

## An Abstract of the Thesis of

Stephanie L. Gunckel for the degree of Masters of Science in Fisheries Science presented on October 31, 2000. Title: Feeding Behavior and Diet of Native Bull Trout *Salvelinus confluentus* and Introduced Brook Trout *S. fontinalis* in Two Eastern Oregon Streams

Abstract approved: \_\_\_\_\_

Judith L. Li

One of the greatest threats to native bull trout *Salvelinus confluentus* populations is the presence of non-native brook trout *S. fontinalis*. This study, conducted in two second-order Eastern Oregon streams, investigates the effect of brook trout on the feeding behavior and diet of bull trout. Feeding behavior, microhabitat use, and agonistic interactions were examined in a controlled in-stream experiment where twenty enclosures were randomly assigned one of three treatments: two bull trout, four bull trout, or a mix of two bull trout and two brook trout. Results provide little evidence of a niche shift for bull trout in the presence of brook trout or of resource partitioning between sympatric bull trout and brook trout. All fish held focal feeding points in similar microhabitats and fed primarily from the water column. Brook trout showed the greatest growth, were highly aggressive, and consistently dominated bull trout of equal size. Examination of stomach contents revealed allopatric bull trout, sympatric bull and brook trout fed primarily on larvae of Ephemeroptera, Trichoptera, and aquatic Diptera and terrestrial insects. Sympatric bull trout and brook trout had a high degree of dietary overlap. All fish exhibited size selective predation, and piscivory was rare. Similar habitat use, feeding behavior and diet of bull trout and brook trout, and aggressive interactions between these species suggest that, when habitat and prey resources are scarce, direct interference competition is likely, and the dominant behavior of brook trout may potentially displace bull trout.

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Feeding Behavior and Diet of Native Bull Trout *Salvelinus confluentus* and Introduced  
Brook Trout *S. fontinalis* in Two Eastern Oregon Streams

by

Stephanie L. Gunckel

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APPROVED:

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Major Professor, representing Fisheries Science

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Chair of Department of Fisheries and Wildlife

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Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Stephanie L. Gunckel, Author

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## Table of Contents

	<u>Page</u>
Introduction .....	1
Chapter 1: Feeding Behavior of Sympatric Bull Trout <i>Salvelinus confluentus</i> and Non-native Brook Trout <i>S. fontinalis</i> .....	4
Abstract .....	5
Introduction.....	6
Methods .....	8
Study Site .....	8
Study Design .....	10
Observations .....	13
Statistical Analysis .....	13
Results .....	15
Observations of Free-Ranging Fish.....	15
In-Stream Experiment.....	19
Discussion.....	26
Acknowledgements .....	31
Chapter 2: Dietary Overlap of Co-occurring Bull Trout <i>Salvelinus confluentus</i> and Brook Trout <i>S. fontinalis</i> in Eastern Oregon Streams .....	32
Abstract .....	33
Introduction.....	34
Methods .....	35
Study Site .....	35
Fish and Prey Collection .....	36
Description of Diet.....	40
Dietary Overlap.....	41
Electivity.....	41
Results .....	42

## Table of Contents (continued)

	<u>Page</u>
Description of Diet.....	42
Dietary Overlap.....	45
Prey Electivity.....	45
Discussion.....	51
Acknowledgements .....	58
Overview/Conclusion.....	59
Bibliography .....	63
Appendix .....	71

## List of Figures

<u>Figure</u>	<u>Page</u>
1.1. Relative distribution of allopatric bull trout (=) and sympatric bull trout and brook trout (••) in a) Meadow Fork of Big Creek in the Malheur River Basin and b) North Powder River in the Powder River Basin, Oregon.....	9
1.2. Frequency distribution of percent total depth of focal feeding points for free-ranging allopatric bull trout, sympatric bull trout and brook trout. 0% = stream bottom, 100% = surface.....	16
1.3. Velocity and maximum velocity of focal feeding points for free-ranging bull trout (solid) and brook trout (open) in the allopatric and sympatric reaches measured in centimeters/second. The difference between velocity and maximum velocity represents the velocity differential. All values are means $\pm$ 1 SE. ....	17
1.4. Percent of foraging attempts directed at the benthos, water column, and surface for free-ranging bull trout (solid) and brook trout (hatched) in the allopatric and sympatric reaches. ....	18
1.5. Number of interactions that were a) dominant and b) subordinate for bull trout (black) and brook trout (white) in experimental enclosures. Values are treatment means $\pm$ 1 SE. See text for interaction definitions.....	22
1.6. Relative frequency of dominant interactions between equal sized bull trout and brook trout in the Mix treatment. See text for details .....	24
1.7. Percent change in body weight for bull trout (solid) and brook trout (open) in experimental enclosures. Values are treatment means $\pm$ 1 SE.....	25
1.8. Percent change in body weight for bull (solid) and brook trout (open) in experimental enclosures in North Powder River and Meadow Fork of Big Creek. Values are treatment means $\pm$ 1 SE. ....	27
2.1. Relative distribution of allopatric bull trout (=) and sympatric bull trout and brook trout (••) in a) Meadow Fork of Big Creek in the Malheur River Basin and b) North Powder River in the Powder River Basin, Oregon.....	37
2.2. Average percent abundance of major insect families and life stages in the diet of allopatric bull trout, sympatric bull trout and sympatric brook trout for all study sites combine. Error bars represent standard error. ....	44

## List of Figures (continued)

<u>Figure</u>	<u>Page</u>
2.3. Values of electivity for prey families compared to the relative abundance available. Includes diet of all bull trout and brook trout.....	46
2.4. North Powder River NMS ordinations of Johnson's indices for individual fish in prey space. Electivity patterns of allopatric bull trout (▼), sympatric bull trout (●)and brook trout (□) are illustrated. Direction of the gradient for explanatory taxa on each axis indicated by arrows. ....	49
2.5. Meadow Fork NMS ordinations of Johnson's indices for individual fish in prey space. Electivity patterns of allopatric bull trout (▼), sympatric bull trout (●)and brook trout (□) are illustrated. Direction of the gradient for explanatory taxa on each axis indicated by arrows. ....	50
2.6. Size distribution for prey items in the drift and stomach contents of bull trout and brook trout in the a) allopatric and b) sympatric reaches of Meadow Fork of Big Creek in 1997.....	52
2.7. Origin of prey in the stomach contents of all trout in Meadow Fork of Big Creek 1997 by size class. 'Aquatic derived terrestrials' represent the terrestrial stages of aquatic insects.....	53

## List of Tables

<u>Table</u>	<u>Page</u>
1.1. Habitat characteristics of study streams.....	11
1.2. Number of replicate treatments in each stream per year.....	12
1.3. Nontransformed treatment means $\pm$ SE from the in-stream experiment. Behavior of bull trout in all treatments (2Bull, 4Bull, MixBull) compared using 3-way GLM ANOVA (factors = treatment, year, and stream without interaction). Pairwise comparisons made using Tukey HSD. Groups with differing superscripts (x or y) within variables are significantly different. Behavior of bull trout and brook trout in the Mix treatment (MixBull and MixBrook) compared with paired t-test. Percent water column use compared by G-test of heterogeneity. ....	20
2.1. Habitat characteristics of study streams.....	38
2.2. Dates, number of fish sampled, and Schoener's Index of Overlap (D) for bull trout and brook trout in the sympatric reach for each sample period. ....	39
2.3. Prey taxa elected based on the average Johnson's Index. Prey taxa included in the analysis were >1% of the diet.....	48

## List of Appendix Tables

<u>Table</u>	<u>Page</u>
A.1. Fish diet and prey availability data, North Powder River, July 23-24, 1996. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m <sup>2</sup> ) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m <sup>2</sup> ) represent the mean density of each taxa in three drift samples. See chapter 2 for collection protocol.....	72
A.2. Fish diet and prey availability data, Meadow Fork of Big Creek, August 20-21, 1996. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m <sup>2</sup> ) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m <sup>2</sup> ) represent the mean density of each taxa in three drift samples. See chapter two for collection protocol. ....	78
A.3. Fish diet and prey availability data, North Powder River, July 23-23, 1997. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m <sup>2</sup> ) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m <sup>2</sup> ) represent the mean density of each taxa in three drift samples. See chapter two for collection protocol.....	84
A.4. Fish diet and prey availability data, Meadow Fork of Big Creek, July 3-5, 1997. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m <sup>2</sup> ) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m <sup>2</sup> ) represent the mean density of each taxa in three drift samples. See chapter two for collection protocol. ....	91

# Feeding Behavior and Diet of Native Bull Trout *Salvelinus confluentus* and Introduced Brook Trout *S. fontinalis* in Two Eastern Oregon Streams

## Introduction

Historically, the distribution of bull trout *Salvelinus confluentus* (Suckley) extended from the Sacramento River in Northern California to the headwaters of the Yukon River (Cavender 1978; Haas and McPhail 1991). Currently, bull trout exist throughout their historic range but many populations are depressed and highly fragmented (Rieman and McIntyre 1995). Few bull trout populations in the United States are considered abundant and without risk of extinction (Buchanan *et al.* 1997; Rieman *et al.* 1997). Of special concern are the populations near the southern margins of their range: Oregon, California, and Nevada. The McCloud River (California) population is now considered extinct (Haas and McPhail 1991), and the United States Fish and Wildlife Service listed all remaining populations in the United States as threatened (Office of the Federal Register 64 [November 1, 1999]: 58910).

The fragmentation and decline of bull trout populations can be attributed to habitat degradation, migration barriers, and introduction of non-native fish, though other factors also exist (Ratliff and Howell 1992; Rieman and McIntyre 1993). Bull trout are highly stenotopic, requiring cold water temperatures, complex and stable habitats, and uninterrupted migratory corridors. Because of habitat degradation and barriers to migration, many bull trout populations are limited to headwater streams (Rieman and McIntyre 1993). These small and isolated bull trout populations are the most susceptible to the effects of non-native species, particularly those of introduced salmonids.

Non-native fish often have deleterious effects on the structure and organization of aquatic communities. Successful introductions of non-native species have resulted in the reduced growth, decreased reproduction, or elimination of native species through competition, predation, hybridization, introduction of pathogens, and

environmental modifications (Moyle *et al.* 1986). Because non-native species are not co-adapted with predators, may have less specific resource requirements, or have greater tolerances to degraded habitat, they are often superior competitors (Moyle *et al.* 1986). If two species are not naturally sympatric within their geographic distribution, then effects of non-native fish are most dramatic because they have not co-evolved mechanisms of co-existence (Fausch 1988). Furthermore, introduced salmonids may have an even greater impact on native salmonid populations because they are similar in morphology and often ecological analogs, increasing potential for direct competitive interaction.

Bull trout exist in sympatry with introduced brook trout *S. fontinalis*, brown trout *Salmo trutta*, and lake trout *Salvelinus namaycush*, all of which have deleterious effects on bull trout populations. Lake trout displaced and eliminated bull trout from many large lakes in Canada (Donald and Alger 1993) and are possibly related to declines of bull trout in some Oregon lakes (Buchanan *et al.* 1997). Brown trout are associated with the decline and eventual extinction of the McCloud River bull trout population (Bond 1992). Brook trout pose the greatest threat to native bull trout populations because their distribution is widespread throughout the range of bull trout (Rieman and McIntyre 1993). In streams with sympatric brook trout, hybridization (Leary *et al.* 1993) and competition for resources (Dambacher *et al.* 1992; Ratliff and Howell 1992) have been cited as reasons for the decline of bull trout.

Brook trout are native to eastern United States and Canada. The first brook trout introductions on record in eastern Oregon were in 1925 (Oregon Department of Fish and Wildlife, unpublished data) though they likely occurred before the turn of the century. The ability of brook trout to spawn in lakes made them desirable game fish for high elevation lakes without permanent inlets, where native trout could not exist without regular stocking programs (Dill and Cordone 1997). Since then brook trout have become naturalized in many high elevation lakes and streams of Oregon.

Where bull trout and brook trout co-occur hybridization is probable. Both species are fall spawners and choose low gradient streams with cold water, a groundwater influence, and loosely compacted beds of gravel as spawning habitat

(Fraley and Shepard 1989; Kitano *et al.* 1994). The high instance of hybridization can result in the decline of genetically pure bull trout. In addition, brook trout tend to be younger at maturity than bull trout. Generally brook trout mature at 3 years and bull trout at 5 years (Buchanan *et al.* 1997). Because of their shorter generation time, brook trout can quickly swamp bull trout, further increasing the probability of hybridization and potential for displacement (Leary *et al.* 1993).

The effects of non-native brook trout on the resource use and performance of bull trout is not well understood and poorly documented. Evidence of direct competition is lacking; however, similarities in life history, food habits, and habitat use make direct competition likely. In streams at Crater Lake National Park, bull trout and brook trout had very similar diets (Wallis 1948), and both species preferred pools over riffles and glides (Dambacher *et al.* 1992). In Montana, a limited removal experiment suggested an ecological release for bull trout after the removal of brook trout, indicating brook trout may be the dominant species (Nakano *et al.* 1998). Unfortunately, the results of this study were confounded by changes in density, so empirical evidence was only suggestive of brook trout dominance over bull trout.

The primary focus of this research was to investigate the effects of brook trout on the feeding behavior and diet of bull trout. Behavior and diet were compared between allopatric bull trout and bull trout sympatric with brook trout. In addition, comparisons were made between the diet and behavior of sympatric bull trout and brook trout. The specific research objectives were to:

1. Identify any differences in feeding focal point characteristics, feeding behaviors, and agonistic interactions between allopatric bull trout and sympatric bull trout and brook trout.
2. Describe the diet and prey electivity of allopatric bull trout and bull trout sympatric with brook trout, and determine the degree of dietary overlap between sympatric bull trout and brook trout.

**Chapter 1**  
**Feeding Behavior of Sympatric Bull Trout *Salvelinus confluentus* and Non-  
native Brook Trout *S. fontinalis***

Stephanie L. Gunckel

## Abstract

Observations of free-ranging sympatric bull trout *Salvelinus confluentus* and brook trout *S. fontinalis* in two eastern Oregon headwater streams provided little evidence of resource partitioning. Both species held focal feeding points in similar microhabitats, and fed primarily from the water column. In a stream experiment, 20 enclosures were randomly assigned one of three treatments: two bull trout, four bull trout, or a mix of two bull trout and two brook trout. Macroinvertebrate drift in the enclosures was restricted, creating an environment of limited food resources. Brook trout were highly aggressive, maintained dominance in 75% of the enclosures with both species, and grew significantly faster than bull trout. There was no indication of a niche shift for bull trout; feeding behavior and habitat use did not differ among bull trout in the presence or absence of brook trout. Although bull trout sympatric with brook trout experienced more agonistic interactions than allopatric bull trout, the effects of intra- and interspecific interactions on growth were equivalent. Given the absence of resource partitioning despite obvious interference competition, I suggest that the aggressive behavior of brook trout combined with their shorter generation time and hybridization may significantly impact bull trout on a population scale.

## Introduction

Introduced salmonids are frequently implicated in the declining abundance of native bull trout *Salvelinus confluentus*. Bull trout exist in sympatry with lake trout *S. namaycush*, brown trout *Salmo trutta*, and brook trout *Salvelinus fontinalis*, all of which have had deleterious effects on bull trout populations. Lake trout displaced and eliminated bull trout from large lakes in Western Canada (Donald and Alger 1993) and are possibly related to declines of bull trout in some Oregon lakes (Buchanan *et al.* 1997). Brown trout were associated with the eventual extinction of the McCloud River bull trout population in California (Bond 1992). Brook trout pose the greatest threat to stream-dwelling bull trout populations because their distribution is widespread throughout the range of bull trout (Rieman *et al.* 1997; Thurow *et al.* 1997) and are present in many of the same basins (Rieman and McIntyre 1993).

Typically, hybridization and competition between bull trout and brook trout are cited as mechanisms of bull trout displacement into the uppermost headwater streams (Ratliff and Howell 1992; Buchanan *et al.* 1997). Bull trout x brook trout hybrids are commonly found where both species co-occur. Because brook trout tend to be younger at maturity than bull trout, their shorter generation time may allow them to quickly out-number bull trout (Leary *et al.* 1993; Buchanan *et al.* 1997). High abundance of brook trout increases the probability of hybridization, posing a significant threat to isolated bull trout populations (Leary *et al.* 1993).

Brook trout are assumed to impact bull trout negatively through competitive interactions. However, competition between the two species has not been clearly demonstrated, and the outcome of potential agonistic interactions is unknown. Dambacher *et al.* (1992) found both bull trout and brook trout prefer pools over riffles and glides, and both species typically maintain positions near the channel margins. Although bull trout and brook trout occupy similar habitats, co-occurring salmonids typically partition habitats on the finer scale of depth, water velocity, cover types, and location of prey. For instance, in an Idaho stream, brook trout and cutthroat trout *Oncorhynchus clarki* segregated according to differences in velocity and total depth

(Griffith 1972). Also, in Newfoundland, brook trout occupied focal points with lower water velocities and greater cover than sympatric rainbow trout *Oncorhynchus mykiss* in Newfoundland (Cunjak and Green 1983).

A limited removal experiment suggested an ecological release for bull trout after the removal of brook trout (Nakano *et al.* 1998), indicating brook trout may be the dominant species. Unfortunately, the results of this study were confounded by differences in fish size and changes in density, so empirical evidence was only suggestive of brook trout dominance over bull trout.

The objective of my study was to examine the effect of brook trout on bull trout feeding behavior, focusing on habitat use, foraging rates, and agonistic interactions. I assumed that individuals compete for focal feeding positions based on their value as food acquisition sites (Chapman 1966; Fausch and White 1981). Drift feeding fish face the trade-off of minimizing the cost of maintaining position by choosing a foraging position (focal point) at low velocities, while maximizing the benefit of macroinvertebrate drift by feeding from high velocity water (Everest and Chapman 1972; Smith and Li 1983; Fausch 1984). In addition to feeding behavior, growth is an important measure of net energy gain and performance (Werner and Hall 1977), and in my study was considered an important measure of competitive success. For both a controlled in-stream experiment and observations of free-ranging fish, I compared behavior and growth of allopatric bull trout with that of bull trout sympatric with brook trout. My hypotheses were that bull trout in the presence of brook trout would 1) feed in less profitable feeding sites, 2) change feeding positions from the water's surface or column to the benthos, 3) experience more agonistic interactions, and 4) exhibit less growth than allopatric bull trout. I also expected to see fine scale microhabitat partitioning between bull trout and brook trout.

## Methods

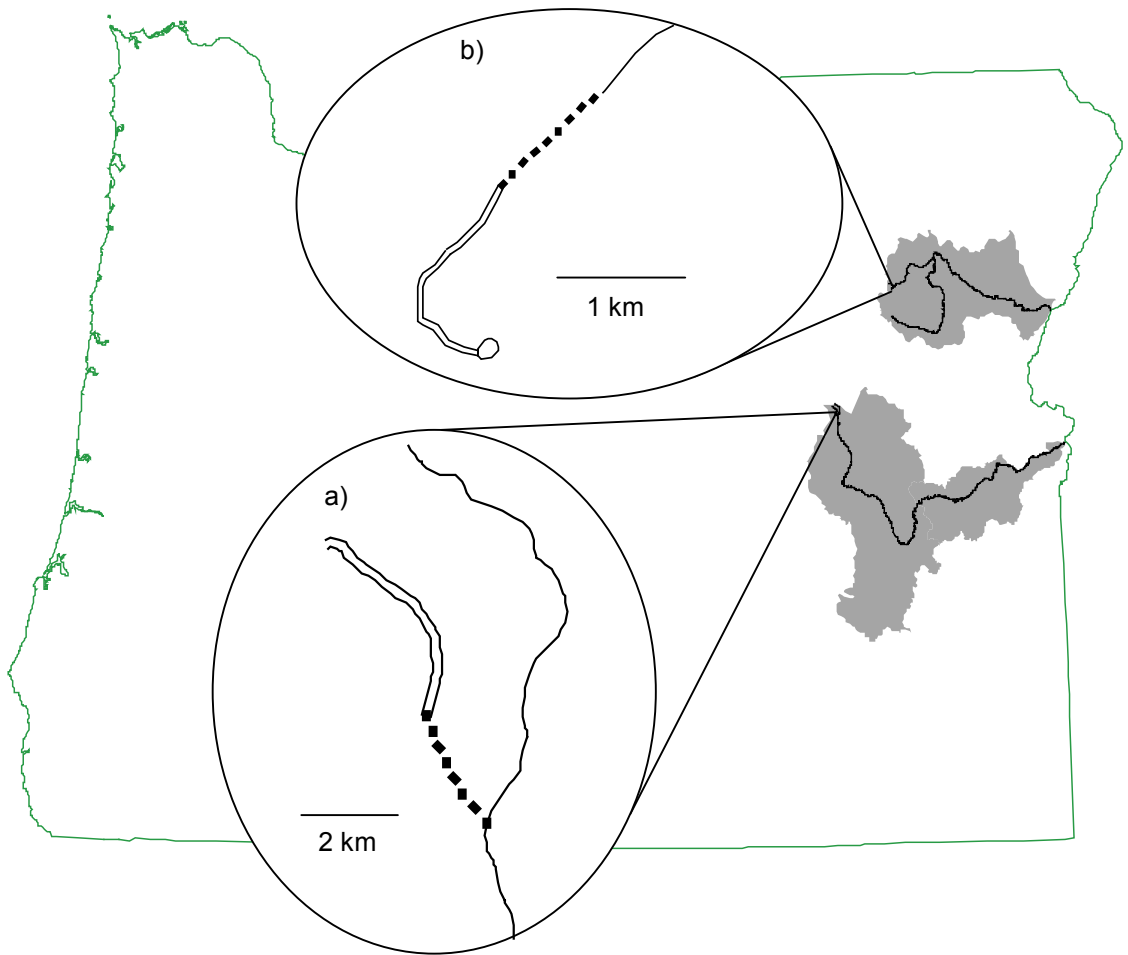
### *Study Site*

The study was conducted in Meadow Fork of Big Creek and North Powder River in eastern Oregon. These streams shared characteristic fish distribution, where bull trout were allopatric in the upper segments and sympatric with brook trout in the middle segments. Both streams were selected for their relatively high densities of trout species, zones of trout sympatry and allopatry, and relative ease of access.

Meadow Fork of Big Creek is a tributary of the Malheur River. The sympatric reach was 2.6 km long where bull trout, brook trout, rainbow trout, and shorthead sculpin *Cottus confusus* were present. Directly upstream, the allopatric reach was 4.3 km with only bull trout. The experiment was located in the sympatric reach approximately 1.5 km upstream from the confluence of Big Creek (Fig. 1.1a) (UTM 11T0369750, 4899573).

The North Powder River is a headwater stream in the Powder River Basin. The sympatric reach was 1.0 km long where bull trout and brook trout were present. The allopatric bull trout reach extended 2.6 km upstream from the top of the sympatric reach. The experiment was located in the sympatric reach, 2.8 km downstream from the headwater source lake (Fig. 1.1b) (UTM 11T0405501, 4971227).

Habitat was assessed using survey methodology based on protocol developed by Hankin and Reeves (1988; Moore *et al.* 1997). Electronic temperature loggers (OnSet computer Co.) were placed in the middle of each reach and recorded stream temperature every half hour for the duration of the study. In 1998 the macroinvertebrate community was described in the allopatric and sympatric reach of each stream. Three drift samples were collected during peak drift at dawn. A 250  $\mu$  m drift net with an opening of 0.1 m<sup>2</sup> was set for 30 minutes in the thalweg just upstream from the head of three randomly selected pools. Depth and water velocity were measured at each net using a Marsh-McBirney flow meter. Six benthic samples were collected in pools in each reach using a 0.095 m<sup>2</sup> surber sampler with a 250  $\mu$  m net.



**Figure 1.1.** Relative distribution of allopatric bull trout (—) and sympatric bull trout and brook trout (••) in a) Meadow Fork of Big Creek in the Malheur River Basin and b) North Powder River in the Powder River Basin, Oregon.

Sites within each pool were randomly selected. Habitat characteristics for all reaches are described in Table 1.1.

### *Study Design*

The study was comprised of observations of free-ranging fish and a controlled in-stream experiment. During 1998, bull trout and brook trout in Meadow Fork of Big Creek were observed in their natural environment. The sympatric reach and two segments of the allopatric reach were snorkeled once a week for six weeks. A snorkel diver moved upstream and conducted five minute observations on every undisturbed fish until a minimum of ten fish of each species were observed.

The controlled in-stream experiment consisted of twenty enclosures, averaging 3.6 m<sup>2</sup> in area, built in pools or slow water habitats in the sympatric reach of each stream. Each enclosure was constructed with four to six wood frame panels that were 4 ft<sup>2</sup> and covered with 3/4 inch mesh nylon screen. An erosion-proof cloth was attached to the underside of the panels which were secured to the stream bottom with re-bar and stabilized with 2x4 braces. Substrate was piled on top of the cloth to prevent fish from escaping, and sandbags were placed on the downstream edge of the panels to minimize undercutting. In most cases the stream bank served as one side of the enclosures to provide elements of natural cover and input of terrestrial insects. Each enclosure contained a variety of microhabitats including slow water refuges, portions of the thalweg, and areas with cover.

Experimental fish were collected from the sympatric reaches by angling. Electrofishing was avoided to prevent any behavioral aberrations (Mesa and Schreck 1989). Each animal was weighed, measured, and uniquely marked with a phototonic dye (NewWest Technology) injected between the caudal rays to ensure positive identification during the experiment. One of three treatments was randomly assigned to each enclosure: 2 bull trout (hereafter 2Bull), 4 bull trout (hereafter 4Bull), or a combination of 2 bull trout and 2 brook trout (hereafter Mix). In 1997 there were

**Table 1.1.** Habitat characteristics of study streams.

	Meadow Fork		North Powder	
	Sympatric	Allopatric	Sympatric	Allopatric
Stream Order	3	2	2	2
Mean Elevation (ft)	5640	6180	6110	6380
Length (km)	2.6	4.3	1.0	2.6
Gradient (%)	4.2	6.5	6.1	7.7
Mean Width (m)	4.5	3.8	*	4.0
Pools: % of total surface area	17	14	*	10
Rapids: % of total surface area	52	38	*	46
Dominant Substrates	Cobble 45% Gravel 44%	Cobble 48% Gravel 41%	*	Gravel 24% Cobble 23% Sand 22%
Mean Daily Max. Temp. C (SD) <sup>c</sup>	10.7 (0.94) <sup>a</sup> 12.0 (0.82) <sup>b</sup>	*	11.7(0.95) <sup>c</sup>	11.4 (1.08) <sup>c</sup>
Mean Daily Min. Temp. C (SD) <sup>c</sup>	7.2 (0.64) <sup>a</sup> 7.6 (0.68) <sup>b</sup>	*	8.7 (0.78) <sup>c</sup>	8.4(0.87) <sup>c</sup>
Mean invertebrate drift density /100 m <sup>3</sup>	875.4 <sup>a</sup>	1334.1 <sup>a</sup>	1484.3 <sup>a</sup>	1904.3 <sup>a</sup>
Mean benthic invertebrate density /m <sup>2</sup>	5829.8 <sup>a</sup>	9266.7 <sup>a</sup>	2486.0 <sup>a</sup>	2259.6 <sup>a</sup>
Species Present	Bull, Brook, and Rainbow trout, Shorthead Sculpin	Bull trout	Bull trout, Brook trout	Bull trout

<sup>a</sup> 1997<sup>b</sup> 1998<sup>c</sup> Measured every 30 minutes during the experiment.

\* Information is not available

four replicates of each treatment, two in each stream. In 1998 only the 4Bull and Mix treatments were applied and each was replicated four times in Meadow Fork Big Creek (Table 1.2). Experimental animals were introduced to enclosures simultaneously, and fish in each enclosure were of similar size to minimize size-structured dominance hierarchies (Fausch 1988). Fish size among enclosures ranged from 153mm to 253mm, and the average difference between the largest and smallest fish within an enclosure was 13mm. Fish acclimated in the enclosures for seven days before the first observations were conducted. Fish behavior in the enclosures was observed by snorkeling 1-8 times per week for a period of six weeks. All observations were systematically scheduled to ensure each enclosure was observed during all periods of the day.

**Table 1.2.** Number of replicate treatments in each stream per year.

Year	Stream	Dates	Treatment <sup>a</sup>		
			2Bull	4Bull	Mix
97	Meadow Fork	Jul 4 – Aug 18	2	2	2
	North Powder	Jul 23 – Sept 8	2	2	2
98	Meadow Fork	Jun 27 – Aug 12	-	4	4

<sup>a</sup>2Bull = 2 bull trout per enclosure, 4Bull = 4 bull trout per enclosure, Mix = 2 bull trout and 2 brook trout per enclosure.

During 1998, macroinvertebrate drift was collected in Meadow Fork of Big Creek to compare food availability inside to outside enclosures. One drift net (250  $\mu$ m mesh) was set directly upstream of each enclosure, and one inside each enclosure at the upstream end. The average distance between the inside and outside drift net was approximately 1.5 meters. Drift was collected inside the enclosures on August 3 and 5 and outside on August 4 and 6 at 04:50 to 05:20 each day. Samples were preserved in 95% ethanol. In the laboratory, insects were sorted out of drift samples, dried at 55°C, and weighed for measures of biomass.

### *Observations*

During a snorkel dive, focal animal observations (Altmann 1974) were conducted on each fish for five minutes. Foraging attempts were counted and classified as directed at either 1) surface macroinvertebrate drift, 2) water column drift, or 3) benthic invertebrates on the substrate. Because prey were not always visible, all foraging attempts were counted regardless of capture success. Interactions between fish were counted and categorized as dominant or subordinate. An interaction was considered dominant when an observed fish gained or maintained feeding territory through aggression. An interaction was subordinate when a fish was displaced or lost feeding territory by aggression from another.

After observations were completed, physical characteristics of the focal points were measured. Locations of focal points were marked with a bobber attached to a fishing weight with monofilament line. The bobber was positioned at the height of the focal feeding point. The distance from the bobber to the substrate defined the holding depth. Water velocity at the focal point and maximum velocity within 0.6 m from the focal point were measured using a flow meter (Marsh-McBirney). The difference between the two values defined the velocity differential (Fausch and White 1981). The percent of the feeding territory with cover was recorded in categories of 0, 1-25, 26-50, 51-75, or 76-100%. After six weeks, fish in the enclosures were weighed, measured, and released.

### *Statistical Analysis*

#### Free-Ranging Fish

Behaviors of free-ranging fish in Meadow Fork of Big Creek during 1998 were summarized by averaging observations for each species in the allopatric and sympatric reach. Holding depth was standardized by dividing by total depth to yield a relative

position in the water column. Differences in behaviors between allopatric and sympatric bull trout were detected using a non-parametric Mann-Whitney U- test because data were highly skewed. Behaviors of sympatric bull trout and brook trout were treated similarly. Differences in cover use and the proportion of feeding attempts directed at the surface, water column, and benthos were detected using the log-likelihood ratio test (G-test for heterogeneity)(Sokal and Rohlf 1981).

### In-stream Experiment

Since enclosures were the experimental unit, observations for each variable were averaged first for individual fish, then for each species per enclosure, resulting in one value for every species in each enclosure. Treatments differences were detected by a three-way GLM ANOVA (factors = treatment, stream, year). Interaction terms were not included in the analysis due to insufficient degrees of freedom. When significant differences were found, Tukey HSD was used for pairwise comparisons. A non-parametric Kruskal-Wallis test was used in cases where distributions were highly skewed. Differences in cover use and the proportion of feeding attempts directed at the surface, water column, and benthos were detected using the log-likelihood ratio test (G-test for heterogeneity)(Sokal and Rohlf 1981). Significant differences between bull trout and brook trout behaviors in the mixed treatment and macroinvertebrate drift biomass inside and outside of the enclosures were detected using paired t-tests.

During the experiment, six fish from four enclosures disappeared, and one fish died. The average value for each behavior variable was calculated using only the data collected when each fish was present. For enclosures with missing fish, growth of the remaining fish was used to represent the overall growth of the enclosure. In two instances, fish escaped during the first three weeks of the experiment. Replacement fish were introduced to these enclosures to maintain proper density but their behaviors and growth were not included in the analysis.

All tests were two-tailed and significance was determined at  $p \leq 0.05$ . Systat 8.0 was used for all statistical analyses (SPSS 1998).

## **Results**

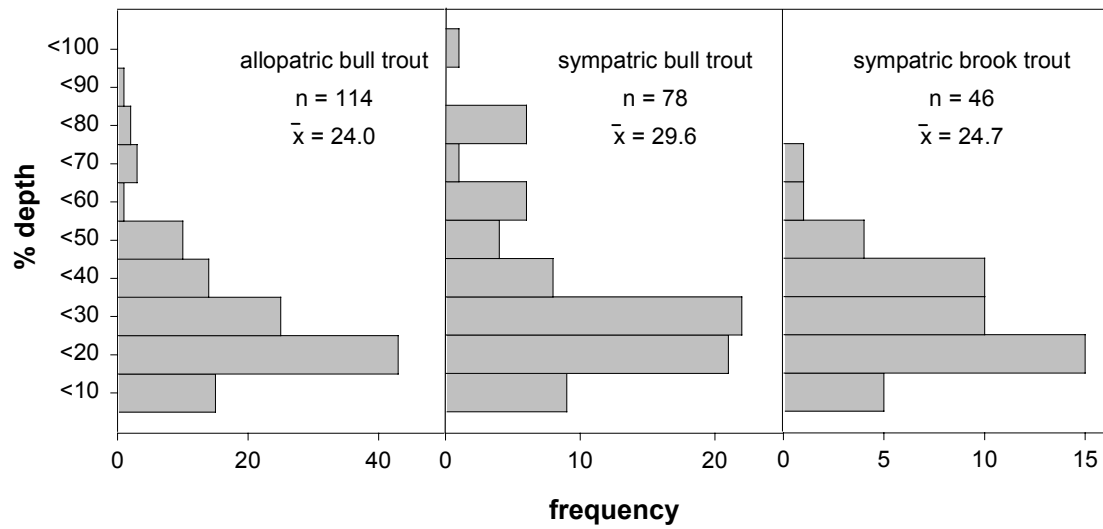
### *Observations of Free-Ranging Fish*

#### Habitat-associated Behaviors

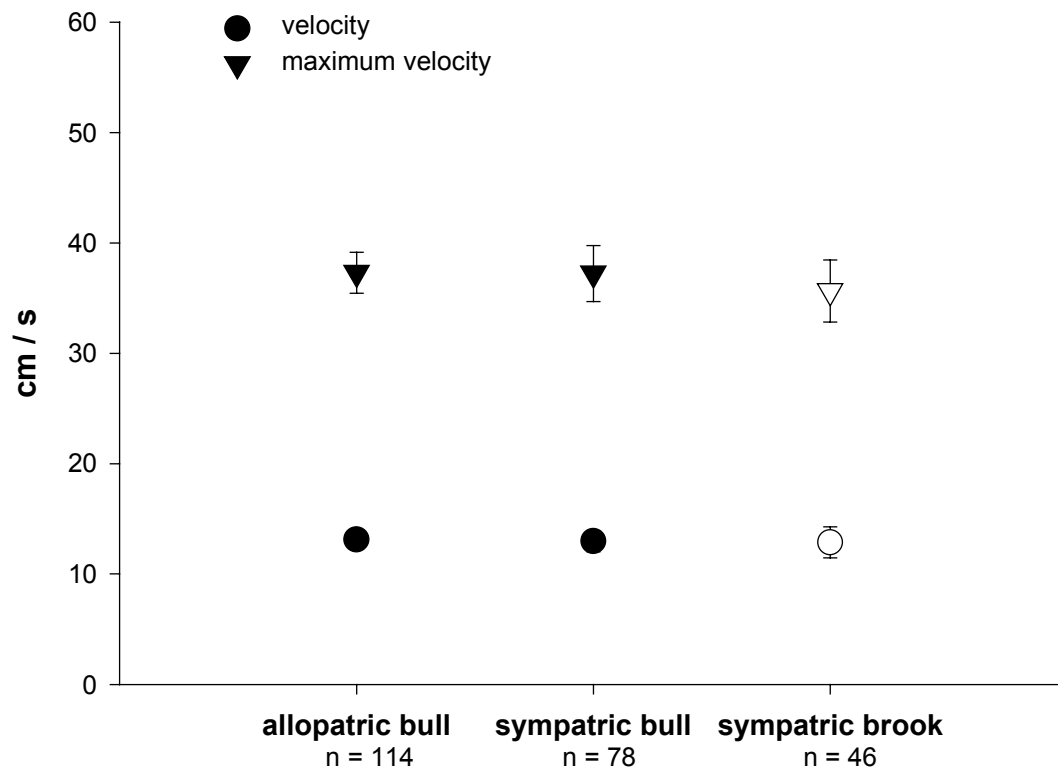
The physical characteristics of focal feeding positions were similar among allopatric bull trout, sympatric bull trout, and brook trout. On average, fish in all groups held positions in the lower third of the water column (Kruskal-Wallis,  $p=0.193$ ) (Fig. 1.2). Average focal point velocity did not differ among allopatric and sympatric bull trout (Mann-Whitney,  $p=0.845$ ) or sympatric bull trout and brook trout (Mann-Whitney,  $p=0.626$ ) (Fig. 1.3). Similarly there were no differences between the average maximum velocity within 60 cm of the focal feeding points (Mann-Whitney,  $p=0.765$  and  $0.851$ , respectively) and hence the velocity differential (Mann-Whitney,  $p=0.488$  and  $0.923$ , respectively) (Fig. 1.3). Cover use was consistent between allopatric and sympatric bull trout (G-test,  $p>0.1$ ) and sympatric bull trout and brook trout (G-test,  $p>0.1$ ). Seventy-nine percent of the allopatric bull trout, 76% of the sympatric bull trout, and 64% of brook trout maintained a feeding territory with  $\leq 25\%$  cover.

#### Feeding Behaviors

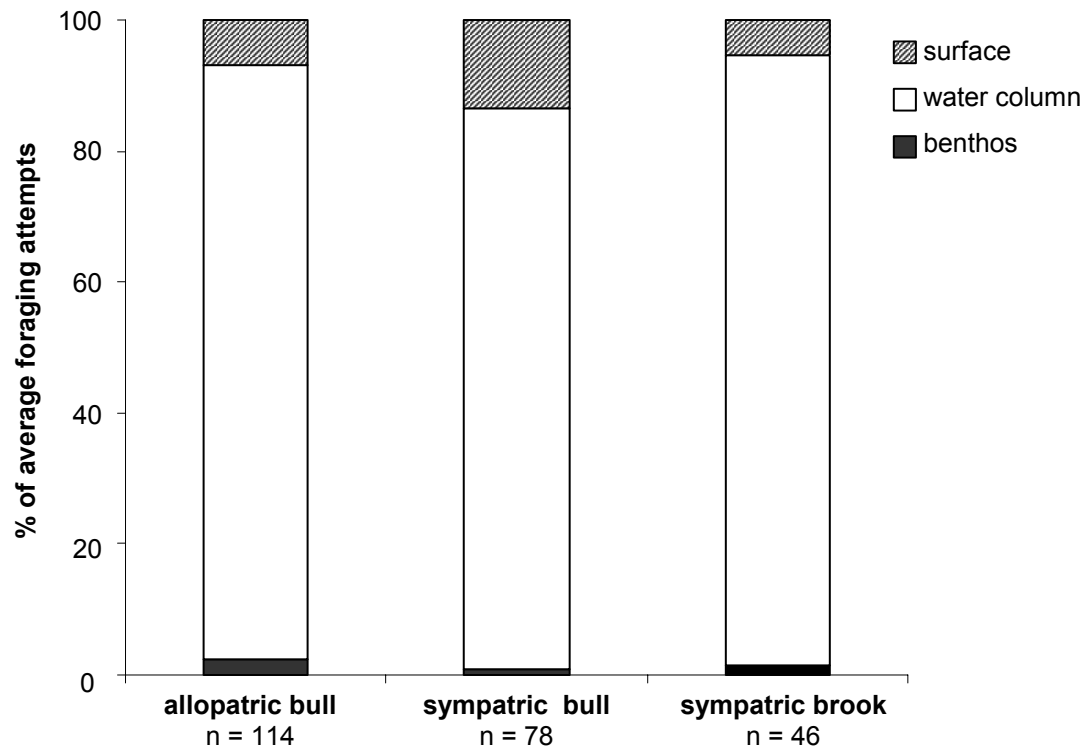
Allopatric bull trout, sympatric bull trout, and brook trout fed primarily from the water column (Fig. 1.4). Seldom did they feed from the benthos or directly from the surface. These patterns did not vary statistically between allopatric and sympatric bull trout (G-test,  $p>0.5$ ) or sympatric bull trout and brook trout (G-test,  $p>0.5$ ).



**Figure 1.2.** Frequency distribution of percent total depth of focal feeding points for free-ranging allopatriic bull trout, sympatric bull trout and brook trout. 0% = stream bottom, 100% = surface.



**Figure 1.3.** Velocity and maximum velocity of focal feeding points for free-ranging bull trout (solid) and brook trout (open) in the allopatric and sympatric reaches measured in centimeters/second. The difference between velocity and maximum velocity represents the velocity differential. All values are means  $\pm$  1 SE.



**Figure 1.4.** Percent of foraging attempts directed at the benthos, water column, and surface for free-ranging bull trout (solid) and brook trout (hatched) in the allopatric and sympatric reaches.

However, sympatric bull trout fed from the surface 12% of the time, twice that of brook trout and allopatric bull trout.

### Interactions

Sympatric bull trout experienced a greater average number of subordinate interactions ( $\bar{x}$  = 0.15 per 5 min.) than allopatric bull trout ( $\bar{x}$  = 0.03 per 5 min.; Mann-Whitney,  $p=0.014$ ) or brook trout ( $\bar{x}$  = 0.02 per 5 min.; Mann-Whitney,  $p=0.102$ ); 88% of these interactions were instigated by brook trout. Eighty seven percent of all interactions observed were size-dominant interactions. The remaining 13% were between fish of similar size.

### *In-stream Experiment*

Prey availability in the enclosures was restricted. Biomass of invertebrate drift inside ( $\bar{x}$  = 0.015 g) the enclosures was on average 52.5% (sd = 20.1) less than outside ( $\bar{x}$  = 0.029 g) of the enclosures (paired t-test,  $p<0.001$ ).

### Habitat-associated Behaviors

Bull trout occupied similar habitats whether they were allopatric at different densities or sympatric with brook trout. Mean velocity, maximum velocity, and velocity differential of bull trout focal points did not vary significantly between treatments (Table 1.3). Cover use did not differ among bull trout in all treatments (G-test,  $p>0.1$ ). Greater than 75% of bull trout in all treatments utilized a feeding territory with  $\leq 25\%$  cover. All bull trout maintained focal feeding positions in the lower third of the water column, though positions of bull trout in the 4Bull treatment were statistically higher

**Table 1.3.** Nontransformed treatment means  $\pm$  SE from the in-stream experiment. Behavior of bull trout in all treatments (2Bull, 4Bull, MixBull) compared using 3-way GLM ANOVA (factors = treatment, year, and stream without interaction). Pairwise comparisons made using Tukey HSD. Groups with differing superscripts (x or y) within variables are significantly different. Behavior of bull trout and brook trout in the Mix treatment (MixBull and MixBrook) compared with paired t-test. Percent water column use compared by G-test of heterogeneity.

Variable	Treatment Means			Test Statistics		
	2Bull (n=4)	4Bull (n=8)	MixBull (n=8)	MixBrook (n=8)	F	t
<b>Habitat Associated Behaviors</b>						
Percent Depth	16.4 $\pm$ 2.3 <sup>xy</sup>	25.0 $\pm$ 2.6 <sup>y</sup>	17.4 $\pm$ 1.1 <sup>x</sup>	18.7 $\pm$ 2.3	5.107*	-0.619
Velocity - cm/s	8.1 $\pm$ 1.4	9.7 $\pm$ 1.8	11.5 $\pm$ 1.3	10.3 $\pm$ 1.6	0.648	0.789
Max Velocity - cm/s	21.4 $\pm$ 3.0	26.9 $\pm$ 2.7	31.1 $\pm$ 3.6	29.3 $\pm$ 3.5	1.078	0.948
Velocity Differential <sup>a</sup> - cm/s	13.3 $\pm$ 3.9	17.3 $\pm$ 2.6	19.6 $\pm$ 3.0	18.9 $\pm$ 4.0	0.897	0.330
<b>Feeding Behaviors</b>						
Foraging Rate <sup>b</sup> - #/5min	5.1 $\pm$ 1.5	6.6 $\pm$ 1.3	4.6 $\pm$ 0.9	5.6 $\pm$ 1.1	0.922	-0.683
% Benthos	4.0 $\pm$ 2.5	2.4 $\pm$ 0.5	1.0 $\pm$ 0.5	1.7 $\pm$ 0.6	0.310 <sup>c</sup>	0.004 <sup>c</sup>
% Water Column	87.8 $\pm$ 4.1	84.1 $\pm$ 2.7	88.0 $\pm$ 3.1	89.1 $\pm$ 0.9		
% Surface	8.1 $\pm$ 3.2	13.4 $\pm$ 2.8	10.9 $\pm$ 3.3	9.2 $\pm$ 1.0		
<b>Interactions</b>						
Dominant Interactions <sup>b</sup> - #/5min	0.0 $\pm$ 0.0 <sup>x</sup>	0.09 $\pm$ 0.03 <sup>y</sup>	0.03 $\pm$ 0.01 <sup>xy</sup>	0.33 $\pm$ 0.15	6.697 <sup>ad</sup>	2.268 <sup>ae</sup>
Subordinate Interactions <sup>b</sup> - #/5min	0.03 $\pm$ 0.03 <sup>x</sup>	0.16 $\pm$ 0.05 <sup>xy</sup>	0.29 $\pm$ 0.08 <sup>y</sup>	0.04 $\pm$ 0.02	3.648*	4.363*
<b>Growth</b> % change in body weight	-7.44 $\pm$ 4.1	-12.15 $\pm$ 1.5	-12.99 $\pm$ 2.8	3.42 $\pm$ 3.6	2.461	-6.282**

\* significance at  $p \leq 0.05$

\*\*significance at  $p \leq 0.001$

<sup>a</sup> log base 10 transformation

<sup>b</sup> square root transformation

<sup>c</sup> G-test for heterogeneity

<sup>d</sup> Kruskal Wallis Z-statistic

<sup>e</sup> Mann Whitney U test statistic

than those of bull trout in the Mix treatment (Tukey HSD,  $p=0.018$ ) (Table 1.3). Similarly, there were no differences in habitat associated behaviors of bull trout when dominant individuals in each enclosure were not included in the analysis.

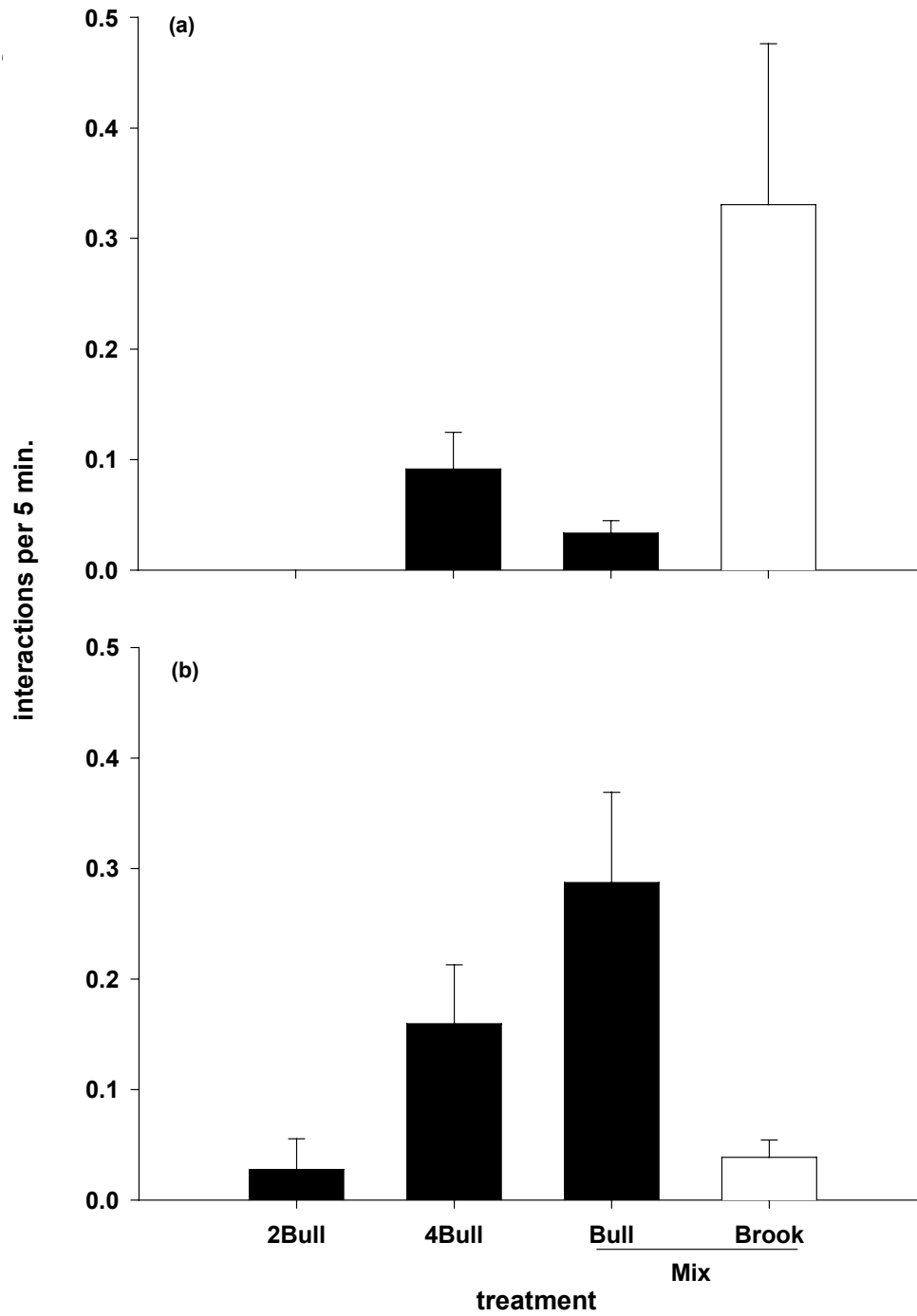
Brook trout in the Mix treatment displayed habitat associated behaviors similar to sympatric bull trout. Both species selected focal feeding points at similar positions in the water column, and with equivalent velocity measures (Table 1.3). Cover use was similar for both species (G-test,  $p>0.1$ ).

### Feeding Behaviors

Bull trout in all treatments exhibited comparable feeding behaviors (Table 1.3). Mean foraging rates were similar among experimental treatments. All bull trout fed primarily from the water column and the proportion of time spent feeding from the benthos, water column, or surface did not differ among treatments. Likewise, bull trout and brook trout in the Mix treatment had comparable foraging rates and fed similarly from the benthos, water column, and surface (Table 1.3).

### Interactions

Interactions of bull trout in the enclosures were not only density-dependent but also species-specific. Bull trout in the low density treatment (2Bull) had low rates of interaction compared to both high-density treatments. There were no dominant interactions among fish in the 2Bull treatment, and interactions in the 4Bull treatment were significantly more than in the 2Bull treatment (Mann-Whitney,  $p=0.014$ ) (Fig. 1.5a). Average displacement rates in the 2bull treatment were significantly less than those for bull trout in the Mix treatment (Tukey HSD,  $p=0.041$ ) (Fig. 1.5b). Bull trout



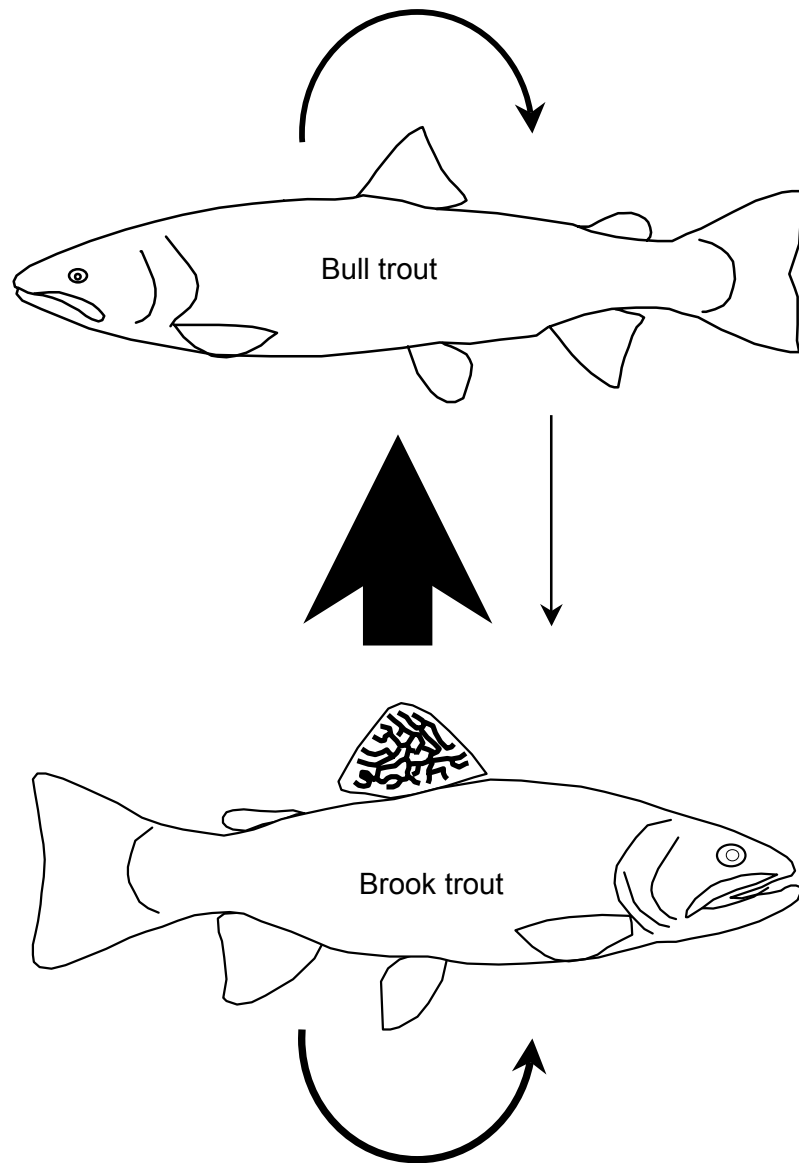
**Figure 1.5.** Number of interactions that were a) dominant and b) subordinate for bull trout (black) and brook trout (white) in experimental enclosures. Values are treatment means  $\pm$  1 SE. See text for interaction definitions.

more frequently than bull trout in the 4Bull treatment, though differences were not statistically significant (Fig. 1.5, Table 1.3).

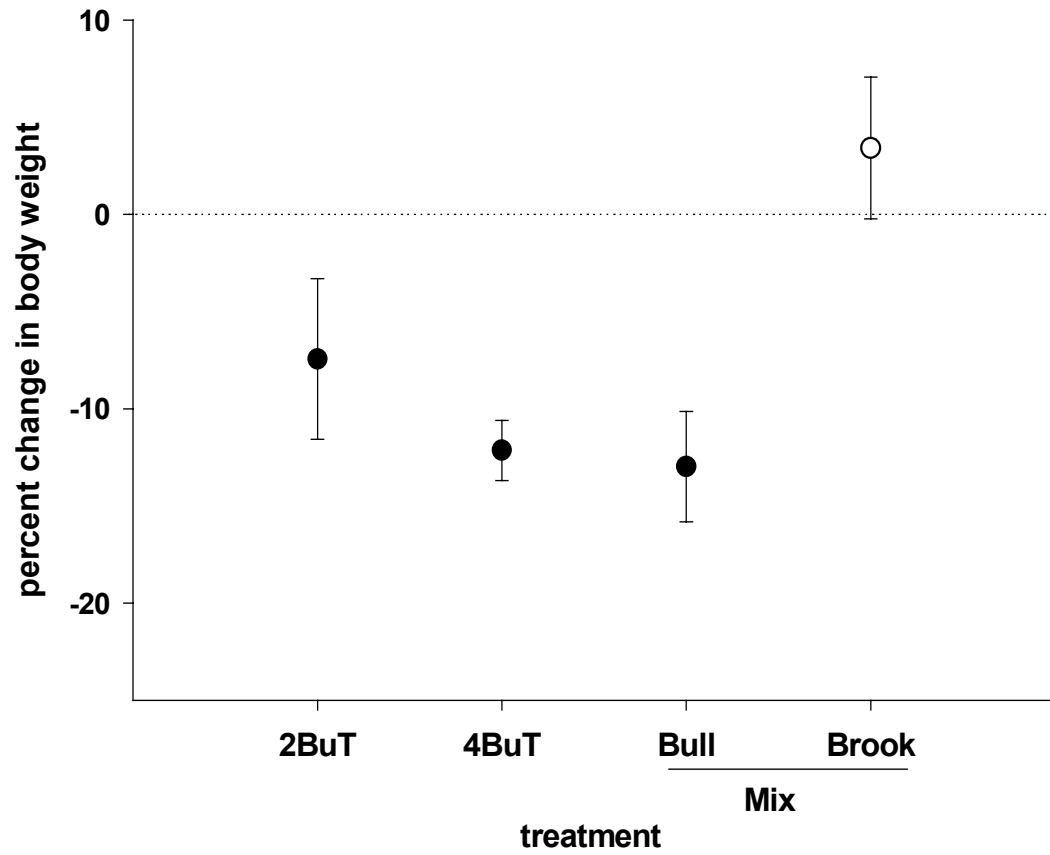
A brook trout was the dominant fish in six of the eight Mix treatment enclosures. The fish in the remaining two enclosures never established strong social dominance hierarchies. The dominant brook trout consistently maintained feeding territories in the front third of the pool. The subordinate fish resided in the rear, visually isolated from the dominant brook trout. Compared to bull trout, brook trout in the mixed treatment initiated a significantly greater number of dominant interactions (Fig. 1.5a, Table 1.3); a disproportionate number of those interactions, 90.3%, were over bull trout. Brook trout harassed or displaced bull trout at an average rate of 0.26 dominant interactions every five minutes. In contrast, bull trout in the Mix treatment were displaced more frequently than brook trout (Fig. 1.5b, Table 1.3), 91.9% by brook trout. Rarely did bull trout successfully defend their feeding territory from intruding brook trout or displace brook trout. Bull trout harassed or displaced brook trout at an average rate of 0.01 interactions every five minutes. These rates of agonistic interactions observed in the Mix treatment are symbolized in Figure 1.6.

### Growth

Fifty two of the 60 bull trout in the enclosures lost weight over the duration of the experiment. Bull trout in the 2Bull treatment lost an average of 7.4% of their body weight, which was less than bull trout in the 4Bull and Mix treatment which lost 12.15% (Tukey HSD,  $p= 0.164$ ) and 12.99% (Tukey HSD,  $p= 0.114$ ) respectively. Growth of bull trout was similar in high-density allopatric and sympatric treatments. Results were similar when dominant fish were factored out of the analysis. Brook trout in enclosures gained an average of 3.4% of their body weight (Fig. 1.7). The difference between growth of bull trout and brook trout in the Mix treatment was statistically significant (paired t-test,  $p<0.001$ ).



**Figure 1.6.** Relative frequency of dominant interactions between equal sized bull trout and brook trout in the Mix treatment. See text for details.



**Figure 1.7.** Percent change in body weight for bull trout (solid) and brook trout (open) in experimental enclosures. Values are treatment means  $\pm 1$  SE.

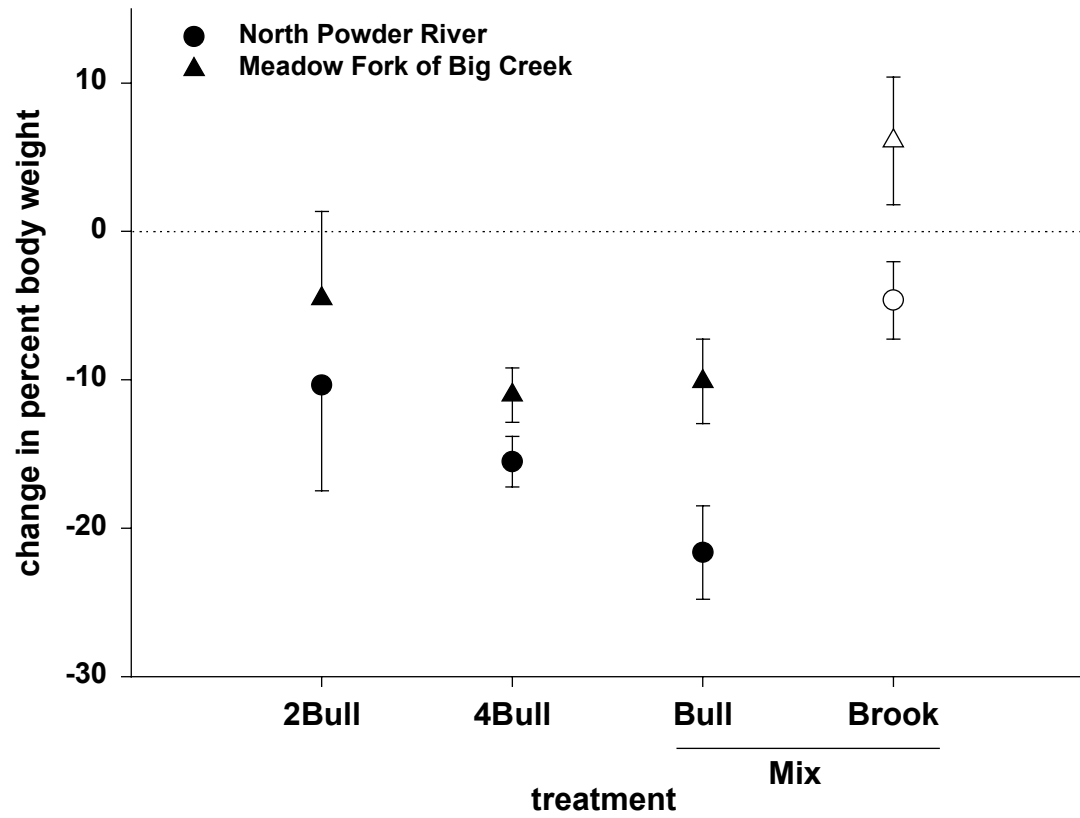
Compared to fish in Meadow Fork of Big Creek, bull trout and brook trout in North Powder River lost a greater proportion of body weight (Fig.1.8). In the North Powder River growth of bull trout in the Mix treatment was less than the 4Bull treatment. Statistical comparisons were not possible due to insufficient degrees of freedom.

## Discussion

Observations of free-ranging fish revealed that sympatric bull trout and brook trout exhibited similar feeding and habitat associated behaviors. Contrary to my hypothesis, I saw little evidence of resource partitioning. The slightly greater focus of sympatric bull trout on the surface was not statistically significant, and not sufficient to ameliorate competitive interactions or suggest a niche shift for bull trout (see Fausch and White 1981 and Nakano *et al.* 1992 for examples). Both species fed primarily from the water column and held focal feeding points with similar velocity measures, relative depth, and cover. With such similar feeding behaviors, intense interference competition is likely when food and space are scarce.

In the experimental enclosures, macroinvertebrate drift was reduced by 52%, creating an environment with reduced food resources and a high potential for competition. Under these conditions bull trout and brook trout still exhibited similar feeding and habitat-associated behaviors. The lack of resource partitioning in the enclosures further emphasizes the high likelihood of direct interference competition when habitat and prey resources are limiting.

Shared resource use is not surprising because 1) bull trout are native and brook trout are introduced and 2) both species are congeners. Closely related species that do not exist in sympatry, but in similar environments, have the greatest potential for interference competition (Hearn 1987; Fausch 1988). Naturally sympatric species are more likely to have evolved mechanisms for partitioning limited resources (DeWald and Wilzbach 1992). For example, bull trout and westslope cutthroat trout *O. c. lewisi*



**Figure 1.8.** Percent change in body weight for bull (solid) and brook trout (open) in experimental enclosures in North Powder River and Meadow Fork of Big Creek. Values are treatment means  $\pm$  1 SE.

co-occur naturally in Idaho and Montana streams. In sympatry, juvenile bull trout hold positions closer to the substrate and feed predominantly from the benthos, whereas cutthroat hold positions higher in the water column and feed from the surface (Pratt 1984; Nakano *et al.* 1992). In addition, closely related species with similar morphology typically exploit food and habitat resources in the same manner and overlap in resource use (Werner 1977).

The results of the in-stream experiment clearly show brook trout were dominant and aggressive over bull trout of similar size. In the Mix treatment, brook trout consistently were dominant over bull trout, and bull trout were seldom observed to be dominant over brook trout. Bull trout were displaced more frequently than brook trout, and disproportionately more often by brook trout rather than other bull trout (Fig. 1.6). In addition, bull trout in the presence of brook trout experienced a greater number of agonistic interactions than allopatric bull trout. Likewise, brook trout have been shown to be more aggressive than rainbow trout (Magoulick and Wilzbach 1998) and cutthroat trout at warmer temperatures (DeStaso and Rahel 1994).

Compared to bull trout, brook trout in the experimental pens grew more. Confined bull trout lost weight while brook trout gained weight during the experiment. This was the result of brook trout's greater ability to maintain and defend more profitable foraging positions at the front of the pool. The greater growth of brook trout is a measure of the competitive advantage over bull trout. It may also illustrate the greater ability of brook trout to tolerate confinement, high densities, and stressful conditions (McNicol and Noakes 1984; Schroeter 1998).

If the difference in growth between bull trout and brook trout in the experimental pens reflected a similar difference in free-ranging fish, then brook trout likely grow faster, which will confer greater fitness, than bull trout in these streams. Because the outcomes of 87% of the interactions between free-ranging fish were determined by size, I infer that brook trout in the same cohort as bull trout may eventually attain dominance over bull trout based on size alone.

The growth of an individual cannot be equated to the growth of a population (Fausch 1984). Even though this study documents the effects of brook trout on the

feeding behavior and growth of individual bull trout it provides no measure of the effect of brook trout on the demographic parameters of bull trout, e.g. emigration or mortality rates. However, the aggressive behavior and the reproductive advantage of brook trout, in combination with hybridization, suggest brook trout may eventually out-number and dominate bull trout (Leary *et al.* 1993). On the population scale, these factors may force bull trout to emigrate, ultimately leading to displacement and the eventual decline of bull trout. In scenarios where bull trout are limited to headwater streams, downstream displacement of bull trout may force them to reside in heavily degraded habitat (Ratliff and Howell 1992) and warmer water temperatures, decreasing their chances for survival. Displacement of bull trout upstream into the allopatric reaches may increase bull trout densities, which as this study shows, negatively affects growth through density-dependant interactions. To fully understand population level consequences of brook trout, a study designed specifically to examine immigration and emigration rates and population dynamics of bull trout is required.

Observations of free-ranging fish also reveal consistent resource use between allopatric and sympatric bull trout. There was no evidence of a niche shift of bull trout caused by the presence of brook trout. Similarly, in the experimental enclosures, where prey resources were reduced and size and density of fish controlled, I saw no evidence of a niche shift. Bull trout in all treatments fed primarily on macroinvertebrate drift in the water column and held focal points with the same relative depth, velocity measures, and cover. I accepted my null hypothesis that allopatric bull trout compared to bull trout sympatric with brook trout exhibit similar habitat and feeding associated behaviors.

Nakano *et al.* (1998) demonstrated a shift in resource use of bull trout after the removal of brook trout from two pools. In the absence of brook trout, bull trout increased foraging rates and distances, and occupied more exposed focal points. They concluded brook trout were dominant over bull trout, and interspecific interactions were important in the regulation of bull trout density. Unfortunately, their results were confounded by fish size and density. On average, brook trout in their study were larger than bull trout, making the distinction between dominance based on size or

species difficult. The shift in resource use by bull trout also may have been a result of lower densities after brook trout were removed.

My study resolved these issues by controlling for both fish density and size. Comparisons of treatments with two bull trout to those with two bull trout and two brook trout established conditions for interspecific competition. I tested the intensity of interspecific interactions relative to intraspecific interactions by keeping density constant and comparing bull trout in enclosures with four bull trout to those with two bull trout and two brook trout (Fausch 1998). Because body size can determine the outcome of interactions between stream salmonids (Noakes 1980), fish in each enclosure were similar sizes.

In this study the effects of interspecific interactions on individual bull trout performance were equivalent to those of intraspecific interactions (Fausch 1998). The presence of similar-sized brook trout did not affect the growth of sympatric bull trout any more than other bull trout. Bull trout in the high density allopatric and sympatric treatments experience comparable growth (weight loss). Regardless of the presence of brook trout bull trout in both treatments experienced a similar net energy loss where the cost of occupying and defending a focal feeding point was greater than the energy gain from foraging on drift.

There is evidence that interspecific interactions are mediated by abiotic factors (Dunson and Travis 1991). My study suggests habitat complexity can play an important role in determining the outcome of competitive interactions between bull trout and brook trout. In the North Powder River, bull trout in the Mix treatment enclosures grew less than bull trout in the 4Bull treatment. This pattern was not observed in Meadow Fork of Big Creek (Fig. 1.8). However, the enclosures in the North Powder had predominantly gravel substrate with few boulders for cover. The habitat in the enclosures in Meadow Fork of Big Creek was more complex with large cobble and boulder substrate and wood or vegetation as cover. Individual bull trout may be negatively affected by the aggressive behavior of brook trout in habitat where they cannot visually isolate themselves. Degradation, simplification, and homogenization of habitat gives an added advantage to brook trout. Thus, the

conservation and restoration of complex stream habitat may allow bull trout to avoid the negative effects of dominance by introduced brook trout.

Decreased growth in the North Powder River enclosures was correlated to lower prey densities as compared to Meadow Fork of Big Creek (Table 1.1). Another possible explanation of less bull trout growth in the Mix treatment was the increased competition between bull trout and brook trout induced by the reduced (and potentially limiting) prey resources. Because brook trout were the more aggressive species they were able to out-compete bull trout and better exploit prey resources.

My study clearly documents the aggressive behavior of introduced brook trout and their competitive dominance over similar-sized bull trout in two eastern Oregon headwater streams. I saw no evidence of resource partitioning between bull trout and brook trout or a niche shift of bull trout in the presence of brook trout. Hence, during periods of resource scarcity, competition between bull trout and brook trout is likely and displacement of bull trout eminent. Further research should consider the role of habitat complexity in interactions between bull trout and brook trout and also clearly identify the impact of brook trout on the demographic parameters of bull trout.

## **Acknowledgements**

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Chapter 2  
Dietary Overlap of Co-occurring Bull Trout *Salvelinus confluentus* and Brook  
Trout *S. fontinalis* in Eastern Oregon Streams

Stephanie L. Gunckel

## Abstract

To quantify the impacts to native bull trout by introduced brook trout, diet similarity of the two species was evaluated. I examined the stomach contents of 82 allopatric bull trout, 74 sympatric bull trout, and 73 sympatric brook trout. Drifting and benthic macroinvertebrates were sampled to measure prey availability. Diets of all fish were dominated numerically by aquatic Diptera and Trichoptera larvae, Ephemeroptera nymphs, and terrestrial insects. Bull trout and brook trout showed strong size selective predation, with both terrestrial and aquatic insects >5 mm occurring more frequently in the diet than were available. Substantial dietary overlap of sympatric bull and brook trout was indicated by high values of Schoener's Index (0.46 – 0.68). Both populations had completely overlapping patterns of electivity, though brook trout elected families of Trichoptera more frequently than bull trout. The study provides little evidence of food resource partitioning between bull trout and brook trout, and little evidence of changes in bull trout diet when brook trout are present. Instead, my study demonstrates high potential for interspecific competition when prey resources are scarce.

## Introduction

One of the most significant threats to declining native bull trout *Salvelinus confluentus* populations is the presence of non-native salmonids (Howell and Buchanan 1992). Brook trout *S. fontinalis* particularly cause great concern because they are widely distributed throughout the range of bull trout (Rieman and McIntyre 1993) and the two species can hybridize (Leary *et al.* 1993). In addition, competition between bull and brook trout for habitat and prey resources has been implicated in the decline of bull trout populations (Ratliff and Howell 1992; Dambacher *et al.* 1992). My work reveals bull trout and brook trout utilize similar feeding microhabitats and exhibit feeding behaviors in common, demonstrating a high potential for competition when resources are scarce (Chapter 1). However, the specific diet of introduced brook trout and native bull trout and the potential competition for prey has received minimal attention (except Wallis 1948).

Other diet studies reveal stream-dwelling trout feed primarily on the most abundant aquatic insect orders, terrestrial insects and, occasionally, fish (Elliot 1967; Griffith 1974; Allan 1981; Boag 1987; Angradi and Griffith 1990; Nakano *et al.* 1992; Bozek *et al.* 1994). Though salmonids commonly have similar diets, naturally sympatric species typically partition resources. Native co-occurring salmonids have evolved mechanisms for partitioning food and habitat resources; each species exploits a unique set of the available resources, thereby reducing potential for direct interaction (Nilsson 1967; Dolloff and Reeves 1990). For example, juvenile coho salmon *Oncorhynchus kisutch* and Dolly Varden *S. malma* selectively segregated according to cover use, water column use and feeding microhabitat (Dolloff and Reeves 1990). Each species occupied exclusive habitats alone and in sympatry; interspecific interaction rates between species were minimal. When two species are brought together through introductions, but do not exist naturally in sympatry, there is greater potential for shared resource use (Fausch 1988). The result is either displacement of one species or coexistence through interactive segregation (Everest and Chapman 1972). Nilsson's (1967) interactive segregation hypothesis suggests segregation is due

to direct competition, territoriality, or predation. A shift in diet based on the presence or absence of a competitor would be an example of interactive segregation.

Current data are inadequate to determine whether the interactive segregation hypothesis applies to the diets of native bull trout and introduced brook trout. Allopatric bull trout and brook trout have been shown to feed primarily from the water column (Allan 1981; Boag 1987) suggesting that both species exploit the same prey resources. In studies where bull trout and brook trout were separately sympatric with cutthroat trout *O. clarki*, each species exhibited a benthic-oriented diet (Andrusak and Northcote 1971; Griffith 1974; Nakano *et al.* 1992). No single study has focused on the diet of bull trout in allopatry and in sympatry with brook trout.

This study examined the diet of bull trout and brook trout to document the potential degree of competitive interaction between the two species. The objectives were to 1) determine the dietary overlap between sympatric bull trout and brook trout, and 2) describe the diet of bull trout in allopatry and sympatry with brook trout. I hypothesized that due to interactive segregation, bull trout and brook trout diets would differ and resource overlap would be minimal. Also, I expected bull trout diet and patterns of electivity to differ in allopatry and sympatry with brook trout.

## **Methods**

### *Study Site*

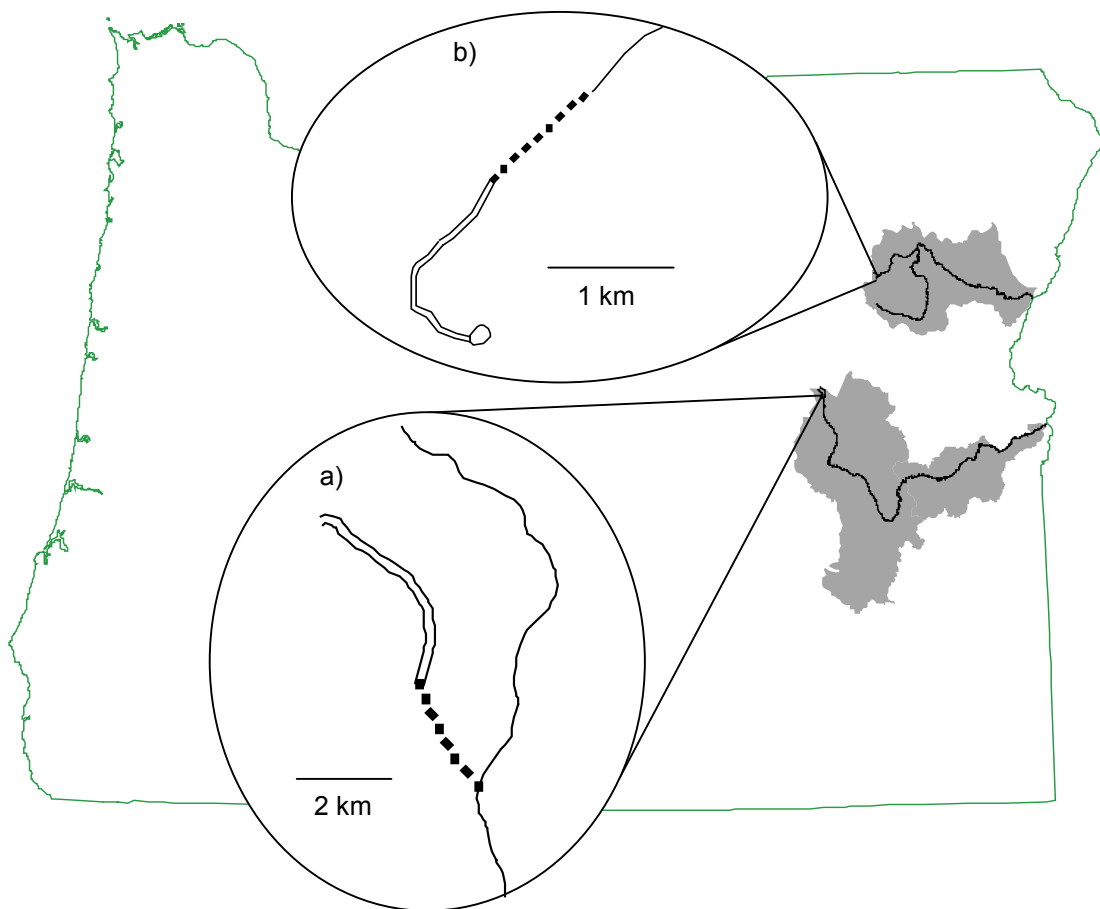
Bull and brook trout stomach contents, macroinvertebrate drift and benthic samples were collected in two streams in eastern Oregon, the North Powder River and Meadow Fork of Big Creek. These streams shared a characteristic fish distribution where bull trout were allopatric in the upper segments and sympatric with brook trout in the middle segments. Both streams were selected for their relatively high densities of trout species, zones of trout allopatry and sympatry, and relative ease of access.

Meadow Fork of Big Creek is a tributary of the Malheur River. The sympatric reach was 2.6 km long where bull trout, brook trout, rainbow trout *O. mykiss*, and shorthead sculpin *Cottus confusus* were present. Immediately upstream the allopatric reach was 4.3 km long with only bull trout (Fig. 2.1a). The allopatric and sympatric study sites were separated by 2.0 km.

The North Powder river is a headwater stream in the Powder River Basin. The 1.0 km long sympatric reach had bull and brook trout. The allopatric reach extended 2.6 km upstream of the sympatric reach where only bull trout were present (Fig. 2.1b). The allopatric and sympatric study sites were separated by <0.5 km. Habitat was assessed using survey methodology based on protocol developed by Hankin and Reeves (1988; Moore 1997). Habitat characteristics for all reaches are described in Table 2.1.

#### *Fish and Prey Collection*

Fish and prey samples were collected in mid-summer of 1996 and 1997 (Table 2.2). For each sample date, stomach contents were collected from allopatric bull trout and sympatric bull trout and brook trout. Concurrently, drift and benthic samples were collected to quantify availability.



**Figure 2.1.** Relative distribution of allopatric bull trout (—) and sympatric bull trout and brook trout (••) in a) Meadow Fork of Big Creek in the Malheur River Basin and b) North Powder River in the Powder River Basin, Oregon.

**Table 2.1.** Habitat characteristics of study streams.

	Meadow Fork		North Powder	
	Sympatric	Allopatric	Sympatric	Allopatric
Mean Elevation (ft)	5640	6180	6110	6380
Stream Order	3	2	2	2
Length (km)	2.6	4.3	1.0	2.6
Gradient (%)	4.2	6.5	6.1	7.7
Mean Width (m)	4.5	3.8	*	4.0
Pools: % of total surface area	17	14	*	10
Rapids: % of total surface area	52	38	*	46
Dominant Substrates	Cobble 45% Gravel 44%	Cobble 48% Gravel 41%	*	Gravel 24% Cobble 23% Sand 22%
Mean invertebrate drift density /100 m <sup>3</sup>	781.5 <sup>a</sup> 875.4 <sup>c</sup>	494.2 <sup>a</sup> 1334.1 <sup>c</sup>	362.5 <sup>b</sup> 1484.3 <sup>c</sup>	706.2 <sup>b</sup> 1904.3 <sup>c</sup>
Mean benthic invertebrate density /m <sup>2</sup>	8401.8 <sup>a</sup> 5829.8 <sup>c</sup>	9645.6 <sup>a</sup> 9266.7 <sup>c</sup>	3254.4 <sup>b</sup> 2486.0 <sup>c</sup>	4894.7 <sup>b</sup> 2259.6 <sup>c</sup>
Fish Species Present	Bull, Brook, and Rainbow trout, Shorthead Sculpin	Bull trout	Bull trout, Brook trout	Bull trout

\* Quantitative information is not available

<sup>a</sup> August 1996

<sup>b</sup> July 1996

<sup>c</sup> July 1997

**Table 2.2.** Dates, number of fish sampled, and Schoener's Index of Overlap (D) for bull trout and brook trout in the sympatric reach for each sample period.

Stream	Date	Reach	Bull Trout	Brook Trout	D
Meadow Fork	Aug 20, 1996	Allopatric	11	-	-
	Aug 21, 1996	Sympatric	10	11	0.46
	Jul 3, 1997	Sympatric	26	23	0.65
	Jul 5, 1997	Allopatric	20	-	-
North Powder	Jul 23, 1996	Sympatric	10	9	0.61
	Jul 24, 1996	Allopatric	18	-	-
	Jul 23, 1997	Sympatric	28	31	0.68
	Jul 24, 1997	Allopatric	33	-	-

All fish were caught between 0700 and 1200. Trout were collected during the morning hours in order to capture the diet following the dawn peak in macroinvertebrate drift. In 1996, all fish were captured by angling with insect-mimicking flies. During 1997, equal sample sizes were captured using insect-mimicking flies, fish-mimicking flies, and an electrofisher to test for bias in capture method. No difference in diet was found between capture methods. Fish were anesthetized in tricaine methanesulfonate (MS-222), weighed, and measured. Stomach contents were flushed into a 250  $\mu\text{m}$  sieve, and preserved in 95% ethanol (sensu Meehan and Miller 1978). Fish were held in a recovery tank until fully recovered from anesthesia and returned to the stream. To calculate the efficiency of the stomach flushing technique a sub-sample of 10 sampled brook trout were killed, their stomachs removed, and preserved in 95% ethanol.

Three drift samples were collected during peak drift at dawn the morning prior to sampling fish in each study reach. Peak drift was roughly determined by measuring the volume of macroinvertebrates in 10 minute intervals for the hour before and during sunrise. A 250  $\mu\text{m}$  drift net with an opening of 0.1  $\text{m}^2$  was set for 30 minutes in the thalweg just upstream from the head of three randomly selected pools. In all

cases the height of the drift net exceeded water depth, effectively sampling the entire water column. Depth and water velocity were measured at each net using a Marsh-McBirney flow meter. Six benthic samples were collected in pools in each reach using a 0.095 m<sup>2</sup> surber sampler with a 250  $\mu$ m net. Sites within each pool were randomly selected. Drift and benthic samples were preserved in 95% ethanol.

Invertebrates from stomach, drift, and benthic samples were sorted, identified to genus, categorized by lifestage (larvae, pupae, or adult), and counted in the laboratory using a Zeiss dissecting microscope (10-40x). In some cases sub-samples of 50% were used to speed processing of drift and benthic samples with a high volume of silt and sand or FPOM. Drift and benthic samples were split using a plankton splitter and Caton tray (Caton 1991) respectively. Identification of invertebrates was determined using Merritt and Cummins (1996), Borror et al. (1989), Stewart and Stark (1993), Thorp and Covich (1991) and Wiggins (1995). Insects also were classified as terrestrial, aquatic origin terrestrials (adult aerial stages of aquatic insects), or aquatic insects. To examine size selective predation lengths of insects (not including antennae or cerci) were measured to the nearest 0.5mm for stomach and drift samples from only Meadow Fork of Big Creek in 1997.

#### *Description of Diet*

Often the condition of insects in the stomach samples only allowed identification to the family or order taxonomic levels. Diets of individual fish were described by family and life stage of the prey species present. The average numeric proportions of prey taxa in the diet of all allopatric bull trout and sympatric bull trout and brook trout were compared using the log-likelihood ratio test (G-test)(Sokal and Rohlf 1981). Empty stomachs were not included in the analysis.

### *Dietary Overlap*

Dietary overlap of sympatric bull trout and brook trout on each sample date was calculated based on family and life stage of prey using Schoener's overlap index (D):

$$D = 1 - 0.5 \left( \sum_{i=1}^s |p_{ij} - p_{ik}| \right),$$

where,  $P_{ij}$  and  $P_{ik}$  are the proportions of the resource category ( $i$ ) used by species ( $j$ ) and ( $k$ ), and ( $s$ ) is the total number of resource categories used by both species (Schoener 1968). Values of  $D$  range from 0, representing no overlap, to 1, for complete overlap. The index provides a comparative measure rather than a statistical measure (Townsend and Hildrew 1976) where values greater than 0.60 are generally considered to indicate biologically significant overlap in the resource use of two species (Wallace 1981; Wilhelm *et al.* 1999).

### *Electivity*

Prey availability was determined by averaging the mean proportion of each taxa present in the benthos and the drift. Johnson's Index (JI) was used to determine the relative preference for life stages of each prey family for allopatric bull trout and sympatric bull trout and brook trout (Johnson 1980). The index expresses the difference between rank usage and availability for each prey taxa. Values  $>0$  indicate preference and  $<0$  avoidance. The advantages of this rank procedure are 1) it avoids the difficulties and inaccuracies common in measurements of availability (Strauss 1979; Wallace 1981) and 2) comparisons of relative values of the index prevent incorrect absolute statements of preference (Johnson 1980). The JI was averaged across all fish in each reach each year to obtain a mean index for each prey component.

Non-metric multidimensional scaling (NMS), a non-parametric ordination technique, was used to determine whether the collective patterns of preference were

similar between populations of allopatric bull trout and sympatric bull and brook trout (Kruskal 1964; McCune and Mefford 1999). NMS was chosen because it is appropriate for data that are non-normal or on scales that are discontinuous or otherwise questionable (McCune and Mefford 1999). Each study stream each year was ordinated separately using Johnson's Index for prey families and life stages of each individual fish (fish by prey family matrix of JI). The NMS ordinations were performed using Euclidean (Pythagorean) distance measure. Three hundred iterations were used for each run to evaluate stability, and each analysis was conducted ten times to ensure the lowest possible stress, a measure of fit. The dimensionality of each data set was determined at the point where additional dimensions provide only small reductions in stress. Each ordination was orthogonally rotated so the maximum variation was loaded on the first axis. Correlation coefficients of the prey taxa to the ordination axes were used to describe the relationship of fish electivity in prey space.

## **Results**

Stomach contents of 82 allopatric bull trout, 74 sympatric bull trout and 73 sympatric brook trout were examined. Fork lengths of fish ranged from 85-238 mm and did not differ statistically among groups (3 way ANOVA,  $f = 0.48$ ,  $p=0.6$ ). Only one allopatric bull trout and two brook trout had empty stomachs.

Of the ten brook trout stomachs dissected after stomach flushing, 70% were completely empty. For the remaining 30% with partially flushed stomachs, 23% of the insects remained ( $\bar{x} = 3$  insects).

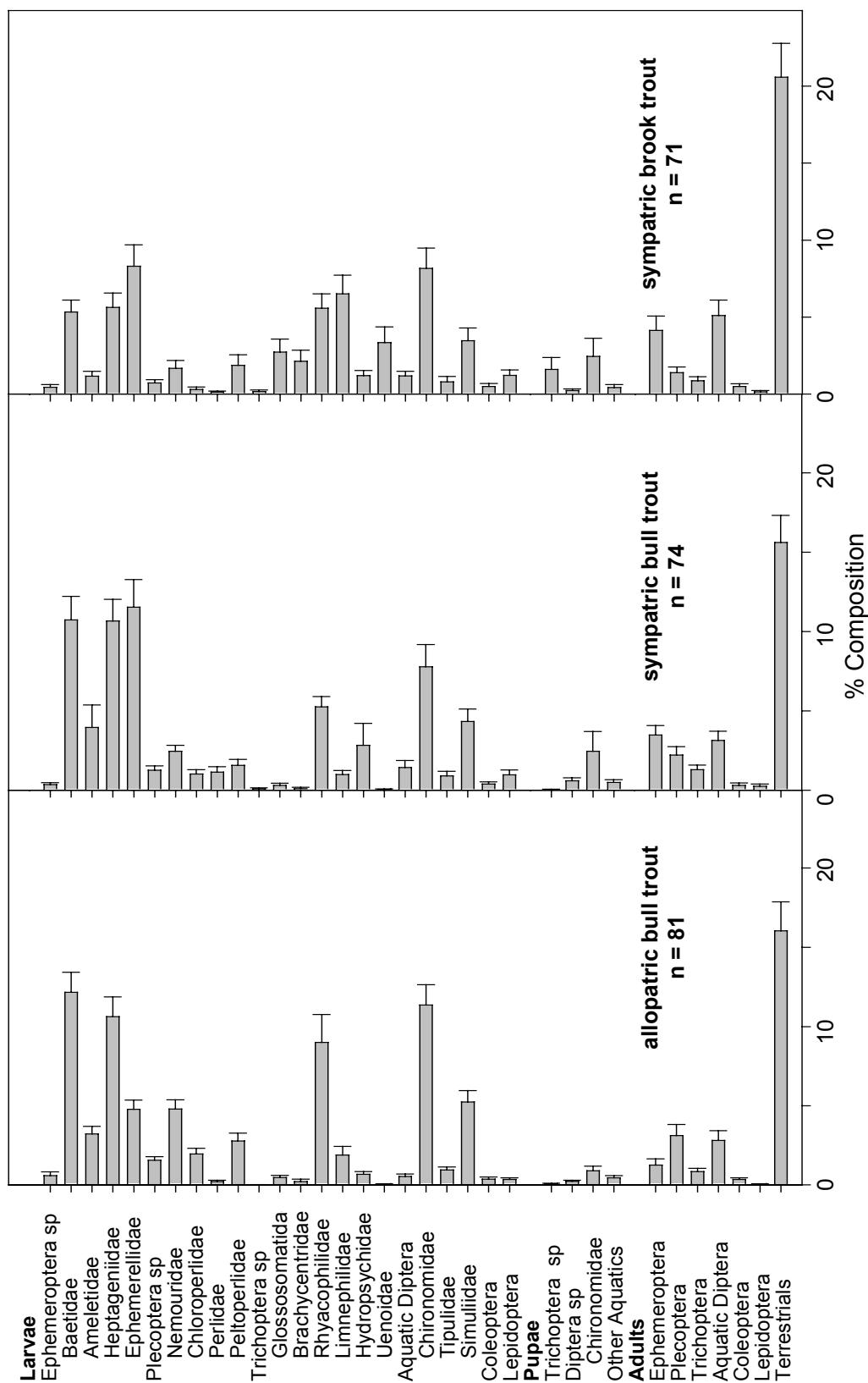
### *Description of Diet*

Bull trout and brook trout fed on a wide variety of prey. Each species in each stream each year consumed an average of 85 (range 67-94) different prey families and

life stages. No one family averaged more than 13% of the diet, and only 13% of the 85 families exceeded an average of 2% of the diet. Though relative proportions of specific prey varied between individual fish, larval stages of Ephemeroptera, aquatic Diptera and Trichoptera, and terrestrial insects dominated the stomach samples. Together these orders averaged 72.3 - 74.1% of the diets for trout in the study. Vertebrate prey were rare; two brook trout from Meadow Fork of Big Creek each consumed one shorthead sculpin.

For the purpose of comparison between diets, less dominant prey taxa were combined into groups of similar taxa. The adult stages of aquatic insect orders were combined into their respective groups (e.g. Ephemeroptera adults, Plecoptera adults, etc.) Ostracods, copepods, clams, mites, oligochaetes and platyhelminthes were combined into an 'other aquatic insects' category. A 'terrestrial insects' grouping comprised all insects without an aquatic life stage, including families of Hymenoptera, Hemiptera, Homoptera, Collembola, Thysanoptera, and Chilapoda.

Diet composition of bull trout was consistent between allopatric and sympatric reaches ( $G_{H(34)} = 23.21$ ,  $p > 0.90$ ). Both allopatric and sympatric bull trout fed primarily on Baetidae (12.2% and 10.7%, respectively), Heptageniidae (10.6% and 10.7%), Rhyacophilidae (9.0% and 5.3%), Chironomidae (11.3% and 7.7%) and terrestrial insects (16.0% and 15.6%) (Fig. 2.2). Sympatric bull trout also consumed a large proportion of Ephemerellidae (11.5%). Sympatric bull trout diet did not differ statistically from the diet of brook trout ( $G_{H(34)} = 35.85$ ,  $p > 0.10$ ). However, compared to sympatric bull trout, brook trout diet had a greater proportion of terrestrial insects (20.5%) and total Trichoptera families (23% compared to 9% for sympatric bull trout). Brook trout also had a smaller proportion of total Ephemeroptera (20.8% compared to 37.2% for sympatric bull trout) (Fig. 2.2).



**Figure 2.2.** Average percent abundance of major insect families and life stages in the diet of allopatric bull trout, sympatric bull trout and sympatric brook trout for all study sites combine. Error bars represent standard error.

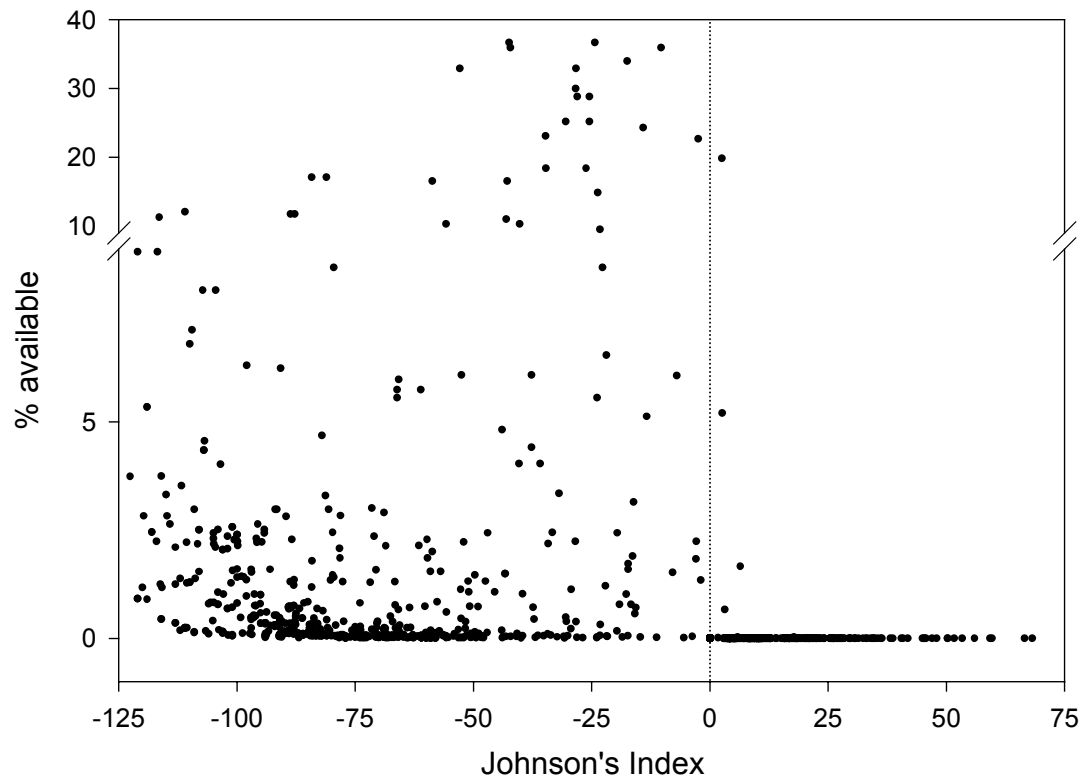
### *Dietary Overlap*

Similarity in consumption of particular prey families was reflected in measures of diet overlap. Bull trout and brook trout diets overlapped considerably in each stream each year. Schoener's index of overlap (D) for sympatric bull and brook trout ranged between 0.46 and 0.68. The only sample when  $D < 0.60$  was Meadow Fork of Big Creek 1996 (Table 2.2).

### *Prey Electivity*

Johnson's Index shows bull trout and brook trout primarily elected prey taxa rarely available. Almost all taxa with a Johnson's Index  $> 0$  were not present in both the drift and benthic samples (Fig. 2.3). Terrestrial insects comprised 51.8% of these taxa, 28.9% were adult stages of aquatic insects, and 19.3% were rare aquatic insects (e.g. Blephariceridae pupae, and Pelecorhynchidae larvae). These data demonstrate not only the strong preference of trout for rare and land dwelling prey species, but also the bias of electivity indices towards rare taxa.

My objective was to examine potential interaction between bull trout and brook trout over common prey. In order to reduce the emphasis on insects rarely encountered but retain a measure of electivity for terrestrial insects as a group, all allochthonous prey items were combine into a 'terrestrial insects' category. This group includes families of Hymenoptera, Hemiptera, Homoptera, terrestrial Coleoptera, Collembola, Arachnida, Thysanoptera, and terrestrial Diptera (primarily Brachycera). In addition, adult stages of each aquatic order were combined into respective groups (e.g. Ephemeroptera adults, Plecoptera adults etc.). An 'other aquatics' category included ostracods, copepods, clams, mites, oligochaetes and platyhelminthes. Prey taxa consisting  $< 1.0\%$  of the diet of each species were not included in the analysis.



**Figure 2.3.** Values of electivity for prey families compared to the relative abundance available. Includes diet of all bull trout and brook trout.

Terrestrial insects were preferred by all trout. On average, Johnson's Index showed most fish elected for terrestrials (Table 2.3). In the North Powder sympatric bull trout (1996,1997) and brook trout (1997) samples terrestrial insects in the diet equaled those available. Similarly terrestrial adult stages of aquatic taxa, particularly Ephemeroptera, were consistently elected among all groups of fish.

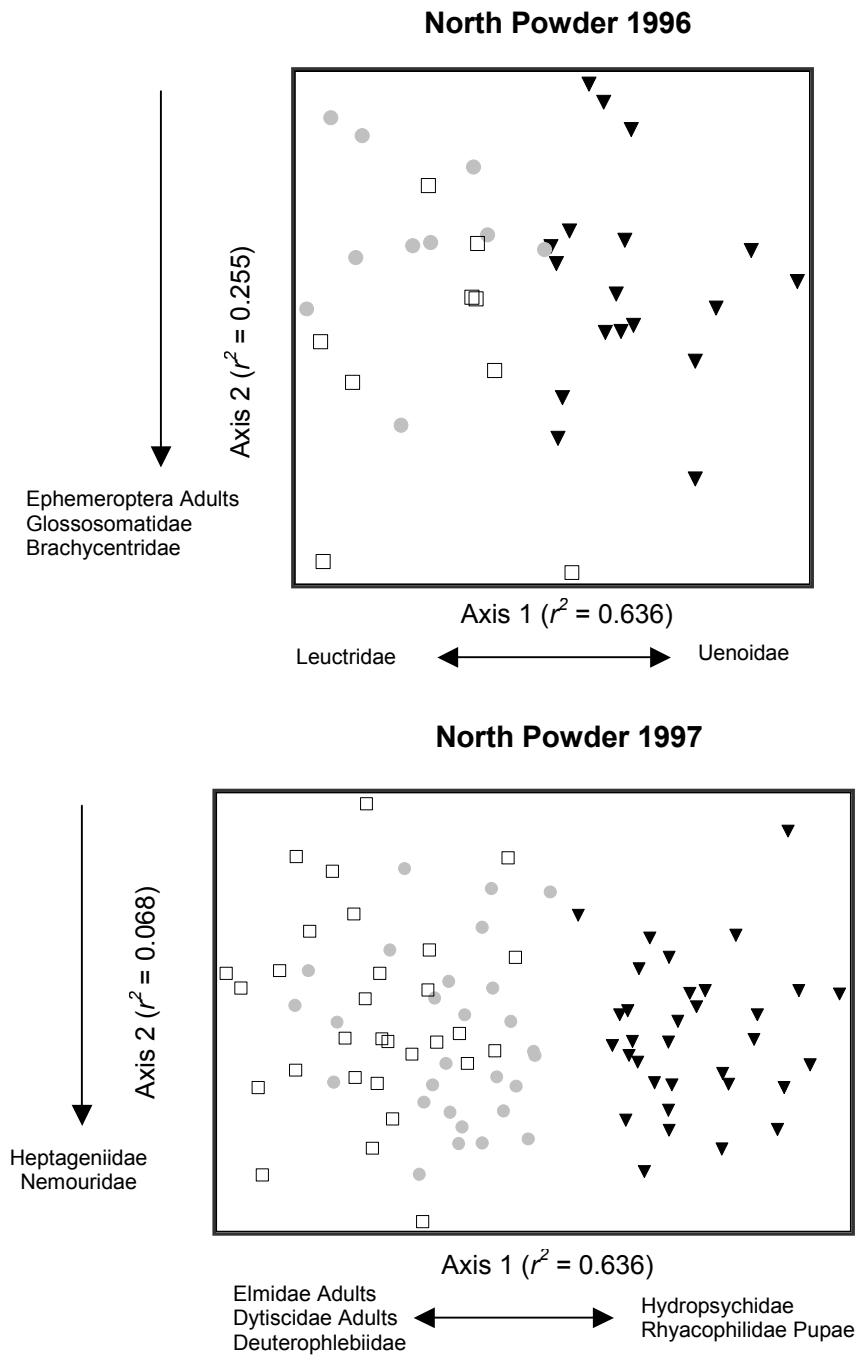
Sympatric bull trout and brook trout elected slightly different prey. Compared to bull trout, sympatric brook trout consistently showed a strong preference for Trichoptera families, Hydropsychidae, Limnephilidae, Glossosomatidae, Brachycentridae and Uenoidae (Table 2.3). However, the degree of dissimilarity between bull trout and brook trout varied among streams and years. For example, Meadow Fork 1996 electivity of sympatric bull trout and brook trout differed only in the election of Hydropsychidae by bull trout. Electivity of prey families overlapped by 83%. For comparison, in North Powder 1997, bull trout and brook trout had only Ephemeroptera adults in common out of seven families. Bull trout elected for Perlidae and Simuliidae larvae and brook trout elected four families of Trichoptera.

Compared to sympatric bull trout, allopatric bull trout more frequently elected families of Plecoptera and Ephemeroptera. Differences in taxa elected by allopatric and sympatric bull trout varied between streams (Table 2.3). In Meadow Fork 1997, allopatric and sympatric bull trout elected a similar suite of insects. Five of the nine families (55%) elected by allopatric and sympatric bull trout were common to both groups. In contrast, in North Powder 1997, allopatric and sympatric bull trout only elected for Simuliidae larvae in common.

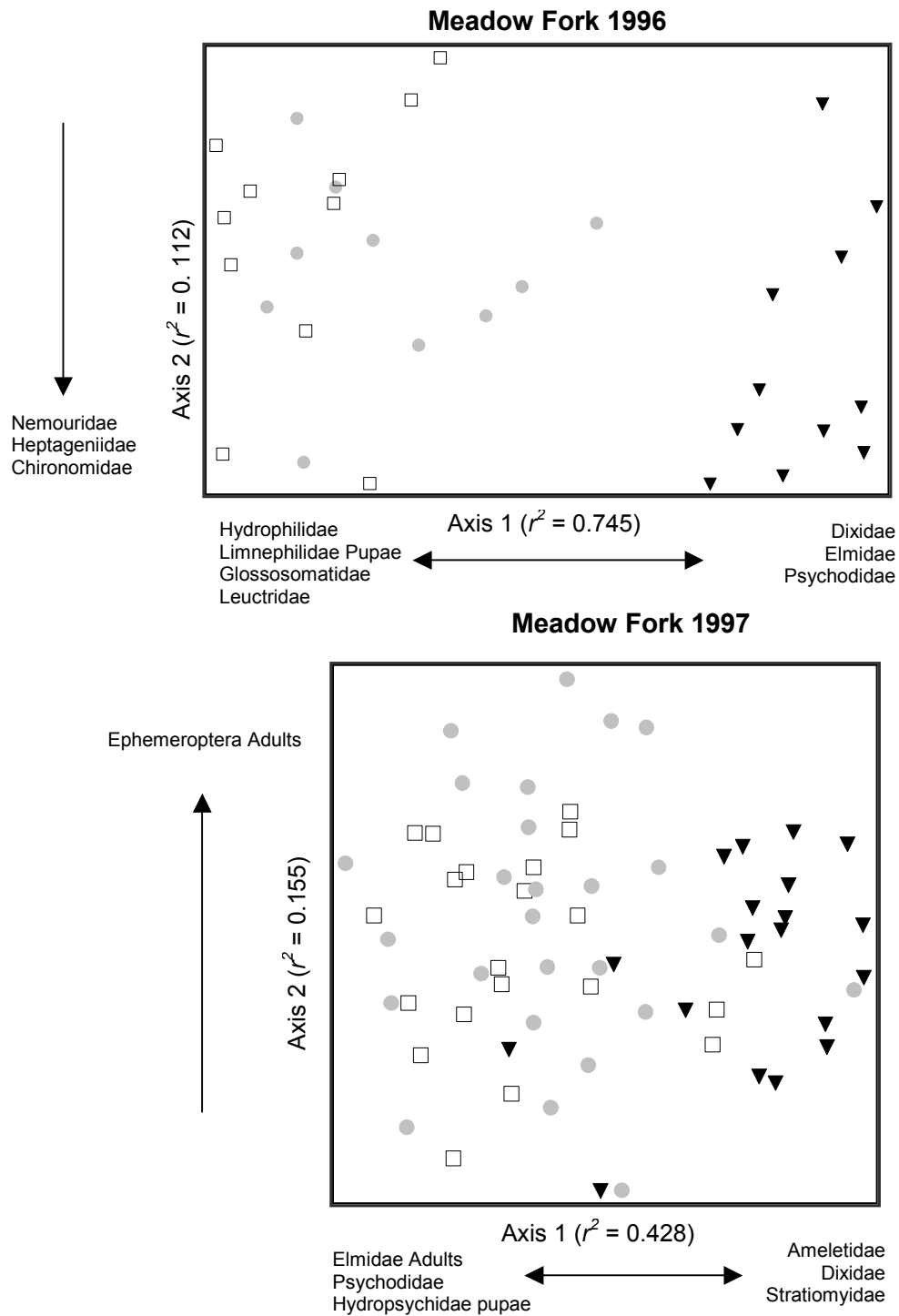
NMS shows that collective electivity patterns for individual allopatric bull trout were distinctly different than those of both sympatric species (Fig. 2.4, 2.5). The ordinations explained 68-85% of the variation. Meadow Fork 1996 and North Powder 1997 data matrices were best described with two dimensions. Meadow Fork 1997 and North Powder 1996 data matrices were best described with three dimensions, however, the third axis (not illustrated) explained only a small proportion of the variation, 9% and 18% respectively. Allopatric bull trout were clustered on axis

**Table 2.3.** Prey taxa elected based on the average Johnson's Index. Prey taxa included in the analysis were >1% of the diet.

	<b>Allopatric Bull Trout</b>	<b>Sympatric Bull trout</b>	<b>Sympatric Brook trout</b>
<b>North Powder 1996</b>			
	<u>n = 18</u>	<u>n = 10</u>	<u>n = 10</u>
Plecoptera – Nemouridae	X		
Trichoptera - Limnephilidae	X		X
Glossosomatidae			X
Rhyacophilidae		X	
Hydropsychidae		X	X
Aq. Diptera - Blephariceridae			X
Ephemeroptera - Adults	X	X	X
Plecoptera - Adults	X	X	X
Aq. Diptera - Adults			X
Lepidoptera – Adults			X
Coleoptera - Adults	X	X	
Terrestrial Insects	X		X
<b>North Powder 1997</b>			
	<u>n = 33</u>	<u>n = 28</u>	<u>n = 30</u>
Ephemeroptera – Ameletidae	X		
Plecoptera – Perlidae		X	
Trichoptera - Limnephilidae			X
Glossosomatidae			X
Uenoidae			X
Brachycentridae			X
Aq. Diptera – Simuliidae	X	X	
Tipulidae	X		
Ephemeroptera – Adults		X	X
Terrestrial Insects	X		
<b>Meadow Fork 1996</b>			
	<u>n = 11</u>	<u>n = 10</u>	<u>n = 10</u>
Ephemeroptera – Heptageniidae	X		
Baetidae	X		
Trichoptera - Hydropsychidae		X	
Aq. Diptera – Tipulidae	X		
Ephemeroptera - Adults	X		X
Plecoptera - Adults			X
Trichoptera - Adults	X	X	X
Aq. Diptera - Adults		X	X
Terrestrial Insects	X	X	X
<b>Meadow Fork 1997</b>			
	<u>n = 19</u>	<u>n = 25</u>	<u>n = 21</u>
Ephemeroptera - Ephemerellidae	X	X	
Plecoptera - Chloroperlidae	X		
Peltoperlidae			X
Trichoptera– Hydropsychidae	X	X	X
Limnephilidae			X
Rhyacophilidae	X	X	X
Aq. Diptera – Tipulidae	X		
Simuliidae	X		
Lepidoptera - Pyralidae		X	X
Ephemeroptera – Adults	X	X	X
Terrestrial Insects	X	X	X



**Figure 2.4.** North Powder River NMS ordinations of Johnson's indices for individual fish in prey space. Electivity patterns of allopatric bull trout ( $\blacktriangledown$ ), sympatric bull trout ( $\bullet$ ) and brook trout ( $\square$ ) are illustrated. Direction of the gradient for explanatory taxa on each axis indicated by arrows.



**Figure 2.5.** Meadow Fork NMS ordinations of Johnson's indices for individual fish in prey space. Electivity patterns of allopatric bull trout ( $\blacktriangledown$ ), sympatric bull trout ( $\bullet$ ) and brook trout ( $\square$ ) are illustrated. Direction of the gradient for explanatory taxa on each axis indicated by arrows.

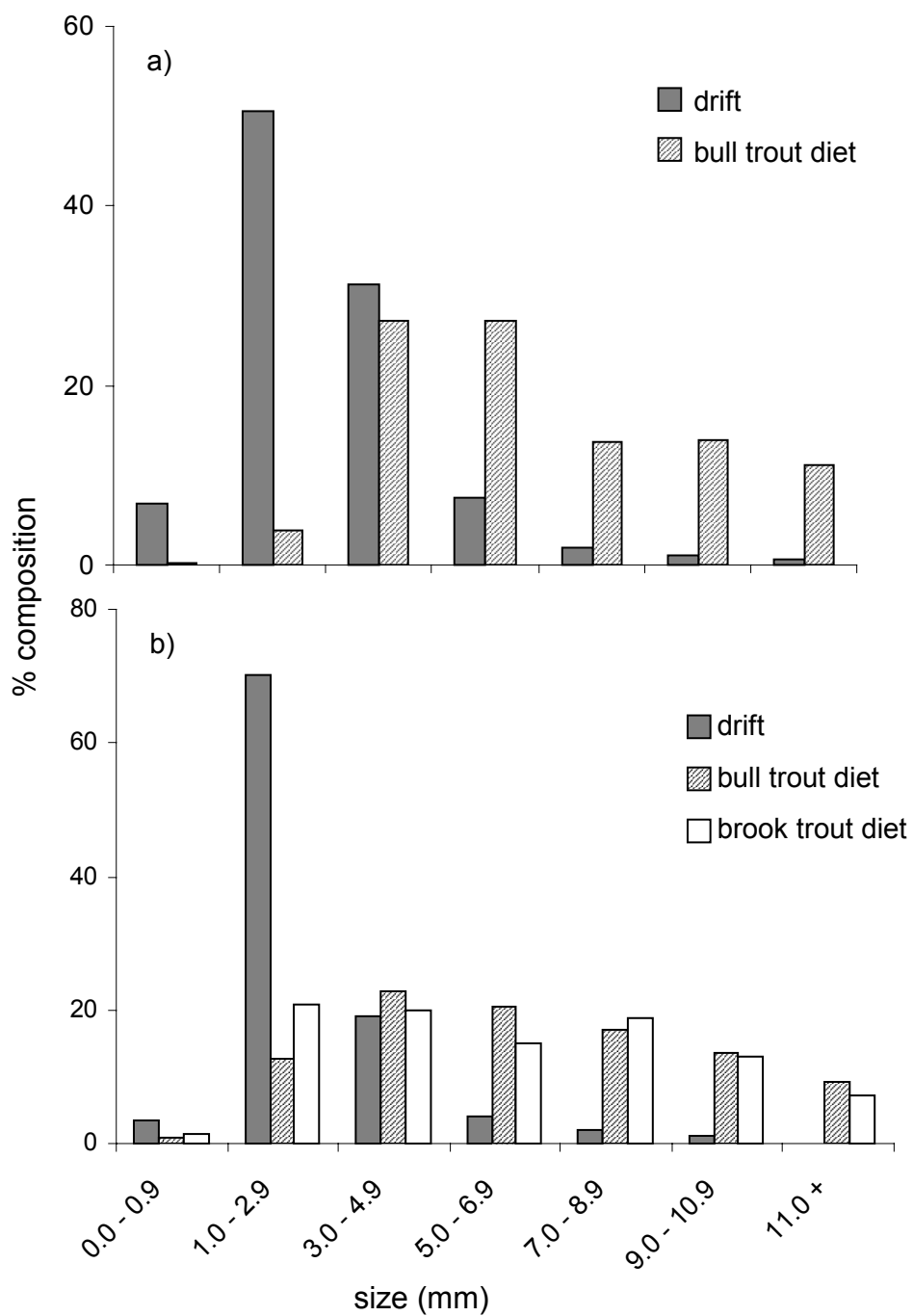
one opposite from sympatric fish. In all cases axis one was correlated with insects present in the availability of one reach but not the other. The electivity for sympatric bull trout and brook trout completely overlapped. There was no distinct separation between the two species in the ordination along axis two.

Allopatric bull trout, sympatric bull trout, and brook trout in Meadow Fork of Big Creek during 1997 exhibited size selective predation (Fig. 2.6). All fish ate insects > 5mm in greater proportions than they appeared in the drift. Small prey, < 3 mm, were underrepresented in the diet of all trout. Selection appeared to be strictly for size. Aquatic insects, aquatic derived terrestrials (terrestrial stages of aquatic insects), and terrestrial insects all were represented in size classes >3mm for all trout diets (Fig. 2.7). However, aquatic insects comprised at least 75% of each size class.

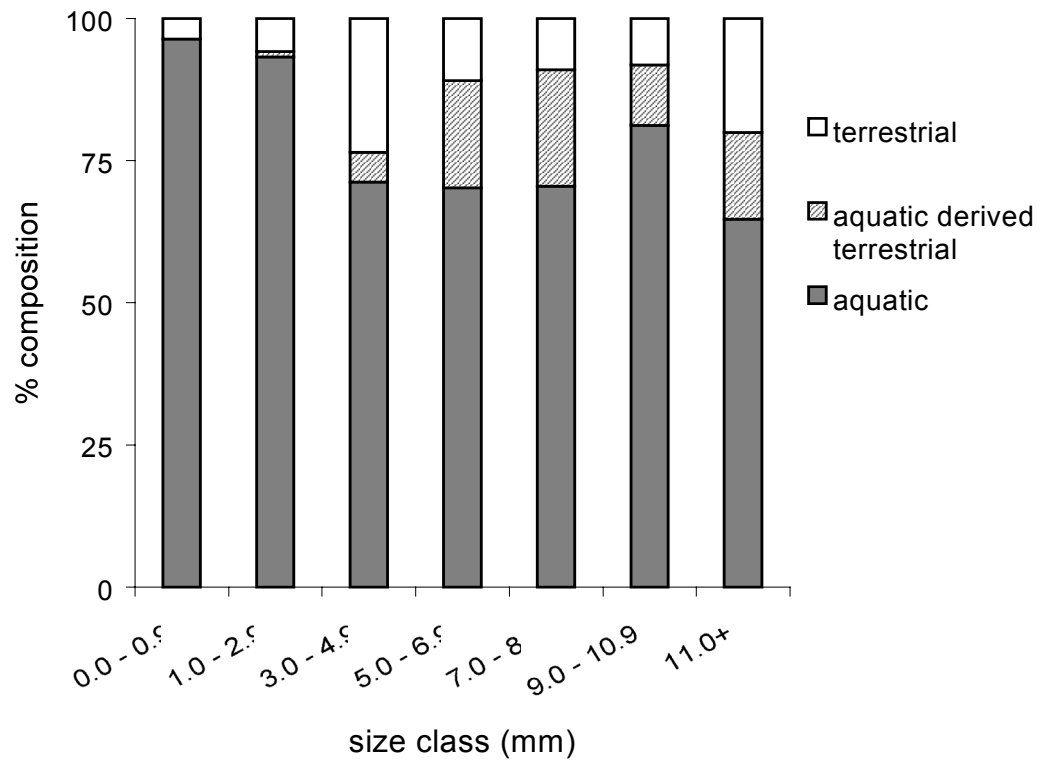
## **Discussion**

In two second order montane streams where non-native brook trout are colonizing threatened bull trout territory, diet overlap and election for the same prey resources demonstrated high potential for direct competition. NMS ordinations provide convincing evidence of shared resource use between bull trout and brook trout on the population scale. The ordinations graphically summarize individual prey preferences for trout in both allopatric and sympatric reaches. Each trout ate only part of the spectrum of prey consumed by the entire population. However, the collective electivity patterns of the sympatric populous completely overlap. This population-level pattern of overlap was consistent among both streams during both years, and demonstrated the persistence of dietary overlap in environments of differing prey assemblages.

The high dietary overlap of bull trout and brook trout was further indicated by Schoener's overlap index. Values of the index for sympatric bull trout and brook trout in this study were equivalent to those calculated for co-occurring lake-dwelling bull



**Figure 2.6.** Size distribution for prey items in the drift and stomach contents of bull trout and brook trout in the a) allopatric and b) sympatric reaches of Meadow Fork of Big Creek in 1997.



**Figure 2.7.** Origin of prey in the stomach contents of all trout in Meadow Fork of Big Creek 1997 by size class. 'Aquatic derived terrestrials' represent the terrestrial stages of aquatic insects.

trout and lake trout *S. namaycush* in Alberta, Canada (0.69 and 0.53 for two lakes)(Donald and Alger 1993). Substantial overlap in diet and resulting potential for competition in the latter study was suggested as the primary mechanism of bull trout displacement by lake trout. Three size classes of Colorado River cutthroat trout *O. clarki pleuriticus* demonstrated a similar degree of overlap in a high-elevation stream (0.64 - 0.87) (Bozek *et al.* 1994). The authors concluded food may be limiting in those unproductive streams and the high degree of overlap suggested strong intraspecific competition among size classes.

Schoener's overlap index was similar for all samples collected in early July. However, for the Meadow Fork of Big Creek August 1996 sample, sympatric bull trout and brook trout diets overlapped less. The difference may be due to the small size of the latter sample (21 individuals), but may also indicate temporal differences. Though sampling was not designed to measure changes in overlap over time the results suggested diet, electivity, and the degree of overlap were not constant. Temporal differences in invertebrate drift are common; the abundance and accessibility of prey fluctuates according to insect lifecycles and seasons (Allan 1972; 1981). Trout diet can vary seasonally with availability (Elliot 1973; Bridcut and Giller 1995; Duffield and Nelson 1998). During periods of resource scarcity individuals may broaden their diet (Werner and Hall 1977) and ultimately increase the degree of overlap. Thus the diet of bull trout and brook trout likely vary over time and potential for direct interference increases during times of limited prey availability.

The ordinations also illustrate that individual trout may specialize on certain prey items. For example, an individual bull trout fed on 339 Chironomidae pupae, 88.1% of it's diet, and other fish showed a similar degree of specialization. The inherent patchiness of local microhabitats and insect distributions may help explain the variability found between individual trout (Bryan and Larkin 1972; Bridcut and Giller 1995; Wilhelm *et al.* 1999). Thus the diet of bull trout and brook trout with focal points in close proximity (in the same patch) may overlap to an even greater degree, intensifying the potential for interspecific interactions.

Coinciding with significant overlap of bull trout and brook trout diets, evidence of resource partitioning and interactive segregation was minimal. My hypothesis - sympatric bull trout and brook trout diets differ due to interactive segregation - was rejected. The diets and patterns of electivity for bull trout and brook trout were statistically similar. Even though brook trout more frequently elected for larvae of Trichoptera families, they were not exclusive to the diet of brook trout (Fig. 2.1, Appendix A.1-A.4). Trichoptera larvae were commonly preyed upon by both bull trout and brook trout.

In other studies, brook trout also were noted to feed on a significant proportion of Trichoptera larvae, and it was suggested brook trout were benthic-oriented foragers (Griffith 1974; Hubert and Rhodes 1989). In my study, the Trichoptera component of brook trout diet consisted primarily of Limnephilidae, Rhyacophilidae, Glossosomatidae, Hydropsychidae and Uenoidae species. Intuitively the presence of these families may indicate a benthic-oriented diet, however, all families appeared both in drift and benthic samples. These Trichoptera families characteristically reside in microhabitats with high exposure to flow, but not necessarily on the exposed surface of the substrate (Radar 1997). As a result the larvae may have a higher likelihood of being preyed upon as accidental drift rather than as an epibenthic organism. Moreover, during underwater observations both brook trout and bull trout were documented feeding primarily from the water column (chapter 1). Thus, this study gives little indication that either brook trout or bull trout were benthic-oriented foragers, providing little evidence of resource partitioning.

Both bull trout and brook trout exhibited strong size-selective predation. Most importantly the selection of large prey was not limited to just terrestrial insects but was dominated by both the aquatic and terrestrial stages of aquatic invertebrates. This pattern was illustrated by the frequency of large insects in their diet and the selection for larger taxonomic orders and life stages, Ephemeroptera and Plecoptera adults, Trichoptera larvae, and terrestrial insects. However, small insects can be digested quickly resulting in differential evacuation rates that may bias the results toward larger

insects (Elliot 1967; Hyslop 1980). Additionally, insects with a heavy cuticle and higher fat content digest at a lower rate (Elliot 1972).

The obvious selection for large prey items corroborates many studies that document size selective predation in stream dwelling salmonids (Allan 1978; Bisson 1978; Allan 1981; Newman and Waters 1984) and is consistent with optimal foraging models (Angradi and Griffith 1990). Feeding efficiency increases with larger insects (Allan 1978; Ringler 1979; Allan 1981). Evidence of size selective predation in the diet of bull trout and brook trout demonstrates prey selection is not necessarily based on taxonomic organization. Other factors such as size, abundance, accessibility, and hunger (Angradi and Griffith 1990) significantly influence diet.

No bull trout in this diet analysis were found to be piscivorous, and only two brook trout consumed sculpin. Although these findings contradict other bull trout diet studies (Boag 1987), my snorkel observations (chapter 1) documented bull trout will prey on smaller size classes when available (typically rainbow trout). The degree of piscivory depends on the abundance and accessibility of small forage fish. In montane streams young-of-the-year fish reside frequently near stream margins and are not found often in the same microhabitat with large fish (Mundie 1969; Moore and Gregory 1988; Hubert and Rhodes 1992). The difference in microhabitat use between size classes decreases the likelihood of predation on small trout by older/larger trout.

Lack of resource partitioning between bull trout and brook trout is not surprising. Because bull trout and brook trout did not evolve in sympatry anywhere within their respective range they would not have evolved different feeding behaviors to ameliorate the effects of competition (Fausch 1988; DeWald and Wilzbach 1992). In addition, in studies where significant differences in diet were found between sympatric salmonid species, there was often corresponding partitioning of habitat (Andrusak and Northcote 1971; Hindar *et al.* 1988; Nakano *et al.* 1992; Nakano and Kaeriyama 1995; Haugen and Rygg 1996). Differences in the diet of bull trout and westslope cutthroat trout *O. clarki lewisi* corresponded to differences in foraging mode and microhabitat use (Nakano *et al.* 1992). Bull trout often (but not always) fed from the benthos whereas cutthroat trout fed primarily from the drift and surface. The specialization in habitat

use was evident in the drastically greater proportions of terrestrial insects in diet of westslope cutthroat trout. Such clear and obvious differences in habitat use (chapter 1) and diet composition were not evident between bull trout and brook trout in this study.

A shift in bull trout diet in the presence and absence of brook trout also was not apparent. Diet of allopatric bull trout did not differ qualitatively or statistically from sympatric bull trout. Though this observation may suggest brook trout do not cause a change in bull trout diet, this causal inference is not justified by my study because of its observational nature. Composition of the prey community differed between the allopatric and sympatric reach of both study streams, affecting the overall diet and the electivity for fish. The separation of allopatric and sympatric bull trout in the ordinations is explained by the presence of prey taxa in one reach but not the other, thereby affecting electivity. The difference in prey resources impedes direct comparison of the diets and electivity of bull trout in both reaches. A removal experiment would provide the added rigor necessary to demonstrate a change (or lack thereof) in diet for bull trout in the presence of brook trout (Fausch 1988; 1998).

This study clearly demonstrates shared resource use between bull trout and brook trout, particularly during the summer months. Since evidence of resource partitioning is lacking, high potential for competitive interspecific interactions exists. During periods of resource scarcity when the selection for large prey is most intense, brook trout will likely have an advantage over smaller or equal size bull trout because of their aggressive behavior (chapter 1). Brook trout consistently occupied positions near the head of the pool where large surface drifting insects are more accessible (Furukawa-Tanaka 1992). Greater access to preferred resources based on dominance can result in increased growth and fitness among dominant brook trout (Bridcut and Giller 1995). Thus, the lack of resource partitioning, aggressive behavior by bull trout, and potentially increased growth of brook trout, bull trout may ultimately be displaced during periods of limiting prey resources.

The potential for direct interactions between bull trout and brook trout may be reduced by conserving pristine and complex habitats. Heterogeneous habitat is positively correlated with total diversity and abundance of macroinvertebrates (Allan

1995). A diverse and abundant insect community of various life histories will potentially maximize the continual availability of larger instars. Adequate conservation of complex habitat also will preserve the structural and biological function of the riparian zone. The diversity and abundance of insects common to intact riparian zones serves as the exclusive source of terrestrial insects to aquatic communities. As this study demonstrated, terrestrial insects constitute a significant portion of trout diet. Thus, through the preservation of heterogeneous and complex stream habitat, the abundance and diversity of macroinvertebrate prey may minimize the severity and duration of periods of limited prey resources for trout, and ultimately minimize potential for interspecific interaction.

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## Overview/Conclusion

Shared diet and common feeding behaviors of native bull trout and introduced brook trout make direct interference competition likely during periods of resource scarcity in two second order montane streams. Focal feeding points occupied by bull trout and brook trout had equivalent velocity measures and were at the same relative depths and cover. Both species captured prey primarily in the water column and seldom fed directly from the surface or benthos. Reflecting the similarity in feeding behavior and habitat use, bull trout and brook trout diets had a high degree of overlap. Both species fed predominantly on aquatic insect larvae – Ephemeroptera, Trichoptera, and aquatic Diptera - and terrestrial insects. Moreover bull trout and brook trout exhibited strong size selective predation demonstrating similar mechanisms of prey choice. Thus, there was very little evidence of resource partitioning or interactive segregation between bull trout and brook trout.

The feeding behavior, growth and diet of bull trout did not fluctuate in the presence and absence of brook trout. The growth results suggest that for fish of equal size the effects of brook trout were equivalent to those of bull trout. However, bull trout sympatric with brook trout experienced a greater number of agonistic interactions and were displaced more frequently than allopatric bull trout at the same densities. Over 80% of these interactions were initiated by brook trout. Moreover, brook trout occupied preferred focal points at the head of the pool and maintained the top position in the dominance hierarchy. Their competitively superior behavior was reflected in their greater growth as compared to bull trout. Brook trout was clearly the more aggressive and dominant species.

The clear interpretation and applicability of these results is due to the design, where the rigor of a controlled manipulative experiment, conducted in the natural environment, was supplemented with unintrusive observation of wild fish behavior. The lack of resource partitioning documented in the in-stream experiment was confirmed by similar results observed in the diet and feeding behavior of unconfined

fish. As a consequence, the phenomena documented in the study can be directly applicable to a natural and wild context. Furthermore the controlled experiment clearly demonstrated the aggressive behavior of brook trout, a conclusion difficult to document in a solely observational study.

The most significant implication of brook trout aggression is the potential displacement of bull trout. Interaction between similar stream fishes can result in either displacement of one species or co-existence through segregation (Everest and Chapman 1972). Evidence of shared habitat use and diet between bull trout and brook trout does not support the co-existence hypothesis. Instead the aggressive and dominant nature of brook trout, compared to bull trout, in combination with shared resource use deems displacement probable. Furthermore, earlier maturation and shorter generation times of brook trout enables them to out number bull trout populations (Leary *et al.* 1993). In these scenarios not only will brook trout be able to occupy and defend the preferred focal feeding points, but their greater abundance will increase the chance of hybridization with bull trout resulting in a loss of genetically pure bull trout and a decrease in abundance.

Given the negative effect of interactions with brook trout on bull trout all reasonable efforts should be made to minimize further impacts. The conservation and restoration of complex stream habitats are critical to minimizing direct interaction between bull trout and brook trout. Heterogeneous and complex stream habitat offers an abundance and variety of microhabitats, providing bull trout the ability to visually isolate themselves from brook trout and reducing the potential of competition for preferred focal feeding points. In degraded and simplified habitats bull trout are subject to the aggressive and dominant behavior of brook trout and will potentially compete for limited microhabitats (Chapter 1). In addition, bull trout are also more susceptible to increases in water temperature. Although temperature preference data for bull trout is lacking, bull trout are known to be stenothermic, requiring cold water to rear and reproduce (Buchanan and Gregory 1997). In temperatures warmer than those optimal for bull trout, brook trout may be able to maintain a competitive advantage (Dunson and Travis 1991).

Complex and heterogeneous stream habitat also is positively correlated with diverse and abundant macroinvertebrates. Varying life histories in these communities will potentially maximize the continual availability of large instars, minimizing direct competition for large prey. Adequate conservation of complex habitat will preserve riparian zone structural and biological functions. Streamside vegetation and old growth canopy at my study sites provided habitat for terrestrial insects and the adult stages of aquatic insects and served as the source of terrestrial insect input. As my research demonstrated, terrestrial insects constitute a significant proportion of trout diet (Chapter 2). Habitat conservation will not necessarily reduce the abundance of brook trout, but it will potentially enable bull trout populations to maintain their abundance and minimize the potential for interspecific competition.

Similarly, the preservation of the migratory life histories of bull trout is crucial. Bull trout returning to spawn after rearing in large rivers and lakes are substantially larger than resident bull trout and brook trout. Because size plays a determining role in the outcome of interspecific interactions (Chapter 1; Noakes 1980) large migratory fish will be able to out compete, displace and potentially consume small brook trout. Resource requirements of large migratory fish differ from those of resident fish reducing resource overlap and potential for competition (Werner and Gilliam 1984). Through assortative mating, larger migratory fish will likely pair up with a similar sized mate, reducing the potential of hybridization with a smaller brook trout (Kitano *et al.* 1994). Lastly, large migratory fish have greater fecundity than smaller resident fish, possibly counteracting the reproductive advantage brook trout have over bull trout.

In conjunction with adequate management of bull trout populations, further research of bull trout/brook trout interactions should continue. Future research should identify the impact of brook trout on bull trout at the population level, including effects on emigration and mortality rates. In addition, studies of interactions between 0+ fish in natural systems may provide critical insight. Finally, there is a need to consider the role abiotic factors, primarily habitat complexity and temperature, play in the interactions of these two species.

Because bull trout have a low tolerance for habitat degradation and thrive in pristine habitats they serve as a valuable indicator of fully functioning cold water stream systems. The recent decline in abundance of bull trout signifies the erosion and degradation of entire aquatic ecosystems. Conservation of bull trout not only guarantees the preservation of a unique and intriguing animal but also guarantees the persistence of increasingly rare and valuable stream communities.

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## Appendix

**Table A.1.** Fish diet and prey availability data, North Powder River, July 23-24, 1996. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m<sup>2</sup>) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m<sup>3</sup>) represent the mean density of each taxa in three drift samples. See chapter 2 for collection protocol.

Code	Order	Family	Genus	Life stage	Fish Diet				Average Benthic Density /m <sup>2</sup>		Average Drift Density / 100m <sup>3</sup>	
					Total n = 18		Total Sympatric n = 10		Allopatric Reach	Sympatric Reach	Allopatric Reach	Sympatric Reach
					Allopatric Bull Trout	Sympatric Bull Trout	Allopatric Bull Trout	Sympatric Brook Trout				
EpSp	Ephemeroptera		species	larvae	10	2	1	1.75	17.54	0.00	0.00	
EpSpAD	Ephemeroptera		species	adult	28	2	5	0.00	0.00	0.00	0.00	
EpBasp	Ephemeroptera	Baetidae	species	larvae	7	0	0	1.75	10.53	0.00	3.30	
EpBaspAD	Ephemeroptera	Baetidae	species	adult	1	0	0	1.75	0.00	0.00	0.00	
EpBala	Ephemeroptera	Baetidae	<i>Labriobaetis</i>	larvae	144	23	12	110.53	101.75	326.49	153.76	
EpAmAm	Ephemeroptera	Ameletidae	<i>Ameletus</i>	larvae	9	13	2	110.53	80.70	6.92	1.07	
EpSiSi	Ephemeroptera	Siphonuridae	<i>Siphonurus</i>	larvae	0	0	0	0.00	3.51	0.56	4.59	
EpHesp	Ephemeroptera	Heptageniidae	species	larvae	1	4	1	5.26	5.26	0.53	0.38	
EpHespAD	Ephemeroptera	Heptageniidae	species	adult	1	0	0	0.00	0.00	0.00	0.00	
EpHeCl	Ephemeroptera	Heptageniidae	<i>Cinygmula</i>	larvae	19	7	4	54.39	40.35	12.12	2.68	
EpHeEp	Ephemeroptera	Heptageniidae	<i>Epeorus</i>	larvae	5	2	3	3.51	8.77	33.04	18.91	
EpHeRh	Ephemeroptera	Heptageniidae	<i>Rhithrogena</i>	larvae	4	0	1	0.00	3.51	0.00	0.00	
EpHeCi	Ephemeroptera	Heptageniidae	<i>Cinygma</i>	larvae	0	0	0	0.00	7.02	0.00	0.00	
EpEpsp	Ephemeroptera	Ephemerellidae	species	larvae	0	1	0	0.00	0.00	0.00	9.41	
EpEpspAD	Ephemeroptera	Ephemerellidae	species	adult	0	1	4	0.00	0.00	0.00	0.00	
EpEpsE	Ephemeroptera	Ephemerellidae	<i>Serratella</i>	larvae	0	1	6	0.00	0.00	0.00	0.00	
EpEpDr	Ephemeroptera	Ephemerellidae	<i>Drunella</i>	larvae	9	15	9	249.12	173.68	42.19	16.92	
EpEpEp	Ephemeroptera	Ephemerellidae	<i>Ephemerella</i>	larvae	2	0	0	0.00	0.00	0.00	0.00	
EpEpCa	Ephemeroptera	Ephemerellidae	<i>Caudatella</i>	larvae	0	1	0	0.00	0.00	1.32	0.38	

Table A.1. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
PIsp	Plecoptera		species	larvae	6	2	3	0.00	0.00	0.00	0.00
PIspAD	Plecoptera		species	adult	5	0	0	0.00	0.00	0.00	0.00
PINesp	Plecoptera	Nemouridae	species	larvae	2	2	0	0.00	3.51	0.00	0.99
PINespAD	Plecoptera	Nemouridae	species	adult	1	0	0	0.00	0.00	0.00	0.00
PINeZa	Plecoptera	Nemouridae	Zapada	larvae	103	6	3	35.09	17.54	15.37	7.96
PINeVi	Plecoptera	Nemouridae	Visoka	larvae	2	1	0	10.53	28.07	3.42	0.69
PINeViAD	Plecoptera	Nemouridae	Visoka	adult	2	0	0	0.00	0.00	0.00	0.00
PINeZaAD	Plecoptera	Nemouridae	Zapada	adult	18	2	0	0.00	0.00	0.00	0.00
PICHsp	Plecoptera	Chloroperlidae	species	larvae	11	1	0	170.18	100.00	5.59	4.52
PICHspAD	Plecoptera	Chloroperlidae	species	adult	9	2	0	0.00	0.00	0.00	0.00
PICHsw	Plecoptera	Chloroperlidae	Sweltsa	larvae	2	2	0	21.05	35.09	0.00	0.00
PICHBi	Plecoptera	Chloroperlidae	Bisancora	larvae	0	0	0	0.00	3.51	0.00	0.00
PICHPa	Plecoptera	Chloroperlidae	Paraperla	larvae	0	1	0	42.11	14.04	0.79	0.00
PICHKaAD	Plecoptera	Chloroperlidae	Kathroperla	adult	0	0	1	0.00	0.00	0.00	0.00
PIPesp	Plecoptera	Perlidae	species	larvae	3	0	0	17.54	5.26	0.00	0.00
PIPespAD	Plecoptera	Perlidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
PIPeCa	Plecoptera	Perlidae	Calineuria	larvae	0	2	0	3.51	0.00	0.00	0.00
PIPdsp	Plecoptera	Perlidae	species	larvae	1	1	0	0.00	0.00	0.00	0.00
PIPdspAD	Plecoptera	Perlidae	species	adult	2	1	0	0.00	0.00	0.00	0.00
PIPdMeAD	Plecoptera	Perlidae	Magarcys	adult	5	0	1	0.00	0.00	0.00	0.00
PIPdIs	Plecoptera	Perlidae	Isoperla	larvae	0	1	0	0.00	0.00	0.00	0.00
PIPdSe	Plecoptera	Perlidae	Setvena	larvae	1	0	0	0.00	0.00	0.00	0.00
PILeCa	Plecoptera	Leuctridae/Capniidae	species	larvae	0	1	0	1.75	0.00	0.00	0.00
PIPpSp	Plecoptera	Peltoperlidae	species	larvae	0	0	1	1.75	0.00	0.00	0.00
PIPpYa	Plecoptera	Peltoperlidae	Yoroperla	larvae	15	5	0	105.26	10.53	9.60	6.20
PLPpYaAD	Plecoptera	Peltoperlidae	Yoroperla	adult	10	2	4	0.00	0.00	0.00	0.00
Trisp	Trichoptera		species	larvae	2	0	1	0.00	0.00	0.00	0.00
TrispP	Trichoptera		species	pupae	0	0	0	1.75	0.00	0.00	0.00

Table A.1. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
TrspAD	Trichoptera		species	adult	1	0	0	0.00	0.00	0.00	0.00
TrGlsp	Trichoptera	Glossomatidae	species	larvae	0	0	3	0.00	0.00	0.00	0.00
TrGIGI	Trichoptera	Glossomatidae	<i>Glossosoma</i>	larvae	0	0	1	0.00	0.00	0.00	0.00
TrBmI	Trichoptera	Brachycentridae	<i>Micrasema</i>	larvae	2	0	2	133.33	47.37	1.57	3.29
TrRhRh	Trichoptera	Rhyacophilidae	<i>Rhyacophila</i>	larvae	66	28	22	140.35	71.93	7.61	7.88
TrRhP	Trichoptera	Rhyacophilidae	species	pupae	0	0	0	8.77	0.00	0.00	0.00
TrRhAD	Trichoptera	Rhyacophilidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
TrLisp	Trichoptera	Linnephilidae	species	larvae	56	0	3	21.05	10.53	0.79	1.76
TrLIP	Trichoptera	Linnephilidae	species	pupae	0	0	9	0.00	0.00	0.00	0.00
TrLI Mo	Trichoptera	Linnephilidae	<i>Moselyana</i>	larvae	1	0	0	0.00	8.77	0.00	0.00
TrLIPs	Trichoptera	Linnephilidae	<i>Psychoglypha</i>	larvae	8	1	1	1.75	5.26	0.00	0.00
TrHySp	Trichoptera	Hydropsychidae	species	larvae	0	1	1	0.00	0.00	0.00	0.00
TrHyPa	Trichoptera	Hydropsychidae	<i>Parapsyche</i>	larvae	5	1	1	0.00	0.00	0.00	0.00
TrUeNe	Trichoptera	Uenoidae	<i>Neophylax</i>	larvae	1	0	5	0.00	10.53	0.00	0.00
TrUeNeP	Trichoptera	Uenoidae	<i>Neophylax</i>	pupae	0	0	1	0.00	0.00	0.00	0.00
TrUeNt	Trichoptera	Uenoidae	<i>Neothremma</i>	larvae	0	1	0	0.00	0.00	0.00	0.00
Disp	Diptera		species	larvae	1	0	3	0.00	0.00	0.00	0.00
DiChsp	Diptera	Chironomidae	species	larvae	0	0	0	15.79	33.33	0.00	0.00
DiChP	Diptera	Chironomidae	species	pupae	17	1	1	203.51	19.30	0.00	0.00
DiChAD	Diptera	Chironomidae	species	adult	17	7	5	8.77	15.79	4.01	5.21
DiChOr	Diptera	Chironomidae	Orthoclaadiinae	larvae	63	28	11	1049.12	610.53	22.69	9.03
DiChOrP	Diptera	Chironomidae	Orthoclaadiinae	pupae	3	0	0	0.00	52.63	0.00	0.00
DiChTp	Diptera	Chironomidae	Tanypodinae	larvae	5	8	0	131.58	187.72	4.12	2.98
DiChTpP	Diptera	Chironomidae	Tanypodinae	pupae	2	0	0	0.00	31.58	0.00	0.00
DiChTt	Diptera	Chironomidae	Tanytarsini	larvae	7	1	2	645.61	1192.98	24.13	39.66
DiTisp	Diptera	Tipulidae	species	larvae	2	0	0	56.14	12.28	0.00	0.00
DiTispAD	Diptera	Tipulidae	species	adult	4	2	2	0.00	0.00	0.00	0.00
DiTITI	Diptera	Tipulidae	<i>Tipula</i>	larvae	0	0	0	0.00	5.26	0.00	0.00

Table A.1. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
DTITDi	Diptera	Tipulidae	<i>Dicranota</i>	larvae	1	0	0	0.00	5.26	0.56	0.00
DTTiAn	Diptera	Tipulidae	<i>Antocha</i>	larvae	2	0	0	0.00	0.00	0.00	0.00
DIEmsp	Diptera	Empididae	species	larvae	0	2	0	0.00	0.00	0.00	0.00
DIEmspAD	Diptera	Empididae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiCesp	Diptera	Ceratopogonidae	species	larvae	0	0	0	38.60	0.00	0.00	0.00
DiCéPt	Diptera	Ceratopogonidae	<i>Probezzia</i>	larvae	0	0	0	3.51	8.77	0.00	0.00
DiSisp	Diptera	Simuliidae	species	larvae	4	2	2	0.00	5.26	0.00	0.31
DISIPt	Diptera	Simuliidae	<i>Prosimulium</i>	larvae	25	4	0	1.75	3.51	14.13	15.31
DISIP	Diptera	Simuliidae	species	pupae	3	0	0	0.00	0.00	0.00	0.00
DiSiAD	Diptera	Simuliidae	species	adult	5	1	0	0.00	0.00	0.00	0.00
DiStsp	Diptera	Stratiomyidae	species	larvae	0	0	0	0.00	0.00	0.56	0.00
DiBrAD	Diptera - Brachycera		species	adult	9	24	4	1.75	1.75	1.57	3.68
DiNeAD	Diptera - Nematocera		species	adult	17	2	0	0.00	0.00	0.00	0.00
DiMyspAD	Diptera	Mycetophilidae	species	adult	1	4	5	0.00	0.00	0.00	0.00
DiDiDi	Diptera	Dixidae	<i>Dixa</i>	larvae	0	0	0	0.00	0.00	1.12	0.00
DiBlsp	Diptera	Blephariceridae	species	larvae	4	0	1	0.00	0.00	0.00	0.00
DiBIAg	Diptera	Blephariceridae	<i>Agathon</i>	larvae	0	0	2	0.00	0.00	0.00	0.00
DiBlspAD	Diptera	Blephariceridae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiMuspAD	Diptera	Muscidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiSyspAD	Diptera	Syrphidae	species	adult	2	1	0	0.00	0.00	0.00	0.00
DiSrspAD	Diptera	Sciaridae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiScspAD	Diptera	Scathophagidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiAsspAD	Diptera	Asilidae	species	adult	5	0	0	0.00	0.00	0.00	0.00
DiHespAD	Diptera	Heleomyzidae	species	adult	29	7	6	0.00	0.00	0.00	0.00
Cosp	Coleoptera		species	larvae	3	0	1	0.00	0.00	0.00	0.00
CospAD	Coleoptera		species	adult	14	5	0	1.75	0.00	0.00	0.00
CoHysp	Coleoptera	Hydrophilidae	species	larvae	1	0	0	0.00	0.00	0.00	0.00
CoCasp	Coleoptera	Carabidae	species	larvae	7	0	0	0.00	0.00	0.00	0.00

Table A.1. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
CoDyspAD	Coleoptera	Dytiscidae	species	adult	2	0	1	0.00	0.00	0.00	0.00
CoStspAD	Coleoptera	Staphylinidae	species	adult	10	1	3	0.00	0.00	0.00	0.00
CoCuspAD	Coleoptera	Curculionidae	species	adult	8	1	0	0.00	0.00	0.00	0.00
CoCusp	Coleoptera	Curculionidae	species	larvae	0	0	0	0.00	1.75	0.00	0.38
CoCispAD	Coleoptera	Cicindelidae	species	adult	5	0	0	0.00	0.00	0.00	0.00
CoScspAD	Coleoptera	Scarabaeidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
CoNospAD	Coleoptera	Noteridae	species	adult	1	0	0	0.00	0.00	0.00	0.00
CoChspAD	Coleoptera	Chrysomelidae	species	adult	0	2	0	0.00	0.00	0.00	0.00
CoEtspAD	Coleoptera	Elatridae	species	adult	1	0	2	0.00	0.00	0.00	0.00
CoElisp	Coleoptera	Elmidae	species	larvae	0	0	0	10.53	0.00	0.00	0.00
CoEHe	Coleoptera	Elmidae	<i>Heterilimnius</i>	larvae	0	0	0	0.00	3.51	0.00	1.46
CoCnspAD	Coleoptera	Cantharidae	species	adult	1	1	0	0.00	0.00	0.00	0.00
CoTrspAD	Coleoptera	Trogossitidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
Hosp	Hornoptera		species	adult	2	0	0	0.00	0.00	0.00	0.31
HoApsp	Hornoptera	Aphididae	species	adult	6	2	1	0.00	0.00	0.00	1.84
HoCisp	Hornoptera	Cicadellidae	species	adult	64	15	5	0.00	0.00	1.57	0.31
HoAdsp	Hornoptera	Adelgidae	species	adult	0	0	0	0.00	1.75	1.09	0.38
Hemisp	Hemiptera		species	adult	7	1	0	0.00	0.00	0.00	0.00
HeThspAD	Hemiptera	Thyreocoridae	species	adult	2	0	0	0.00	0.00	0.00	0.00
HeSaspAD	Hemiptera	Saldidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
HeMespAD	Hemiptera	Mesovelliidae	species	adult	4	0	0	0.00	0.00	0.00	0.00
HeLysp	Hemiptera	Lygaeidae	species	adult	0	2	1	0.00	0.00	0.00	0.00
HyspAD	Hymenoptera		species	adult	11	4	0	0.00	0.00	0.00	0.00
HyFosp	Hymenoptera	Formicidae	species	adult	33	9	5	0.00	0.00	0.00	0.00
HyChsp	Hymenoptera	Chalcididae	species	adult	0	0	0	0.00	0.00	1.09	0.00
HyCesp	Hymenoptera	Cephidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
HyBrsp	Hymenoptera	Braconidae	species	adult	7	2	2	0.00	0.00	0.00	0.00
HyDisp	Hymenoptera	Diapriidae	species	adult	0	1	0	0.00	0.00	0.00	0.00

Table A.1. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
HyIcsp	Hymenoptera	Ichneumonidae	species	adult	3	2	0	0.00	0.00	0.00	0.00
HyTesp	Hymenoptera	Tenthredinidae	species	larvae	1	2	0	0.00	0.00	0.00	0.00
LePysp	Lepidoptera	Pyralidae	species	larvae	4	2	0	0.00	0.00	0.00	0.38
LePyCr	Lepidoptera	Pyralidae	species	larvae	1	0	0	0.00	0.00	0.00	0.00
LePyAD	Lepidoptera	Pyralidae	species	adult	0	0	2	0.00	0.00	0.00	0.00
Lesp	Lepidoptera		species	larvae	1	1	0	0.00	0.00	0.00	0.00
LespAD	Lepidoptera		species	adult	1	0	0	0.00	0.00	0.00	0.00
Collern	Collembola		species	adult	3	0	0	0.00	1.75	11.12	12.31
Mites	Acari		species		2	0	0	177.19	56.14	4.38	7.19
Ostra	Ostracoda		species		0	0	0	12.28	0.00	0.00	0.00
Arachnida	Arachnida		species		20	10	2	1.75	3.51	0.00	1.60
Arps	Pseudoscorpiones		species		1	0	0	0.00	1.75	0.00	0.00
Amphipods	Amphipoda		species		0	0	0	0.00	3.51	0.56	0.31
ThripsAD	Thysanoptera		species	adult	0	0	2	0.00	0.00	2.18	0.31
Oligoc	Oligochaeta		species		0	0	0	1152.63	152.63	2.36	0.77
Platy	Platyhelminthes		species		0	0	0	101.75	10.53	5.28	0.69
misc	misc. Terrestrial		species		0	2	0	0.00	0.00	0.00	0.00

**Table A.2.** Fish diet and prey availability data, Meadow Fork of Big Creek, August 20-21, 1996. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m<sup>2</sup>) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m<sup>3</sup>) represent the mean density of each taxa in three drift samples. See chapter two for collection protocol.

Code	Order	Family	Genus	Life stage	Fish Diet				Average Benthic Density /m <sup>2</sup>		Average Drift Density / 100m <sup>3</sup>	
					Total Allopatric Bull Trout n = 11	Total Sympatric Bull Trout n = 10	Total Sympatric Brook Trout n = 11	Allopatric Reach	Sympatric Reach	Allopatric Reach	Sympatric Reach	
Epsp	Ephemeroptera			larvae	12	6	5	14.04	24.56	5.43	0.00	
EpspAD	Ephemeroptera			adult	5	5	12	1.75	0.00	4.42	0.00	
EpBasp	Ephemeroptera	Baetidae	species	larvae	1	3	0	5.26	24.56	12.82	44.63	
EpBaspAD	Ephemeroptera	Baetidae	species	adult	0	5	3	0.00	0.00	0.00	0.00	
EpBaBa	Ephemeroptera	Baetidae	<i>Baetis</i>	larvae	0	0	0	0.00	0.00	0.00	8.47	
EpBaLa	Ephemeroptera	Baetidae	<i>Labiobaetis</i>	larvae	246	99	19	585.96	700.00	169.33	440.67	
EpAmAm	Ephemeroptera	Ameletidae	<i>Ameletus</i>	larvae	54	7	1	277.19	119.30	4.20	1.66	
EpHesp	Ephemeroptera	Heptageniidae	species	larvae	11	4	1	14.04	43.86	0.00	0.00	
EpHespAD	Ephemeroptera	Heptageniidae	species	adult	0	5	0	0.00	0.00	0.00	0.00	
EpHeCl	Ephemeroptera	Heptageniidae	<i>Cinygmula</i>	larvae	55	30	9	291.23	442.11	5.21	5.88	
EpHeEp	Ephemeroptera	Heptageniidae	<i>Epeorus</i>	larvae	45	7	3	161.40	49.12	17.60	48.68	
EpHeRh	Ephemeroptera	Heptageniidae	<i>Rhithrogena</i>	larvae	3	0	0	63.16	289.47	5.43	2.12	
EpHeIr	Ephemeroptera	Heptageniidae	<i>Ironodes</i>	larvae	0	0	0	0.00	0.00	0.00	0.60	
EpEpsp	Ephemeroptera	Ephemerellidae	species	larvae	0	0	0	0.00	5.26	0.00	0.00	
EpEpsSe	Ephemeroptera	Ephemerellidae	<i>Serratella</i>	larvae	0	0	0	0.00	3.51	0.00	0.00	
EpEpDr	Ephemeroptera	Ephemerellidae	<i>Drunella</i>	larvae	3	9	6	1007.02	764.91	10.43	11.49	
EpEpEp	Ephemeroptera	Ephemerellidae	<i>Ephemerella</i>	larvae	0	0	0	0.00	0.00	0.00	6.35	
Plsp	Plecoptera		species	larvae	2	1	0	19.30	349.12	3.62	3.60	
PlspAD	Plecoptera		species	adult	0	3	2	0.00	0.00	0.00	0.00	
PlNesp	Plecoptera	Nemouridae	species	larvae	1	0	0	1.75	0.00	0.00	0.00	
PlNeZa	Plecoptera	Nemouridae	<i>Zapada</i>	larvae	16	7	1	98.25	94.74	6.81	8.30	

Table A.2. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
PINeVi	Plecoptera	Nemouridae	<i>Visoka</i>	larvae	1	0	0	350.88	182.46	0.00	0.60
PINeZaAD	Plecoptera	Nemouridae	<i>Zapada</i>	adult	1	0	0	0.00	0.00	0.00	0.00
PIChsp	Plecoptera	Chloroperlidae	species	larvae	2	1	0	207.02	119.30	7.17	11.15
PIChspAD	Plecoptera	Chloroperlidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
PIChSw	Plecoptera	Chloroperlidae	<i>Swetsta</i>	larvae	3	0	0	136.84	103.51	0.00	1.05
PIChSu	Plecoptera	Chloroperlidae	<i>Suwalla</i>	larvae	0	0	0	5.26	0.00	0.00	0.00
PIChBi	Plecoptera	Chloroperlidae	<i>Bisancora</i>	larvae	0	0	0	0.00	3.51	0.00	0.00
PIChPa	Plecoptera	Chloroperlidae	<i>Paraperla</i>	larvae	0	0	0	10.53	64.91	0.00	0.00
PIChHa	Plecoptera	Chloroperlidae	<i>Haploperla</i>	larvae	0	0	0	1.75	0.00	0.00	0.00
PIPesp	Plecoptera	Perlidae	species	larvae	0	0	0	8.77	28.07	0.00	0.00
PIPeCa	Plecoptera	Perlidae	<i>Calineuria</i>	larvae	1	1	0	5.26	43.86	0.00	0.60
PIPeHe	Plecoptera	Perlidae	<i>Hesperoperla</i>	larvae	0	0	1	0.00	0.00	0.00	0.00
PIPdsp	Plecoptera	Perlodidae	species	larvae	0	0	1	14.04	0.00	0.00	1.06
PIPdspAD	Plecoptera	Perlodidae	species	adult	0	2	2	0.00	0.00	0.00	0.00
PIPdMe	Plecoptera	Perlodidae	<i>Magarcys</i>	larvae	0	0	0	1.75	0.00	0.00	1.51
PIPdRi	Plecoptera	Perlodidae	<i>Rickera</i>	larvae	0	0	0	1.75	0.00	0.00	0.00
PIPdKo	Plecoptera	Perlodidae	<i>Kogotus</i>	larvae	1	0	0	0.00	0.00	0.00	0.00
PIPdIs	Plecoptera	Perlodidae	<i>Isoperla</i>	larvae	3	0	0	0.00	0.00	0.00	0.00
PIPePd	Plecoptera	Perlidae/Perlodidae	species	larvae	5	0	0	0.00	0.00	0.00	0.00
PILeCa	Plecoptera	Leuctridae/Capniidae	species	larvae	2	1	0	36.84	3.51	0.00	0.91
PILesp	Plecoptera	Leuctridae	species	larvae	0	0	0	29.82	1.75	0.00	0.00
PILeDe	Plecoptera	Leuctridae	<i>Despaxia</i>	larvae	0	0	0	70.18	14.04	0.00	0.00
PIPpsp	Plecoptera	Peltoperlidae	species	larvae	0	0	1	0.00	0.00	3.40	0.00
PIPpYa	Plecoptera	Peltoperlidae	<i>Yoroperla</i>	larvae	9	0	2	57.89	17.54	0.00	0.00
Trsp	Trichoptera		species	larvae	0	0	1	3.51	0.00	3.62	0.00
TrspP	Trichoptera		species	pupae	2	0	0	0.00	0.00	0.00	0.00
TrspAD	Trichoptera		species	adult	3	0	2	0.00	0.00	0.00	0.00
TrGlsp	Trichoptera	Glossosomatidae	species	larvae	0	0	0	52.63	0.00	0.00	0.00
TrGlspP	Trichoptera	Glossosomatidae	species	pupae	0	0	0	33.33	17.54	0.00	0.00
TrGlspAD	Trichoptera	Glossosomatidae	species	adult	9	1	0	3.51	0.00	0.00	0.00

Table A.2. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
TrBrMi	Trichoptera	Brachycentridae	<i>Micrasema</i>	larvae	0	0	1	0.00	5.26	0.00	0.00
TrRhRh	Trichoptera	Rhyacophilidae	<i>Rhyacophila</i>	larvae	14	6	0	268.42	261.40	3.19	12.50
TrRHP	Trichoptera	Rhyacophilidae	species	pupae	0	0	0	5.26	3.51	0.00	0.00
TrRhAD	Trichoptera	Rhyacophilidae	species	adult	2	5	3	0.00	0.00	0.00	0.60
TrLisp	Trichoptera	Limnephilidae	species	larvae	3	1	1	94.74	108.77	21.94	26.10
TrLJP	Trichoptera	Limnephilidae	species	pupae	0	0	0	1.75	0.00	0.00	0.00
TrLjCr	Trichoptera	Limnephilidae	<i>Cryptochia</i>	larvae	0	0	0	0.00	5.26	0.00	0.60
TrLjEc	Trichoptera	Limnephilidae	<i>Ecclisomyia</i>	larvae	0	0	0	19.30	100.00	0.00	0.00
TrLjGo	Trichoptera	Limnephilidae	<i>Goeracea</i>	larvae	0	0	0	1.75	0.00	0.00	0.00
TrLjHo	Trichoptera	Limnephilidae	<i>Homophylax</i>	larvae	0	0	0	7.02	0.00	0.00	0.00
TrHySp	Trichoptera	Hydropsychidae	species	larvae	2	0	3	0.00	5.26	0.00	0.00
TrHyPa	Trichoptera	Hydropsychidae	<i>Parapsyche</i>	larvae	2	5	2	0.00	0.00	0.00	0.00
TrHySpAd	Trichoptera	Hydropsychidae	species	adult	0	0	0	0.00	0.00	0.00	1.06
Disp	Diptera		species	larvae	0	2	0	0.00	0.00	0.00	0.00
DiChsp	Diptera	Chironomidae	species	larvae	0	0	1	1.75	0.00	1.81	0.00
DiChP	Diptera	Chironomidae	species	pupae	2	3	69	392.98	208.77	6.01	4.68
DiChAD	Diptera	Chironomidae	species	adult	2	3	24	122.81	12.28	10.43	9.94
DiChOr	Diptera	Chironomidae	Orthocladiinae	larvae	84	3	4	2142.11	1621.05	36.79	49.77
DiChOrP	Diptera	Chironomidae	Orthocladiinae	pupae	5	1	0	0.00	0.00	0.00	0.00
DiChTp	Diptera	Chironomidae	Tanypodinae	larvae	0	0	0	15.79	31.58	0.00	0.00
DiChTt	Diptera	Chironomidae	Tanytarsini	larvae	0	0	0	1008.77	650.88	7.03	2.57
DiTisp	Diptera	Tipulidae	species	larvae	5	3	1	1.75	17.54	0.00	0.00
DiTispAD	Diptera	Tipulidae	species	adult	2	3	13	1.75	0.00	1.81	0.60
DiTispP	Diptera	Tipulidae	species	pupae	0	0	2	0.00	0.00	0.00	0.00
DiTTI	Diptera	Tipulidae	<i>Tipula</i>	larvae	0	0	0	3.51	3.51	0.00	0.60
DiTIDi	Diptera	Tipulidae	<i>Dicranota</i>	larvae	2	0	0	0.00	0.00	0.00	0.00
DiTIAN	Diptera	Tipulidae	<i>Antocha</i>	larvae	5	0	1	0.00	7.02	0.00	0.00
DiEmsp	Diptera	Empididae	species	larvae	0	0	4	0.00	0.00	0.00	0.00
DiEmspAD	Diptera	Empididae	species	adult	2	0	7	0.00	0.00	0.00	1.20
DiEmCl	Diptera	Empididae	<i>Clinocera</i>	larvae	0	0	0	15.79	7.02	0.00	0.00

**Table A.2.** (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
DiCesp	Diptera	Ceratopogonidae	species	larvae	0	1	0	0.00	0.00	0.00	0.00
DiCeAD	Diptera	Ceratopogonidae	species	adult	2	0	0	0.00	0.00	3.40	0.00
DSjPr	Diptera	Simuliidae	<i>Prosimulium</i>	larvae	9	1	4	1.75	5.26	0.80	0.45
DiSIP	Diptera	Simuliidae	species	pupae	1	0	0	0.00	1.75	0.00	0.00
DiSiAd	Diptera	Simuliidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiPsPe	Diptera	Psychodidae	<i>Pericoma</i>	larvae	0	0	0	10.53	10.53	0.00	0.00
DiPhAD	Diptera	Phoridae	species	adult	0	1	2	0.00	0.00	0.00	0.00
DiBrAD	Diptera- Brachycera		species	adult	13	6	7	1.75	0.00	0.80	1.66
DiNeAD	Diptera- Nematocera		species	adult	1	1	1	0.00	5.26	0.00	0.60
DiMyspAD	Diptera	Mycetophilidae	species	adult	12	3	17	0.00	0.00	0.00	0.00
DiDiDI	Diptera	Dixidae	<i>Dixa</i>	larvae	0	0	0	0.00	0.00	0.80	2.86
DiBlspAD	Diptera	Blephariceridae	species	adult	0	3	0	0.00	0.00	0.00	0.00
DiThspAD	Diptera	Thaumaleidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
DiMuspAD	Diptera	Muscidae	species	adult	7	0	8	0.00	0.00	0.00	0.00
DiTaspAD	Diptera	Tachinidae	species	adult	1	0	1	0.00	0.00	0.00	0.00
DiSyspAD	Diptera	Syrphidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiSmmspAD	Diptera	Sciomyzidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiSrspAD	Diptera	Sciariidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiSzspAD	Diptera - Schizophora		species	adult	0	7	0	0.00	0.00	0.00	0.00
DiRhspAD	Diptera	Rhagionidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiCospAD	Diptera	Cecidomyiidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiHespAD	Diptera	Heleomyzidae	species	adult	4	11	21	0.00	0.00	0.00	0.00
DiAnspAD	Diptera	Anthomyiidae	species	adult	2	0	0	0.00	0.00	0.00	0.00
Cosp	Coleoptera		species	larvae	1	0	1	0.00	1.75	0.00	0.00
CospAD	Coleoptera		species	adult	0	0	2	0.00	0.00	0.00	0.00
CoHyspAD	Coleoptera	Hydrophilidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
CoHysp	Coleoptera	Hydrophilidae	species	larvae	0	0	0	0.00	0.00	3.62	0.00
CoCasp	Coleoptera	Carabidae	species	larvae	0	0	0	3.51	0.00	0.00	0.00
CoStspAD	Coleoptera	Staphylinidae	species	adult	0	1	5	0.00	0.00	0.00	0.00
CoStsp	Coleoptera	Staphylinidae	species	larvae	0	0	0	3.51	0.00	1.59	0.00

**Table A.2.** (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
CoCuspAD	Coleoptera	Curculionidae	species	adult	1	0	10	0.00	0.00	0.00	0.00
CoCusp	Coleoptera	Curculionidae	species	larvae	0	0	0	0.00	1.75	0.00	0.00
CoEtspAD	Coleoptera	Elateridae	species	adult	0	2	0	0.00	0.00	0.00	0.00
CoElsp	Coleoptera	Elmidae	species	larvae	0	0	0	0.00	28.07	0.80	0.00
CoElspAd	Coleoptera	Elmidae	species	adult	0	0	0	0.00	10.53	0.00	4.37
CoElHe	Coleoptera	Elmidae	<i>Heterlimnius</i>	larvae	0	0	0	87.72	205.26	0.00	0.60
Hosp	Homoptera		species	adult	0	0	1	0.00	1.75	0.80	0.00
HoApsp	Homoptera	Aphididae	species	adult	1	1	1	3.51	1.75	0.00	0.60
HoCisp	Homoptera	Cicadellidae	species	adult	12	0	3	5.26	3.51	9.05	4.37
HoAdsp	Homoptera	Adeigidae	species	adult	1	3	2	0.00	0.00	0.00	0.00
HeResp	Hemiptera	Reduviidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
HyspAD	Hymenoptera		species	adult	0	0	1	0.00	0.00	0.00	0.00
HyFosp	Hymenoptera	Forficidae	species	adult	3	6	15	0.00	0.00	0.00	0.00
HyMusp	Hymenoptera	Mutillidae	species	adult	0	0	0	0.00	0.00	1.81	0.00
HyBrsp	Hymenoptera	Braconidae	species	adult	0	3	4	0.00	0.00	0.00	0.00
HyPosp	Hymenoptera	Pompilidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
HyIcsp	Hymenoptera	Ichneumonidae	species	adult	3	0	1	0.00	0.00	0.00	0.00
HyTesp	Hymenoptera	Tenthredinidae	species	larvae	5	1	3	0.00	0.00	0.00	0.00
LePyAD	Lepidoptera	Pyralidae	species	larvae	1	0	0	0.00	0.00	0.00	0.00
LePyAD	Lepidoptera	Pyralidae	species	adult	0	2	0	0.00	0.00	0.00	0.00
Lesp	Lepidoptera		species	larvae	0	0	2	0.00	0.00	0.00	0.00
Collem	Collembola		species		0	0	0	0.00	3.51	2.61	5.11
Mites	Acari		species		2	0	0	198.25	200.00	7.82	18.75
Ostra	Ostracoda		species		0	0	0	1017.54	670.18	11.01	5.58
Clam	Bivalvia		species		0	0	0	33.33	126.32	0.00	0.00
Arachnida	Arachnida		species		3	4	5	1.75	0.00	0.00	0.60
Arps	Pseudoscorpiones		species		0	0	0	1.75	0.00	0.00	0.00
ThripsAD	Thysanoptera		species	adult	0	0	2	0.00	0.00	0.00	0.00
Thrips	Thysanoptera		species	larvae	0	1	0	5.26	0.00	0.00	0.00
Psocids	Psocoptera		species		0	0	1	0.00	0.00	0.00	0.00

**Table A.2.** (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
Oligoc	Oligochaeta		species		0	3	0	343.86	336.84	0.80	6.65
Platy	Platyhelminthes		species		0	1	0	187.72	221.05	0.00	0.60
OdLesp	Odonata	Lestidae	species		0	0	1	0.00	0.00	0.00	0.00
Fish	Scorpaeniformes	Cottidae	species		0	0	1	0.00	0.00	0.00	0.00
LiHesp	Lithobiomorpha	Henicopidae	species		3	0	0	0.00	0.00	0.00	0.00
misc	misc. terrestrials				7	7	7	0.00	0.00	7.24	0.45

**Table A.3.** Fish diet and prey availability data, North Powder River, July 23-23, 1997. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m<sup>2</sup>) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m<sup>3</sup>) represent the mean density of each taxa in three drift samples. See chapter two for collection protocol.

Code	Order	Family	Genus	Life stage	Fish Diet				Average Benthic Density /m <sup>2</sup>		Average Drift Density / 100m <sup>3</sup>	
					Total Allopatric Bull Trout n = 33	Total Sympatric Bull Trout n = 28	Total Sympatric Brook Trout n = 30	Allopatric Reach	Sympatric Reach	Allopatric Reach	Sympatric Reach	
					Allopatric Bull Trout n = 33	Sympatric Bull Trout n = 28	Sympatric Brook Trout n = 30	Allopatric Reach	Sympatric Reach	Allopatric Reach	Sympatric Reach	
EpSp	Ephemeroptera		species	larvae	1	1	2	1.75	0.00	0.00	0.00	
EpSpAD	Ephemeroptera		species	adult	9	11	15	0.00	0.00	0.00	0.00	
EpBasp	Ephemeroptera	Baetidae	species	larvae	0	0	0	15.79	12.28	76.42	185.72	
EpBaspAD	Ephemeroptera	Baetidae	species	adult	1	0	0	0.00	0.00	0.00	0.00	
EpBala	Ephemeroptera	Baetidae	<i>Labiobaetis</i>	larvae	158	80	37	24.56	207.02	770.74	646.81	
EpAmAm	Ephemeroptera	Ameletidae	<i>Ameletus</i>	larvae	39	27	15	24.56	78.95	9.26	15.83	
EpAmAmAD	Ephemeroptera	Ameletidae	<i>Ameletus</i>	adult	0	9	1	0.00	0.00	0.00	0.00	
EpHesp	Ephemeroptera	Heptageniidae	species	larvae	23	14	6	15.79	8.77	3.35	4.05	
EpHespAD	Ephemeroptera	Heptageniidae	species	adult	2	1	0	0.00	0.00	0.00	0.00	
EpHeCl	Ephemeroptera	Heptageniidae	<i>Cinygmula</i>	larvae	124	52	28	15.79	45.61	46.28	33.23	
EpHeEp	Ephemeroptera	Heptageniidae	<i>Epeorus</i>	larvae	47	13	8	28.07	45.61	94.69	59.96	
EpHeRh	Ephemeroptera	Heptageniidae	<i>Rhithrogena</i>	larvae	0	0	1	1.75	0.00	5.94	0.88	
EpHeCl	Ephemeroptera	Heptageniidae	<i>Cinygma</i>	larvae	0	1	1	0.00	1.75	0.76	0.00	
EpEpsp	Ephemeroptera	Ephemerellidae	species	larvae	0	0	0	66.67	136.84	321.95	99.72	
EpEpspAD	Ephemeroptera	Ephemerellidae	species	adult	1	0	0	0.00	0.00	0.00	0.00	
EpEpsSe	Ephemeroptera	Ephemerellidae	<i>Serratella</i>	larvae	0	1	0	0.00	0.00	10.04	1.99	
EpEpdR	Ephemeroptera	Ephemerellidae	<i>Drunella</i>	larvae	65	48	28	29.82	64.91	17.89	71.16	
EpEpcA	Ephemeroptera	Ephemerellidae	<i>Caudatella</i>	larvae	25	3	3	0.00	0.00	0.00	0.00	
EpEpcAAd	Ephemeroptera	Ephemerellidae	<i>Caudatella</i>	adult	2	0	0	0.00	0.00	0.00	0.00	
PlSp	Plecoptera		species	larvae	12	12	3	1.75	10.53	0.00	0.00	
PlSpAD	Plecoptera		species	adult	0	2	0	0.00	0.00	0.00	0.00	

Table A.3. (continued)

Code	Order	Family	Genus	Life stage	Allopatric		Sympatric		Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
					Bull Diet	Bull Diet	Bull Diet	Brook Diet					
PIEspAD	Plecoptera	Nemouridae	species	adult	1	0	0	0	0.00	0.00	0.00	0.00	
PINeZa	Plecoptera	Nemouridae	Zapada	larvae	121	40	11	11	1.75	10.53	81.54	42.14	
PINeVi	Plecoptera	Nemouridae	Visoka	larvae	5	0	0	0	42.11	14.04	6.39	5.30	
PINeZaAD	Plecoptera	Nemouridae	Zapada	adult	2	5	2	2	0.00	0.00	0.00	0.00	
PIChsp	Plecoptera	Chloroperlidae	species	larvae	6	0	0	0	35.09	10.53	2.22	3.87	
PIChSw	Plecoptera	Chloroperlidae	Sweltsa	larvae	7	3	3	3	42.11	15.79	4.09	3.39	
PIChSu	Plecoptera	Chloroperlidae	Suwallia	larvae	2	0	0	0	0.00	0.00	0.00	0.00	
PIChPa	Plecoptera	Chloroperlidae	Paraperla	larvae	0	0	0	0	3.51	0.00	0.00	0.00	
PIChKa	Plecoptera	Chloroperlidae	Kathroperla	larvae	2	1	0	0	0.00	0.00	0.00	0.00	
PIEsp	Plecoptera	Pertidae	species	larvae	2	3	0	0	3.51	0.00	0.00	0.00	
PIPeCa	Plecoptera	Pertidae	Calineuria	larvae	4	6	0	0	0.00	0.00	0.00	0.00	
PIPeDo	Plecoptera	Pertidae	Doroneuria	larvae	0	4	1	1	0.00	0.00	0.00	0.00	
PIPeHe	Plecoptera	Pertidae	Hesperoperla	larvae	0	0	0	0	0.00	0.00	0.00	0.44	
PIPdsp	Plecoptera	Perlodidae	species	larvae	1	0	0	0	0.00	0.00	0.00	0.00	
PIPdMe	Plecoptera	Perlodidae	Magarcys	larvae	0	1	0	0	0.00	0.00	0.00	0.00	
PIPdKo	Plecoptera	Perlodidae	Kogotus	larvae	0	0	0	0	0.00	1.75	0.00	0.00	
PIPdls	Plecoptera	Perlodidae	Isoperla	larvae	12	1	2	2	0.00	0.00	2.58	0.22	
PIPePd	Plecoptera	Pertidae/Perlodidae	species	larvae	7	0	0	0	10.53	17.54	7.49	15.61	
PILeCa	Plecoptera	Leuctridae/Capniidae	species	larvae	2	1	0	0	7.02	1.75	1.13	1.29	
PICaAd	Plecoptera	Capniidae	species	adult	3	0	0	0	0.00	0.00	0.00	0.99	
PIPpYa	Plecoptera	Peltoperlidae	Yoroperla	larvae	71	26	13	13	31.58	14.04	15.18	12.64	
PLPpYaAD	Plecoptera	Peltoperlidae	Yoroperla	adult	0	0	1	1	0.00	0.00	0.00	0.00	
PITaDoAD	Plecoptera	Taeniopterygidae	Daddisia	adult	0	0	1	1	0.00	0.00	0.00	0.00	
TrspP	Trichoptera		species	pupae	0	0	1	1	0.00	0.00	0.00	0.00	
TrspAD	Trichoptera		species	adult	3	2	0	0	0.00	0.00	0.38	0.29	
TrGlspP	Trichoptera	Glossosomatidae	species	pupae	0	0	2	2	0.00	0.00	0.00	0.00	
TrGIGI	Trichoptera	Glossosomatidae	Glossosoma	larvae	2	5	30	30	0.00	0.00	0.00	0.00	
TrBrisp	Trichoptera	Brachycentridae	species	larvae	1	1	1	1	1.75	1.75	0.00	0.00	

Table A.3. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
TrBtMi	Trichoptera	Brachycentridae	<i>Micrasema</i>	larvae	2	0	17	3.51	3.51	3.36	3.83
TrRhRh	Trichoptera	Rhyacophilidae	<i>Rhyacophila</i>	larvae	109	48	42	28.07	42.11	25.10	16.68
TrRhP	Trichoptera	Rhyacophilidae	species	pupae	0	0	0	0.00	1.75	0.00	0.00
TrRhAD	Trichoptera	Rhyacophilidae	species	adult	4	3	4	0.00	5.26	1.51	1.22
TrLespAD	Trichoptera	Lepidostomatidae	species	adult	2	0	0	0.00	0.00	0.00	0.00
TrLisp	Trichoptera	Limnephilidae	species	larvae	7	7	13	5.26	5.26	1.49	2.17
TrLiCr	Trichoptera	Limnephilidae	<i>Cryptochia</i>	larvae	0	1	0	0.00	0.00	2.24	0.00
TrLiEc	Trichoptera	Limnephilidae	<i>Ecclisomyia</i>	larvae	0	0	1	0.00	0.00	0.00	0.00
TrLiEl	Trichoptera	Limnephilidae	<i>Ecclisocosmoecus</i>	larvae	0	1	1	0.00	0.00	0.00	0.00
TrLiEo	Trichoptera	Limnephilidae	<i>Ecosmoecus</i>	larvae	0	0	0	0.00	0.00	1.84	0.59
TrLiPs	Trichoptera	Limnephilidae	<i>Psychoglypha</i>	larvae	1	0	10	10.53	1.75	0.00	0.00
TrHyPa	Trichoptera	Hydropsychidae	<i>Parapsyche</i>	larvae	9	9	5	0.00	1.75	0.00	0.44
TrUesp	Trichoptera	Uenoidae	species	larvae	0	0	1	0.00	3.51	0.38	0.74
TrUespAD	Trichoptera	Uenoidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
TrUeNe	Trichoptera	Uenoidae	<i>Neophylax</i>	larvae	0	0	6	0.00	0.00	0.00	0.00
TrUeNt	Trichoptera	Uenoidae	<i>Neothremma</i>	larvae	0	0	47	0.00	0.00	0.00	0.00
TrUeNfP	Trichoptera	Uenoidae	<i>Neothremma</i>	pupae	0	0	9	0.00	0.00	0.00	0.00
Disp	Diptera		species	larvae	3	2	0	0.00	0.00	0.00	0.00
DispP	Diptera		species	Pupae	0	1	0	0.00	0.00	0.00	0.00
DiChsp	Diptera	Chironomidae	species	larvae	1	4	3	26.32	1.75	0.00	0.00
DiChP	Diptera	Chironomidae	species	pupae	23	7	3	29.82	45.61	4.05	7.93
DiChAD	Diptera	Chironomidae	species	adult	33	19	9	12.28	94.74	19.78	16.07
DiChOr	Diptera	Chironomidae	<i>Orthocladinae</i>	larvae	308	185	78	338.60	726.32	80.86	54.83
DiChOrP	Diptera	Chironomidae	<i>Orthocladinae</i>	pupae	0	0	1	0.00	0.00	0.00	0.00
DiChTp	Diptera	Chironomidae	<i>Tanypodinae</i>	larvae	12	2	1	142.11	75.44	16.08	9.90
DiChTt	Diptera	Chironomidae	<i>Tanytarsini</i>	larvae	9	4	1	1010.53	317.54	36.91	53.68
DiTisp	Diptera	Tipulidae	species	larvae	3	2	4	8.77	10.53	0.00	0.00
DiTispAD	Diptera	Tipulidae	species	adult	2	1	1	0.00	0.00	0.73	0.00

Table A.3. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
DiTispP	Diptera	Tipulidae	species	pupae	0	2	0	0.00	0.00	0.00	0.00
DiTTI	Diptera	Tipulidae	<i>Tipula</i>	larvae	8	2	1	0.00	0.00	0.00	0.00
DiTTiDi	Diptera	Tipulidae	<i>Dicranota</i>	larvae	6	4	1	1.75	5.26	0.75	2.69
DiTiAn	Diptera	Tipulidae	<i>Antocha</i>	larvae	3	0	0	3.51	1.75	0.00	0.00
DiTiPe	Diptera	Tipulidae	<i>Pedicia</i>	larvae	0	1	0	0.00	0.00	0.00	0.00
DiEnsp	Diptera	Empididae	species	larvae	7	6	2	0.00	0.00	0.00	0.00
DiEnspAD	Diptera	Empididae	species	adult	15	1	0	0.00	0.00	0.00	0.00
DiCesp	Diptera	Ceratopogonidae	species	larvae	4	0	2	0.00	0.00	0.00	0.00
DiCePt	Diptera	Ceratopogonidae	<i>Probezzia</i>	larvae	1	4	0	5.26	1.75	0.00	0.00
DiCeAD	Diptera	Ceratopogonidae	species	adult	3	4	0	0.00	3.51	0.73	0.00
DiSisp	Diptera	Simuliidae	species	larvae	24	2	2	0.00	0.00	0.00	0.00
DiSiPt	Diptera	Simuliidae	<i>Prosimulium</i>	larvae	120	54	24	1.75	0.00	20.52	11.37
DiSiP	Diptera	Simuliidae	species	pupae	3	3	0	5.26	3.51	0.00	0.00
DiSiAD	Diptera	Simuliidae	species	adult	5	1	1	0.00	0.00	0.00	0.00
DiPhAD	Diptera	Phoridae	species	adult	0	3	0	0.00	0.00	0.76	0.00
DiBrAD	Diptera - Brachycera		species	adult	8	2	3	0.00	0.00	0.00	0.00
DiNeAD	Diptera - Nematocera		species	adult	8	5	4	0.00	0.00	0.76	0.44
DiMyspAD	Diptera	Mycetophilidae	species	adult	13	2	3	0.00	0.00	0.00	0.00
DiDiDi	Diptera	Dixidae	<i>Dixa</i>	larvae	0	0	0	3.51	0.00	0.00	1.29
DiDispAD	Diptera	Dixidae	species	adult	0	0	0	0.00	0.00	0.00	0.99
DiPeGl	Diptera	Pelecorhynchidae	<i>Glutops</i>	larvae	0	0	1	0.00	0.00	0.00	0.00
DiDospAD	Diptera	Dolichopodidae	species	adult	2	0	2	0.00	0.00	0.00	0.00
DiBlspP	Diptera	Blephariceridae	species	pupae	2	1	0	0.00	0.00	0.00	0.00
DiBlAg	Diptera	Blephariceridae	<i>Agathon</i>	larvae	3	1	2	0.00	0.00	0.00	0.00
DiBlPh	Diptera	Blephariceridae	<i>Philorus</i>	larvae	0	0	0	0.00	0.00	0.00	0.99
DiDesp	Diptera	Deuterophlebiidae	species	larvae	0	0	0	0.00	0.00	0.73	0.00
DiCuspAD	Diptera	Culicidae	species	adult	3	0	0	0.00	0.00	0.00	0.00
DiThspAD	Diptera	Thaumaleidae	species	adult	0	0	1	0.00	1.75	0.00	0.00

Table A.3. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
DiMuspAD	Diptera	Muscidae	species	adult	0	0	0	0.00	0.00	2.20	0.00
DiTaspAD	Diptera	Tachinidae	species	adult	1	0	1	0.00	0.00	1.52	0.00
DiSyspAD	Diptera	Syrphidae	species	adult	2	1	0	0.00	0.00	0.76	0.00
DiSrspAD	Diptera	Sciaridae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiSzspAD	Diptera - Schizophora		species	adult	1	2	0	0.00	0.00	0.00	0.00
DiCospAD	Diptera	Cecidomyiidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
DiAsspAD	Diptera	Asilidae	species	adult	1	1	0	0.00	0.00	0.00	0.00
DiTpspAD	Diptera	Tephritidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiHespAD	Diptera	Heleomyzidae	species	adult	3	0	0	0.00	0.00	0.00	0.00
Cosp	Coleoptera		species	larvae	1	1	0	0.00	1.75	0.00	0.00
CospAD	Coleoptera		species	adult	5	1	4	0.00	0.00	0.00	0.00
CoHyspAD	Coleoptera	Hydrophilidae	species	adult	0	0	0	1.75	0.00	0.00	0.00
CoHysp	Coleoptera	Hydrophilidae	species	larvae	2	0	1	0.00	0.00	1.11	0.00
CoCaspAD	Coleoptera	Carabidae	species	adult	5	3	1	0.00	0.00	0.00	0.00
CoCasp	Coleoptera	Carabidae	species	larvae	2	1	0	0.00	0.00	0.00	0.00
CoDysp	Coleoptera	Dytiscidae	species	larvae	0	2	0	0.00	0.00	0.00	0.00
CoStspAD	Coleoptera	Staphylinidae	species	adult	16	4	2	0.00	0.00	0.00	0.00
CoStsp	Coleoptera	Staphylinidae	species	larvae	4	0	0	0.00	0.00	0.76	0.29
CoCuspAD	Coleoptera	Curculionidae	species	adult	7	4	3	3.51	0.00	0.38	0.00
CoCusp	Coleoptera	Curculionidae	species	larvae	0	0	0	0.00	0.00	1.47	0.00
CoCrspAD	Coleoptera	Cerambycidae	species	adult	4	0	0	0.00	0.00	0.00	0.00
CoScspAD	Coleoptera	Scarabaeidae	species	adult	1	1	0	0.00	0.00	0.00	0.00
CoEtspAD	Coleoptera	Elateridae	species	adult	3	0	1	0.00	0.00	0.00	0.00
CoElisp	Coleoptera	Elmidae	species	larvae	0	0	0	5.26	1.75	0.00	0.00
CoElispAD	Coleoptera	Elmidae	species	adult	0	0	0	1.75	0.00	0.75	0.00
CoEHe	Coleoptera	Elmidae	<i>Heterimnius</i>	larvae	1	0	0	0.00	5.26	0.00	0.00
CoCnspAD	Coleoptera	Cantharidae	species	adult	4	4	0	0.00	0.00	0.00	0.00
CoAmsp	Coleoptera	Amphizoidae	species	larvae	7	2	1	0.00	0.00	0.00	0.00

**Table A.3.** (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
CoCispAD	Coleoptera	Cleridae	species	adult	0	1	0	0.00	0.00	0.00	0.00
CoByspAD	Coleoptera	Byrrhidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
CoCpspAD	Coleoptera	Cryptophagidae	species	adult	2	0	3	0.00	0.00	0.00	0.00
Hosp	Homoptera		species	adult	0	0	0	0.00	19.30	0.00	0.44
HoApsp	Homoptera	Aphididae	species	adult	68	22	9	1.75	10.53	2.65	0.29
HoCisp	Homoptera	Cicadellidae	species	adult	9	3	1	0.00	0.00	0.00	2.17
HoAdsp	Homoptera	Adelgidae	species	adult	2	0	0	0.00	0.00	0.00	3.98
HoErsP	Homoptera	Eriosomatidae	species	adult	3	1	0	0.00	0.00	0.73	0.00
Hemisp	Hemiptera		species	adult	0	2	1	0.00	0.00	0.00	0.00
HeThspAD	Hemiptera	Thyreocoridae	species	adult	0	0	1	0.00	0.00	0.00	0.00
HeLysp	Hemiptera	Lygaeidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
HyspAD	Hymenoptera		species	adult	2	6	0	0.00	3.51	0.00	0.00
HyFosp	Hymenoptera	Formicidae	species	adult	53	13	13	0.00	1.75	0.00	0.22
HyBrsp	Hymenoptera	Braconidae	species	adult	5	4	0	0.00	0.00	0.76	0.29
HyPosp	Hymenoptera	Pompilidae	species	adult	0	1	0	0.00	0.00	0.00	0.00
HyVesp	Hymenoptera	Vespidae	species	adult	0	0	2	0.00	0.00	0.00	0.00
HyDisp	Hymenoptera	Diapriidae	species	adult	3	1	0	0.00	0.00	0.00	0.00
HyEusp	Hymenoptera	Eurytomidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
HyElisp	Hymenoptera	Eulophidae	species	adult	2	0	0	0.00	0.00	0.00	0.00
HyIcsp	Hymenoptera	Ichneumonidae	species	adult	7	4	1	0.00	0.00	0.38	0.00
HyTesp	Hymenoptera	Tenthredinidae	species	larvae	1	0	0	0.00	0.00	0.00	0.00
LePysp	Lepidoptera	Pyralidae	species	larvae	5	1	1	0.00	0.00	0.00	0.29
LePyCr	Lepidoptera	Pyralidae	species	larvae	1	0	0	0.00	0.00	0.00	0.00
LePyAD	Lepidoptera	Pyralidae	species	adult	2	1	0	0.00	0.00	0.00	0.99
Lesp	Lepidoptera		species	larvae	1	1	2	0.00	0.00	0.00	0.00
LespAD	Lepidoptera		species	adult	0	1	0	0.00	0.00	0.00	0.00
NeHeChsp	Neuroptera	Hemerobiidae	species	larvae	9	8	2	0.00	0.00	0.00	0.00
OrspAD	Orthoptera		species	adult	0	1	0	0.00	0.00	0.00	0.00

**Table A.3.** (continued)

Code	Order	Family	Genus	Life stage	Allopatric		Sympatric		Brook Diet	Allopatric		Sympatric		Allopatric Drift	Sympatric Drift
					Bull Diet	Bull Diet	Bull Diet	Bull Diet		Benthos	Benthos	Benthos	Benthos		
Collemb	Collembola		species		8	6	3	3.51	7.02	134.00	7.02	32.52	134.00	32.52	
Mites	Acari		species		7	4	2	87.72	63.16	87.63	63.16	42.47	87.63	42.47	
Ostra	Ostracoda		species		0	0	0	7.02	3.51	1.52	3.51	0.00	1.52	0.00	
Clam	Bivalvia		species		0	0	0	1.75	0.00	0.00	0.00	0.00	0.00	0.00	
Arachnida	Arachnida		species		14	10	5	0.00	0.00	0.76	0.00	0.00	0.76	0.00	
ThripsAD	Thysanoptera		species	adult	0	0	1	0.00	1.75	0.75	1.75	2.28	0.75	2.28	
Thrips	Thysanoptera		species	larvae	0	0	0	3.51	5.26	2.28	5.26	3.50	2.28	3.50	
Oligoc	Oligochaeta		species		1	0	1	185.96	52.63	0.00	52.63	0.22	0.00	0.22	
Platy	Platyhelminthes		species		0	0	0	5.26	14.04	1.52	14.04	1.29	1.52	1.29	
LiHesp	Lithobiomorpha	Henicopidae	species		1	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
misc	misc. terrestrials				14	3	4	0.00	0.00	0.73	0.00	0.00	0.73	0.00	

**Table A.4.** Fish diet and prey availability data, Meadow Fork of Big Creek, July 3-5, 1997. Fish diet represents the total number of prey taxa found in the stomach of all allopatric bull trout, sympatric bull trout, and sympatric brook trout. Average benthic densities (per m<sup>2</sup>) represents the mean density of each taxa of six surber samples. Average drift densities (per 100 m<sup>3</sup>) represent the mean density of each taxa in three drift samples. See chapter two for collection protocol.

Code	Order	Family	Genus	Lifestage	Fish Diet			Average Benthic Density /m <sup>2</sup>		Average Drift Density / 100m <sup>3</sup>	
					Allopatric Bull Trout n = 19	Sympatric Bull Trout n = 27	Sympatric Brook Trout n = 20	Allopatric Reach	Sympatric Reach	Allopatric Reach	Sympatric Reach
EpSp	Ephemeroptera			larvae	0	1	1	1.75	3.51	0.38	0.00
EpSpAD	Ephemeroptera			adult	3	55	18	0.00	0.00	0.00	0.00
EpBasp	Ephemeroptera	Baetidae	species	larvae	0	0	0	0.00	12.28	0.00	0.00
EpBaspAD	Ephemeroptera	Baetidae	species	adult	0	1	3	0.00	0.00	0.00	0.00
EpBaLa	Ephemeroptera	Baetidae	<i>Labiobaetis</i>	larvae	159	34	12	587.72	187.72	305.20	79.53
EpAmAm	Ephemeroptera	Ameletidae	<i>Ameletus</i>	larvae	63	13	3	108.77	47.37	19.03	17.04
EpHesp	Ephemeroptera	Heptageniidae	species	larvae	19	12	5	28.07	28.07	8.90	0.00
EpHeCl	Ephemeroptera	Heptageniidae	<i>Cinygmula</i>	larvae	45	9	3	491.23	568.42	38.81	18.71
EpHeEp	Ephemeroptera	Heptageniidae	<i>Epeorus</i>	larvae	22	61	22	480.70	1475.44	128.90	2.53
EpHeRh	Ephemeroptera	Heptageniidae	<i>Rhithrogena</i>	larvae	6	17	4	129.82	78.95	4.63	4.28
EpHeCi	Ephemeroptera	Heptageniidae	<i>Cinygma</i>	larvae	0	0	0	5.26	0.00	5.21	1.45
EpHelr	Ephemeroptera	Heptageniidae	<i>Ironodes</i>	larvae	0	0	0	0.00	0.00	0.00	0.00
EpEpsp	Ephemeroptera	Ephemerellidae	species	larvae	0	0	1	0.00	10.53	0.00	0.00
EpEpspAD	Ephemeroptera	Ephemerellidae	species	adult	1	4	3	0.00	0.00	0.00	0.00
EpEpSe	Ephemeroptera	Ephemerellidae	<i>Serratella</i>	larvae	1	1	0	7.02	0.00	0.00	10.70
EpEpDr	Ephemeroptera	Ephemerellidae	<i>Drunella</i>	larvae	143	129	77	335.09	247.37	39.63	17.21
EpEpCa	Ephemeroptera	Ephemerellidae	<i>Caudatella</i>	larvae	12	33	35	0.00	3.51	19.19	1.22
EpEpCaAD	Ephemeroptera	Ephemerellidae	<i>Caudatella</i>	adult	0	1	0	0.00	0.00	0.00	0.00
PlSp	Plecoptera		species	larvae	8	5	4	40.35	12.28	3.79	0.00
PlSpAD	Plecoptera		species	adult	7	0	0	0.00	0.00	0.00	0.00



Table A.4. (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
Trsp	Trichoptera		species	larvae	0	2	1	0.00	0.00	0.00	0.00
TrspAD	Trichoptera		species	adult	1	1	4	0.00	0.00	0.00	0.00
TrGlspP	Trichoptera	Glossosomatidae	species	pupae	1	0	0	71.93	80.70	0.00	0.00
TrGlspAD	Trichoptera	Glossosomatidae	species	adult	2	10	0	0.00	0.00	0.00	0.00
TrGIGI	Trichoptera	Glossosomatidae	<i>Glossosoma</i>	larvae	29	5	8	191.23	75.44	1.01	1.45
TrBtMi	Trichoptera	Brachycentridae	<i>Micrasema</i>	larvae	0	0	4	0.00	0.00	0.00	0.00
TrRhRh	Trichoptera	Rhyacophiliidae	<i>Rhyacophila</i>	larvae	196	50	31	310.53	91.23	21.97	10.57
TrRhP	Trichoptera	Rhyacophiliidae	species	pupae	0	1	0	17.54	8.77	0.00	0.35
TrRhAD	Trichoptera	Rhyacophiliidae	species	adult	17	7	5	0.00	0.00	0.00	0.00
TrLespAD	Trichoptera	Lepidostomatidae	species	adult	0	0	0	0.00	0.00	0.00	0.00
TrLisp	Trichoptera	Limnephiliidae	species	larvae	12	2	20	5.26	66.67	1.40	2.33
TrLispAD	Trichoptera	Limnephiliidae	species	adult	2	0	0	0.00	0.00	0.00	0.00
TrLiP	Trichoptera	Limnephiliidae	species	pupae	0	0	1	0.00	0.00	0.00	0.00
TrLiCr	Trichoptera	Limnephiliidae	<i>Cryptochia</i>	larvae	0	0	0	1.75	0.00	11.88	0.00
TrLiEc	Trichoptera	Limnephiliidae	<i>Ecclisomyia</i>	larvae	0	6	61	1.75	8.77	0.26	0.00
TrLiEcP	Trichoptera	Limnephiliidae	<i>Ecclisomyia</i>	pupae	0	0	6	0.00	0.00	0.00	0.00
TrLiCh	Trichoptera	Limnephiliidae	<i>Chyranda</i>	larvae	0	0	7	0.00	0.00	0.00	0.00
TrLiHo	Trichoptera	Limnephiliidae	<i>Homophylax</i>	larvae	0	1	0	0.00	0.00	0.00	0.00
TrLiAm	Trichoptera	Limnephiliidae	<i>Amphicosmoecus</i>	larvae	0	0	0	0.00	1.75	0.00	0.00
TrLiPs	Trichoptera	Limnephiliidae	<i>Psychoglypha</i>	larvae	2	0	0	0.00	0.00	0.26	0.00
TrLiDi	Trichoptera	Limnephiliidae	<i>Dicosmoecus</i>	larvae	0	1	0	0.00	0.00	0.00	0.00
TriHyPa	Trichoptera	Hydropsychidae	Parapsyche	larvae	23	21	12	5.26	7.02	4.96	0.38
TriHyPaP	Trichoptera	Hydropsychidae	Parapsyche	pupae	0	0	0	10.53	0.00	0.00	0.00
TriPhspAD	Trichoptera	Philopotamidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
Disp	Diptera		species	larvae	0	1	0	0.00	0.00	0.00	0.00
DispP	Diptera		species	pupae	1	0	0	0.00	0.00	0.00	0.00
DiChsp	Diptera	Chironomidae	species	larvae	1	0	0	0.00	12.28	0.00	0.00
DiChP	Diptera	Chironomidae	species	pupae	2	346	2	107.02	59.65	36.33	6.78

Table A.4. (continued)

Code	Order	Family	Genus	Life stage	Allopatric		Sympatric		Allopatric		Sympatric	
					Bull Diet	Bull Diet	Brook Diet	Brook Diet	Benthos	Benthos	Drift	Drift
DiChAD	Diptera	Chironomidae	species	adult	2	7	5	61.40	3.51	24.39	19.42	
DiChOr	Diptera	Chironomidae	Orthodadiinae	larvae	107	10	7	931.58	349.12	72.97	20.53	
DiChTp	Diptera	Chironomidae	Tanytopodinae	larvae	5	2	3	28.07	59.65	17.09	3.50	
DiChTt	Diptera	Chironomidae	Tanytarsini	larvae	2	1	1	810.53	947.37	170.40	1.22	
DiTisp	Diptera	Tipulidae	species	larvae	4	1	1	0.00	15.79	0.38	0.00	
DiTispAD	Diptera	Tipulidae	species	adult	0	1	2	0.00	1.75	0.00	0.48	
DiTispP	Diptera	Tipulidae	species	pupae	0	1	1	0.00	0.00	0.00	0.00	
DiTITI	Diptera	Tipulidae	<i>Tipula</i>	larvae	3	1	1	0.00	0.00	0.00	0.00	
DiTIDi	Diptera	Tipulidae	<i>Dicranota</i>	larvae	14	4	0	15.79	5.26	0.00	0.96	
DiTiAn	Diptera	Tipulidae	<i>Antocha</i>	larvae	0	2	0	1.75	19.30	4.45	0.83	
DiTiHo	Diptera	Tipulidae	<i>Holorusia</i>	larvae	1	0	0	0.00	0.00	0.00	0.00	
DiTiPe	Diptera	Tipulidae	<i>Pedicia</i>	larvae	2	1	0	0.00	0.00	2.48	0.00	
DiEmnp	Diptera	Empididae	species	larvae	5	5	0	3.51	0.00	0.00	0.00	
DiEmnpP	Diptera	Empididae	species	pupae	1	0	0	3.51	3.51	0.00	0.00	
DiEmnpAD	Diptera	Empididae	species	adult	5	0	0	0.00	0.00	0.00	0.00	
DiEmOr	Diptera	Empididae	<i>Oreogeton</i>	larvae	0	0	0	5.26	0.00	0.00	0.00	
DiCesp	Diptera	Ceratopogonidae	species	larvae	6	0	0	0.00	0.00	0.00	0.48	
DiCePt	Diptera	Ceratopogonidae	<i>Probezzia</i>	larvae	0	1	2	0.00	1.75	0.00	0.00	
DiCeAD	Diptera	Ceratopogonidae	species	adult	0	0	0	0.00	0.00	0.00	0.35	
DiSisp	Diptera	Simuliidae	species	larvae	64	29	22	0.00	0.00	5.31	10.73	
DiSiPt	Diptera	Simuliidae	<i>Prosimulium</i>	larvae	8	1	0	26.32	10.53	8.79	18.76	
DiSiP	Diptera	Simuliidae	species	pupae	2	4	1	7.02	3.51	0.26	0.00	
DiSiAd	Diptera	Simuliidae	species	adult	1	1	0	0.00	1.75	0.00	0.38	
DiStAd	Diptera	Stratiomyidae	species	adult	0	0	0	0.00	1.75	0.00	0.00	
DiPsPe	Diptera	Psychodidae	<i>Pericoma</i>	larvae	0	0	0	1.75	12.28	0.00	0.00	
DiPsAD	Diptera	Psychodidae	species	adult	0	0	0	0.00	0.00	0.64	0.00	
DiPHAD	Diptera	Phoridae	species	adult	1	1	0	0.00	0.00	0.00	0.48	
DiBrAD	Diptera - Brachycera		species	adult	9	1	2	0.00	0.00	0.00	0.00	

**Table A.4.** (continued)

Code	Order	Family	Genus	Life stage	Allopatric Bull Diet	Sympatric Bull Diet	Sympatric Brook Diet	Allopatric Benthos	Sympatric Benthos	Allopatric Drift	Sympatric Drift
DiNeAD	Diptera - Nematocera		species	adult	3	2	0	0.00	1.75	2.22	0.00
DiMyspAD	Diptera	Mycetophilidae	species	adult	3	2	4	0.00	0.00	1.27	0.00
DiDiD	Diptera	Dixidae	<i>Dixa</i>	larvae	0	0	0	0.00	1.75	3.62	0.00
DiPeGI	Diptera	Pelecorhynchidae	<i>Glutops</i>	larvae	0	4	2	0.00	0.00	0.00	0.00
DiBlsp	Diptera	Blephariceridae	species	larvae	0	0	0	0.00	1.75	0.00	0.00
DiBlspP	Diptera	Blephariceridae	species	pupae	0	2	2	0.00	0.00	0.00	0.00
DiBlAg	Diptera	Blephariceridae	<i>Agathon</i>	larvae	4	3	3	0.00	0.00	0.00	0.38
DiBlspAD	Diptera	Blephariceridae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiMusp	Diptera	Muscidae	species	larvae	0	1	0	0.00	0.00	0.00	0.00
DiMuspAD	Diptera	Muscidae	species	adult	1	1	0	0.00	0.00	0.00	0.00
DiTaspAD	Diptera	Tachinidae	species	adult	0	2	0	0.00	0.00	0.00	0.00
DiSyspAD	Diptera	Syrphidae	species	adult	1	2	2	0.00	0.00	0.00	0.00
DiSrspAD	Diptera	Sciaridae	species	adult	0	1	0	0.00	0.00	0.00	0.00
DiAsspAD	Diptera	Asilidae	species	adult	1	2	0	0.00	0.00	0.00	0.00
DiTbspAD	Diptera	Tabanidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiTpspAD	Diptera	Tephritidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
DiHespAD	Diptera	Heleomyzidae	species	adult	8	4	1	0.00	0.00	0.38	0.00
DiAnspAD	Diptera	Anthomyiidae	species	adult	2	0	0	0.00	0.00	0.00	0.00
DiCbsp	Diptera	Chaoboridae	species	adult	0	0	0	0.00	0.00	0.26	0.00
Cosp	Coleoptera		species	adult	5	5	5	0.00	0.00	2.48	0.77
CospAD	Coleoptera		species	adult	2	3	4	0.00	0.00	0.00	0.00
CoHyspAD	Coleoptera	Hydrophilidae	species	adult	0	0	1	0.00	0.00	0.00	0.00
CoCaspAD	Coleoptera	Carabidae	species	adult	2	0	4	0.00	0.00	0.00	0.00
CoCasp	Coleoptera	Carabidae	species	larvae	3	0	0	0.00	0.00	0.00	0.00
CoDyspAD	Coleoptera	Dytiscidae	species	adult	1	0	0	0.00	0.00	0.00	0.00
CoStspAD	Coleoptera	Staphylinidae	species	adult	12	3	3	3.51	0.00	0.64	0.83
CoStsp	Coleoptera	Staphylinidae	species	larvae	0	1	0	0.00	0.00	0.00	0.35
CoPtspAD	Coleoptera	Ptilodactylidae	species	adult	0	0	0	0.00	0.00	0.38	0.00

Table A.4. (continued)

Code	Order	Family	Genus	Life stage	Allopatric		Sympatric		Allopatric		Sympatric		Allopatric		Sympatric	
					Bull Diet	Bull Diet	Brook Diet	Brook Diet	Benthos	Benthos	Drift	Drift				
CoCuspAD	Coleoptera	Curculionidae	species	adult	15	0	3	0.00	0.00	0.38	0.00	0.38	0.00			
CoScspAD	Coleoptera	Scarabaeidae	species	adult	1	0	0	0.00	0.00	0.38	0.00	0.38	0.00			
CoEtspAD	Coleoptera	Elateridae	species	adult	0	2	4	0.00	0.00	0.00	0.00	0.00	0.00			
CoElsp	Coleoptera	Elmidae	species	larvae	0	1	0	0.00	12.28	0.00	0.48	0.00	0.48			
CoElspAD	Coleoptera	Elmidae	species	adult	0	0	0	1.75	1.75	0.00	1.31	0.00	1.31			
CoElHe	Coleoptera	Elmidae	<i>Heterirmnius</i>	larvae	0	0	0	198.25	149.12	1.52	1.44	1.52	1.44			
CoCnspAD	Coleoptera	Cantharidae	species	adult	9	1	2	0.00	0.00	0.00	0.00	0.00	0.00			
CoSospAD	Coleoptera	Scolytidae	species	adult	0	1	0	0.00	0.00	2.48	0.00	2.48	0.00			
CoCospAD	Coleoptera	Coccinellidae	species	adult	0	0	1	0.00	0.00	0.00	0.00	0.00	0.00			
CoEnspAD	Coleoptera	Endomychidae	species	adult	1	0	0	0.00	0.00	0.00	0.00	0.00	0.00			
Hosp	Homoptera		species	adult	0	0	0	0.00	0.00	1.28	0.00	1.28	0.00			
HoApsp	Homoptera	Aphididae	species	adult	6	20	21	15.79	7.02	6.98	0.70	6.98	0.70			
HoCisp	Homoptera	Cicadellidae	species	adult	0	0	2	1.75	1.75	0.64	0.73	0.64	0.73			
HoAdsp	Homoptera	Adelgidae	species	adult	0	0	0	0.00	0.00	5.92	0.00	5.92	0.00			
HoErsp	Homoptera	Eriosomatidae	species	adult	0	0	0	0.00	0.00	3.36	0.00	3.36	0.00			
HeThspAD	Hemiptera	Thyreocoridae	species	adult	0	1	1	0.00	0.00	0.00	0.00	0.00	0.00			
HeSaspAD	Hemiptera	Salicidae	species	adult	0	3	2	0.00	0.00	0.00	0.00	0.00	0.00			
HeNaspAD	Hemiptera	Nabidae	species	adult	0	1	1	0.00	0.00	0.00	0.00	0.00	0.00			
HeLysp	Hemiptera	Lygaeidae	species	adult	44	4	1	0.00	0.00	0.00	0.00	0.00	0.00			
HyspAD	Hymenoptera		species	adult	1	2	1	0.00	0.00	0.00	0.00	0.00	0.00			
HyFosp	Hymenoptera	Formicidae	species	adult	58	23	57	0.00	3.51	5.21	0.70	5.21	0.70			
HyMusp	Hymenoptera	Mutillidae	species	adult	0	0	1	0.00	0.00	0.00	0.00	0.00	0.00			
HyBrsp	Hymenoptera	Braconidae	species	adult	2	0	2	0.00	0.00	0.00	0.00	0.00	0.00			
HyVesp	Hymenoptera	Vespidae	species	adult	0	0	2	0.00	0.00	0.00	0.00	0.00	0.00			
HyIcsp	Hymenoptera	Ichneumonidae	species	adult	7	5	3	0.00	0.00	0.00	0.00	0.00	0.00			
HyTesp	Hymenoptera	Tenthredinidae	species	larvae	0	3	1	0.00	0.00	0.00	0.00	0.00	0.00			
HyTespAD	Hymenoptera	Tenthredinoidea	species	adult	0	0	0	0.00	0.00	2.22	0.00	2.22	0.00			
LePysp	Lepidoptera	Pyralidae	species	larvae	2	13	7	0.00	1.75	2.48	0.38	2.48	0.38			

