could exacerbate the severity of nonnative freshwater invasions. Introduced fishes that become invasive are one of the most serious threats to native fish populations (Allan & Flecker 1993; Peterson & Fausch 2003). Brook charr, a native of eastern North America, were introduced into western watersheds during the 19th century, and have subsequently expanded throughout western montane coldwater streams (Kennedy et al. 2003). In many parts of the inland western United States brook charr invasions, in conjunction with habitat destruction and genetic introgression with exotic rainbow trout (*Oncorhynchus mykiss*), have resulted in the extirpation of cutthroat trout from at least 95% of their historic ranges (Kennedy et al. 2003; Young 1995). In Montana’s streams, water temperature, fine sediment, and the abundance of pools and woody debris have all been correlated with brook charr invasion, and the concomitant displacement of westslope cutthroat trout (Shepard 2004). These habitat factors implicate the presence of beaver in a watershed as facilitators of brook charr invasion.

It is well documented that brook charr tend to monopolize lower stream elevations, displacing cutthroat to colder refuges in colder headwater reaches of invaded watersheds (Dunham et al. 2002; Fausch 1989; Paul & Post 2001; Rieman et al. 2006). Indeed, many of the remaining cutthroat populations within the upper Missouri basin are now isolated in high elevation headwater habitats (Shepard et al. 1997). Gradual upstream declines in growth rates associated with declining water temperatures may define the upstream limit for brook charr invasions of coldwater stream systems (Adams 1999). However, beaver ponds may allow brook charr to circumvent their upstream minimum temperature threshold through provision of warmer habitats, particularly in middle and higher elevations of montane streams (Adams 1999). Thus beaver ponds could function as reproductive source areas from which to colonize high elevation, colder sink sections of watersheds (Schlosser 1995). In addition to altering the invasion success of brook charr, beaver ponds may influence the outcome of species interactions between cutthroat and brook charr. If beaver pond habitat increases brook charr abundance and distribution in a stream, then their negative impacts on westslope cutthroat may be larger. Increased temperature has also been implicated in enhancing the ability of brook charr to outcompete cutthroat trout (De Staso III & Rahel 1994; Novinger 2000). Therefore if beaver ponds increase stream temperature to a degree that has been shown to affect the interspecific competitive ability of cutthroat trout with brook charr (Thomas 1996), this may confer brook charr with a greater competitive advantage. Chapter 3 examines how beaver mediate the effects of brook charr invasion on cutthroat trout stream distributions and somatic growth rates. I found that in watersheds with beaver impoundments, cutthroat trout exhibited increased stream distributions and higher somatic growth rates. Chapter 4 expands upon these observed differences in cutthroat distributions and growth rates, exploring how beaver alter the impacts of brook charr invasion on cutthroat trout demography and extinction risk. Cutthroat populations in beaver streams had higher survival rates, higher growth rates, and hence reduced extinction risk relative to a non-beaver control.

There are therefore myriad ramifications of beaver activity for freshwater ecosystems, and several of these have been used to justify their active transplantation into degraded ecosystems of the Pacific northwest (Pollock et al. 1995). This represents a cost-effective and innovative watershed management strategy, perhaps offering a more environmentally benign and sustainable method of mitigating wetland loss in the face of declining annual streamflow (Luce & Holden 2009) and ultimately a changing climate (Hood & Bayley 2008). However, we must inform management actions using a sound scientific understanding of how such systems operate so that we maintain environmental quality and functional food webs, without exacerbating threats from exotic species. My dissertation therefore addresses deficiencies in our understanding of the role that beaver disturbance plays in these basic ecosystem processes of conservation relevance.

CHAPTER 2
BEAVER EXPAND AQUATIC CARBON RESOURCE SHEDS

Abstract

Fluxes of resource subsidies between aquatic and terrestrial habitats can be modified by disturbance events, producing measurable effects on consumer dynamics in receiving systems. Beaver (*Castor canadensis*) considerably alter stream habitat characteristics and aquatic resource availability. However, it is unclear how the quantity and areal dispersal (resource shed) of aquatic nutrients translate to terrestrial systems. I examined how beaver influence macroinvertebrate emergence patterns, and determined impacts on focal terrestrial consumers. I examined differences in abundance and community composition of aquatic macroinvertebrates, as well as differences in the abundances of focal terrestrial consumers (Lycosid spiders and *Peromyscus maniculatus*) between beaver and non-beaver sites. I used stable isotope analysis to identify feeding relationships at these sites, and to track the flow of carbon from autotrophs to heterotrophic consumers. Beaver systems had higher abundances and emergence densities of Diptera and Trichoptera than non-beaver sites. Beaver sites also had 55 % and 75 % higher abundances of Lycosids and *P. maniculatus,* respectively. Lycosids showed enrichment in aquatic carbon 75 % further from the water's edge at beaver sites. I document how beaver habitat modification enhances macroinvertebrate abundances and emergence distances from the water's edge, leading to increased subsidization of focal terrestrial consumers. This work defines a novel example of a ubiquitous agent of landscape disturbance leading to alterations in nutrient subsidies in small stream ecosystems. I demonstrate that beaver have a major role in ecosystem functioning, providing direction for management efforts that seek to maintain natural ecosystems in the face of drying climatic conditions.

Introduction

The importance of allochthonous subsidization of aquatic biota is well documented (Cummins et al. 1973; Eberle & Stanford 2009; Fisher & Likens 1973; Mason & MacDonald 1982; Nakano et al. 1999; Wallace et al. 1997, 1999), and is a crucial component of early models of longitudinal biotic and abiotic gradients in river systems (Vannote et al. 1980). As our conceptual understanding of aquatic systems has developed (see Junk et al. 1989; Stanford et al. 2005; Stanford & Ward 1993), it has become clear that nutrient subsidies are not unidirectional, but rather follow omnidirectional resource gradients (e.g. Nakano & Murakami 2001). This has led to a burgeoning body of research elucidating the importance of reciprocal energy transfers between aquatic and terrestrial food webs, which have the capacity to influence growth rates, population sizes, and community structure of receiving systems (e.g., Baxter et al. 2005; Baxter et al. 2004; Burdon & Harding 2008; Darimont & Reimchen 2002; Gray 1993; Hilderbrand et al. 1999; Iwata et al. 2003; Kato et al. 2003; Nakano & Murakami 2001; Power 2001; Richardson et al. 2009; Roth 2003; Stapp & Polis 2003). Trans-ecotone fluxes inextricably bind aquatic and terrestrial habitats together, and disruption or alteration of these fluxes are likely to propagate widely throughout the linked food webs.

Research is beginning to elucidate the role of ecological disturbances in mediating trans-ecotone fluxes. Disruption of subsidies has been associated with several anthropogenically related disturbances. For instance, exotic species invasions can intercept terrestrial subsidies to aquatic habitats, leading to trophic cascades that ultimately reduce riparian consumer densities (Baxter et al. 2004), as well as fundamentally changing terrestrial nutrient dynamics and hence influencing plant productivity and composition (Maron et al. 2006). Deforestation has been shown to weaken terrestrial-aquatic linkages through reductions in allochthonous organic material entering the aquatic system, which support native stream food webs (England & Rosemond 2004). In a similar fashion, natural flood disturbance has been shown to influence cross-habitat nutrient flux. Varying flood magnitude modifies the degree of aquatic prey subsidization to riparian fishing spiders, whereby a trade-off between spider habitat quality (which increases with high magnitude flood) and subsidy availability (highest at low flood magnitude) causes fishing spiders to attain peak biomass at intermediate levels of disturbance (Greenwood & McIntosh 2008). Whilst there are relatively few known examples of natural disturbance influencing cross-habitat nutrient flux, it is likely that other periodic disturbances affect this integral component of ecosystem dynamics.

As a ubiquitous and strongly interactive element on the North American continent, beaver (*Castor canadensis*) drive a natural disturbance regime that has the potential to have large effects on these nutrient fluxes. Beaver feeding and dam-building behaviours have considerable effects on freshwater ecosystems (Collen & Gibson 2001; McKinstry & Anderson 2002). Beaver dams create lentic habitat in otherwise lotic systems, increasing landscape heterogeneity (Johnston & Naiman 1990) by driving changes in channel geomorphology and hydrology (Naiman et al. 1986), sediment characteristics (Rosell et al. 2005), and nutrient cycling (Coleman & Dahm 1990). These effects have been found to enhance algal production (Coleman & Dahm 1990), and modify riparian vegetation structure and dynamics (McKinstry & Anderson 2002). In addition to impacting riparian successional processes, and hence the structure and species composition of riparian plant communities (e.g., Huntly 1995), beaver have numerous other and far-reaching effects in the terrestrial ecosystem (for a full review see Rosell et al. 2005). For example, increased production of cottonwood (*Populus* spp.) chemical defence compounds through beaver feeding counterintuitively acts to stimulate terrestrial leaf beetle (*Chrysomela confluens*) production (Martinsen et al. 1998). Beaver also shape the dynamics of many bird species through the provision of high levels of invertebrate production (McKinstry et al. 2001), cover, and habitat (Carr 1940).

In ponds formed by beaver, macroinvertebrate community structure transitions from lotic to lentic assemblages (Harthun 1999; Margolis et al. 2001; McDowell & Naiman 1986; Sprules 1941), whilst invertebrate communities associated with the dam structure itself can exhibit assemblages typical of a more free-flowing environment (Clifford et al. 1993). Indeed, diversity of invertebrate fauna can be highest in the dam structure relative to adjacent lotic and beaver pond habitats of the stream, with beaver dams in Germany exhibiting median invertebrate emergence densities 3.2 and 5.5 times higher than in stream and pond sections respectively (Rolauffs et al. 2001). However, it is unknown how these increases in macroinvertebrate emergence densities influence trans-ecotone subsidies to the terrestrial system.

The areal extent to which resources disseminate from a given source are defined as their “resource shed”. The cross-habitat movement of aquatic resources via macroinvertebrates provides an intuitive mechanism for how aquatic productivity, altered by beaver activity, may change the size of aquatic resource sheds. The goals of this study were to ascertain how beaver disturbance affects trans-ecotone transport of aquatic carbon via aquatic invertebrates, and to measure concomitant changes in terrestrial consumer food sources and biomass. I tracked aquatic carbon flow through focal species (Figure 2.1) to assess how prominent members of the terrestrial food web may be influenced by beaver disturbance. Insectivorous wolf spiders (family Lycosidae) provided an abundant and easily captured taxon that have been shown to be important terrestrial consumers of aquatic macroinvertebrate prey (e.g. Paetzold et al. 2005). Similarly, omnivorous deer mice (*Peromyscus maniculatus*) were targeted due to their prominent role in terrestrial food webs. In addition to being a major prey item, voracious seed predators, and disease reservoir (Pearson & Callaway 2006), these rodents are also highly mobile and have a great reproductive potential, making them potentially important vectors of inland transport of aquatic nutrients (Stapp & Polis 2003). Delineating how beaver disturbance influences these focal species is an important step towards understanding how broader communities are structured on the landscape in the presence of this keystone species. I investigated the hypothesis that beaver-created wetlands increase nutrient subsidization of the terrestrial system compared with unmodified stream sections. By comparing non-beaver and beaver sites, I addressed the following specific questions:

(1) Do beaver sites exhibit different aquatic invertebrate emergence patterns, in terms of community composition and abundance?

(2) Do focal terrestrial consumers ingest more aquatically derived carbon at beaver sites, and are there differences in the scale of aquatic resource sheds?

(3) Are abundances of focal terrestrial consumers higher at beaver sites?

Methods

Study sites

I studied three beaver (B), and three non-beaver (NB) sites in the Beaverhead-Deerlodge National Forest. Beaver pond sites were located in the upper Ruby River (B) (UTM: 12T 420882E 4969250N), and at two sites on Seymour Creek (B1 – UTM: 12T 330758E 5095795N; B2 – UTM: 12T 328939E 5097955N). Beaver sites were selected to include a simple beaver complex, comprising a single main dam impounding a discrete single pond with no lateral areas of standing water. I also chose non-beaver control sites that had no current discernible signs of beaver activity in the upper Ruby River (NB) (UTM: 12T 420695E 4969329N), Coal Creek (NB) (UTM: 12T 421560E 4966490N), and Twelvemile Creek (NB) (12T 336795E 5094675N). Given home range size and terrestrial dispersal behaviours of the taxa central to this study (aquatic macroinvertebrates (see Bilton et al. 2001), Lycosid spiders (Kuenzler 1958), *Peromyscus maniculatus* (Abramson et al. 2006)), I ensured independence among sites by selecting sites greater than 2 km from each other. All study streams were approximately the same size and gradient at study sites, and had abundant salmonid populations (Ruby River and Coal Creek: *Oncorhynchus clarkii lewisi, Thymallus arcticus*, and Seymour Creek and Twelvemile Creek: *O. clarkii lewisi, Salvelinus fontinalis*).

Aquatic sampling at each site was designed to elucidate isotopic signatures of primary production at each site, as well as isotopic signatures and abundance estimates of aquatic invertebrates. I established three terrestrial transects at each site, along which I sampled vegetation, Lycosid spider, and *P. maniculatus* individuals for isotope analysis and abundance estimates (Figure 2.2).

Vegetation sampling

To establish baseline carbon isotopic signatures ($\delta^{13}C$) of each habitat type, vegetation was sampled at Coal Creek and Ruby River sites from 06-Jul-2005 to 08-Jul-2005. Seymour Creek and Twelvemile Creek were sampled during the period 02-Aug-2005 to 06-Aug-2005. I stratified the water body at each site, collecting aquatic vegetation from 5 random points along the margins (within 1 m of the bank) as well as at 5 random points in the channel (Figure 2.2). Where they occurred, I collected biofilm, filamentous algae, and macrophytes. I collected terrestrial vegetation at each site along three transects extending away from the water body (Figure 2.2). I placed 1 m^2 quadrats every 10 m along each transect up to 100 m. Vegetation in quadrats were identified to the genus level, and representative samples of each were removed.

Aquatic macroinvertebrate sampling

I sampled aquatic macroinvertebrates, during the periods of 06-Jul-2005 to 08-Jul-2005 in Coal Creek and Ruby River and 02-Aug-2005 to 06-Aug-2005 in Seymour Creek and Twelvemile Creek. I used kick net sampling (using a D-net, mesh size: 500 μm) at non-beaver sites, and D-net (mesh size: 500 μm) sweeps at beaver sites to collect macroinvertebrates from 10 random 1 m^2 points. To initially quantify macroinvertebrate emergence, I used terrestrial light traps (CDC Miniature Light Trap Model 512) situated at 0 m and 100 m on each of the three transects at each site (Figure 2.2). To ensure light traps characterized consistent patterns of aquatic invertebrate emergence, I also sampled aquatic invertebrates during the period of 01-Jun-2007 to 29-Jun-2007, using three randomly placed floating emergence traps (effective capture area: 400 cm^2) (Cushman 1983) at each site. The emergence traps were checked at weekly intervals. Captured macroinvertebrates were collected and traps were reset. Whole invertebrate specimens from each of these sampling methods were preserved in 75% ethanol and returned to the laboratory, where they were dried for 48 hours at 50 °C, and sorted to order or family.

To estimate relative macroinvertebrate abundances from D-net samples, I averaged counts of each taxon from the ten 1 m^2 sample points at each site. Counts of each taxa captured by the three emergence traps at each site were averaged, scaled to number caught per square meter, and expressed as the number caught per day. Invertebrates captured by light traps at 0 and 100 m from the water's edge were expressed in terms of the number of different individuals captured per unit trapping effort (CPUE) (Equation 1). Estimates were calculated separately for each transect, then averaged among the three transects to obtain an average abundance for each site.

Trapping effort was therefore 3 trap nights per distance point (0 and 100 m) per transect (based on 1 trap, set for 3 days).

$$CPUE = \frac{captures}{trap\,nights} \times 100 \qquad \text{Equation 1}$$

Terrestrial Lycosid sampling

I sampled Lycosid spiders using two pitfall traps at each trapping point at 5 m intervals from 0 – 50 m along the three 100 m stream-to-upland transects. To ensure that truly terrestrial Lycosid signatures were established, pitfall traps at 100 m were positioned on each transect. Lycosid trapping occurred 06-Jul-2005 to 08-Jul-2005 at Coal Creek and Ruby River and 02-Aug-2005 to 08-Aug-2005 at Seymour Creek and Twelvemile Creek. Traps were checked daily, captured spiders removed, and traps reset. Spiders were stored in dry, cold for return to the laboratory. To estimate the relative abundance of Lycosid spiders within 100 m of the aquatic-terrestrial ecotone at each site, I used the number of individuals captured per unit trapping effort (CPUE) as an index of abundance (Equation 1) for each transect, then averaged across transects to obtain an average site abundance. Trapping effort was therefore 33 trap nights per transect (based on 11 traps, set for 3 days).

P. maniculatus sampling

I used 30 Sherman live-traps arranged along each of the three stream-to-upland transects at each site to derive isotopic signatures and abundance of *P. maniculatus*. Two traps, baited with sunflower seeds, were located at each transect point. Trap points were spaced at 5 m intervals along the first 50 m of each transect, then at 10 m intervals up to 100 m from the water's edge.

Traps were set for three-consecutive nights at all sites. I baited traps each evening with sunflower seeds, and closed them each morning to reduce trapping mortality rates. I collected a 2 – 3 mm piece of tail tissue from each new capture for stable isotope analysis, following protocols approved by the Institutional Animal Care and Use Committee at the University of Montana. All captured individuals were released immediately at their location of capture. Tail tissue samples consisting of bone, cartilage, and skin were stored in cold dry conditions for return to the laboratory.

To estimate relative *P. maniculatus* abundance within 100 m of the aquatic-terrestrial ecotone at each site, I used the number of unique captures per unit effort on each transect to calculate a relative abundance index. To account for sprung traps, and thus a loss of trapping effort, I used a corrected index ($\mathrm{CPUE}_{\mathrm{corrected}}$) (Cunningham & Moors 1996). Total trapping effort on each transect was 102 trap nights (based on 30 traps, set for 3 nights). Half a night was subtracted for each sprung trap (whether it had captured an animal or not) based on the assumption that it had been sprung for at least half a night (Equation 2). The index was calculated separately for each transect, then averaged among the three transects to obtain the average abundance at each site. I averaged *P. maniculatus* abundances at each site and grouped them according to the presence/absence of beaver.

$$CPUE_{corrected} = \frac{captures}{trap\,nights - \frac{sprung\,traps}{2}} \times 100 \qquad \text{Equation 2}$$

Isotope analysis

In the laboratory, I dried all vegetation and consumer samples at 50°C for 48 hours. I sub-sampled dried aquatic and terrestrial vegetation by randomly selecting at least 3 samples of all vegetation types from each site. Dried samples were ground to powder, and 2 – 3 mg of vegetation, and 1 mg of aquatic invertebrates, Lycosid spiders, and *P. maniculatus* were measured into tin capsules (Costech Analytical Technologies, Inc.) for isotopic analysis.

I conducted isotopic analysis on samples from two beaver (Ruby River – B and Seymour Creek – B1) and two non-beaver sites (Ruby River – NB and Coal Creek – NB). Dried and ground samples of vegetation, invertebrates, and small mammals from these sites were sent to the UC Davis Stable Isotope Facility for analyses. Samples were analyzed for natural abundances of ^{13}C and ^{15}N using a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd. Cheshire, UK).

Stable isotope composition of analyzed samples were expressed as δ values, which refers to the difference in parts per thousand (‰) between the isotopic ratio of the sample and that of a standard (PeeDee Belemnite formation for C and atmospheric nitrogen for N):

$$\delta^{13}C \text{ or } \delta^{15}N = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \qquad \text{Equation 3}$$

The δ^{13}C and δ^{15}N values of the aquatic and terrestrial resource base, as well as aquatic invertebrates, Lycosid spiders, and *P. maniculatus* were averaged and associated variances calculated. To determine how Lycosids and *P. maniculatus* utilized carbon from aquatic versus terrestrial primary sources at each site, I used a two source mass balance mixing model for carbon isotopes (Equation 4) (Phillips and Koch 2002) to calculate the proportional contribution of aquatic carbon to Lycosids and *P. maniculatus*, extending from 0 – 100 m from the water's edge at each site.

$$\delta^{13}\mathrm{C}_M = f_X(\delta^{13}\mathrm{C}_X + \Delta^{13}\mathrm{C}_{tissue\text{-}X}) + f_Y(\delta^{13}\mathrm{C}_Y + \Delta^{13}\mathrm{C}_{tissue\text{-}Y}); \qquad \text{Equation 4}$$
$$1 = f_X + f_Y$$

where:

X = Aquatic vegetation isotope signature
Y = Terrestrial vegetation isotope signature
M = mixture (consumer)
f = proportion of C mass from a food source
$\Delta^{13}\mathrm{C}_{tissue\text{-}X}$ = trophic fractionation (approximately 1 ‰ for C)

One-way Analysis of Variance (ANOVA) and Tukey's HSD post-hoc pairwise comparisons were used to determine how proportional aquatic tissue carbon of terrestrial consumers changed with distance from the water's edge for each site individually. The percent aquatic tissue carbon signature at the trapping point closest to the water's edge was used as a baseline to which all other distance signatures were compared using

Tukey's HSD pairwise comparisons. To evaluate how beaver activity and distance influenced the proportion of aquatic carbon in *P. maniculatus* and Lycosid spider tissues at beaver versus non-beaver sites, I grouped the data according to beaver presence, and used univariate nested ANOVA to assess aquatic carbon tissue proportions within 35 m of the water's edge for Lycosids and within 100 m for *P. maniculatus* (distance thresholds derived from one-way ANOVA above). Beaver presence/absence was treated as a fixed factor, with transect nested within this as a random factor.

Results

Vegetation

Isotopic signatures

Macrophytes and filamentous algae constituted the aquatic basal resource base, and I assumed that their δ^{13}C represented 100% autochthonous organic carbon. Aquatic primary production at each site was considerably enriched in ^{13}C compared with terrestrial primary productivity (Figure 2.3), which was derived from dominant terrestrial vegetation: *Salix* spp., Poaceae spp., *Artemisia tridentata, Lupinus* spp., *Achillea millefolium, Fragaria virginiana, Potentilla* spp.

Aquatic macroinvertebrates

Abundances

Of the five macroinvertebrate taxa captured in their nymphal form using D-net sampling, all exhibited significant differences in abundance between beaver and non-beaver sites (Figure 2.4a). Ephemeroptera dominated non-beaver sites, comprising 45 – 50 % of the overall communities at these sites, compared with 2 – 5 % at beaver sites (t = 5.85, P = 0.004). Plecoptera were also more common in non-beaver environments (t = 7.07, P = 0.002) constituting 15 – 20 % of the community. Contrastingly, I found significantly higher abundances of nymphal Diptera (t = -16.52, df = 4, P < 0.001) and Trichoptera (t = -6.04, df = 4, P = 0.004) at beaver ponds relative to non-beaver sites, with approximately 3- and 7-fold more individuals per unit area, respectively. I also found that Odonata comprised between 7 – 14 % of nymphal macroinvertebrate taxa at beaver sites, whilst Ephemeroptera nymphs were a minor community component at beaver sites (2 – 9 %).

I quantified relative differences in emerging macroinvertebrate abundances between beaver and non-beaver sites using emergence traps to capture three taxa present at both site types (Figure 2.4b). Based on these taxa, I found that overall daily emergence rates from beaver ponds were 3.5 times higher than at non-beaver sites. Approximately twice as many Ephemeroptera emerged per day at beaver sites (t = -4.94, df = 4, P = 0.008). At the non-beaver sites, Trichoptera emerged at 3 times the rate at beaver sites (t = -4.90, df = 4, P = 0.008), and Diptera at almost 4.5 times (t = -4.95, df = 4, P = 0.008) the rates of non-beaver sites.

In the case of airborne, adult aquatic invertebrates, I found no differences in Ephemeroptera or Plecoptera abundances at distances of 0 and 100 m of the water's edge, between beaver and non-beaver sites (Figures 2.4c and 2.4d). However, Diptera were considerably more numerous at beaver sites, with around 4 times the number immediately adjacent to the beaver pond (t = -4.77, df = 4, P = 0.009), and twice as many at 100 m (t = -2.96, df = 4, P = 0.04). Trichoptera exhibited even larger differences in abundance at beaver sites, with approximately 5.5 times the number at non-beaver areas (t = -2.99, df = 4, P = 0.04). Whilst more Trichoptera individuals were captured 100 m from the water's edge at beaver sites (Figure 2.4d), these were not statistically different from non-beaver sites (t = -0.90, df = 4, P = 0.42).

Isotopic signatures

Five taxonomic groups of aquatic macroinvertebrates were used for stable isotope analysis (Figure 2.3). These represented over 95% of the total insect biomass found at each site, and comprised taxa likely to be important in the transfer of energy across the ecotone boundary. Overall, δ^{13}C values of Ephemeroptera (grazers) reflected the values of aquatic primary productivity, whilst Plecoptera and Trichoptera (detritivores) exhibited strong terrestrially derived δ^{13}C values. Diptera (predominantly comprised of Simuliidae, Culicidae Chironomidae (filter feeders)) exhibited δ^{13}C values intermediate between aquatic and terrestrial basal resource values. However, Dipterans at beaver sites were approximately 18 % more enriched in δ^{13}C than in non-beaver sites, implying a larger contribution of aquatic carbon to Dipteran production at beaver pond sites. Similarly, Odonata, which were found only at beaver sites, also exhibited intermediate $\delta^{13}C$ signatures.

Focal terrestrial consumers

Isotopic signatures

Within each site, Lycosid spiders and *P. maniculatus* exhibited similar $\delta^{13}C$ signatures, and these showed enrichments in $\delta^{13}C$ at beaver sites, indicating increased importance of aquatic carbon resources, likely the result of increased reliance on Dipterans and Ephemeropterans (Figure 2.3).

Abundances

I found that relative abundances of Lycosid spiders and *P. maniculatus* were positively related to beaver presence, with approximately 55 % and 75 % higher abundances at beaver sites relative to non-beaver sites respectively (Lycosid: Levene's test: $P = 0.97$; $t = -3.69$, $df = 4$, $P = 0.02$; *P. maniculatus*: Levene's test: $P = 0.11$; $t = -3.75$, $df = 4$, $P = 0.02$; Figure 2.5).

Tracing aquatic subsidies

In beaver systems, I detected a higher overall trend in the mean proportions of aquatic carbon in terrestrial consumer tissues, for both Lycosids (Figure 2.6a) and *P. maniculatus* (Figure 2.6b). The effect of distance from water's edge on the proportion of aquatic carbon in Lycosid tissue was highly variable (Figure 2.7), exhibiting no statistically significant differences among the various distance points measured at non-beaver sites (Coal Creek: $F_{10,22} = 1.30$, $P = 0.29$; Ruby R. – NB: $F_{10,28} = 1.83$, $P = 0.10$). Proportional aquatic tissue carbon of *P. maniculatus* was also variable, with no significant differences evidenced at Coal Creek ($F_{7,16} = 1.69$, $P = 0.18$), yet the Ruby River – NB site indicated significant differences in aquatic tissue composition with distance ($F_{9,20} = 3.72$, $P = 0.007$). Tukey's HSD post hoc multiple comparisons for Ruby river – NB indicated that this trend of decreased *P. maniculatus* aquatic carbon signatures with distance was driven by significant pairwise differences between three sets of trapping points: 10 m and 15 m ($P = 0.03$), 10 m and 60 m ($P = 0.02$), and between 10 m and 80 m ($P = 0.01$).

At beaver sites, I detected a negative relationship between distance from water body and percent aquatic tissue carbon in terrestrial consumers. Lycosids exhibited distinct reductions in aquatic carbon tissue content (Ruby River – B: $F_{10,25} = 8.70$, $P < 0.001$; Seymour Creek – B: $F_{10,35} = 8.34$, $P < 0.001$; Figure 2.7), while *P. maniculatus* manifested significant reductions in aquatic carbon with distance at Seymour Creek ($F_{7,16} = 2.78$, $P = 0.043$), although the trend of reduced percent aquatic carbon with distance was not significant at the Ruby River – B site ($F_{7,16} = 1.43$, $P = 0.26$), although a paucity of captures at several trapping points within 50 m of the water's edge may also have played a role in this result (Figure 2.8). Tukey's HSD post-hoc multiple comparisons revealed that high Lycosid aquatic carbon signatures were statistically indistinguishable from the water's edge to a distance of 35 m (0 m to 40 m: $P = 0.001$) at the Ruby River – B site and up to a distance of 30 m (0 m to 35 m: $P = 0.03$) from the water's edge at Seymour. After these distance thresholds, proportional aquatic tissue carbon signatures at beaver sites were statistically indistinguishable from those at non-beaver sites (Figure 2.7). *P. maniculatus* also manifested reductions in percent aquatic tissue carbon with distance (Figure 2.8). This trend was statistically significant at Seymour Creek – B, although determining the distance threshold at which aquatic subsidy was important was hindered by patchy capture success at certain distances. Since no captures were recorded between 60 m and 100 m, the first statistically distinct carbon signature occurred at 100 m (0 m to 100 m: $P = 0.04$). I also found that beaver activity imparted significantly higher proportions of aquatic carbon to Lycosids ($F_{1,4} = 89.3$, $P = 0.001$) and *P. maniculatus* ($F_{1,4} = 52.67$, $P = 0.002$) within 35 m and 100 m of the water's edge, respectively.

Discussion

My research links a keystone species to the modification of nutrient subsidies, and shows the importance of disturbance and landscape heterogeneity to the process of trans-ecotonal nutrient flux. I documented the novel example of beaver engineering resulting in altered community composition and increased emergence rates of aquatic macroinvertebrates. Although aquatic subsidies have been documented in other studies, my work indicates that beaver increase the scale of aquatic resource sheds, evidenced by a broader extent of emergence as well as aquatic and terrestrial consumers attaining higher abundances, with an increased reliance on aquatic energy sources. Although I have presented clear evidence of elevated macroinvertebrate emergence rates corresponding with increased abundance of terrestrial consumers, there may be other pathways by which beaver activity influence community structure. The propensity for beaver to alter structural aspects of stream ecosystems suggests that nutrient dynamics may be modified by increased preponderance of discrete lateral standing water bodies, and/or aggregation and direct consumption of aquatic emergent vegetation by terrestrial consumers. While these factors may generally have ecosystem-structuring roles in beaver systems, increased macroinvertebrate emergence are well established as the dominant vector of aquatic nutrient translation due to the simple structure of beaver ponds chosen for study, and the enriched nitrogen signatures of terrestrial consumers relative to aquatic macroinvertebrate signatures at beaver sites (Figure 2.3).

As in other studies (Clifford et al. 1993; Harthun 1999; Margolis et al. 2001; McDowell & Naiman 1986; Rolauffs et al. 2001; Sprules 1941), I found that beaver sites exhibited altered macroinvertebrate community compositions, and increased abundances (Figure 2.4). Mean emergence densities of 379 individuals m^{-2} d^{-1} in beaver areas were 3.5 times larger than those at non-beaver sites. Trichoptera and Diptera exhibited the largest differences in abundance for individual macroinvertebrate taxa amongst all sampling methods (Figure 2.4a – d). These taxa were present at beaver sites in considerably higher densities at all life stages (nymphal, emerging, and adult) although Trichoptera were not significantly more abundant 100 m from the water's edge (Figure 2.3d). Given the isotopic signatures of these taxa (Figure 2.3), Dipterans, which were more enriched in aquatic carbon and extended further into the terrestrial environment, appear to be the major link organisms responsible for the transference of aquatic carbon to terrestrial consumers. Detritivorous Trichopterans at all sites exhibited strongly terrestrial isotopic signatures, and likely benefit in beaver systems through enhanced accumulation of terrestrial detritus. Therefore, since Trichoptera achieve higher abundances in beaver systems, but ultimately derive carbon from primarily terrestrial sources, the actual amount of subsidization emanating from beaver ponds via aquatic invertebrates was underestimated by this study, as this would have shown up in terrestrial consumer tissue as terrestrial carbon.

In lotic systems, the importance of emerging aquatic insects to riparian predators is well established (e.g. Lynch et al. 2002), and have been known to contribute up to 90 % of a predators diet (Kato et al. 2004). I show that disturbance of lotic systems caused by beaver in small stream ecosystems can have measurable effects on the stream-to-upland flux of aquatic carbon subsidies, and thus alter the resource shed of aquatic resources.

While other studies (Briers et al. 2005; Collier et al. 2002; Sanzone et al. 2003) have detected large aquatic subsidies influencing Lycosid spiders within approximately 10 m of the stream, my results for Lycosids at non-beaver sites were extremely variable, showing no trend in aquatic carbon content with distance from the stream. This may be due to low sample sizes in conjunction with variability in Lycosid home range sizes. Lycosid home ranges are reported to vary by two orders of magnitude, from 0.6 - 41.8 m^2 (Kuenzler 1958). Lower resource availability at non-beaver sites may lead to larger foraging areas, thereby inflating variances. *P. maniculatus*, also exhibited extremely variable and ill-defined trends at non-beaver sites (Figure 2.8), and may be beset by sample size and home range issues in a similar manner to Lycosids at these sites (diameter of *P. maniculatus* home range = 100 ± 25 m (Abramson et al. 2006)).

At sites with beaver activity, enhanced macroinvertebrate emergence rates extended further from the water's edge, thus increasing availability of aquatic invertebrates to consumers at beaver sites relative to non-beaver sites. Spider abundances were approximately 55 % higher at beaver sites relative to non-beaver controls (Figure 2.5), with a concomitant two-fold increase in the aquatically derived content of their tissues within 20 m of beaver ponds. Overall, Lycosid tissues comprised higher proportions of aquatic carbon (Figure 2.6a), with approximately 25 % of Lycosid diets immediately adjacent to beaver ponds comprised aquatic carbon. This declined with distance, before becoming indistinguishable from non-beaver sites at approximately 35 m (Figure 2.7). This corresponds to a 75 % greater distances compared with previous studies at unmodified lotic sites. Since the home range size of *P. maniculatus* (Abramson et al. 2006) entirely encompassed my sampling transects, thus confounding measurements of isotopic signatures with distance, I did not examine the effect of distance from water's edge on the proportion of aquatic carbon in *P. maniculatus* tissue. However, evaluation of overall aquatic carbon signatures in beaver versus non-beaver sites showed a convincing trend of enhanced proportional contributions of aquatically-derived carbon in *P. maniculatus* tissues associated with beaver systems (Figure 2.6b).

Many studies have documented positive effects of beaver habitat creation for other species. Amphibians species elicit a variety of responses, such as increased occurrence correlated with pond area (Popescu & Gibbs 2009), enhanced survival and production (Karraker & Gibbs 2009), and higher juvenile recruitment (Stevens et al. 2007). Small mammals have been found to have two to three times higher abundances in beaver-influenced willow (*Salix* spp.) shrubland habitats than in adjacent riparian habitat (Medin & Clary 1991), as well as increased abundances associated with beaver lodge structures in Lithuania (Ulevičius & Janulaitis 2007), and ungulates such as moose (*Alces alces*), elk (*Cervus elaphus*), and deer (spp.) benefit from riparian beaver habitat (Baker & Hill 2003). I also detected higher abundances of focal terrestrial consumers, but go further to quantify a distinct expansion of the aquatic carbon resource shed at beaver sites relative to that exhibited by non-beaver sites, tying together the mechanism of enhanced nutrient subsidy from the beaver influenced aquatic system to the altered dynamics of the local consumer populations.

By incorporating cross-habitat nutrient fluxes into the field of food web ecology and recognizing the modifying role that disturbance plays, we are presented with a more complete picture of how natural communities operate. Broadening the scope at which food webs are viewed is already being used to elucidate how spatially discrete populations are receiving subsidization from distant sources. Factoring into this the influence of highly interactive species, such as beaver, provides us with an insight into heterogeneity in trans-ecotone subsidies and the enlargement of resource sheds on the landscape. Through the creation and maintenance of wetlands (see Hood & Bayley 2008), and their effects on resource sheds, beaver may play a pivotal role in structuring wetland communities on the landscape. Therefore, understanding the effects of disturbance regimes and the influence of highly interactive species will be an essential prerequisite in our efforts to predict and manage natural system dynamics under changing environmental conditions.

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Figure Legends

Figure 2.1. Conceptual food web of study system in southwestern Montana. Thick arrows indicate hypothesized pathway of trans-ecotone nutrient subsidization. Dashed boxes indicate focal terrestrial consumers investigated (Lycosid spiders and *Peromyscus maniculatus*).

Figure 2.2. Sampling strategy and trapping methods used at beaver and non-beaver study sites.

Figure 2.3. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures of aquatic and terrestrial primary producers, aquatic macroinvertebrates, Lycosid spiders, and *Peromyscus maniculatus*. Values are means ± 1 SE.

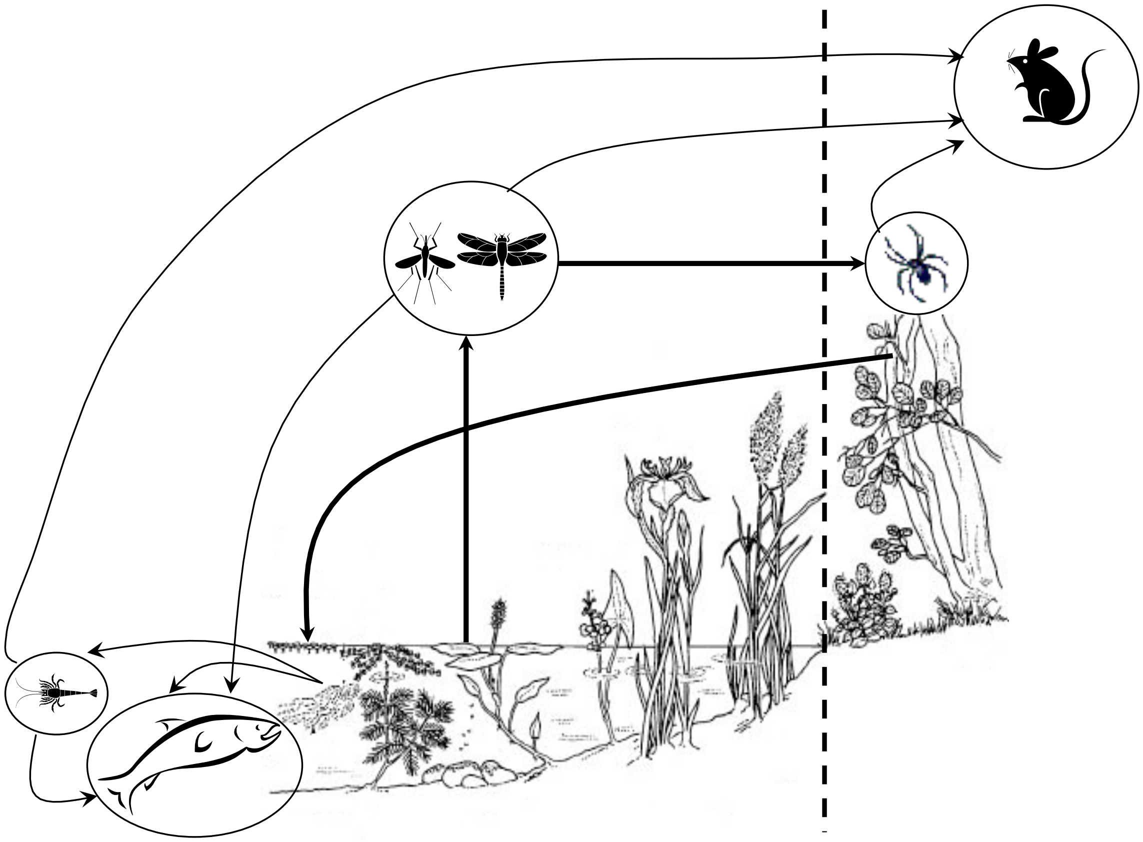
Figure 2.4. Relative abundances of aquatic macroinvertebrates at beaver (🦫) and non-beaver (🚫) sites, using (a) D-net sampling, (b) emergence trap sampling, and light trap sampling situated at (c) 0 m and (d) 100 m from the water's edge. CPUE = Catch Per Unit Effort. Values are means ± 1 SE.

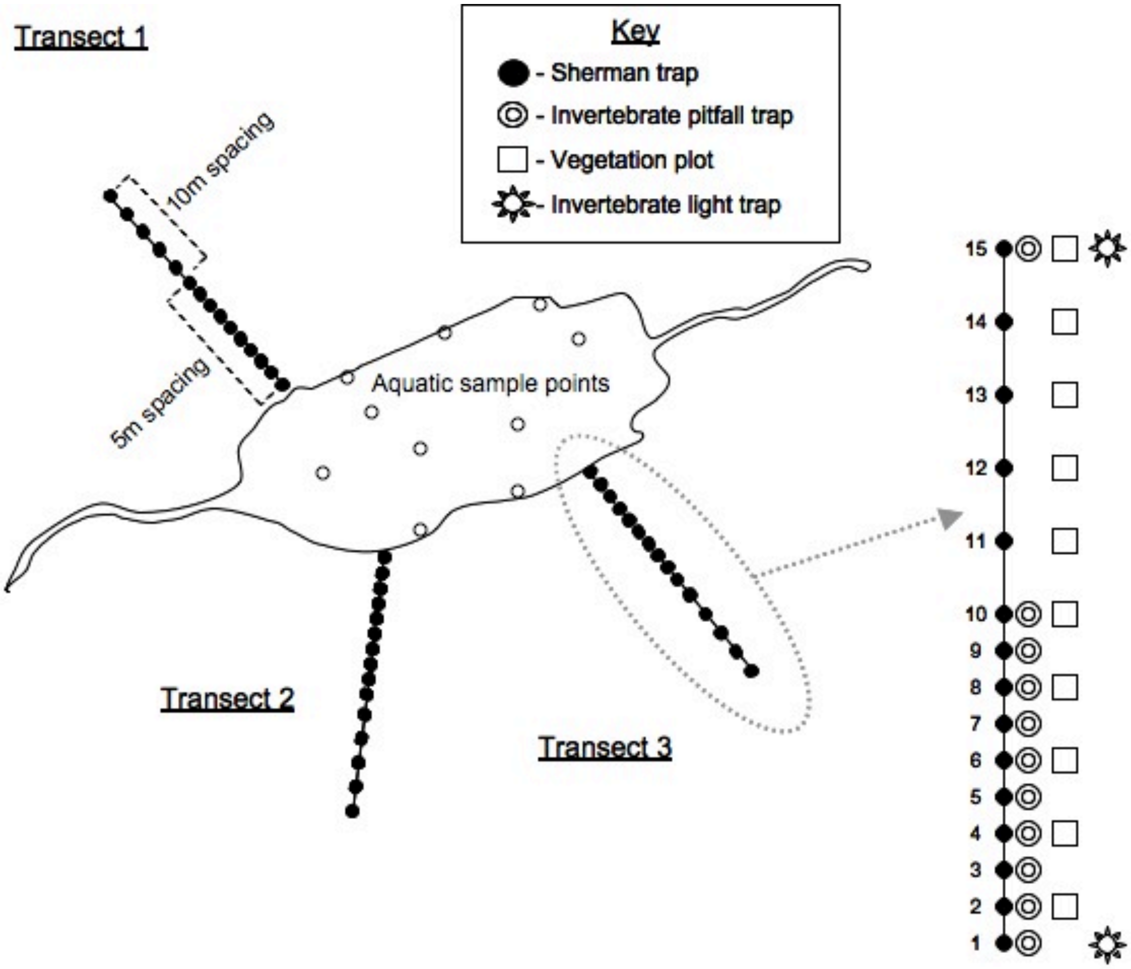
Figure 2.5. Relative abundance of Lycosid spiders and *Peromyscus maniculatus* at beaver (🦫) and non-beaver (🚫) study sites. CPUE = Catch Per Unit Effort. Values are means ± 1 SE.

Figure 2.6. Boxplots of the proportion of (a) Lycosid and (b) *Peromyscus maniculatus* tissue carbon that is derived from aquatic primary production at non-beaver and beaver sites. Boxplots for each taxa show minimum, first quartile, median, third quartile, maximum, and any outliers (circles) for samples collected at non-beaver (🚫) and beaver (🦫) sites.

Figure 2.7. Proportional contribution of aquatically derived carbon in Lycosid spider tissues with lateral distance from the water's edge. Values are means ± 1 SE.

Figure 2.8. Proportional contribution of aquatically derived carbon in *Peromyscus maniculatus* tissues with lateral distance from the water's edge. Values are means ± 1 SE.



Transect 1
Key
● - Sherman trap
◎ - Invertebrate pitfall trap
☐ - Vegetation plot
✹- Invertebrate light trap
10m spacing
5m spacing
Aquatic sample points
Transect 2
Transect 3
15
14
13
12
11
10
9
8
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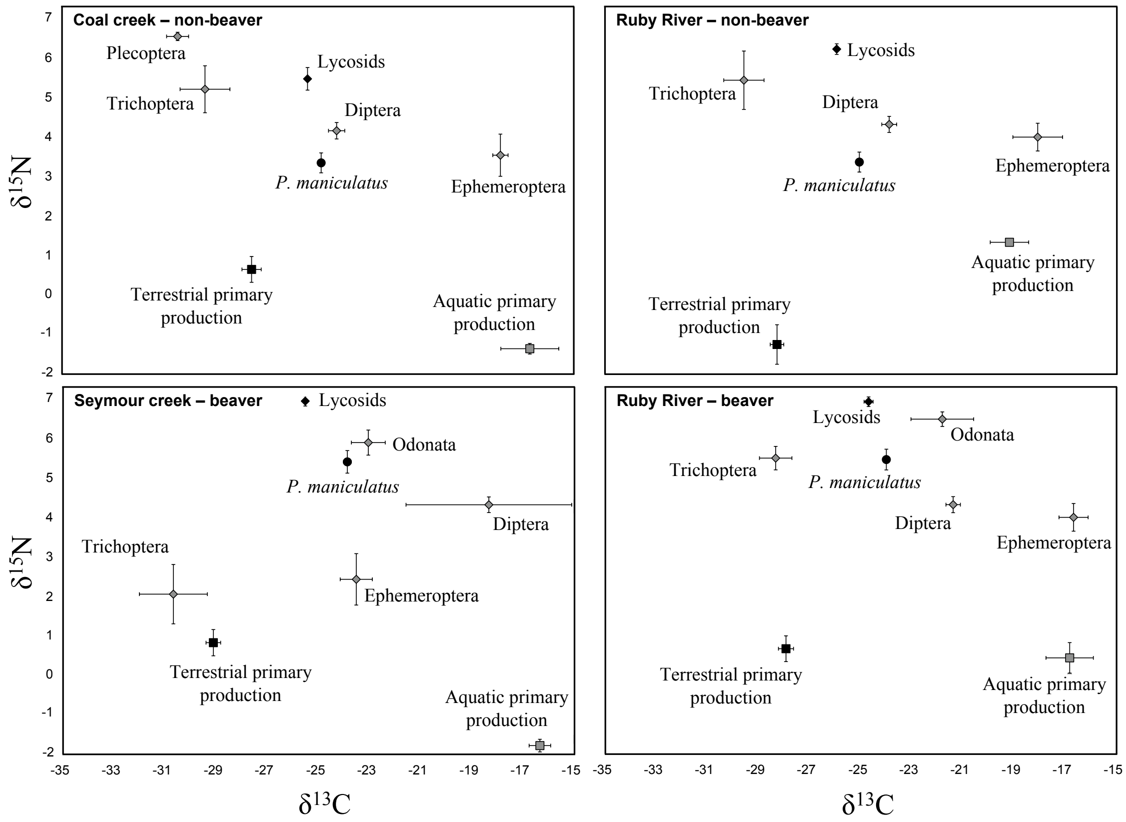
3
2
1


Coal creek – non-beaver
Plecoptera
Lycosids
Trichoptera
Diptera
P. maniculatus
Ephemeroptera
Terrestrial primary production
Aquatic primary production
Ruby River – non-beaver
Lycosids
Trichoptera
Diptera
Ephemeroptera
P. maniculatus
Aquatic primary production
Terrestrial primary production
Seymour creek – beaver
Lycosids
Odonata
P. maniculatus
Diptera
Trichoptera
Ephemeroptera
Terrestrial primary production
Aquatic primary production
Ruby River – beaver
Lycosids
Odonata
Trichoptera
P. maniculatus
Diptera
Ephemeroptera
Terrestrial primary production
Aquatic primary production
δ15N
7
6
5
4
3
2
1
0
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δ13C
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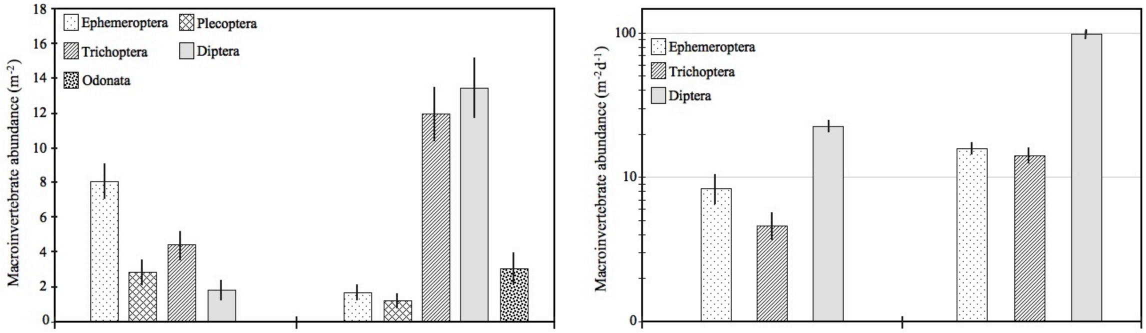
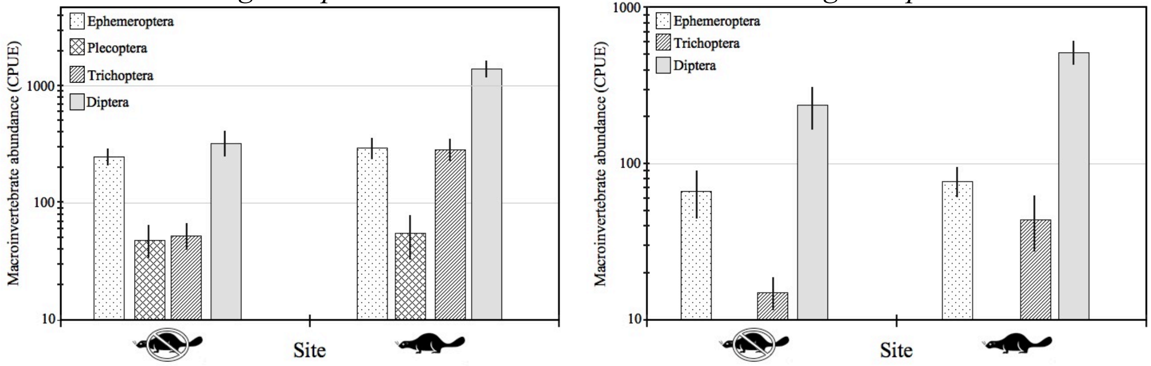
-19
-17
-15



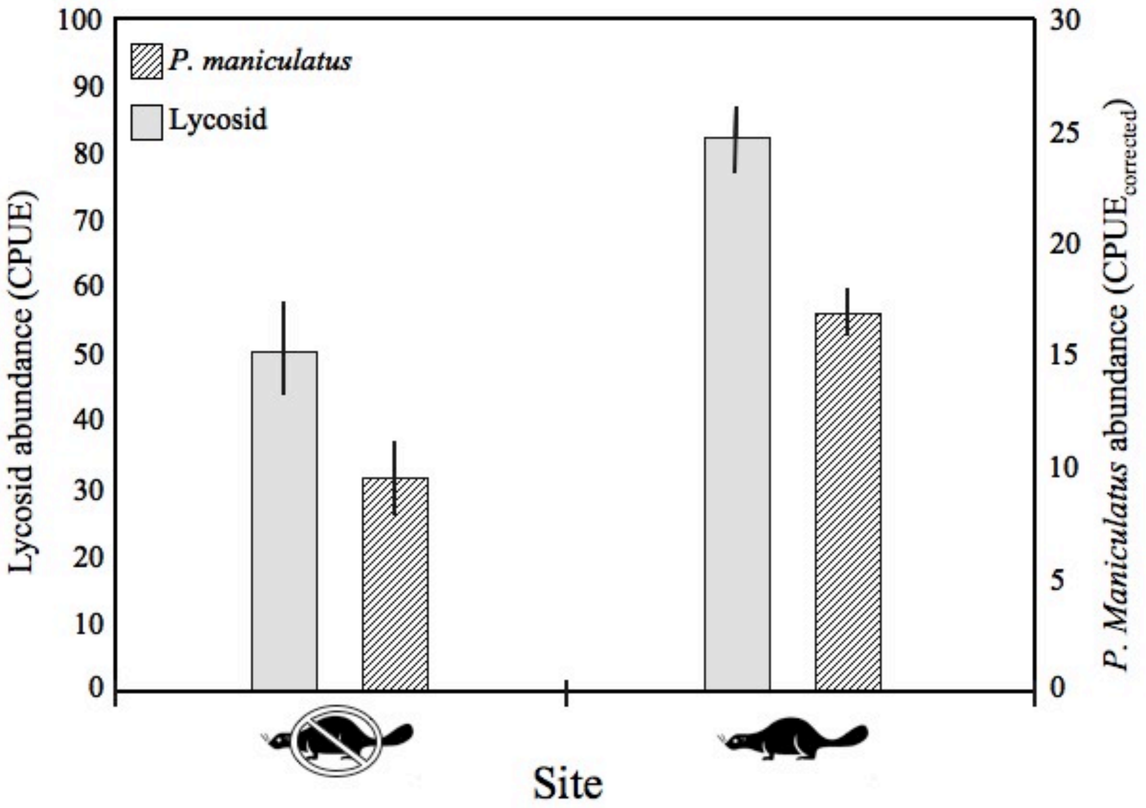
(a) D-net

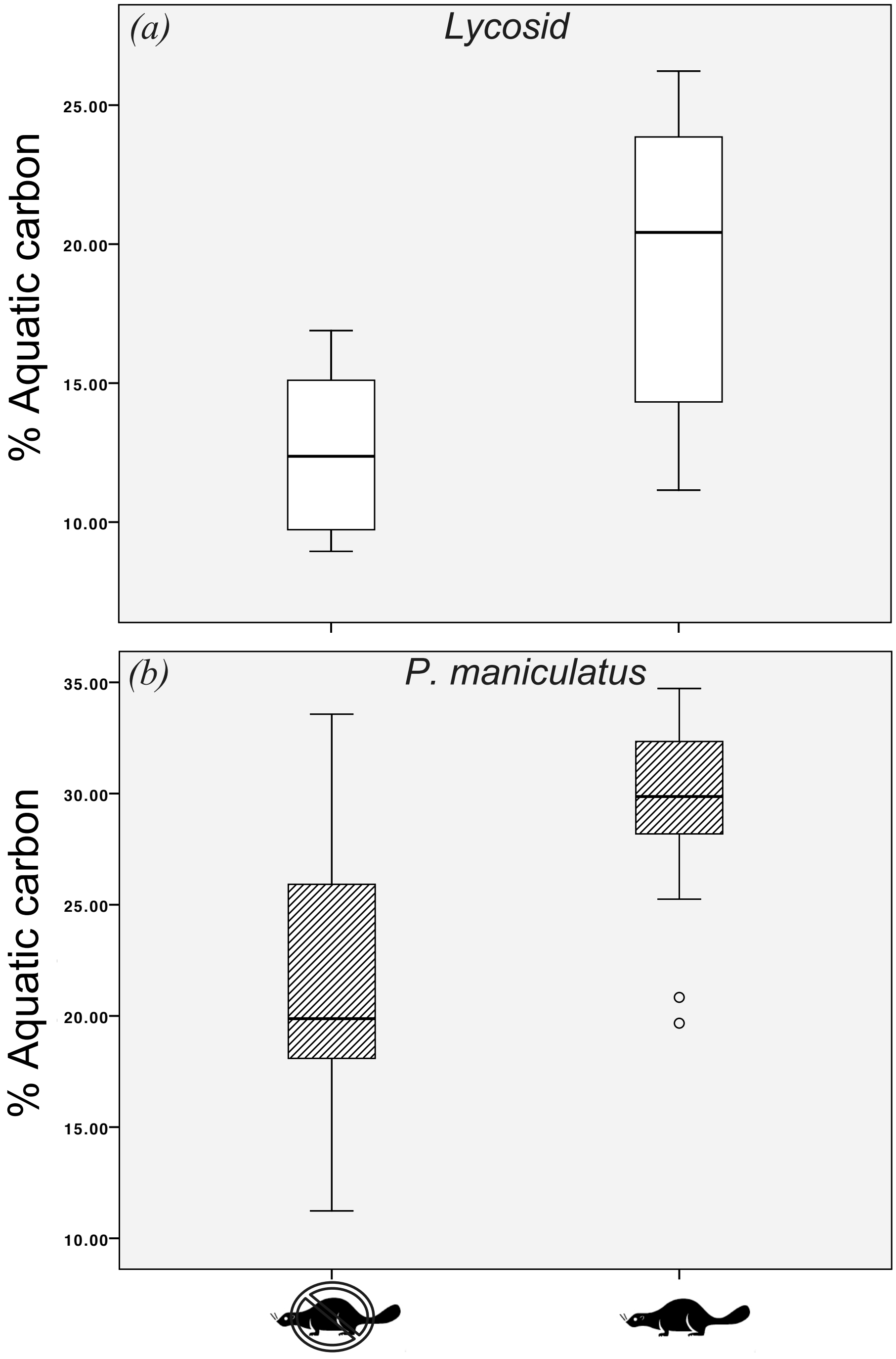
(b) Emergence trap

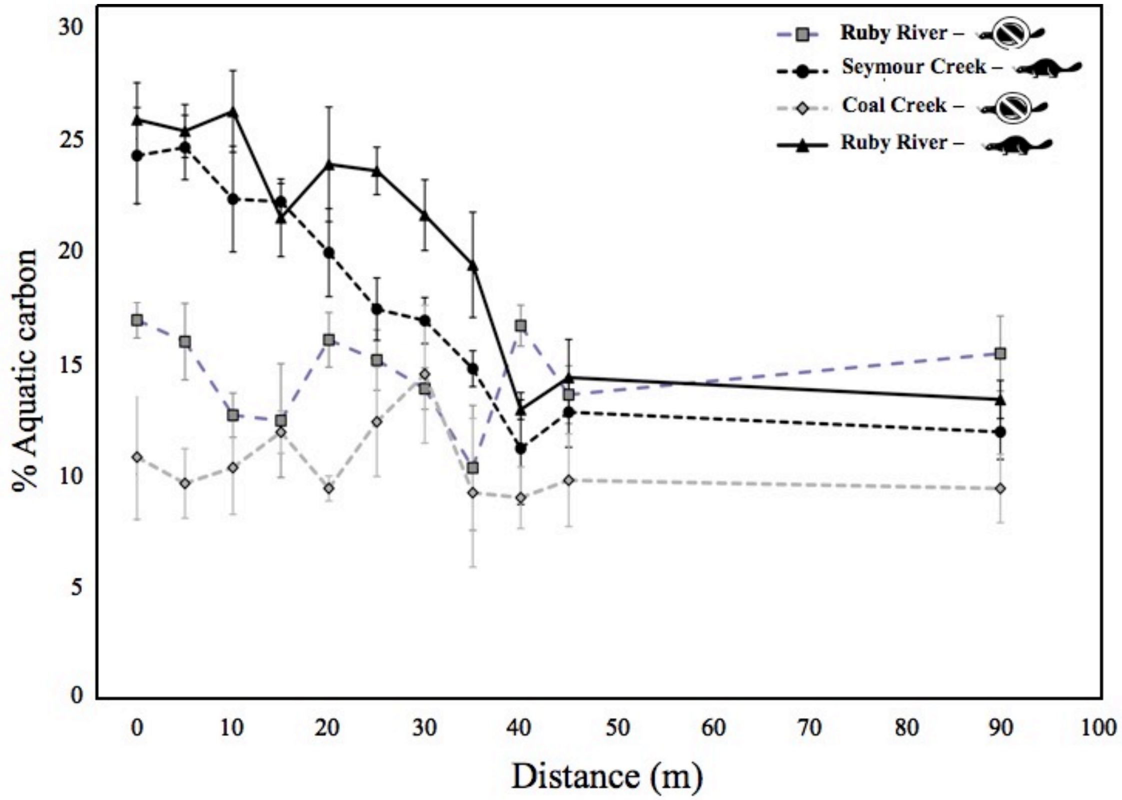


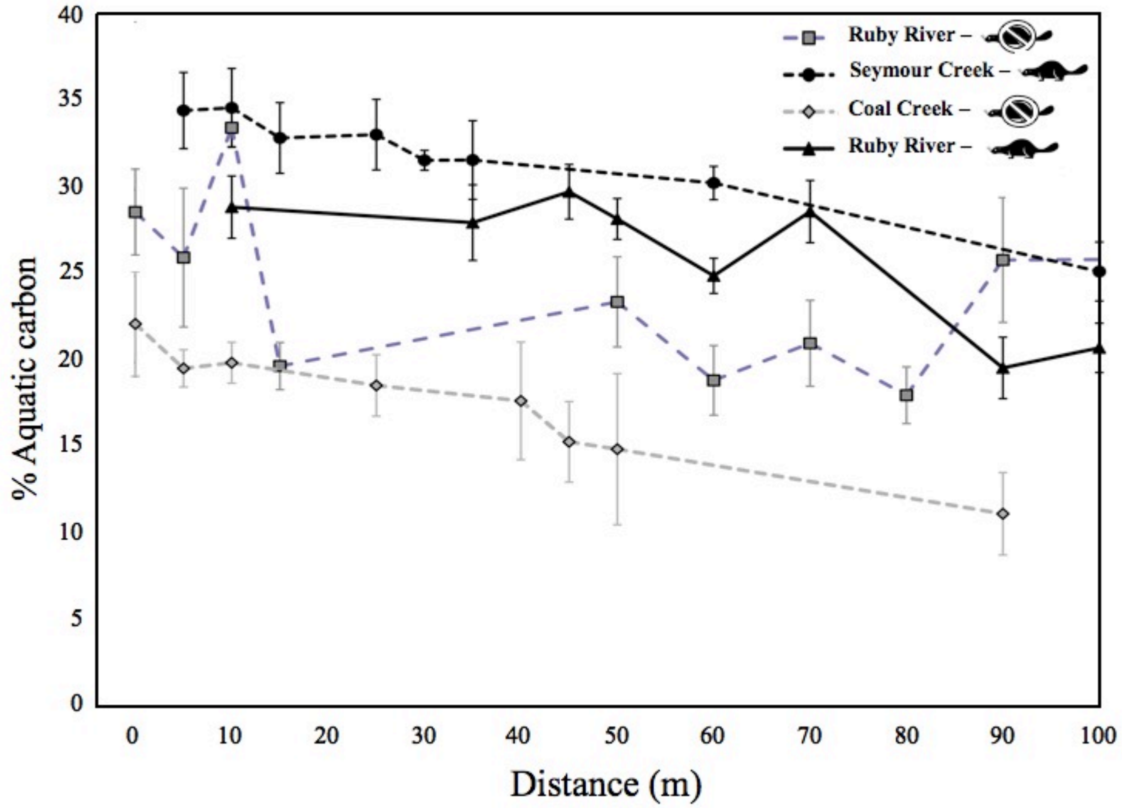
(c) Light trap – 0m

(d) Light trap –100m


100
90
80
70
60
50
40
30
20
10
0
Lycosid abundance (CPUE)
30
25
20
15
10
5
0
P. Maniculatus abundance ($CPUE_{corrected}$)
▨ *P. maniculatus*
□ Lycosid
Site


(a)
Lycosid
% Aquatic carbon
25.00
20.00
15.00
10.00
(b)
P. maniculatus
% Aquatic carbon
35.00
30.00
25.00
20.00
15.00
10.00


Ruby River –
Seymour Creek –
Coal Creek –
Ruby River –
% Aquatic carbon
0
5
10
15
20
25
30
Distance (m)
0
10
20
30
40
50
60
70
80
90
100


40
35
30
25
20
15
10
5
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% Aquatic carbon
0
10
20
30
40
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60
70
80
90
100
Distance (m)
Ruby River –
Seymour Creek –
Coal Creek –
Ruby River –

CHAPTER 3

BEAVER ORCHESTRATE CHANGES IN FISH INVASION DYNAMICS

Abstract

The spread and success of nonnative species may be enhanced by native species in unusual ways. Throughout the western U.S., brook charr (*Salvelinus fontinalis*) invasion has been implicated in the decline of native cutthroat trout (*Oncorhynchus clarkii*). Landscape factors influencing the extent and impact of this invasion need to be determined. Native beaver (*Castor canadensis*) alter streams considerably, but it is unknown how this affects brook charr invasion success, or the consequences for native trout. My objectives were to understand how beaver affect stream temperatures, brook and cutthroat trout distributions, and cutthroat growth rates. During the summers of 2006-2008, I studied brook charr and cutthroat trout in southwestern Montana, in streams both with and without beaver. Using temperature loggers, habitat surveys, and fish depletion sampling methods, I found that beaver presence elevated stream temperatures, increased brook charr densities, and increased the degree of spatial overlap between these species. I also used mark-recapture and scale analysis to determine brook charr effects on cutthroat growth and whether beaver influence cutthroat and brook charr interactions. In brook charr invaded streams, young-of-the-year cutthroat maintained high growth rates when beaver were present, but showed growth reductions without beaver. Thus beaver convey both positive (higher temperature and growth) and negative (increased densities of and overlap with brook charr) impacts to native cutthroat trout. Therefore, beaver mitigate some of the negative effects of brook charr on cutthroat trout. My research elucidates the importance of considering how important landscape modifiers such as beaver alter the outcome of invasions.

Introduction

The global spread of invasive species represents a grave threat to natural ecosystems, and is one of the greatest challenges currently facing conservation biologists and resource managers (Byers et al. 2002; Vitousek et al. 1996). Nonnative invasion can lead to biotic homogenization across the landscape (Rahel 2002), loss of biodiversity (Sakai et al. 2001), behavioral and evolutionary changes in native species, and food web disruption (Baxter et al. 2004; Power 1990; Townsend 1996).

The discipline of invasion ecology relies upon an amalgam of ecological theories (Cadotte et al. 2006; Shea & Chesson 2002), but these have rarely been evaluated with empirical data (Parker 2000; Peterson & Fausch 2003). Recent studies have begun to link quantitative field data to invasion theory in an effort to produce reliable predictions of invasion processes through the development of specific, mechanistic models that describe the invasion of particular taxa, which can then be tested with experimental data (Peterson & Fausch 2003). By incorporating experimental methodology, invasion ecology is striving to develop theoretical tools that will enable conservation practitioners to identify systems that are prone to a given invasive species, and estimate their likely impacts on native members of the invasible community. However, biotic invasions likely result from a complex synergy between exotic species traits, receiving community traits, and abiotic conditions (Lambrinos 2002). Hence, unraveling the Gordian knot of ecological invasion dynamics is stymied by variation in the success of invaders, and responses of natural communities across a heterogeneous landscape (Lambrinos 2002; Lonsdale 1999; Vermeij 1991).

Some of the most successful invasions occur in anthropogenically disturbed habitats, whereby organisms that have a long history of association with human-modified ecosystems are able to invade environments that they are adapted to, but to which native species are not (Sax & Brown 2000). Successful invasions are commonly accompanied by the decline or extirpation of native taxa (Kiesecker et al. 2001; Young 1995). The mechanisms implicated in perceived native declines are likely to be highly context-dependent, but one of the strongest generalizations to emerge from detailed studies of invasion biology is the positive relationship between disturbance and invasion success

(Drake et al. 1989). Invaders have been observed to successfully invade disturbed habitats with concomitant declines in native species, yet are less likely to influence native populations in undisturbed habitats (Davis et al. 2000; Herbold & Moyle 1986; Kiesecker et al. 2001). Despite this, the role that natural disturbance events play in biotic invasion is less clear. For example, responses of native species whose evolutionary history in the presence of local disturbance regimes such as wildfires or flash floods can ameliorate the outcome of invasions, thereby facilitating native resilience (Dunham et al. 2003; Meffe 1984).

In aquatic systems of North America, the natural disturbance regime of native beaver (*Castor canadensis*) populations is an uninvestigated aspect of freshwater invasion ecology. As a keystone species, beaver substantially influence watershed disturbance regimes through their feeding and damming behaviors (Collen & Gibson 2001). Beaver impoundments create lentic habitat in otherwise lotic systems, leading to fundamental alterations in channel geomorphology and hydrology (Naiman et al. 1986), sediment characteristics (Rosell et al. 2005), nutrient cycling, and increases in landscape heterogeneity (Johnston & Naiman 1990). Consequently, it has been shown that beaver can promote changes in succession dynamics, increase biotic productivity, and enhance diversity of floral and faunal assemblages (Collen & Gibson 2001; Naiman 1994; Naiman et al. 1988; Naiman et al. 1986; Schlosser 1995). Increases in water storage through beaver impoundments also alter riparian habitat, and augment water supply and late-season flows (Fouty 2003; Hood & Bayley 2008).

The formation of pool habitat by beaver may increase water temperatures, prey availability, and juvenile rearing habitat for species such as Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*) (Scruton et al. 1998; Winkle et al. 1990), as well as enhance critical winter habitat for fishes such as cutthroat trout (*Oncorhynchus clarkii*) and bull charr (*Salvelinus confluentus*) (Jakober et al. 2000). The potential for beaver to influence stream temperature varies depending on regional characteristics (Collen & Gibson 2001). In conjunction with available physical habitat, temperature is an important stream characteristic that directly influences fish distributions and growth rates (Magnuson et al. 1979). In areas of the western United States, water temperatures in mountain streams often fall below the critical temperatures for trout (e.g. optimal growth temperature: cutthroat trout = 13.6°C (Bear et al. 2007), brook charr = 13 – 16 °C (Baldwin 1956; McCormick et al. 1972)). Temperature increases through beaver activity may benefit both native and nonnative salmonids and have been reported in Utah (Rasmussen 1941), New Mexico (Huey & Wolfrum 1956), and Wyoming (Grasse & Putnam 1955).

Associated with the potential for beaver impoundments to provide high quality habitat conditions for native species, is the possibility that nonnative fishes may benefit disproportionately from the presence of beaver in a watershed. In Montana, streams with higher water temperatures, fine sediment, and the abundance of pools and large wood have been correlated with brook charr invasion (Shepard 2004), hence implicating beaver as facilitators of brook charr invasion.

As an invasive species from eastern North America, brook charr have expanded into numerous montane coldwater streams of the western United States (Kennedy et al. 2003). In invaded systems brook charr and native salmonids have been observed to occur in allopatry, with brook charr dominating warmer downstream water, and native salmonids confined to upstream colder water (Dunham et al. 2002; Fausch 1989; Paul & Post 2001; Rieman et al. 2006). Beaver ponds may allow brook charr to circumvent their upstream minimum temperature limits (Adams 1999), and use beaver ponds as reproductive source areas from which to colonize high elevation, colder sink sections of a watershed (Schlosser 1995).

Any factor that enhances the ability of brook charr to invade watersheds could have serious consequences for native species such as westslope cutthroat trout (*O. c. lewisi*). As brook charr invade aquatic ecosystems in western North America, native cutthroat trout decline (e.g. Dunham et al. 2002; Peterson et al. 2004; Shepard 2004). These declines are generally attributed to three mechanisms: competition, predation, and parasite or disease transmission (Dunham et al. 2002). Studies suggest that brook charr exhibit dominant aggressive behavior over other salmonid species (McMahon et al. 2007), and field experiments have shown reduced feeding efficiency and growth of cutthroat trout in the presence of brook charr (Novinger 2000; Thomas 1996). Size-dependent interspecific competition with brook charr is often cited as the driver of cutthroat trout displacement (Griffith 1988), with smaller cutthroat affected most. Stream temperature has been shown to alter the competitive interaction between these species (De Staso III & Rahel 1994; Novinger 2000), with research suggesting enhanced brook charr competitive ability between 13°C and 17°C (Thomas 1996). This corresponds with brook charr exhibiting comparatively higher growth efficiencies than cutthroat at these temperatures (McMahon, unpublished data). Therefore, if beaver ponds increase overall stream temperatures, brook charr may have a greater competitive advantage over cutthroat trout.

In this study, I used stream comparisons to investigate how beaver modification of fish habitat characteristics influences the potential of brook charr invasion of western watersheds and the consequences for native westslope cutthroat trout. My objectives focused around the questions:

(1) Do beaver alter stream distributions of brook charr and westslope cutthroat trout, and are changes correlated with an altered temperature regime?

(2) What are the impacts of beaver modification on potential and realized growth rates for cutthroat trout?

Methods

Study sites

I selected seven study streams in the Beaverhead-Deerlodge National Forest, adjacent Bureau of Land Management, and private lands of southwestern Montana. Each of these streams included cutthroat trout, with differing combinations of brook charr and beaver to fulfill the treatment criteria: treatment 1 = beaver and cutthroat trout present, treatment 2 = cutthroat trout and brook charr present, and treatment 3 = beaver, cutthroat trout, and brook charr present (Table 3.1). The only salmonid species in treatment streams were westslope cutthroat trout and brook char. Non-salmonid fishes in my study streams included sculpin (*Cottus* spp.) and longnose suckers (*Catostomus catostomus*). All study watersheds with the requisite species assemblages were suitable for beaver habitation, of similar size and gradient, and fell within an elevation range of approximately 1,700 m to 2,400 m (Table 3.1).

Do beaver alter stream distributions of brook charr and westslope cutthroat trout, and are changes correlated with an altered temperature regime?

Stream temperature and habitat sampling

I measured variation in physical factors among streams by conducting habitat surveys in each study stream using protocols adapted from Overton et al. (1997). Proceeding upstream, I described each channel habitat unit (riffle, run, or pool), and measured its length (m), mean wetted width (m), and middle depths of riffles (cm). In addition, I measured channel gradient, and elevation using a compass and Garmin GPS unit respectively. These measurements were corroborated using geographic information system software (GIS, ArcGIS 9) and 30 m resolution digital elevation models (http://nris.mt.gov/gis/). I analyzed for differences in these habitat characteristics among the three treatment types using a one-way analysis of variance (ANOVA) (Zar 1999).

I sampled water temperature along the entire length of all study streams by deploying iButton digital temperature loggers (model DS1920: Maxim Integrated Products, Dallas semi-conductor, Sunnyvale, CA, USA) at intervals ranging from 10 – 800 m. Temperature loggers were placed in the channel thalweg, and shielded from direct solar radiation (Dunham et al. 2005). Loggers recorded water temperature in all study streams (to the nearest 0.5°C; every 30 minutes) from late May through October in 2006, 2007, and 2008 (Table 3.1).

I summarized data from temperature loggers as average daily temperature. Based on movement data from other studies (Gowan & Fausch 1996; Hilderbrand 1998; Young 1996), I assumed some degree of local movement out of my 200 m sample sections and pooled these to give mid- and high elevation temperature values for each stream. I used methods from Coleman and Fausch (2007) to calculate the growing season degree-days (hereafter degree-days) for each elevation strata of each stream by summing the daily mean temperatures over the course of the growing season. The beginning of the growing season was defined as the first week that average stream temperatures exceeded and remained above 5°C for the season. The end of the growing season corresponded to the last day of the first week that average stream temperature remained below 4°C (Coleman & Fausch 2007). These growing season criteria are based on research that adult cutthroat trout spawn when stream temperatures rise to 5-8°C (USFWS 1998), and that in trout, growth typically occurs when temperatures exceed 4°C (Piper et al. 1982). I used Levene's test for equality of variances and conducted a t-test to examine differences in mid- and high-elevation degree-days in beaver and non-beaver streams.

Fish capture

I stratified study streams into low-, mid, and high elevations, and randomly selected three 200 m sections within the mid- and high elevation strata of each stream. Five streams comprised my core capture-mark-recapture sampling systems, and were surveyed over three years (2006-2008; Table 3.1). These five core study streams were sampled twice during each year (once in July and once in August). I added two more streams in 2008 to augment temperature, distribution, and growth data (Table 3.1). I used two-pass depletion electrofishing to capture brook charr and westslope cutthroat trout. During sampling, each section was temporarily enclosed with block-nets, and sampled in an upstream direction using a backpack electrofishing unit (Smith-Root Inc. model 15-D, Vancouver, WA, USA). All brook charr and cutthroat trout captured were measured (total length (TL), nearest 1 mm), weighed (nearest 1 g), and scales were taken for aging and growth analysis, and then fish were released. Additionally, fish greater than 55 mm were individually tagged with a Passive Integrated Transponder (PIT) tag in core streams. During the second (recapture) session of each year, I repeated the above sampling protocol except recaptures were not tagged.

Length-frequency data for cutthroat trout were used to provide insight into the dynamics of my study populations (Figure 3.1). I also summed individual captures from each sample section within mid- and high strata and divided by total stream captures by species within each stream to obtain an estimate of proportionate distributions at mid- versus high elevations, and investigated the relationship between proportional distribution and elevation strata using Pearson's correlations. Densities of brook charr and cutthroat trout per 100 m were calculated in mid- and high elevations of each stream by pooling the number of fish caught in each elevation strata and dividing by the total length of stream sampled.

To investigate whether there was a treatment effect on stream distributions, I then calculated the degree of overlap between cutthroat trout and brook charr using the spatial overlap index (C_{xy}) devised by Schoener (1970):

$$C_{xy} = 1 - \tfrac{1}{2}\left(\sum \left|P_{xi} - P_{yi}\right|\right) \times 100 \qquad \text{Equation 1}$$

Where P_{xi} is the proportional contribution of habitat i to the total habitat occupation of species x, and P_{yi} is the proportional contribution of habitat i to the total habitat occupation of species y. Habitat overlap may range from 0% (no habitat overlap) to 100% (total habitat overlap), and as such were arcsine-square-root transformed for further statistical analyses. Using treatment type, elevation (mid or high), and year as independent variables, I analyzed for differences in degree-days and cutthroat trout density among the three treatment types using multivariate analysis of variance (MANOVA). I investigated pairwise differences between treatments using Tamhane's T2 post hoc comparisons, a conservative test appropriate to analyses incorporating unequal sample sizes among treatments. I used elevation, year, and brook charr treatment type (treatments 2 and 3 only) as independent variables in a second MANOVA with Tamhane's T2 pairwise comparisons, to assess differences in brook charr densities and the degree of cutthroat trout and brook charr overlap between invaded treatment types.

What are the impacts of beaver modification on potential and realized growth rates for westslope cutthroat trout?

Potential cutthroat trout growth rates

I used the pooled mean temperatures for each elevation strata to calculate potential growth rates of cutthroat trout found within each strata, using an experimentally derived growth model for cutthroat trout and the average temperatures for mid- and high-elevations of each stream (Equation 2: Bear et al. 2007). This model predicts daily growth rates for westslope cutthroat trout in the approximate size range of 100–130 mm across a range of temperatures assuming non-limiting food resources.

$$\%\ \text{WCT daily growth rate} = -\,4.1727 + 0.9496\text{T} - 0.0348\text{T}^2 \qquad \text{Equation 2}$$

where WCT = westslope cutthroat trout, T = mean daily summertime temperature (°C).

Realized cutthroat trout growth rates

I estimated cutthroat trout growth during the first year of life. I collected scales from the body area near the lateral line between the dorsal and anal fins from cutthroat trout and stored them in envelopes prior to dry mounting on a glass slide with a cover slip. I examined growth to age-1 using 3 to 10 scales from 25 cutthroat trout individuals from each stream (except Hell Roaring creek where only 12 cutthroat were captured). Individuals for this analysis were drawn randomly from each study section, with roughly equal numbers of fish selected from mid- and high-elevations in the beaver treatments. Since cutthroat trout were predominantly distributed in high-elevation stream reaches in my non-beaver streams, the majority of scales in this treatment were derived from fish in the high-elevation strata of these streams. I viewed and digitized the selected mounted scales using an 11.2 Color Mosaic digital camera (Diagnostic Instruments, Inc., Sterling Heights, MI, USA) attached to a Leica MZ16 Stereomicroscope (Leica Microsystems Ltd., Switzerland) at 920X magnification. I then used ImageJ 1.37V software (Wayne Rasband, National Institutes of Health, USA) to measure the distance (mm) from the focus (center) of the scale to the first annulus, and from the focus to the outer edge of the scale (radius). These measurements were taken along the longest axis of the scale. Scale readings were verified by comparing 10% of the scales read to readings of a second reader. I then back-calculated the length of cutthroat trout at age-1 using the Fraser-Lee formula (Equation 4: Fraser 1916; Lee 1920):

$$L_i = \frac{L_c - a}{S_c} S_i + a \qquad \text{Equation 3}$$

where L_i = back-calculated fish body length at age *i*, L_c = fish body length at capture, S_i = mean scale radius at annulus *i*, S_c = mean scale total radius, a = intercept determined from regression of scale radius and fish total length ($R^2 = 0.89$, $y = 254.7x + 30.9$). Values were averaged to determine mean length at age-1 for each stream. I regressed scale radius with fish total length to validate this method of estimating growth to age-1. I used one-way ANOVA and Tamhane's T2 post hoc pairwise comparisons to analyze for differences in cutthroat trout size at age-1 amongst treatments.

I used measurements of TL from within-summer recapture data to estimate relative growth rates (G, expressed as %) of cutthroat trout greater than 1 year old, and up to 150 mm. The lower size-limit of recaptures used was stream-specific, with size-at-age-1 estimates derived from scale analyses providing the lower bound for each stream (age-1_{stream}). The upper size limit of 150 mm was used to allow comparison with potential growth rates based on temperature (equation 2). I then used a relative growth equation (Equation 4) to calculate summer cutthroat growth rates.

$$G = \frac{Y_2 - Y_1}{Y_1 \times t} \times 100 \qquad \text{Equation 4}$$

where Y_1 = initial weight (g), Y_2 = recaptured weight, and t = time interval between captures (days) (Bear et al. 2007). Recapture growth rates were arcsine-square-root transformed for normality and tested for overall stream growth rate differences amongst treatments using nested Univariate ANOVA. I split my data by elevation strata and repeated this procedure to examine for differences amongst treatment by strata. Tamhane's T2 post hoc tests were used to analyze pairwise treatment differences. To remove the effects of temperature on growth differences among my streams, I divided recapture growth rates (equation 4) by the potential growth rate (equation 2) for each study stream.

Results

Do beaver alter stream distributions of brook charr and westslope cutthroat trout, and are changes correlated with an altered temperature regime?

Aside from differences caused by beaver, my study streams generally exhibited similar habitat attributes (Table 3.2). There were no statistically significant differences in habitat characteristics among treatment types (ANOVA: $P > 0.1$), except for higher average summer temperatures at mid- (ANOVA: F = 13.53, df = 2, P = 0.017) and high- (ANOVA: F = 11.51, df = 2, P = 0.022) elevations of beaver systems. This was manifested by average summertime water temperatures approximately 3.5°C and 3.2°C greater in beaver watersheds than watersheds without beaver present in mid- and high-elevation strata respectively. Concomitantly, I found that streams influenced by beaver exhibited approximately one-third higher degree-days values (Levene's test: P = 0.25; t-test: t = 2.4, df = 10, P = 0.03; Figure 3.2).

There was a significant treatment effect on the proportional distribution of cutthroat trout at mid- and high-elevations (ANOVA: F = 33.28, df = 2, P < 0.001), with higher proportions of cutthroat trout distributed in higher-elevations of non-beaver/brook charr streams, relative to streams with both brook charr and beaver present (Tamhane's T2 test: P = 0.004). However, I found no difference in cutthroat distributions between beaver watersheds with and without brook charr (Tamhane's T2 test: P = 0.822) (Figure 3.3). Using these mid/high-elevation proportion data, I calculated that the degree of cutthroat trout/brook charr overlap was significantly higher in beaver versus non-beaver treatments (MANOVA: F = 43.48, df = 1, P < 0.001) (Table 3.3).

I found a significant treatment effect on westlsope cutthroat trout densities (MANOVA: F = 43.29, df = 2, P < 0.001). Using Tamhane's T2 post-hoc pairwise comparisons, I demonstrated significantly higher cutthroat densities in beaver/non-brook charr streams compared with densities found in brook charr invaded streams both with (P < 0.001) and without beaver present (P < 0.001) (Figure 3.4). I found no difference in cutthroat trout densities between beaver and non-beaver streams undergoing brook charr invasion (P = 0.265). On the other hand, brook charr densities were significantly higher in beaver influenced streams relative to non-beaver streams (MANOVA: F = 8.53, df = 1, P = 0.019).

Overall, I found that the effect of beaver in brook charr invaded streams acts to increase stream temperatures and hence degree-days, brook charr densities, and the degree of spatial overlap between brook charr and cutthroat trout. Whereas 80 – 100 % of cutthroat trout were restricted to high-elevation strata of non-beaver invaded streams, with approximately 60 – 75 % species overlap, beaver presence corresponded with the majority (50-80%) of cutthroat trout captured in mid-elevation sections, with approximately 90 % overlap with high density brook charr populations. The effect of brook charr in beaver streams does not appear to influence cutthroat displacement to higher elevations, but corresponds to depressed cutthroat densities.

What are the impacts of beaver modification on potential and realized growth rates of cutthroat trout?

I found differences in size-at-age-1 among treatment types (ANOVA: $F_{2,3}$ = 6.251, P = 0.001). Pairwise treatment comparisons were statistically significant except for between treatments 1 and 3 (Tamhane's T2 test: treatment 1-2: P = 0.025; treatment 1-3: P = 0.980; treatments 2-3: P = 0.017) (Figure 3.5). I therefore found no differences in growth rate between treatments with beaver, regardless of brook charr presence. However, without beaver, cutthroat trout were approximately 15 mm smaller at age-1.

Overall, recaptured cutthroat trout (TL size range: Age-1_{stream} to 150 mm) growth rates were not statistically different among treatments (ANOVA: $F_{1,2}$ = 8.1, P = 0.105), although post-hoc pairwise comparison between treatments 1 and 2, and 2 and 3 were significant (Tamhane's T2 test: treatment 1-2: P < 0.001, treatment 1-3: P = 0.001, treatment 2-3: P = 0.115) (figure 3.6a). Recaptured cutthroat growth rates in the beaver (no brook charr) treatment (treatment 1) were approximately twice as high as those captured in the presence of brook charr. The strata at which these fish were captured in each stream, and their mean size at first capture are reported in Table 3.3. Examination of mid-elevation recaptures in isolation showed similar treatment differences in growth rate (ANOVA: $F_{1,2}$ = 2.261, P = 0.297), with considerably higher growth rates realized in non-brook charr streams (Tamhane's T2 test: treatment 1-2: P < 0.001, treatment 1-3: P = 0.001, treatment 2-3: P = 0.503). High-elevation recapture growth rates also showed this pattern (ANOVA: $F_{1,2}$ = 93.136, P = 0.084), there was stronger support for increased cutthroat growth rates in brook charr invaded streams with beaver (Tamhane's T2 test: treatment 1-2: P = 0.003, treatment 1-3: P < 0.001, treatment 2-3: P = 0.057) (figure 3.6a). I then evaluated the influence of stream temperature on recapture growth rates using proportion of potential growth for each stream (figure 3.6b). These results were consistent with the recapture growth rate analysis, indicating that temperature differences alone among streams do not explain these differences.

Discussion

I shed light on an aspect of invasion ecology in which the dynamics of an exotic invader and a sensitive native species can be mediated by a third species native to that system. In several small, mountain streams of western Montana, I found that beaver disturbance increased both the mid- and high-elevation fish growing season to levels that enhanced juvenile cutthroat growth rates. Faster growth in stream fishes allows larger body sizes to be attained before overwintering, engendering increased survival and higher recruitment success (Crowder et al. 1987; Letcher et al. 1997; Wootton 1990). In contrast to research conducted in Wisconsin that reports beaver dam removal to result in large increases in brook charr and brown trout (*Salmo trutta*) abundances (Avery 2004), I showed that brook charr densities in increased by 2 – 3 fold in beaver dammed streams compared with non-beaver streams (figure 3.4), a result consistent with several other studies conducted in Western States (Grasse & Putnam 1955; Huey & Wolfrum 1956; Rasmussen 1941). This suggests that beaver activity likely influences freshwater fish invasions in a context-dependent fashion (see Collen & Gibson 2001; Snodgrass & Meffe 1998). However, since the brook charr/cutthroat trout invasion scenario essentially encompasses western, cold-water mountain systems, it is likely that my results are applicable to small headwater streams across the extent of this invasion event.

In keeping with other reports of brook charr/cutthroat trout stream distribution, I found that in non-beaver streams there was a clear distinction between elevational stream distributions of brook charr and cutthroat trout (Dunham et al. 2002; Fausch 1989; Paul & Post 2001; Rieman et al. 2006) (Figure 3.3). This was accompanied by reduced species overlap with significantly lower cutthroat individual growth rates. Invasives dominated lower stream sections, with natives predominantly found in higher elevation reaches. This limitation of downstream cutthroat trout distribution corresponds with other empirical evidence that show that brook charr gain a competitive advantage over cutthroat trout at warmer stream temperatures that are associated with lower elevations (De Staso III & Rahel 1994; Novinger 2000).

I found positive implications of beaver presence for cutthroat trout, manifested by significant increases in the length of the growing season at both mid- and high-elevations in the beaver streams (Figure 3.2), a key determinant of recruitment success (Coleman & Fausch 2007). While mid-elevation strata of non-beaver watersheds exhibited growing seasons marginally within the bounds required for strong recruitment success, the high-elevation strata of these streams, where the majority of cutthroat trout were, fell within temperature bounds that bestow a high risk of recruitment failure (Figure 3.3). Length-frequency distributions (Figure 3.1) and estimates of cutthroat density (Figure 3.4) provide ancillary support for the increased occurrence of cutthroat recruitment failure in non-beaver watersheds, with reduced numbers and an under-representation of smaller-sized fish in these streams relative to those influenced by beaver activity.

I therefore provide evidence that under brook charr invasion conditions, cutthroat trout in non-beaver systems are likely to be restricted to higher elevations with curtailed growing season. Where such spatial demarcation exists, a common management strategy employed by fisheries biologists charged with conserving westslope cutthroat trout (particularly east of the Continental Divide in Montana) is to isolate these populations using artificial fish migration barriers (Fausch et al. 2009). This isolation management approach may be justified in moribund cases of cutthroat decline to maintain short-term persistence of fragmented remnant cutthroat populations. However, when applied indiscriminately, an invasion-isolation trade-off emerges in which longer-term consequences of isolation involves loss of fluvial life-history form and genetic diversity (Fausch et al. 2009; Peterson et al. 2008b), with concomitant increases in susceptibility to stochastic processes (Novinger & Rahel 2003) such as recruitment failure. It is generally recommended that where implemented, isolation management should incorporate as large and diverse an area as possible, and that efforts should be made to ensure that critical habitat requirements are met (e.g. Novinger & Rahel 2003). My research suggests that including beaver in the isolation-management process, with the aim of modifying stream temperatures and augmenting complex habitat availability could meet this last criterion, potentially increasing conservation success rates where these drastic actions are warranted.

Realistically, the ubiquity of brook charr invasions across the range of cutthroat trout (Dunham et al. 2002) makes it infeasible to physically remove all these invasives, or fragment and isolate all cutthroat populations. Based on my findings, I propose that the inclusion of beaver on the landscape furnishes a degree of ecological function that both positively and negatively mitigates aspects of this particular invasion scenario. I found that beaver facilitated the spread of brook charr into upper stream reaches, and increased brook charr/cutthroat trout stream overlap (Table 3.3). Cutthroat trout in beaver streams benefited through lower stream distributions. However, even in beaver streams the effect of brook charr presence decreased cutthroat trout densities. This was likely a result of increased interspecific competition due to large increases in brook charr densities, since brook charr are capable of tolerating higher populations densities than cutthroat trout (Schroeter 1998).

By altering stream distributions and hence the degree of overlap between brook charr and cutthroat trout, beaver activity led to changes in interspecific interactions between these species. Other studies have found that effects of brook charr are most severe on smaller cutthroat trout size classes (Griffith 1988; Peterson et al. 2004). However, my results indicated that juvenile cutthroat trout in brook charr invaded beaver streams were able to attain comparable sizes at age-1 as in non-invaded beaver streams. Additionally, these cutthroat trout juveniles were approximately 15 mm larger at age-1 under invasion conditions than individuals in non-beaver invaded streams (Figure 3.5). Thus, beaver appear to alter the interaction dynamics between cutthroat trout and brook charr, mitigating negative effects of this invasion on juvenile trout.

In the case of larger cutthroat trout however, I found a significant negative effect on cutthroat trout growth when in sympatry with brook trout, regardless of beaver presence (Figure 3.6a). This was contrary to my expectations, as other research has reported that larger cutthroat trout survival rates (age-2+) remain unaffected by brook charr invasion (Peterson et al. 2004). However, Peterson et al. (2004) note that sublethal effects of brook charr, such as reduced growth and hence fecundity may have population-level implications for cutthroat trout. Additionally, my results probably suffer from low sample sizes and incorporate cutthroat trout of age-1+, thereby making it difficult to directly compare with Peterson et al.'s (2004) findings. Whilst I found no mitigating effects of beaver on cutthroat trout when examining overall mid- and high-elevation strata together, I did detect a weak trend of increased growth of age-1+ cutthroat in high-elevations of beaver streams compared with non-beaver streams (Figure 3.6a). Thus, moderating effects of beaver on larger cutthroat trout may be dependent on elevation, and should be investigated further.

Examining these growth rates as a proportion of potential growth as predicted by temperature alone, I found that cutthroat trout in non-invaded beaver streams grew at 30-80% of potential growth rates whilst those in brook charr invaded beaver streams reached approximately 15-25% of their potential growth rate, thus implying a brook charr effect. Upon initial inspection, I found no effect of beaver on age-1+ through comparison of non-beaver and beaver invaded streams. However, this is due to cutthroat trout at mid-elevations attaining around 25% of their potential growth rates in each treatment type. Examination of high-elevation strata hints at a weak beaver effect whereby cutthroat at this elevation achieve 5 % of their potential growth compared with around 15% in beaver streams (Figure 3.6b).

My study provides quantitative evidence for how beaver modify the invasion ecology of brook charr in mountain streams of western North America, and provides information for how this habitat modifier can be incorporated into invasion theory. For instance, in the context of invasion, the interaction chain effect is usually used to describe a chain of direct linkages between the effects of habitat modification on invasive species abundance, which in turn has direct effects on native species decline (Didham et al. 2007). Natural beaver disturbance may represent a special case of an interaction chain effect. Although brook charr invaded higher and attained higher densities in the beaver streams, cutthroat trout may benefit enough from warmer water temperatures and more complex habitat in order to persist in the face of this invasion. My research complements another recent study which shows that interactive effects of beaver act to enhance native puye (*Galaxias maculatus*) abundances in Chile, and hence moderate the negative effects of invasive trout on this species (Moorman et al. 2009). In this case, despite the fact that beaver themselves represent an invasive species, this example in conjunction with my research serves to elucidate the integral role that beaver can play in the invasion dynamics of freshwater systems.

Summary/Conclusion

Beaver facilitated the invasion of brook charr, but the presence of this habitat modifier acted to mitigate some of the negative effects of this invasive on cutthroat trout in my study system. The utility of beaver engineering is becoming more prominent in the realm of freshwater restoration efforts that seek to reshape ecosystem functioning of degraded systems (Roni et al. 2008), and to offset the effects of a drying climate (Hood & Bayley 2008). With beaver presence and nonnative fish invasions ubiquitous across the North American landscape, my research highlights the importance of considering beaver in native species conservation plans and invasive species management. Determining how beaver affects size-specific survival rates of these species is a vital next step in these systems. This will allow us to evaluate the implications that beaver activity has for population persistence of native westslope cutthroat trout, and will help to inform effective management strategies for this invasive/native conundrum.

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Table 3.1. Sampling strategies used in study streams of southwestern Montana.

Stream	Treatment[§]	Focal species present	Year(s) sampled	Data collected[ψ]	Elevation range sampled (m)		Stream length sampled for fish capture (m)
					Mid-elevation	High-elevation	
Stone	1		‘06, ‘07, ‘08	D, S, MR, T, H	1800-1899	1900-2200	1,200
Rape	1		‘06, ‘07, ‘08	D, S, MR, T, H	1900-1999	2000-2180	800
Johnson	2		‘06, ‘07, ‘08	D, S, MR, T, H	1840-1999	2000-2170	800
Stine	2		‘08	T, H	1900-1999	2000-2200	500
Hell Roaring	2		‘08	D, S, T, H	1940-2010	2011-2200	800
Lacy	3		‘06, ‘07, ‘08	D, S, MR, T, H	1900-2020	2021-2230	1,000
Squaw	3		‘06, ‘07, ‘08	D, S, MR, T, H	1850-1999	2000-2100	1,020

§ Treatment: 1 = westslope cutthroat trout, beaver present; 2 = westslope cutthroat trout, brook charr, present; 3 = westslope cutthroat trout, beaver, brook charr present

ψ Fish data collected: D = distribution, S = scales sampled, MR = capture-mark-recapture, T = temperature, H = habitat

Table 3.2. Habitat characteristics of study streams in southwestern Montana.

Stream	Treatment[§]	Average Channel gradient (%)	Average width (m)	Midstream depth (cm)	Pool frequency (per 100 m)	Mean summer temperature (°C)[†]	
						Mid-elevation	High-elevation
Stone	1	5	4	22.2	2.7	12.1	8.8
Rape	1	9	2.2	20.8	2.2	13.7	10.9
Johnson	2	9	4.5	21.7	1.6	10.7	8.4
Stine	2	8	3.0	21.3	1.8	9.7	8.0
Hell Roaring	2	6	3.5	24.8	2.8	10.1	7.2
Lacy	3	5	3.6	19.9	1.7	13.5	11.5
Squaw	3	6	2	34.8	3.1	15.3	12.9

§ Treatment: 1 = westslope cutthroat trout, beaver present; 2 = westslope cutthroat trout, brook charr, present; 3 = westslope cutthroat trout, beaver, brook charr present

† Mean summer temperature 1 July – 31 August 2006 – 2008 data

Table 3.3. Fish capture/recapture rates and attributes of fish populations in each stream used in calculation of distribution and growth rate metrics among treatments.

Stream	Treatment[§]	No. fish captured/recaptured Mid-elevation strata						No. fish captured/recaptured High elevation strata						Ave. overlap (%)	Ave. TL (mm) of recaptured WCT[†]
		2006		2007		2008		2006		2007		2008			
		WCT	BKC	WCT	BKC	WCT	BKC	WCT	BKC	WCT	BKC	WCT	BKC		
Stone	1	264/51	—	228/75	—	213/75	—	138/15	—	136/33	—	133/27	—	—	125/(15.9)
Rape	1	51/7	—	90/31	—	34/5	—	43/4	—	54/5	—	35/6	—	—	93/(28.1)
Johnson	2	10/1	43/6	5/3	48/3	5/4	34/4	46/12	29/6	15/6	22/5	10/3	9/3	76.4	139/(10.5)
Hell Roaring	2	—	—	—	—	0	21	—	—	—	—	12	2	59.8	—
Squaw	3	42/9	271/21	48/18	603/46	51/20	319/122	30/9	185/15	45/13	171/16	48/22	165/43	93.0	110/(25.9)
Lacy	3	76/12	258/39	54/25	217/75	33/11	136/45	12/0	80/14	18/6	86/24	5/1	63/18	91.6	129/(16.4)

§ Treatment: 1 = westslope cutthroat trout (WCT), beaver present; 2 = westslope cutthroat trout, brook charr (BKC), present; 3 = westslope cutthroat trout, beaver, brook charr present

† WCT in the size range 55 – 149mm (TL/(SD))

Figure Legends

Figure 3.1. Length-Frequency distributions of westslope cutthroat trout in each treatment type. Treatment type is indicated pictorially (white fish = cutthroat trout, black fish = brook charr, and beaver.

Figure 3.2. Average Growing Season Degree days (+/- SE) in beaver and non-beaver study streams. Hatched temperature zone (900 – 1,200 Celsius degree days) indicates optimal degree-days for westslope cutthroat trout (WCT) recruitment, the white temperature zone (800 – 900 Celsius degree days) indicates variable recruitment success, and the stippled temperature zone (< 800 Celsius degree days) indicates high risk of recruitment failure (Coleman & Fausch 2007).

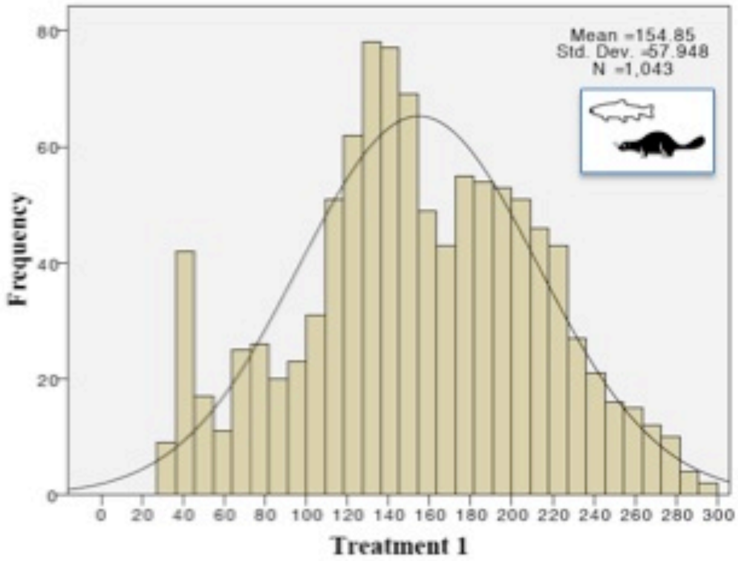
Figure 3.3. Proportions of westslope cutthroat trout (WCT) and brook charr (BKC) captured in mid- and high elevation strata of each stream. Average mid- and high strata degree-days are shown by textured rectangles, with latitudinal length of rectangle denoting range between 2006 and 2008 average degree-days. Streams are grouped according to treatment, with treatment type indicated pictorially (white fish = WCT, black fish = brook charr (BKC), and beaver. Hatched temperature zone (900 – 1,200 Celsius degree days) indicates optimal degree-days for westslope cutthroat trout (WCT) recruitment, the white temperature zone (800 – 900 Celsius degree days) indicates variable recruitment success, and the stippled temperature zone (< 800 Celsius degree days) indicates high risk of recruitment failure (Coleman & Fausch 2007).

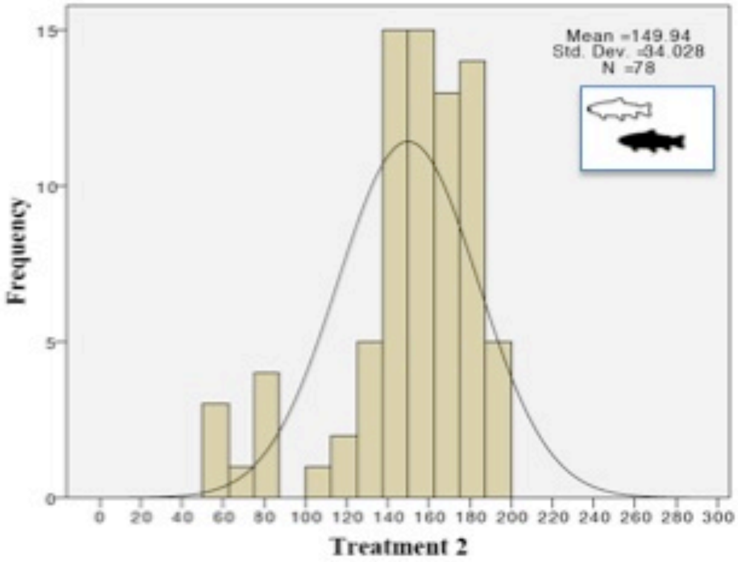
Figure 3.4. Densities of westslope cutthroat trout (+/- SE) (white bars) and brook charr (+/- SE) (grey bars) in each stream. Streams are grouped according to treatment, with treatment type indicated pictorially (white fish = WCT, black fish = brook charr (BKC), and beaver.

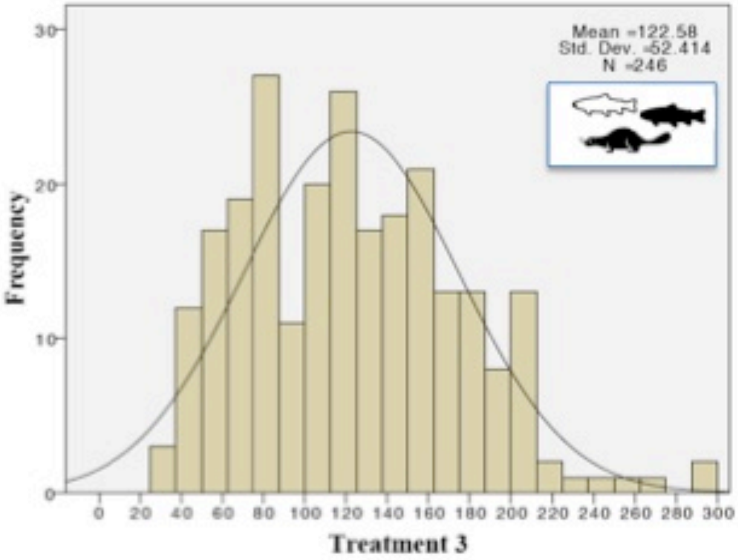
Figure 3.5. Westslope cutthroat trout back-calculated size at age-1 for each stream. Treatment type is indicated pictorially (white fish = WCT, black fish = brook charr

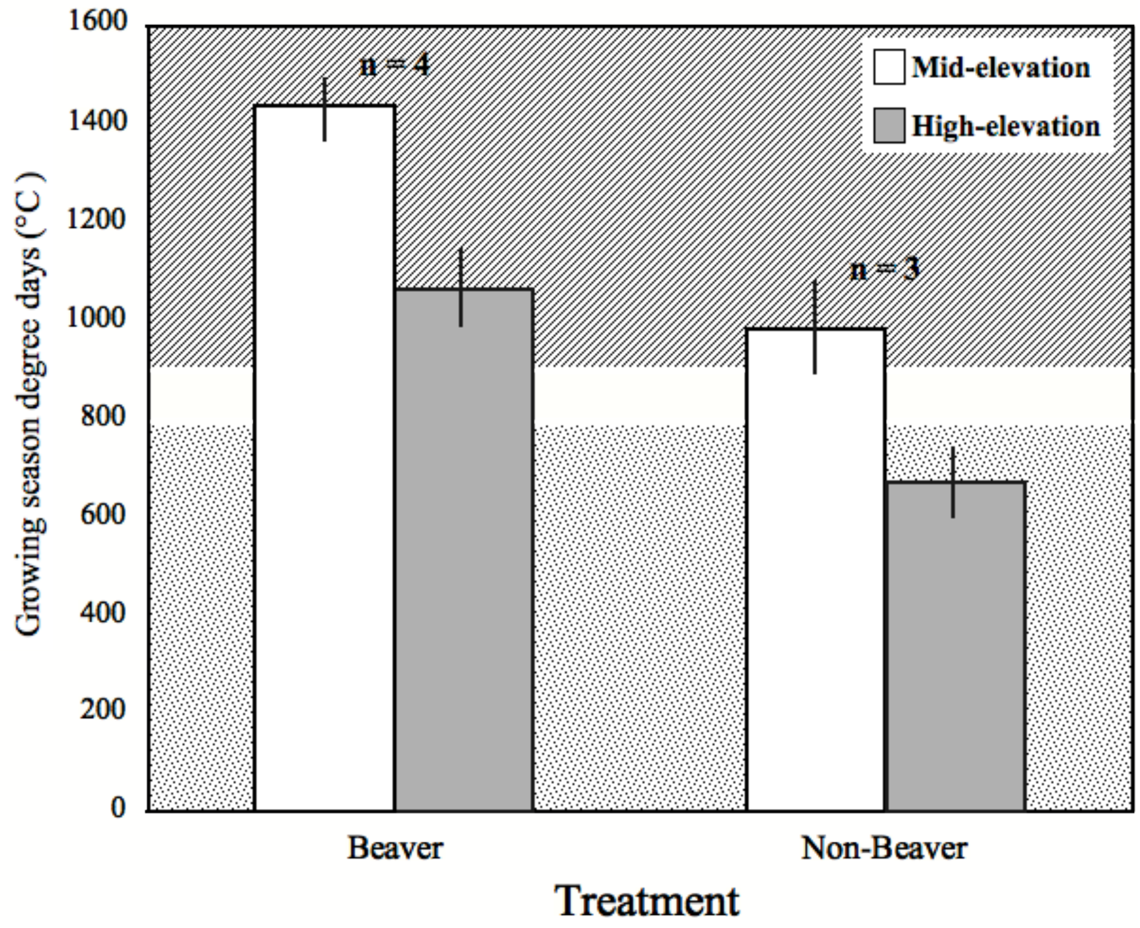
(BKC), and beaver. Letters A and B indicate significant difference between treatments: treatments with different letters are significantly different from one another ($P \leq 0.05$), whilst treatments with the same letter indicate no statistical difference ($P > 0.05$).

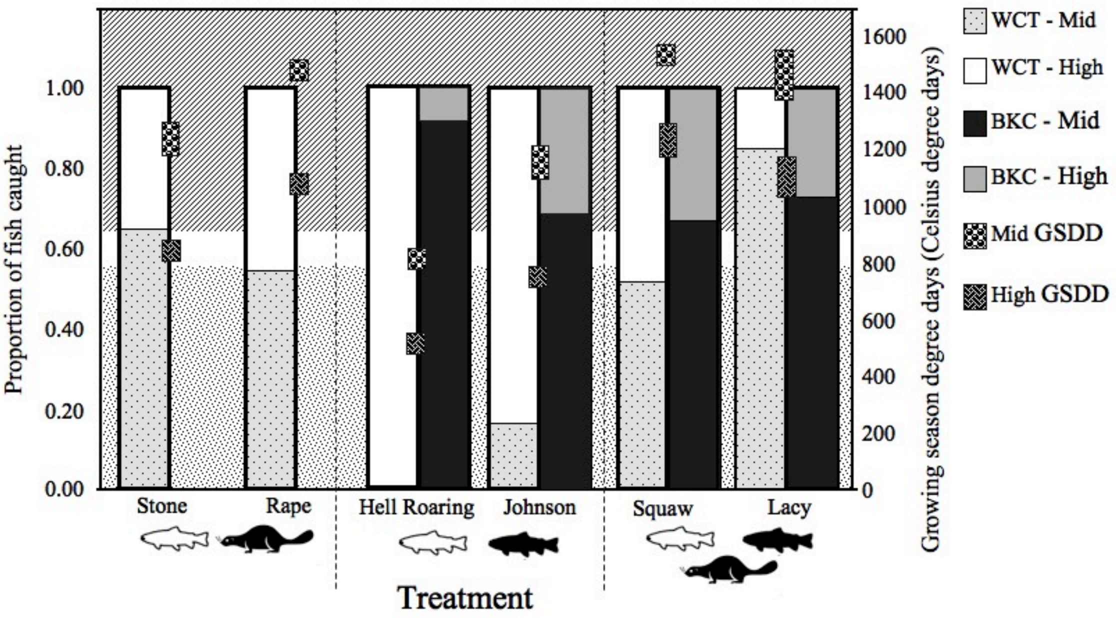
Figure 3.6. (a) Percentage daily growth rate (+/- SE) of westslope cutthroat trout at mid- (white bars) and high-elevations (grey bars) of each stream. (b) The proportion of realized growth to temperature-based potential growth (+/- SE) at mid- (white bars) and high-elevations (grey bars) in each stream. Treatment type is indicated pictorially (white fish = WCT, black fish = brook charr (BKC), and beaver.

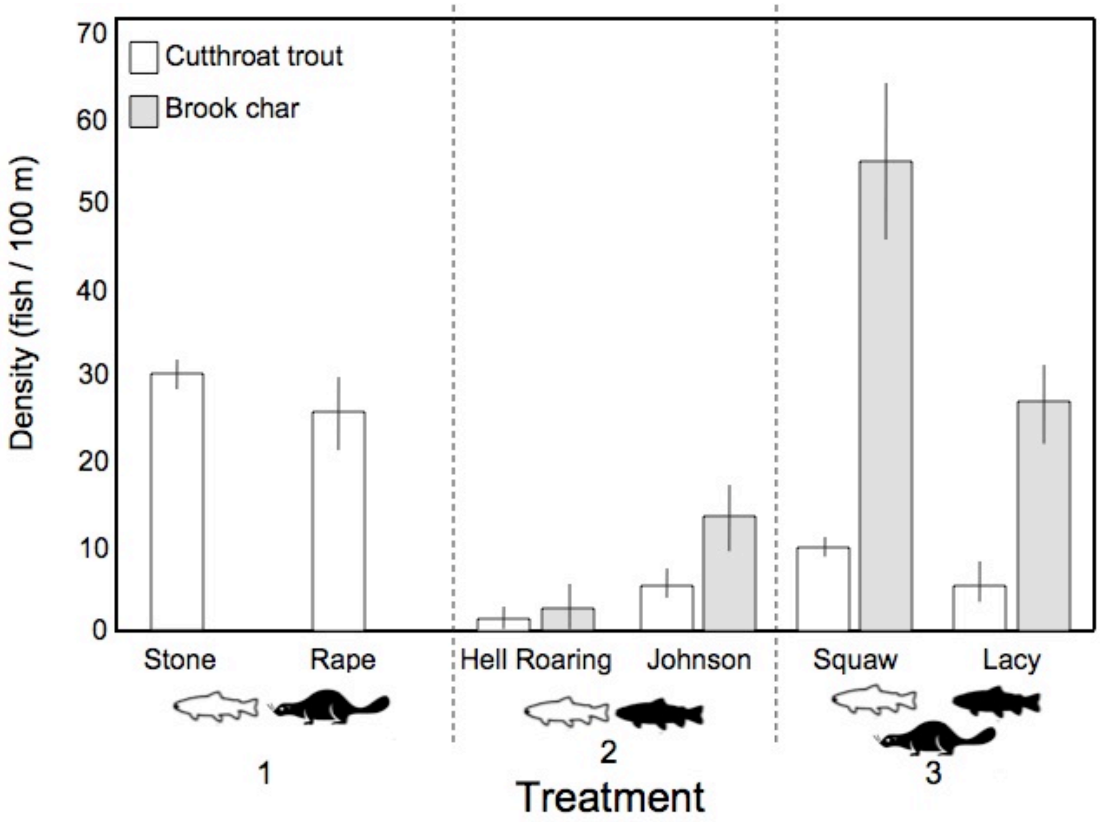

Mean =154.85
Std. Dev. =57.948
N =1,043
Frequency
0
20
40
60
80
0 20 40 60 80 100 120 140 160 180 200 220 240 260 280 300
Treatment 1


Mean =149.94
Std. Dev. =34.028
N =78
Frequency
0
5
10
15
0 20 40 60 80 100 120 140 160 180 200 220 240 260 280 300
Treatment 2

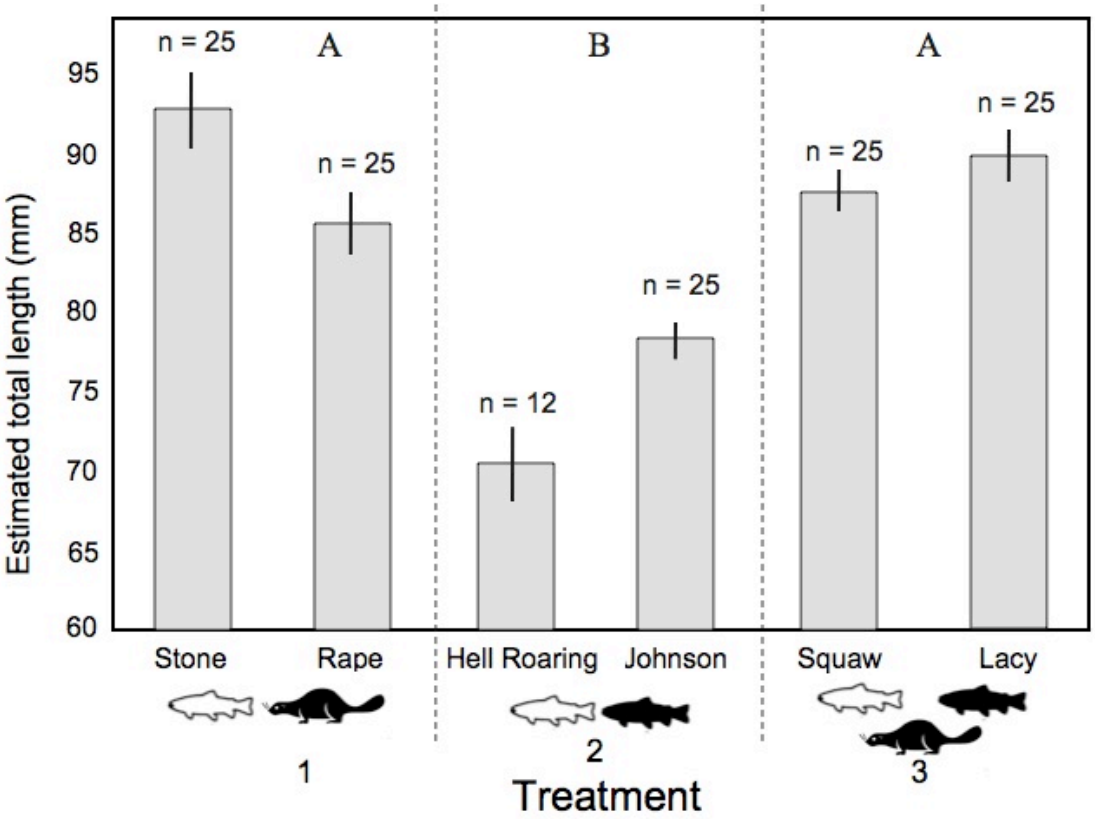

Mean =122.58
Std. Dev. =52.414
N =246
Frequency
0
10
20
30
0 20 40 60 80 100 120 140 160 180 200 220 240 260 280 300
Treatment 3

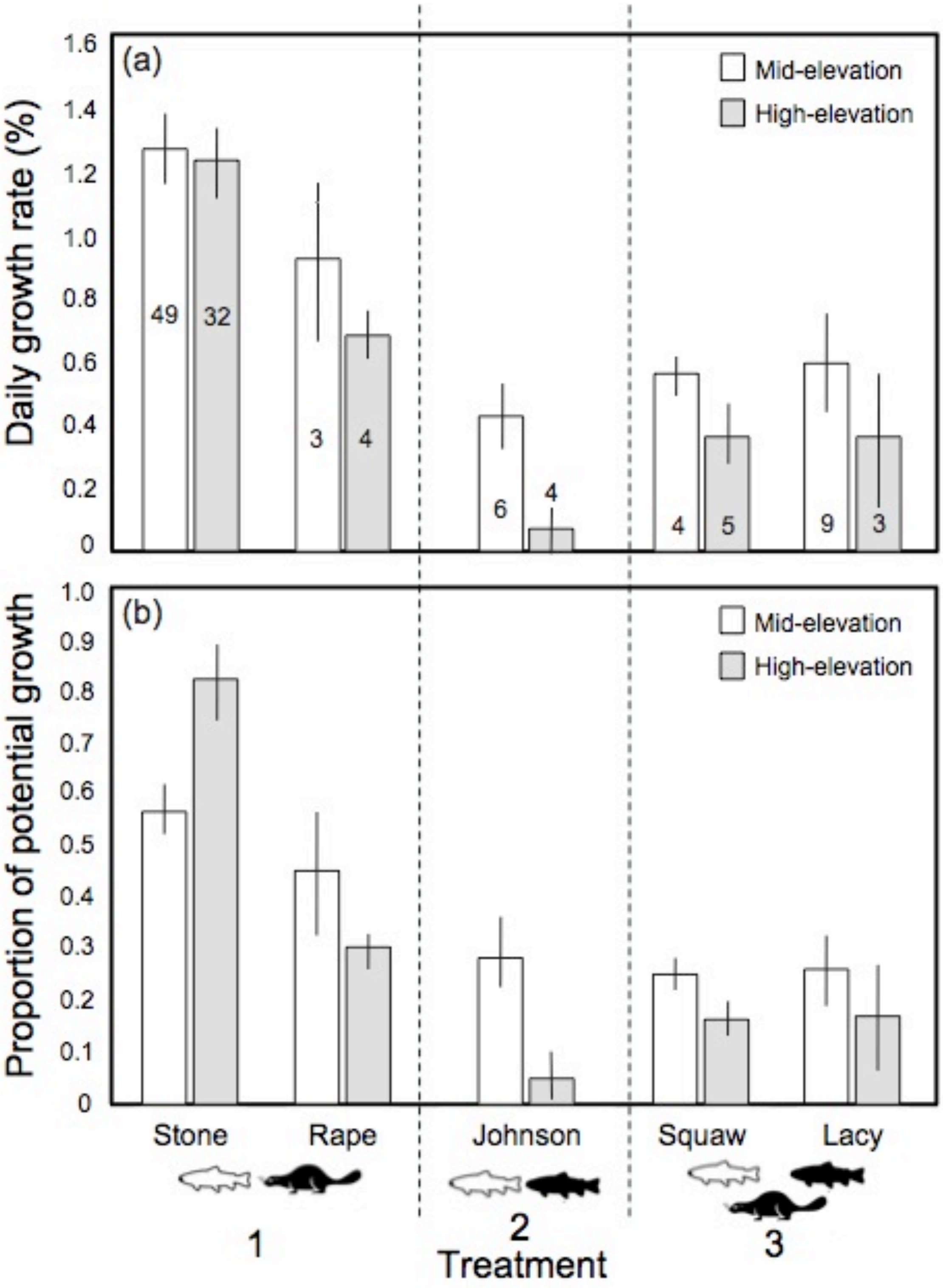

1600
1400
1200
1000
800
600
400
200
0
Growing season degree days (°C)
n = 4
n = 3
Mid-elevation
High-elevation
Beaver
Non-Beaver
Treatment


Proportion of fish caught
1.00
0.80
0.60
0.40
0.20
0.00
1600
1400
1200
1000
800
600
400
200
0
Growing season degree days (Celsius degree days)
Stone
Rape
Hell Roaring
Johnson
Squaw
Lacy
Treatment
WCT - Mid
WCT - High
BKC - Mid
BKC - High
Mid GSDD
High GSDD



Cutthroat trout
Brook char
Density (fish / 100 m)
70
60
50
40
30
20
10
0
Stone
Rape
Hell Roaring
Johnson
Squaw
Lacy
1
2
3
Treatment


Estimated total length (mm)
60
65
70
75
80
85
90
95
n = 25
A
n = 25
B
n = 12
n = 25
A
n = 25
n = 25
Stone
Rape
Hell Roaring
Johnson
Squaw
Lacy
1
2
3
Treatment


(a)
Daily growth rate (%)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
Mid-elevation
High-elevation
49
32
3
4
6
4
4
5
9
3
(b)
Proportion of potential growth
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Mid-elevation
High-elevation
Stone
Rape
Johnson
Squaw
Lacy
1
2
Treatment
3

CHAPTER 4

BEAVER MITIGATE NATIVE FISH DECLINES IN THE FACE OF INVASION

Abstract

An understanding of the parameters that alter demographic consequences of invasions on natural systems is essential as we work to manage exotics and maintain native persistence across the landscape. Brook charr (*Salvelinus fontinalis*) populations have become established throughout the western United States, and have been implicated in native cutthroat trout (*Oncorhynchus clarkii*) declines across their range. Heterogeneity in stream habitat characteristics imposed by beaver (*Castor canadensis*) activity has the potential to alter invasion dynamics between brook charr and cutthroat trout. I examined how beaver influence cutthroat demographic rates and population persistence in invaded and non-invaded streams. I measured vital rates with a 3-year mark-recapture study in southwest Montana to evaluate relative impacts of beaver impoundments on invaded cutthroat demography and developed population models to determine extinction risk. In comparison with non-beaver streams, I found that cutthroat exhibit ~ 40 % higher apparent survival rates in beaver influenced streams. I also found differences in life-stage transition rates, with small to large adult transition probabilities 1.5 and 4 times higher in beaver systems. The invaded non-beaver stream exhibited the lowest population growth rates ($\lambda = 0.89$), and the shortest median time to extinction (8-years). Estimates of population growth rates from invaded beaver streams had 5 – 20 % higher growth rates and longer median times to extinction. Beaver mitigate negative effects of brook charr invasions on cutthroat trout populations. I lend support to an emerging body of evidence that elucidates how spatial heterogeneity on the landscape can lessen the impacts of an invasive species, allowing native persistence. I therefore propose that including beaver in our cutthroat management toolbox could be used to improve population persistence of this sensitive species.

Introduction

Exotic species invasions have devastating effects on native species and ecosystems worldwide, adding to a gamut of stressors on native populations that include habitat degradation, pollution, overexploitation, and disease (Wilcove et al. 1998). Of these stressors, the proliferation of invasive species presents one of the least tractable problems facing ecologists and land managers charged with native species conservation (Byers et al. 2002; Vitousek et al. 1996). Recognition of the magnitude of this threat has stimulated an upsurge in research on ecological invasions (Smith et al. 2006). However, predicting invasions and their impacts, as well as formulation of effective management tools to curtail invasives has proved elusive (Pearson & Fletcher 2008). Understanding the factors and mechanisms that cause invasion success and impacts on native species to be highly context-dependent (Catford et al. 2009; Daehler 2003), may help in the development of efficacious management approaches.

In freshwater systems of the western U.S., invasions by nonnative brook charr (*Salvelinus fontinalis*) have been implicated in native cutthroat trout (*Oncorhynchus clarkii* spp.) population declines, displacement, and range contraction over the past century (Dunham et al. 2002; Kennedy et al. 2003; Young 1995). Consequently, three subspecies of cutthroat trout are formally listed as threatened under the U.S. Endangered Species Act, and the status of cutthroat is a management concern throughout the species' range (Dunham et al. 2002). Interspecific competition is commonly linked to cutthroat displacement by brook charr (Adams et al. 2000; Dunham et al. 2002; Fausch 1988; Griffith 1988), and involves brook charr displaying increased agonistic behavior and occupying preferred feeding positions when sympatric with cutthroat (Chilcote 2004; De Staso III & Rahel 1994; Griffith 1972, 1974; Novinger 2000). Demographic work examining sympatric brook charr-cutthroat populations shows that brook charr depress cutthroat populations through age-specific biotic interactions that reduce juvenile cutthroat survival rates (Figure 4.1) (Peterson et al. 2004). Brook charr monopolize more energetically profitable lower elevations of invaded streams, relegating cutthroat to colder upstream reaches (Dunham et al. 2002; Fausch 1989; Paul & Post 2001; Rieman et al. 2006). Indeed, many of the remaining cutthroat populations within the upper Missouri basin are now restricted to isolated headwater habitats (Shepard et al. 1997).

Aside from direct effects of brook charr competition on native demographic rates, shifts in cutthroat distributions to higher elevations have potential population impacts by reducing somatic growth rates. This has implications for reduced size-at-age (McCaffery, Chapter 3), and hence fecundity values (Downs 1995). Additionally, colder temperatures experienced by displaced cutthroat increase variation in recruitment success, thereby leading to a greater likelihood of recruitment failure (Coleman & Fausch 2007; Peterson et al. 2004). These direct and indirect impacts are hypothesized to increase the risk of extinction. (Rieman & McIntyre 1993; Schaffer 1991; Schaffer & Sampson 1988).

Population dynamics of native cutthroat trout in the face of brook charr invasion pressure varies across the landscape. Understanding the mechanisms behind how population responses vary, and subsequent impacts on cutthroat persistence, is essential to conservation efforts of these natives. Perhaps the most pervasive natural modifier of freshwater stream systems on the North American landscape is habitat engineering associated with beaver (*Castor canadensis*) (Collen & Gibson 2001). As a result of feeding and damming activities, beaver increase landscape heterogeneity (Johnston & Naiman 1990) through the creation of lentic habitat in otherwise lotic systems. The formation of pool habitat increases water temperatures both at the impoundment as well as downstream (McCaffery, Chapter 3), and enhances prey availability and juvenile rearing habitat for all salmonid species (Scruton et al. 1998; Winkle et al. 1990). Stream reaches influenced by beaver have been found to accommodate high abundances of brook charr (Hilderbrand 1998), and beaver pools provide critical winter habitat for cutthroat trout (Jakober et al. 2000). However, quantitative research on the role of beaver habitat modification in aquatic invasive/native fish dynamics is scarce. One example from Chilean watersheds, where beaver themselves are an invasive exotic species, suggests that native puye (*Galaxias maculatus*) attain higher abundances in beaver streams that are under invasion pressure from exotic salmonids (Moorman et al. 2009). These recent findings strongly suggest that beaver activity influences demographic parameters of native populations, and allows them to persist in the sympatry with exotics.

With more natives distributed in lower elevation, warmer stream reaches, juvenile cutthroat in beaver streams display higher somatic growth rates relative to non-beaver systems (McCaffery, Chapter 3), although exhibit a greater degree of spatial overlap with brook charr. Thus I was interested in establishing if these findings propagate to altering cutthroat population persistence.

I examined cutthroat trout populations subject to brook charr invasion in both beaver and non-beaver streams to investigate how habitat modification by beaver might affect cutthroat demographic parameters, and provide insight into cutthroat population viability. Specifically, I assessed how beaver influence cutthroat trout demographic parameters in invaded and non-invaded streams, and evaluated the repercussions for cutthroat population persistence in the face of invasion.

Methods

Study sites

I selected five study streams in the Beaverhead-Deerlodge National Forest, and nearby Bureau of Land Management, and private lands in southwestern Montana. All streams included cutthroat trout, but differed in terms of brook charr and beaver presence in order to fulfill the treatment criteria: 1 = beaver and cutthroat trout present, 2 = cutthroat trout and brook charr present, and 3 = beaver, cutthroat trout, and brook charr present. The only salmonid species inhabiting the study streams were westslope cutthroat trout and brook charr. All study watersheds fell within an elevation range of approximately 1,800 m to 2,200 m and were suitable for beaver habitation. Streams were selected based on the presence of requisite species assemblages, and were of similar size and gradient (Table 4.1).

Data collection

I sampled each study stream using capture-mark-recapture methods during July and August of 2006, 2007, and 2008. I stratified each stream into low, mid, and high elevations, and randomly selected three 200 m sections within the mid and high elevation strata of each stream for study. I used two-pass depletion electrofishing to capture brook charr and westslope cutthroat trout. During the first sampling session, I enclosed each 200 m section temporarily with block-nets, and sampled in an upstream direction using a backpack electrofishing unit (Smith-Root Inc. model 15-D, Vancouver, WA, USA). I measured (total length (TL), nearest 1 mm), and weighed (nearest 1 g) all cutthroat trout. Fish greater than 55 mm were individually tagged with a 12 mm passive integrated transponder tag (PIT tags: Biomark, Inc., Boise, ID, USA) and released. During subsequent recapture sessions, I repeated the established sampling protocol except I recorded recaptures, and PIT tagged new captures.

Demographic parameter estimation

I modeled cutthroat trout populations using a combination of my own nark-recapture field data and vital rates obtained from the literature. Since cutthroat trout exhibit size-specific maturity and fecundity, as well as potential differences in survival, I grouped cutthroat into four life stages categories: stage 1 = Young-of-the-year (YOY), stage 2 = juvenile (treatment 1: TL 89–142 mm, treatment 2: TL 78–142 mm, treatment 3: TL 88–142 mm), stage 3 = small adult (TL 143–173 mm), and stage 4 = large adult (TL 174–265 mm) (Figure 4.2). These stage classes encompassed the range of sizes exhibited by resident cutthroat in my study streams, and approximately correspond to other published cutthroat trout stage-based demographic models (Hilderbrand 2002; Peterson et al. 2008a). I directly measured juvenile, small adult, and large adult stages, and used literature-based vital rate values for the young-of-the-year stage (Hilderbrand 2002; Peterson et al. 2008a; Peterson et al. 2004; Shepard et al. 1997). The variation in juvenile cutthroat trout growth associated with treatment type observed in the field (McCaffery, Chapter 3) was reflected in my model by setting treatment-specific size ranges for juveniles (Figure 4.2).

Given that my sampling design incorporated periods of time between capture sessions during which cutthroat could enter or leave the study reach, I minimized bias in my estimation of demographic vital rates by examining stream capture histories for evidence of transient fish. Transients are individuals that leave the study area after first capture and thus have a subsequent local survival probability equal to zero (Pradel et al. 1997). I used Tmsurviv (Hines 1996) to calculate stage-specific estimates of the proportion of residents (γ), resident survival rates (φ), and associated capture probabilities (p). All possible model combinations, with and without time dependence for each parameter were tested. I found no evidence of overdispersion in any of my capture histories ($\hat{c} = 1$), and I proceeded to assess candidate models using AICc (see White & Burnham 1999). Models with the lowest values of AICc were retained (Lebreton et al. 1992), and any models with AICc differences greater than four were discarded (Anderson et al. 1994). The best models for all streams indicated high cutthroat site fidelity with a negligible influence of transients ($\gamma = 1$).

I then analyzed my capture data using multi-strata mark-recapture models in Program MARK (White & Burnham 1999). Model strata corresponded to juvenile, small adult, and large adult demographic life-stages. Time-independent models that incorporated stage dependence yielded parameter estimates and variances for survival (ϕ), transition rates between life stages (ψ), and capture probability (p), which were then ranked using AICc.

Matrix model construction

I determined the demographic implications of beaver on invaded and non-invaded cutthroat population growth rates using matrix transition models. I constructed post-birth pulse stage-structured matrix models using invaded (low survival (LS)) and non-invaded (high survival (HS)) young-of-the-year survival rates (Peterson et al. 2008a; Shepard et al. 1997), and estimated mean stage-specific survival and transition rates. To calculate reproductive output (F) of adults, I combined estimated adult survival and transition rates with literature values of stage-specific fecundity, sex ratio (assumed to be 1:1), and egg and fry survival rates (Hilderbrand 2002; Peterson et al. 2008a). I obtained estimates of variation in cutthroat vital rates from the literature (Table 4.2; Hilderbrand 2002; Peterson et al. 2008a; Shepard et al. 1997), and used stochastic matrix projection models to determine cutthroat population growth rate for each study stream and explore future population viability. Since previous research has found mitigating effects of beaver for invaded cutthroat trout (McCaffery, Chapter 3), I simulated brook charr invaded systems using both high and low values for young-of-the-year cutthroat survival (Table 4.2). I set the initial population vectors to 2,500 individuals at stable stage distribution for each stream, as this is a realistic carrying capacity for cutthroat populations in small streams (Hilderbrand 2002), and is a reasonable stream-wide total population size based on cutthroat density data for these streams (McCaffery, Chapter 3). I used two metrics to characterize cutthroat population response to invasion, with and without beaver: (i) stochastic lambda (λ_S), and (ii) median time to extinction. Persistence was defined as maintaining a total population size greater than 50. Simulations were run for 100 time steps (years), and iterated 1,000 times using MATLAB version R2007a (MathWorks, Inc.). Projecting the population 100-years into the future is approximately 20 times the generation time of cutthroat trout (Downs et al. 1997), and as such is of sufficient duration to characterize the dynamics of these populations and provide useful indices of extinction risk in the face of invasion. I calculated empirical cumulative distribution functions to elucidate extinction probabilities through time, and expressed overall risk to cutthroat populations in terms of the median time to extinction (Morris & Doak 2002).

Results

Cutthroat trout demographic parameters

I found no evidence of transience in my study areas, and assumed that capture histories comprised only resident cutthroat individuals ($\gamma = 1.0$; Table 4.3). Therefore, I estimated apparent survival and stage transition probabilities using Program MARK (Table 4.4). In comparison to the non-beaver stream, I found that across all stage classes, apparent survival was 40 % and 46 % higher in beaver non-invaded and invaded streams respectively. Examination of mean stage-specific survival rates between beaver and non-beaver systems revealed that estimated juvenile survival was around 36 % higher in non-invaded beaver streams and 20 % higher, though more variable, in invaded beaver streams. I found that stage-specific survival of small and large adults in beaver systems were 40 % higher in non-brook charr invaded streams, and 36 % and 58 % higher respectively in invaded systems (Figure 4.3).

The probability of juveniles transitioning to small adults was relatively similar across all treatments. However, I found that the probability of juveniles transitioning to large adults was around 1.5 times greater in beaver systems. Similarly, I found a 4-fold increase in transition rates of small adults to large adults in beaver influenced systems, relative to the non-beaver stream (Figure 4.4).

Using my mean vital rate estimates, and estimates of vital rate variation from the literature, I constructed stochastic stage-based population matrix models to evaluate the influence of beaver presence on annual cutthroat population growth rates under invasion pressure. Non-invaded beaver streams exhibited positive stochastic annual growth rates of around 2 % per year. The brook charr invaded non-beaver stream, exhibited precipitous population declines of approximately 10 % per year, whilst invaded beaver streams modeled with the same low young-of-the-year survival rates declined at around 1 % and 6 % per year. However, simulations of brook charr invaded beaver streams exhibited annual population growth rates of 2 % and 7 % (Figure 4.5).

Cutthroat trout population persistence

To compare the relative levels of extinction risk associated with the cutthroat populations, I calculated cumulative distribution functions of the extinction probabilities for each stream population (Figure 4.6). In non-invaded beaver streams, I calculated that there was a relatively low likelihood of these populations going extinct within a 100-year timeframe, with cumulative probabilities of approximately 10 % and 45 % after 100-years. However, in brook charr invaded streams, I found that when modeled using low young-of-the-year survival rates, all cutthroat populations had a 100 % probability of extinction within 100-years. The median time to extinction in the invaded non-beaver stream was 8 years, whilst median extinction times in invaded beaver streams were 11 and 23 years. Modeling invaded beaver streams using high young-of-the-year survival rates yielded cumulative extinction probabilities of 0 % and 5 % after 100-years (Figure 4.6).

Discussion

My research provided new insight into the integral role that beaver play in stream ecosystems, and demonstrated the positive implications of this keystone species for cutthroat trout demography in systems that are threatened by brook charr. Since the ultimate metric of invasion impact on a native species is the probability of native extinction, I used demographic analyses to investigate the population-level implications of documented effects that beaver provide critical fish habitat (Jakober et al. 2000), enhance cutthroat somatic growth rates, but increase the degree of overlap with a major competitor (McCaffery, Chapter 3).

In non-beaver streams invaded by brook charr, cutthroat trout exhibited low survival rates across all stage classes. With beaver present in invaded streams, cutthroat exhibited slightly higher mean survival at the juvenile stage, and substantial increases in small and large adult survival rates. Comparison of my low adult survival estimates ($\phi = 0.25$) with the other study streams and to literature values ($\phi \approx 0.35 - 0.55$), is somewhat contrary to previous cutthroat demographic work examining the effects of brook charr invasion. Using brook charr removal experiments, Peterson et al. (2004) found that while juvenile cutthroat suffered lower survival in sympatry with brook charr, adults survival was unaffected by brook charr presence. This discrepancy may be due to the extreme species segregation in the non-beaver stream, whereby all cutthroat in this watershed were displaced into extreme headwater reaches which exhibited cold, less productive fish habitat (McCaffery, Chapter 3). Comparisons of stage-specific cutthroat survival between invaded and non-invaded beaver streams, where cutthroat were distributed throughout the watershed (McCaffery, Chapter 3), showed high adult survival regardless of brook charr presence (Figure 4.3). Mean juvenile survival rates in beaver streams were slightly lower with brook charr present, albeit a weaker effect than evident in the non-beaver stream.

In addition to allowing the projection of future cutthroat population trajectories, evaluation of stage transition rates can also provide us with clues about the mechanisms shaping cutthroat population growth rates. Stage transition probabilities for juvenile to small adults were similar across all treatments. However, transition rates from juvenile to large adult, and small adult to large adult were substantially greater in beaver systems, regardless of brook charr presence. This suggests that cutthroat somatic growth rates are much higher in beaver influenced streams relative to non-beaver, a result that is consistent with previous findings of higher somatic growth rates in these beaver streams, as well as length-frequency data which shows smaller cutthroat size structure in the non-beaver stream relative to beaver systems (McCaffery, Chapter 3).

Translating these vital rates to estimates of population growth, I found that all systems subject to brook charr invasion exhibit negative population growth rates, with the non-beaver stream exhibiting the most precipitous decline (Figure 4.5). This is likely a consequence of both direct competition, and indirect interactions, associated with cutthroat displacement to upstream, colder water, leading to lower somatic growth and survival rates in suboptimal habitat. Additionally, a population of smaller sized fish is less fecund, therefore diminishing resulting population growth rates further. Reductions in somatic growth, fecundity, and population growth with increased elevation are the mechanism that limit upstream brook charr distributions in these stream types (Adams 1999), and this pattern of spatial competitive exclusion of cutthroat to higher elevations by brook charr is not uncommon on the landscape (e.g. Dunham et al. 2002). My results suggest that whilst upstream displacement of cutthroat trout provides a refuge from direct competitive effects of brook charr, it does not represent a viable option for long-term cutthroat persistence.

Since beaver have significant positive effects on somatic growth rates of cutthroat, as well as raising their relative abundances compared with non-beaver streams, I also ran simulations where young-of-the-year cutthroat survival was set at non-invaded levels, whilst keeping all other measured vital rates the same. Resulting population growth rates of cutthroat trout under this scenario are positive, and suggest that beaver could mitigate brook charr effects on cutthroat populations to levels comparable to non-invaded systems, and achieving approximate parity with growth rates reported by Peterson et al. (2008a).

Quantitative risk of extinction provides us with a metric for which to compare relative extinction rates across populations, and is most useful for assessing the relative effects of potential management actions on native persistence (Reed et al. 2002). Non-invaded beaver systems have relatively low probabilities of extinction within the next century. Under brook charr invasion however, all cutthroat populations reached the quasi-extinction threshold within a 100-year timeframe. In brook charr invaded systems with beaver present, I found that median time to extinction was delayed by a few years relative to the non-beaver invaded stream. Based on significantly higher somatic growth rates during the first year (McCaffery, Chapter 3), it is likely that beaver raise young-of-the-year survival rates to some degree. I therefore bounded young-of-the-year survival between low and high young-of-the-year survival rates, and found that cumulative time to extinction in invaded beaver streams using high young-of-the-year survival values, reduced the likelihood of extinction to between 0 and 5 % over 100-years.

The shift to reduced cutthroat extinction risk with beaver presence offers clues to potential management strategies to ensure persistence of native cutthroat populations. Thus far, conventional efforts to maintain cutthroat populations on the landscape have followed a crisis management approach. Struggling populations are subjected to various management interventions, such as translocations to headwater reaches (Coleman & Fausch 2007), installing barriers to nonnative movement, and direct removal actions (Dunham et al. 2002; Peterson et al. 2008a). These actions are variably successful and can have adverse consequences for the native species of concern. Even if beaver do not raise young-of-the-year survival, and I conservatively evaluate invaded cutthroat trout in beaver systems using low survival estimates for this stage class, the presence of beaver increases population growth rates by around 5 and 12 %, corresponding to an extension of 3 – 15 years in time to extinction. In comparison, suppression of brook charr using repeat electrofishing management, can yield as high as 80 % increases in cutthroat population growth (Peterson et al. 2008a). However, benefit-cost ratio analysis of this management strategy for scenarios of periodic repeat suppression over a period of 50-years and low brook charr immigration rates, yields increases in cutthroat population growth of around 1 – 2.5 % per unit effort. I propose that the use of beaver as agents of cutthroat restoration could improve population growth rates, and depending on the strength of the invasion, could be used in concert with periodic suppression and supplementation management actions.

I document an emerging phenomenon in invasion ecology in which spatial heterogeneity in habitat factors can change the competitive effects of invasives on native species, leading to pockets of native persistence in the face of invasion (Metlen, unpublished data, Kolb et al. 2002; Lortie & Cushman 2007). As conservation biologists strive for effective, long-term solutions to mitigate brook charr invasions on cutthroat populations, a holistic approach to conservation that takes account of and maintains essential population and life history processes is essential. I show that the effects of beaver on native species under invasion pressure hints at their potential utility for cutthroat management, and suggests their inclusion in the fisheries management toolbox.

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Table 4.1. Characteristics of study streams in southwestern Montana.

Stream	Treatment §	Focal species present	Elevation range sampled (m)		Stream length sampled (m)	Total number of cutthroat marked	UTM of downstream sample point		
			Mid-elevation	High-elevation			Zone	E	N
Stone	1	🦫	1800-1899	1900-2200	1,200	729	12T	391367	5009731
Rape	1	🦫	1900-1999	2000-2180	800	159	12T	326945	4978266
Johnson	2	🐟	1840-1999	2000-2170	800	101	12T	344216	5079030
Lacy	3	🦫 🐟	1900-2020	2021-2230	1,000	111	12T	331606	5052573
Squaw	3	🦫 🐟	1850-1999	2000-2100	1,020	142	12T	320848	5072475

§ Treatment: 1 = westslope cutthroat trout, beaver present; 2 = westslope cutthroat trout, brook charr present; 3 = westslope cutthroat trout, beaver, brook charr present

Table 4.2. Matrix elements and parameters used in demographic analysis of cutthroat trout. Mean values and associated coefficients of variation (CVs) used in stochastic projections.

Matrix element or parameter			**Mean value**			**CV (%)***
	Stone Creek 🦫	**Rape Creek** 🦫	**Johnson Creek** 🐟	**Lacy Creek** 🦫 🐟	**Squaw Creek** 🦫 🐟	
YOY survival*	0.318	0.318	0.025	0.025/0.318[a]	0.025/0.318[a]	20
Juvenile survival	0.33	0.35	0.25	0.29	0.31	20
Small adult survival	0.35	0.35	0.25	0.39	0.4	10
Large adult survival	0.37	0.35	0.25	0.4	0.41	10
Probability of small adult breeding*	0.75	0.75	0.75	0.75	0.75	10
Probability of large adult breeding*	1.0	1.0	1.0	1.0	1.0	10
Small adult clutch size*	187	187	187	187	187	10
Large adult clutch size*[b]	473	473	473	473	473	10
Egg to age-0 survival from spring spawning to fall census*	0.4	0.4	0.4	0.4	0.4	20
Transition probability (Juvenile to small adult)	0.49	0.49	0.48	0.57	0.71	10
Transition probability (Juvenile to large adult)	0.14	0.1	0.05	0.15	0.1	10
Transition probability (Small adult to large adult)	0.51	0.44	0.08	0.4	0.33	10

* Value obtained from Peterson et al. (2008a).

a – Separate simulations using low and high young-of-the-year (YOY) survival were projected for invaded, beaver streams.

b – My large adult size class encompasses Peterson et al.'s (2008a) medium and large adult size classes. I therefore averaged clutch size values for these stages to gain an average clutch size applicable to my size range for large adults.

Table 4.3. Output from Tmsurviv, showing the best model for each stream, and estimated survival rates and proportion of resident cutthroat trout.

Stream	**Model**	**AIC$_c$**	**No. parameters**	**Estimated survival**			**Proportion of residents**
				Juvenile ϕ (SE)	**Small adult ϕ (SE)**	**Large adult ϕ (SE)**	
Stone	$\phi. \; p_{time} \; \gamma.$	243.5	7	0.33 (0.03)	0.33 (0.03)	0.33 (0.03)	1.0
Rape	$\phi. \; p. \; \gamma.$	126.5	3	0.33 (0.067)	0.33 (0.067)	0.33 (0.067)	1.0
Johnson	$\phi. \; p. \; \gamma.$	88.69	3	0.28 (0.062)	0.28 (0.062)	0.28 (0.062)	1.0
Lacy	$\phi. \; p. \; \gamma.$	139.9	3	0.36 (0.059)	0.36 (0.059)	0.36 (0.059)	1.0
Squaw	$\phi. \; p. \; \gamma.$	87.81	3	0.35 (0.072)	0.35 (0.072)	0.35 (0.072)	1.0

Table 4.4. Output from Program MARK, the best model for each stream and estimated cutthroat trout survival rates and transition probabilities used in matrix projection models.

Stream	**Model**	**AIC$_c$**	**No. parameters**	**Estimated survival**			**Estimated stage transition probability**		
				Juvenile ϕ (SE)	**Small adult ϕ (SE)**	**Large adult ϕ (SE)**	**Juvenile ψ (SE)**	**Juvenile ψ (SE)**	**Juvenile ψ (SE)**
Stone	$\phi_{stage}\ p.\ \psi_{stage}$	342.5	7	0.33 (0.05)	0.35 (0.1)	0.37 (0.07)	0.49 (0.11)	0.14 (0.04)	0.51 (0.12)
Rape	$\phi_{stage}\ p_{stage}\ \psi_{stage}$	358.6	9	0.35 (0.06)	0.35 (0.06)	0.35 (0.06)	0.49 (0.20)	0.10 (0.03)	0.44 (0.18)
Johnson	$\phi.\ p.\ \psi_{stage}$	158.5	5	0.25 (0.07)	0.25 (0.07)	0.25 (0.07)	0.48 (0.21)	0.05 (0.12)	0.08 (0.08)
Lacy	$\phi_{stage}\ p_{stage}\ \psi_{stage}$	338.13	9	0.29 (0.09)	0.39 (0.06)	0.40 (0.05)	0.57 (0.16)	0.15 (0.04)	0.40 (0.08)
Squaw	$\phi_{stage}\ p_{stage}\ \psi_{stage}$	151.42	9	0.31 (0.08)	0.40 (0.07)	0.41 (0.04)	0.71 (0.21)	0.1 (0.05)	0.33 (0.09)

Figure Legends

Figure 4.1. Conceptual diagram of the demography of brook charr invasion and effects on cutthroat trout. Life stages are shown with transitions between stages depicted by arrows. Dashed arrows indicate demographic transitions that are affected by biotic interactions with brook charr. Adapted from Peterson et al. (2004).

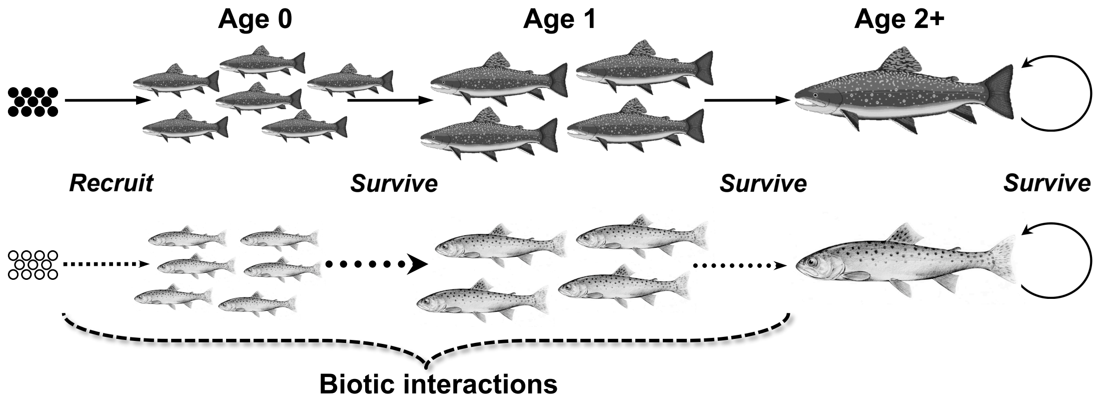
Figure 4.2. Post-birth pulse, stage-structured life cycle diagram for stream-resident cutthroat trout. Stage transitions are the product of surviving and transitioning to the next life stage. Reproductive output (F) for a given stage was the product of probability of breeding, clutch size, spawner survival, and egg survival *plus* reproductive output from the previous stage.

Figure 4.3. Stage-specific cutthroat trout apparent survival (+/- SE) for each study stream.

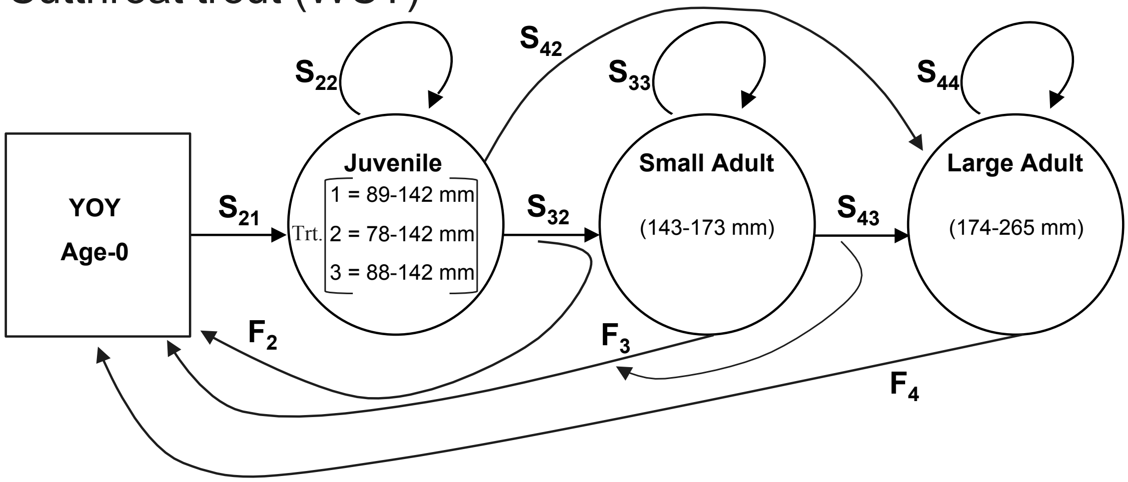
Figure 4.4. Stage-specific cutthroat trout transition probabilities (+/- SE) for each study stream.

Figure 4.5. Stochastic population growth rates (ln(λ)) (+/- SE) for westslope cutthroat trout in each study stream. Invaded beaver streams were modeled using low and high young-of-the-year (YOY) survival values.

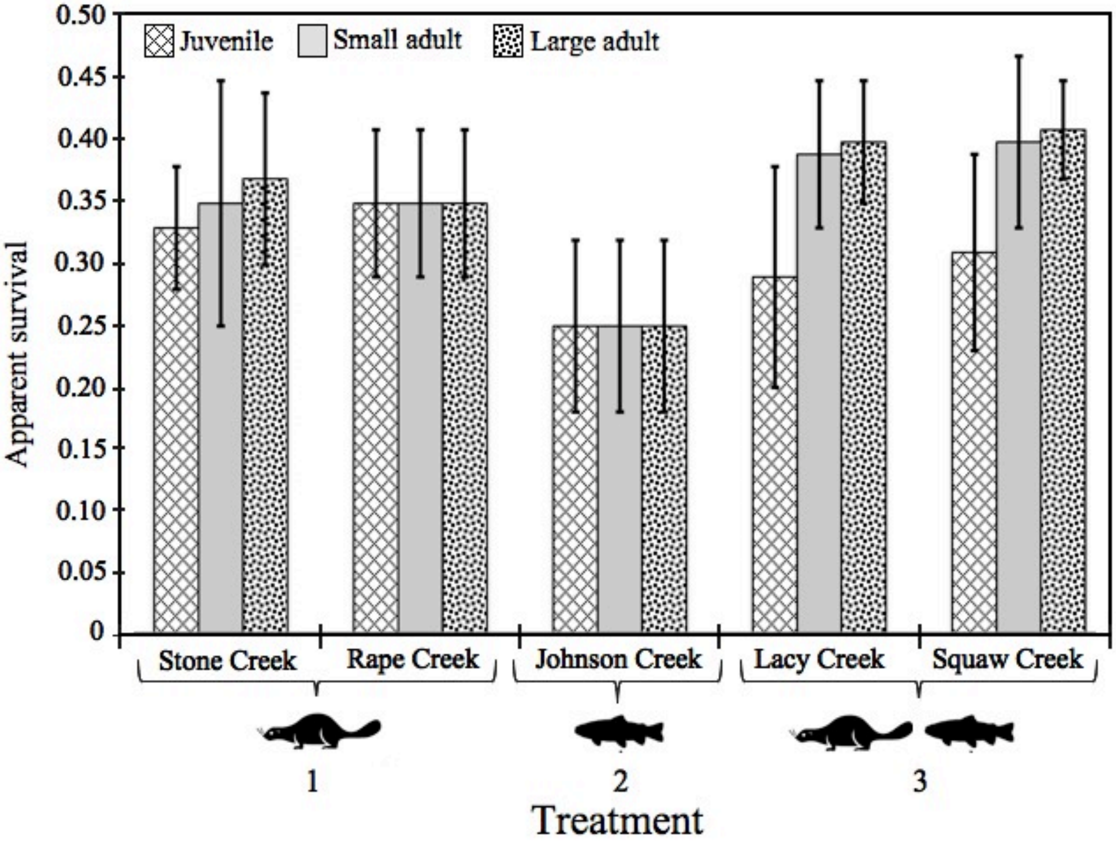
Figure 4.6. Cumulative distribution functions for the probability of cutthroat trout quasi-extinction in each stream. Invaded beaver streams were modeled using low (LS) and high (HS) young-of-the-year (YOY) survival values. Treatment type is indicated pictorially(black fish = brook charr, and beaver).

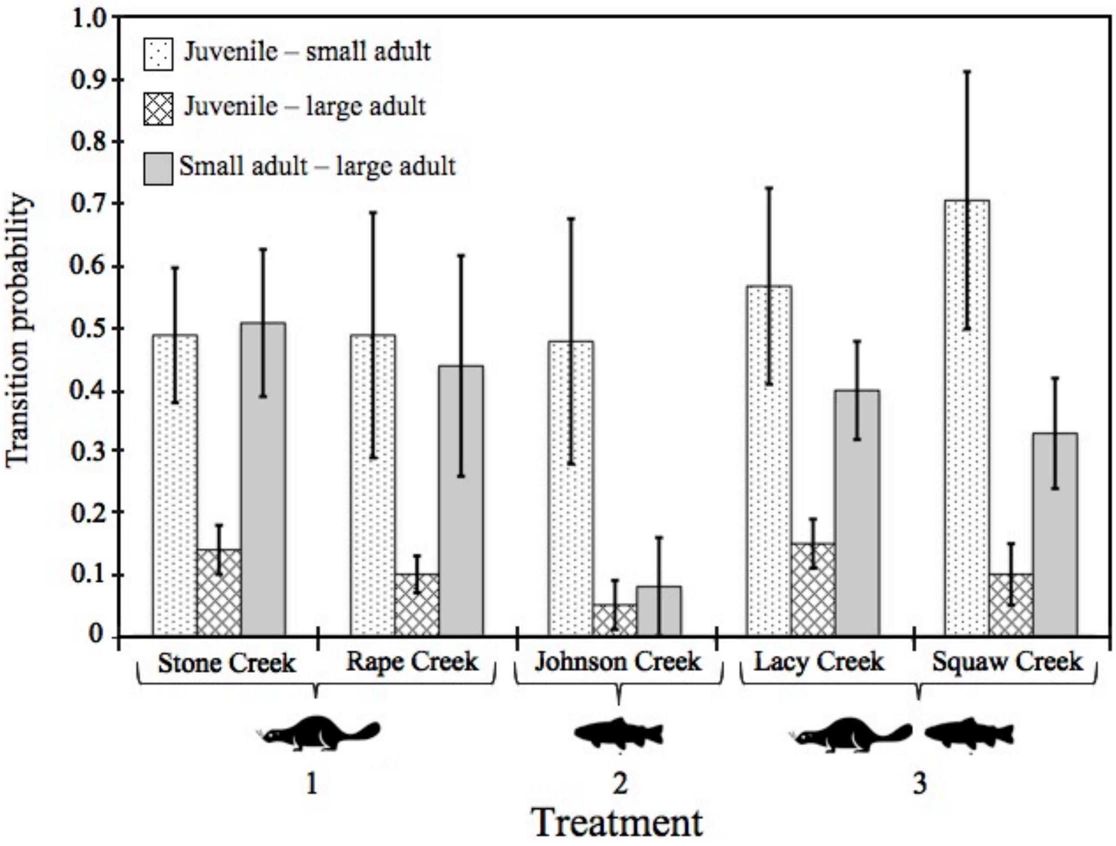

Age 0
Age 1
Age 2+
Recruit
Survive
Survive
Survive
Biotic interactions

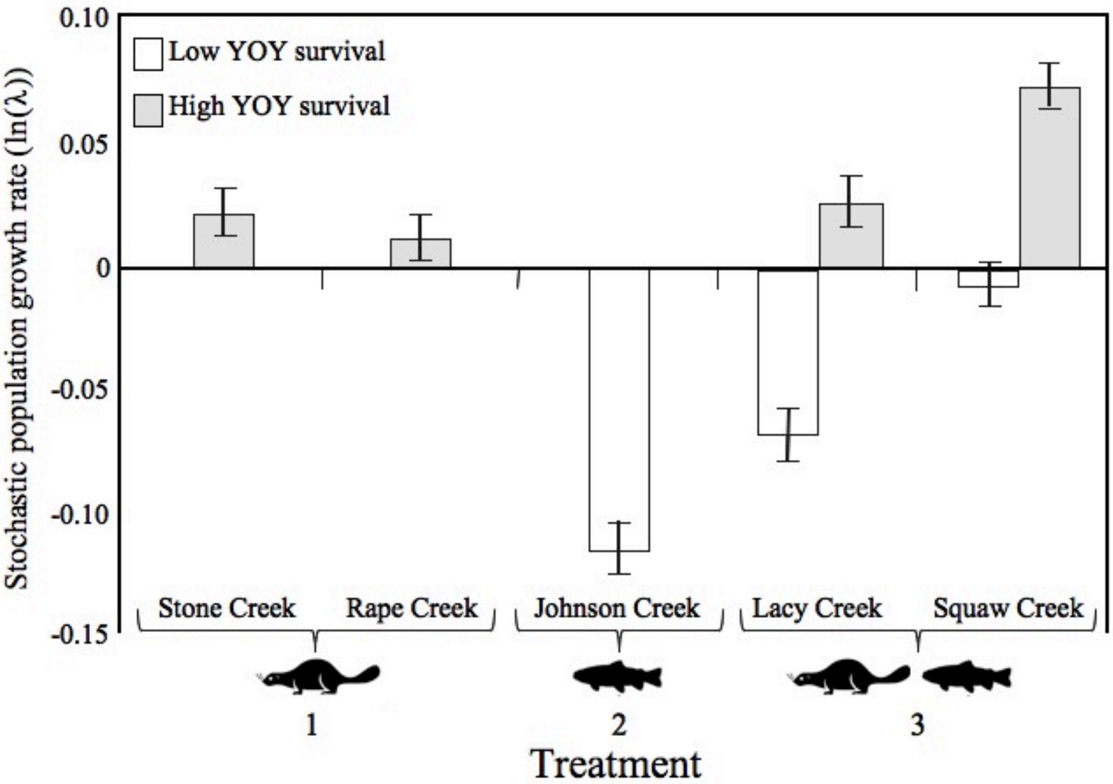
Cutthroat trout (WCT)

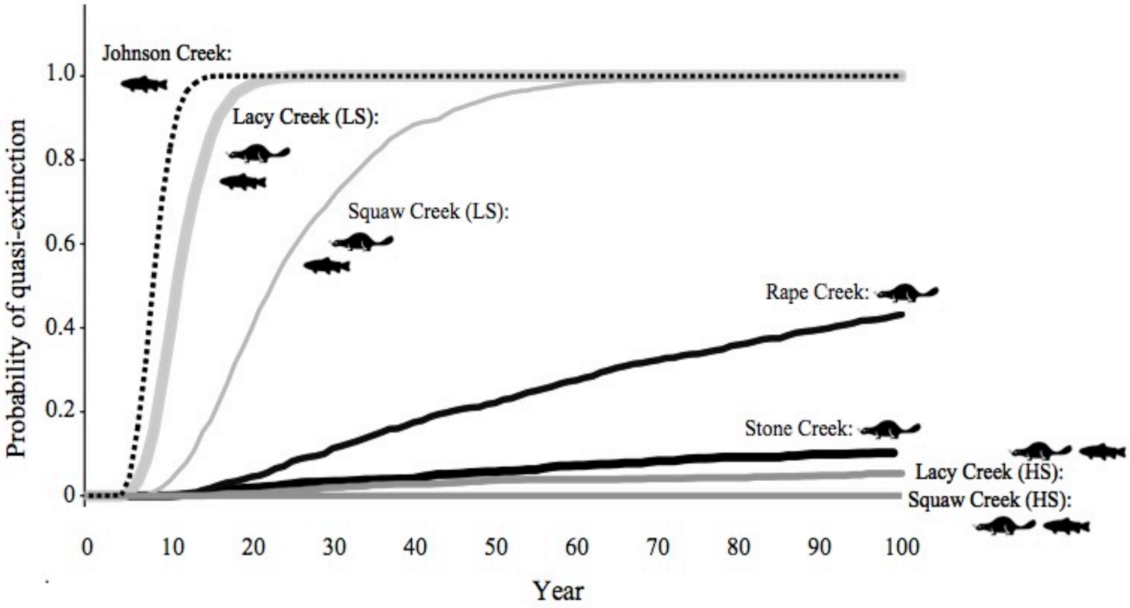


$$\mathbf{A}_{\mathbf{WCT}} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ S_{21} & S_{22} & 0 & 0 \\ 0 & S_{32} & S_{33} & 0 \\ 0 & S_{42} & S_{43} & S_{44} \end{bmatrix}$$


Juvenile
Small adult
Large adult
Apparent survival
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
Stone Creek
Rape Creek
Johnson Creek
Lacy Creek
Squaw Creek
1
2
3
Treatment


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Transition probability
Juvenile – small adult
Juvenile – large adult
Small adult – large adult
Stone Creek
Rape Creek
Johnson Creek
Lacy Creek
Squaw Creek
1
2
3
Treatment


Stochastic population growth rate (ln(λ))
0.10
0.05
0
-0.05
-0.10
-0.15
Low YOY survival
High YOY survival
Stone Creek
Rape Creek
Johnson Creek
Lacy Creek
Squaw Creek
1
2
3
Treatment


Johnson Creek:
Lacy Creek (LS):
Squaw Creek (LS):
Rape Creek:
Stone Creek:
Lacy Creek (HS):
Squaw Creek (HS):
Probability of quasi-extinction
1.0
0.8
0.6
0.4
0.2
0
0
10
20
30
40
50
60
70
80
90
100
Year

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